

**Chemodiversity effects on plant-insect and plant-plant interactions:
Exploring community assembly at plant and plot level**

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Chapter I. General Introduction

Lina Ojeda-Prieto

Understanding the complex interplay between plant species and their associated arthropod communities is fundamental to ecological research. Traditional ecological paradigms have long emphasized the importance of between-species diversity in shaping ecosystem dynamics, examining how different species interact within ecosystems and contribute to overall biodiversity and ecosystem functioning (Weisser et al., 2017; Cardinale et al., 2012; Hooper et al., 2012; Eisenhauer et al., 2011; Schulze & Mooney, 1992). However, recent research has increasingly recognized the importance of intraspecific plant diversity - variation within a single species - in shaping ecological processes and outcomes (Petrén et al., 2023a; Westerband et al., 2021; Müller et al., 2020; Raffard et al., 2019; Koricheva & Hayes, 2018; Siefert et al., 2015; Moore et al., 2014; Violle et al., 2012).

Key areas of study of intraspecific plant diversity are trait variation and adaptation (Konefal et al., 2024; Noto & Hughes, 2020; Jump & Peñuelas, 2005), genetic and evolutionary perspectives (Hughes et al., 2008; Crutsinger et al., 2006), and conservation strategies that emphasize preserving such diversity. Findings indicate that higher intraspecific diversity promotes ecosystem resilience and stability, alters species interactions, and enhances ecosystem services such as pollination and pest control (Govaert et al., 2024; Raffard et al., 2019; Siefert et al., 2015; Bolnick et al., 2011). One component of within-species diversity, and a growing area of interest within this field, is *intraspecific chemical diversity*, or chemodiversity, which focuses on the variation in secondary metabolites within a species (Walker et al., 2022; Whitehead et al., 2021). This chemical diversity is crucial in plant interactions and can significantly influence ecological dynamics (Müller et al., 2020; Moore et al., 2014).

Studying chemodiversity broadens our knowledge of plant defense mechanisms, adaptation, and evolution and offers insights into the possible ecological effects. This introduction aims to provide a comprehensive overview of the concept of chemodiversity, its ecological significance, and the ensuing research questions and hypotheses that guide empirical investigations in this domain.

1.1 Chemical Ecology

1.1.1 Plant Metabolites

Plant metabolites are traditionally categorized into primary and secondary metabolites, each playing distinct roles with different ecological implications (Erb & Kliebenstein, 2020; Fernie & Tohge, 2017). Primary metabolites are compounds directly involved in plant growth, development, and reproduction. These compounds, which include carbohydrates, proteins, lipids, and nucleic acids, are essential for physiological processes such as photosynthesis,

respiration, and nutrient assimilation. However, despite their primary physiological role, they might also influence ecological interactions. For instance, sugars produced during photosynthesis can attract pollinators (Stevenson et al., 2017), while nitrogen-rich amino acids can impact herbivore feeding behavior (Machado et al., 2013).

Secondary metabolites, or specialized metabolites, are compounds not directly involved in primary metabolic processes. They are often associated with key roles in plant defense, signaling, and interactions with the environment, though they might not always be related to a biological effect or at least not known (Pichersky & Raguso, 2018; Wink, 2018). Secondary metabolites are highly diverse and include chemical groups like alkaloids, terpenoids, flavonoids, and phenolic compounds. Secondary metabolites can significantly vary between and within plant species (Hartmann, 2007; Hare, 2011; Tissier et al., 2014). In chemodiversity research, secondary metabolites are often the focus due to their extensive variability and ecological relevance for mediating interactions between plants and interaction partners (Kessler & Kalske, 2018; Yang et al., 2018; Sedio, 2017; Richards et al., 2015).

1.1.2 Chemodiversity

Research on secondary metabolites has traditionally focused on the effect of individual plant compounds and their abundance on ecological interactions (McDanell et al., 1988; Metcalf & Kogan, 1987; Reese, 1978). A combination of new knowledge and methodologies has facilitated a shift to focus on the effects of the overall chemical diversity, including the variety and relative abundance of compounds (Clavijo McCormick et al., 2014; Van Dam et al., 2010; Barker et al., 2006).

In natural settings, plant compounds occur not in isolation but as part of complex chemical mixtures. **Chemodiversity** refers to the variation of those mixtures in terms of the number of metabolites, abundance, and specific mixture composition (Müller & Junker, 2022; Moore et al., 2014), which influences ecological interactions with the environment and other organisms, shaping community structure (Wetzel & Whitehead, 2020). Chemodiversity comprises several dimensions such as richness, as the total number of different chemical compounds present; evenness, referring to the distribution of these compound concentrations; and disparity, as the degree of difference between the chemical compounds in terms of, for instance, their structure, function, metabolic pathway (Figure 1a; Petrén et al., 2023a). The variation of metabolites can be examined at the community level (encompassing multiple species) or intraspecifically (within a single species) (Govaert et al., 2024; Petrén et al., 2023a). This study explores whether increasing intraspecific plot-level chemotype richness results in higher terpenoid richness, evenness, and Shannon diversity (Hypothesis 1.1).

Within plant species, levels of intraspecific chemodiversity are observed at various scales, from individual differences to variations across populations (Eilers, 2021; Müller et al., 2020; Moore et al., 2014). Different tissues and organs within an individual might display differences in their chemical mixtures, which are often associated with specific functions of those tissues (Figure 1b; Rahimova et al., 2024; Jakobs & Müller, 2018; Meindl et al., 2014; Tissier et al., 2014; Kleine & Müller, 2013). Chemodiversity can also refer to differences among individuals within a population, which might be linked to genetic variation and environmental influences (Figure 1c; Calf et al., 2018; Clancy et al., 2016; Kleine & Müller, 2011). Patterns of chemodiversity across populations might provide insights into adaptation and evolutionary processes (Figure 1d; Rahimova, Neuhaus-Harr et al., 2024; Bakhtiari et al., 2019; Wolf et al., 2011; Keskitalo et al., 2001).

In addition to the spatial scale, the temporal scale plays a crucial role in shaping intraspecific chemodiversity (Figure 1e; Wittmann & Bräutigam, 2024; Keefover-Ring, 2022; Gols et al., 2007), with seasonal changes driven by ontogeny and environmental factors contributing to fluctuations in metabolite concentrations and mixture compositions. When individuals within a species exhibit variations in metabolite composition within specific metabolite classes, they are frequently categorized into distinct **chemotypes** (Thon et al., 2024; Eilers, 2021). For instance, studies on plant species such as *Tanacetum vulgare* (Neuhaus-Harr, Ojeda-Prieto, et al., 2024; Kleine & Müller, 2011; Eilers et al., 2021), *Senecio jacobaea* (Macel & Klinkhamer, 2010), *Senecio eurocifolius* (Witte et al., 1992) *Thymus vulgaris* (György et al., 2020; Thompson et al., 2003), *Cannabis sativa* (Lange & Zager, 2022), *Piper arboreum* (Rabelo et al., 2023), *Piper amalago* (Cosmo et al., 2021), *Piper kelleyi* (Glassmire et al., 2016), *Piper marginatum* (Andrade et al., 2008), *Plantago lanceolata* (Medina-van Berkum et al., 2024), and *Salix sachalinensis* (Hayashi et al., 2005) have identified chemotypes characterized by differences in secondary metabolite composition.

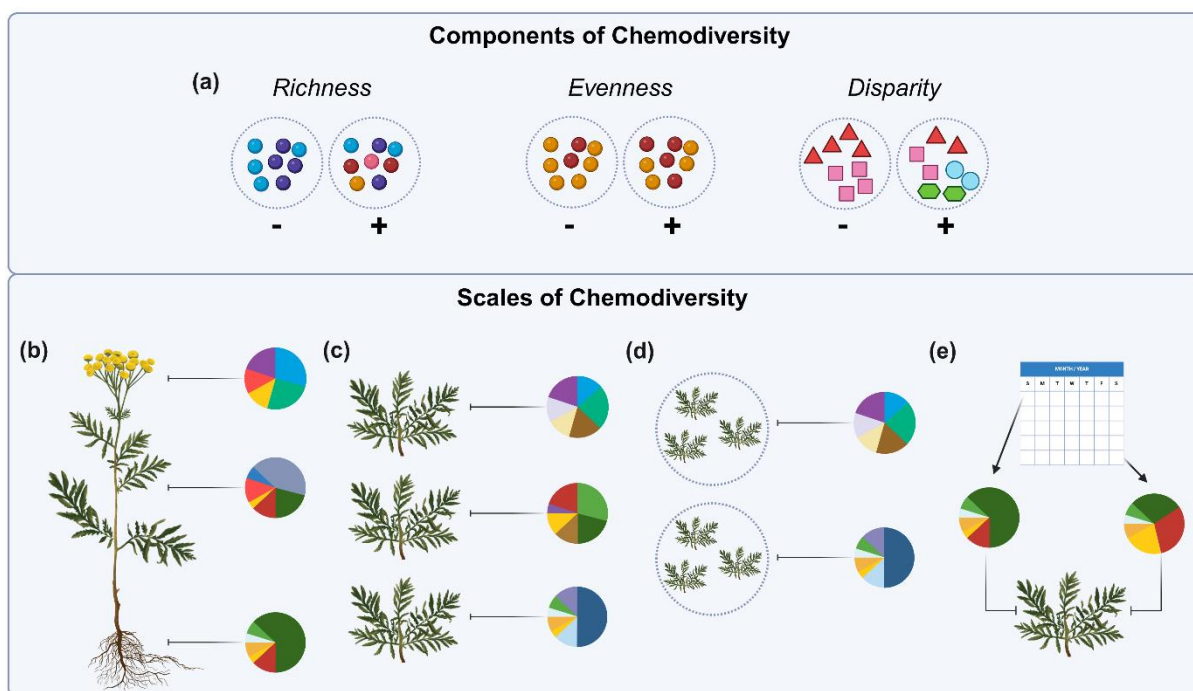


Figure 1. (a) Chemodiversity can be explored through its components. In the illustration, each group contains different compounds (represented by colors). Richness refers to the number of different phytochemicals present, and it increases when more unique phytochemicals are found. Evenness relates to the relative abundance of the phytochemicals; it increases when they become more equal. Disparity reflects the dissimilarity among the phytochemicals in terms of, e.g., molecular structure or biosynthetic metabolic pathway (represented by shapes). It increases, e.g., when more pathways are involved (adapted from Petrén et al., 2023a). Scales of chemodiversity within a species (illustrated here with a pie-chart displaying the relative abundance of secondary metabolites, indicated by color); (b) among different organs within an individual, (c) among individuals within a population, (d) across different populations, and (e) across time (e.g., different time-points or seasons) (adapted from Bielefeld University, 2024). Created with Biorender®.

1.1.3 Chemodiversity in an Ecological Context

Secondary metabolites can further be categorized based on their solubility and volatility, affecting their ecological roles. Non-volatile secondary metabolites are primarily stored in plant tissues like leaves, roots, seeds, and bark and include chemical families like alkaloids, phenolic compounds, and terpenoids (Wink, 2010). Alkaloids, often found in seeds and leaves, can deter herbivores and pathogens due to their toxicity (Mithöfer & Boland, 2012). Phenolic compounds, such as flavonoids and tannins, are typically found in leaves and bark and provide defense against herbivores and pathogens by deterring feeding and inhibiting microbial growth (Treutter, 2006). Terpenoids represent a diverse class of secondary metabolites with volatile

and non-volatile members (Pichersky & Raguso, 2018). Non-volatile terpenoids, often found in leaves, can act as direct defenses against herbivores and pathogens or play roles in plant structural integrity and UV protection (Tholl, 2015).

Volatile organic compounds (VOCs) include terpenoids, green leaf volatiles, and phenolic derivatives (Dudareva et al., 2013). VOCs can attract pollinators, thus facilitating reproduction (Raguso, 2008), and serve as direct defenses by deterring herbivores or inhibiting pathogens (Wetzel et al., 2023; Hare, 2011; Unsicker et al., 2009). They also function as indirect plant defense by attracting predators and parasitoids of herbivores. In plant-plant communication, volatiles can signal neighboring plants to activate their defense mechanisms (Heil, 2014).

The localization and production of secondary metabolites within plant tissues are crucial for their ecological functions. For example, phenolic compounds in cell walls can provide immediate barriers against pathogens, while alkaloids stored in vacuoles can rapidly mobilize upon tissue damage (Underwood, 2012). Similarly, volatile compounds can be produced and released from glandular trichomes or through stomata in leaves and other tissues (Lange & Turner, 2013).

Terpenoid compounds stored in leaves play a critical role in plant interactions with other organisms, especially insects and pathogens (Boncan et al., 2020; A. Cheng et al., 2007; Clancy et al., 2016; Pichersky & Raguso, 2018). Some specialized metabolites, stored in anatomical reservoirs in leaves, can be released in a volatile form due to their chemical properties (volatility and solubility) or the plant physiological or morphological traits, such as the presence of trichomes (Lange & Srividya, 2019; He et al., 2011). Although predicting volatile production is challenging (Dicke et al., 2009; Dudareva et al., 2006), the volatile headspace profile is plausibly related to the compounds found and stored in leaves. However, emitted volatile profiles might differ from those stored in oil reservoirs of trichomes because specific volatile organic compounds are produced only upon attack (known as herbivore-induced plant volatiles, HIPVs, Rashid & Chung, 2017) or induced under abiotic or biotic stress (like green leaf volatiles, benzenoids, and terpenoids). For example, Clancy et al. (2016) found that emitted *T. vulgare* headspace volatiles differed from compounds found in leaves at the individual level by 70%. The extent to which chemotype richness and stored chemical profiles of a group of plants affect the blend of volatiles in their communal headspace remains poorly understood. Higher chemotype richness at the plot level will probably lead to a more chemically diverse VOC headspace, reflecting the variation in stored compounds and their potential volatile emission (Hypothesis 1.2).

1.1.4 Chemical-mediated Interactions

1.1.4.1 Compound-specific Effects on Interactions

Secondary metabolites play crucial roles in plant-arthropod interactions. These compounds can serve as direct defenses against herbivores by deterring feeding or causing toxicity (War et al., 2012; Hartmann, 2007). Alkaloids, phenolics, and terpenoids can disrupt herbivore digestion and metabolism, decreasing herbivory (Müller & Junker, 2022; Mithöfer & Boland, 2012). For example, the glucosinolates in *Brassicaceae* spp. can break down into isothiocyanates after plant physical damage and act as a toxic compound to, for instance, the larvae *Otiorhynchus sulcatus* or as a deterrent to many herbivores such as the generalist *Trichoplusia ni* (Mithöfer & Boland, 2012). The alkaloid nicotine in tobacco plants (*Nicotiana* spp.) can be a potent neurotoxin that deters herbivores (Kessler & Baldwin, 2002). Herbivores, in turn, may adapt to specific chemical defenses, leading to co-evolutionary arms races over evolutionary time (Erb & Robert, 2016). For instance, oral secretions of *Manduca* caterpillars can down-regulate nicotine accumulation in tobacco plants. Furthermore, specialized herbivores may evolve mechanisms to detoxify or sequester plant secondary metabolites, using them to defend against predators (Petschenka & Agrawal, 2016). *Manduca* caterpillars have also developed ways to tolerate high alkaloid concentrations and potentially sequester the metabolite for their defense (Kessler & Baldwin, 2002). Hypothesis 2.4 suggests that aphid species will show species-specific attraction towards tansy chemotypes, with their attraction negatively correlated with increasing chemodiversity.

However, the arms race does not stop there. Natural enemies of herbivores are also attracted to specific VOCs and VOCs mixtures. For instance, after contact with the oral secretions and as a consequence of the nicotine downregulation, the tobacco plant can induce the emission of VOCs that attract *Manduca* caterpillar predators (Kessler & Baldwin, 2001; Halitschke et al., 2000). Many examples across different plant species show that specific compounds released by damaged plants can attract parasitoid wasps and predators that locate herbivorous caterpillars on the plant, thus providing an indirect defense mechanism (Turlings & Erb, 2018; Mithöfer & Boland, 2012; Wu & Baldwin, 2010). Terpenes, such as the sesquiterpene (E)- β -caryophyllene released by maize roots after attack by rootworms, can attract entomopathogenic nematodes (Rasman et al., 2005). Isothiocyanates in *Brassicaceae* spp. can be used by parasitoids of caterpillars that induce those compounds to find their host (Hopkins et al., 2009).

Pollinators may be attracted to soluble compounds in nectar and pollen and specific floral volatiles, which influence plant reproductive success (Kessler & Halitschke, 2007). Different benzenoids in two *Antirrhinum majus* subspecies attract the common bumblebee, *Bombus*

terrestris, differently (Suchet et al., 2011). Phenylacetaldehyde, a common floral volatile in *Silene latifolia*, attracts *Hadena* moths by eliciting antennal responses (Dötterl et al., 2006). Honeybees detected the presence of specific compounds in complex floral mixtures and consistently visited more flowers that produced those compounds (Wright & Schiestl, 2009). Those volatile compounds emitted to attract pollinators can also sometimes have a dual role, whether by inadvertently attracting herbivores or other antagonists that exploit these signals (Schiestl, 2015), such as in the case of *Cirsium arvense*, which produces benzaldehyde and phenylacetaldehyde that attract both pollinating and florivores (Theis, 2006), or by deterring herbivores like in the case of *Nicotiana attenuate* plants that deter nectar thieves like ants but attract hummingbird pollinators (Kessler & Baldwin, 2007).

1.1.4.2 Chemodiversity and its Impact on Interactions

Instead of focusing on individual compounds, some studies investigate the effect of entire chemical profiles on ecological interactions. This approach considers the combined effects of multiple metabolites, which can synergistically or antagonistically affect plant-arthropod and plant-plant interactions (Richards et al., 2015).

Plant chemodiversity affects the interacting arthropod community in terms of its richness, diversity, and structure (Petrén et al., 2023a; Fernandez-Conradi et al., 2022; Dyer & Jeffrey, 2021). In plant-arthropod interactions, higher chemodiversity is hypothesized to attract a more diverse array of arthropods due to the increased likelihood of producing compounds that serve as recognition cues for different species, and thus, probably enhancing reproductive success (Dyer, 2018; Jacobsen & Raguso, 2018). For instance, floral scents are composed of multiple VOCs. Differences in the compound mixture can affect foraging and efficiency pollinator behaviors, drive the specialization of plant-pollinator relationships and their co-evolutionary dynamics, communicate the flower reproductive status, nectar quality, and species identity, and influence the learning and memory processes in insects (Raguso, 2008). Such chemical complexity may also affect herbivore behavior (Segura-Bustos et al., 2017). Increasing the chemotype richness of a plot might increase the occurrence of different arthropod groups, including pollinators, herbivores, and natural enemies (Hypothesis 2.1).

Variations in the chemical profiles of leaves can also influence insect behavior, particularly herbivores, by affecting their attraction, feeding, and reproduction. A diverse chemical profile may also help deter herbivores, providing more comprehensive protection against herbivory (Wetzel & Whitehead, 2020). For example, increased chemodiversity can enhance its resistance to herbivores by making it more difficult for insects to adapt to a single defense compound (Kessler & Halitschke, 2009; Poveda et al., 2003). Thereby, I proposed that higher

plot-level chemotype richness will decrease herbivore and ant abundance but increase predator and flower visitor abundances (Hypothesis 2.2).

Differences in the chemodiversity of plant species caused changes within food webs. For instance, different herbivore and predator communities are associated with different chemotypes of *Tanacetum vulgare* (Senft et al., 2019; Zytynska et al., 2019; Bálint et al., 2016; Benedek et al., 2015; Kos et al., 2011). Hypothesis 2.3 posits that specific chemotypes will have distinct effects on the occurrence and abundance of herbivores, predators, flower visitors, and ants.

Extending the concept of the effects of chemodiversity on plant-arthropod interactions, it can be observed not only in single plants but also across multiple plants within a community and from single chemotypes to a range of chemotypes. Increasing chemodiversity within a plant species in a population can enhance ecosystem resilience, stability, and productivity (Hajjar et al., 2008). For instance, it is positively associated with plant size and herbivore load but negatively with herbivore damage in *Brassicaceae oleraceae* (Bustos-Segura et al., 2017).

Chemodiversity is expected to provide ecosystem resilience against disturbances by supporting diverse community trophic levels (Glassmire et al., 2019; Schuman & Baldwin, 2016). A chemically diverse plant community can support a more complex interaction web, including pollinators, herbivores, and their natural enemies (Richards et al., 2015; Gershenzon et al., 2012). Also, a chemically diverse plant population may better adapt to abiotic and biotic stressors, leading to more stable plant communities (Thibaut & Connolly, 2013; Roger et al., 2012).

In plant-plant interactions, allelopathy is a key mechanism whereby specific secondary metabolites are released into the environment, which might influence plant growth, survival, or reproduction of other plants (Cheng & Cheng, 2015). This process can determine spatial distribution and community structure within plant populations. Plants with higher chemodiversity may exhibit more effective allelopathic effects on neighboring plants, as combining multiple compounds can enhance inhibitory effects on competitors (Gallien, 2017; Mahdavi-Arab et al., 2014). This chemical complexity can contribute to establishing and maintaining plant communities of different or of the same species (Iason et al., 2012a).

Hypothesis 3.1 suggests that individual tansy chemotypes will differ in growth and reproductive traits, which are influenced by the surrounding plot-level chemical richness, possibly due to the combined allelopathic effects enhancing their competitive advantage. Furthermore, plots with higher chemotype richness might be a more favorable environment for plants, potentially increasing overall plant growth (Hypothesis 3.2).

1.1.4.3 Trade-offs in Phytochemical Defense

Although some phytochemicals are the secondary result of chemical reactions, their production commonly involves a metabolic cost on plants, as they require energy and resources (Neilson et al., 2013; Gershenzon, 1994). This allocation of resources to defense compounds can potentially reduce the resources for growth, reproduction, and physiological processes (He et al., 2022; Herms & Mattson, 1992; Coley et al., 1985). Additionally, as explained before, the production of phytochemicals can have ecological costs by affecting interactions with interacting mutualists (Agrawal, 2011), as the same biochemical pathways can mediate multiple interactions within biotic networks (Li et al., 2023; Boncan et al., 2020; Chen et al., 2011). For instance, certain phytochemicals that deter herbivores may also influence the foraging behavior of pollinators (Adler et al., 2012).

Despite their costs, plants still produce phytochemicals with a high variability. It shows that, probably, the costs associated with their production may be compensated by the promotion of beneficial interactions, such as those with pollinators and herbivore predators, leading to greater long-term fitness (Blanchard & Holeski, 2024; Tamburini et al., 2020; Kempel et al., 2011). In some cases, however, the allocation of resources to defense compounds influences competitive interactions within and between plant species. Plants that allocate more resources to phytochemical production might have a competitive advantage in environments with high herbivore pressure but may be outcompeted by plants that allocate resources more towards growth and reproduction in environments with lower herbivore pressure (Züst & Agrawal, 2017; Huot et al., 2014; Boege & Marquis, 2005). Hypothesis 4.1 suggests that there will be a trade-off between the maintenance of chemodiversity and growth-related traits, with resources allocated to phytochemical production potentially limiting those available for growth.

1.2 Introduction to the Model System: *Tanacetum vulgare*

Chemodiversity plays a role in shaping community structure and dynamics at both individual and community levels. At the individual level, a plant chemical profile can determine its interactions with other organisms (Kessler & Kalske, 2018). At the community level, the collective chemical diversity of a population can influence the composition and abundance of associated communities, as well as the competitive dynamics among plant species (Iason et al., 2012b). Empirical studies seek to unravel the mechanisms underpinning the relationship between plant chemodiversity and arthropod-driven ecosystem dynamics involving a variety of methodologies (Wetzel & Whitehead, 2020). This dissertation used *Tanacetum vulgare* L. (tansy), an herbaceous plant known for its intraspecific terpenoid variation (Kleine & Müller, 2011). I study how variation across individuals and the number of tansy chemotypes in a plot

affects insect communities and plant-plant interactions. I conducted several experiments in which the effects of chemodiversity, either at the plant or plot level, were studied. However, this model plant has been the focus of other research lines in chemical ecology; thus, the subsequent section delves deeper into studies conducted in the chemodiversity of *T. vulgare*.

Chemodiversity can be studied at various hierarchical levels, including plant, plot, and community (Figure 1; Iason et al., 2012a). At the plant level, research often focuses on the specific chemical compound profiles produced by individual plants and how the diversity of these compounds affects ecological interactions, such as herbivory and mutualistic relationships (Gershenzon et al., 2012). At the plot or community level, studies examine the combined effects of the chemical diversity of multiple plants and how this influences community dynamics and ecosystem functioning (Richards et al., 2015). Both approaches provide valuable insights into the ecological roles of chemodiversity.

1.2.1 Plant-level Studies

Within the same *T. vulgare* individual, different tissues might produce a different arrangement of chemical compounds differing in one or more chemodiversity components (Figure 1a). This variation might be related to the function of each tissue and its relationship with possible interacting organisms. First of all, the composition and concentration of volatile, stored, and phloem specialized metabolites varied significantly among tansy plant parts and chemotypes, with some metabolites being more dominant in volatile profiles and others in stored forms (Jakobs & Müller, 2019; Clancy et al., 2016), and with leaves containing mainly monoterpenoids and roots containing mainly sesquiterpenoids (Rahimova et al., 2024). Furthermore, variations among different plant parts affect the niche choice of monophagous aphids to the one that maximizes their fitness based on these chemical cues (Jakobs & Müller, 2019). For instance, different aphid species showed distinct preferences for plant parts, with *Macrosiphoniella tanacetaria* preferring stems and *Uroleucon tanacetii* old leaves (Jakobs & Müller, 2019). In a similar way, the high diversity of terpenoids and their tissue-specific distribution, along with the differential inducibility by pipecolic acid to the roots, a known positive regulator of salicylic acid (SA) production that lead to SAR, which application could effectively mimic the SA-dependent response of tansy to aphid attack, suggest that terpenoids play a role in the ecological interactions of tansy and its defense against biotic stressors (Rahimova et al., 2024).

Acknowledging the variation across tissues within an individual and its possible relation to other organisms allows us to define chemotypes based on specific tissues and explore the simultaneous effect of chemodiversity on multiple interacting organisms. For instance, different chemotypes of *T. vulgare*, defined by their leaf terpene profiles, significantly

influenced herbivore abundance and preference, with distinct distribution patterns of aphids and miners and effects on larval development of the last group (Kleine & Müller, 2011). Clancy et al. (2016) investigated tansy plant chemotypes and their effects on aphid colonization and interactions with two ant species, *Myrmica rubra* and *Lasius niger*. The study found that early aphid colonization was associated with specific terpenes (4-terpineol and α -thujone), but mutualistic ants significantly influenced colonization patterns, particularly after the main aphid dispersal phase. Moreover, variation in *T. vulgare* host plant within a plant population can create habitat heterogeneity for specialized herbivores (Clancy et al., 2018) and affect the preference and performance of interacting herbivores (Jakobs & Müller, 2018). For example, *Cassida stigmatica* herbivorous beetle females showed a difference in preference among the 'pure B-thujone' chemotype and mixed chemotypes containing camphor but no difference in performance (larval survival and adult body mass) (Wolf et al., 2012b).

Although tissue variation can occur in plants, there are correlations between compound patterns in leaves and mature flowers (Eilers et al., 2021). In tansy, flower heads showed the same chemotype as the ones defined by the leaf profiles, although the compound mixture was not the same (Sasidharan et al., 2023a). Different tansy chemotypes are also used to explore the differences in flower production, volatile compounds, pollen nutrients, and their relationship with florivory and pollination. A comparison between three tansy chemotypes defined by their leaf terpenoid profile, 'B-thujone', 'Artemisia ketone', and 'Myrox' chemotype (a mixture of (Z)-myroxide, santolina triene, and artemisyl acetate), indicated significant differences also in the terpenoid composition and diversity in flower heads and pollen among these chemotypes (Sasidharan et al., 2023a). Although intraspecific differences in floral traits and their consequences on interactions have not been extensively studied, differences in floral volatile compounds and pollen nutrients can impact the behavior of mutualistic and antagonistic flower visitors (Eilers et al., 2021). For example, in olfactory and contact choice assays, the shining flower beetle, *Olibrus aeneus*, preferred the 'B-thujone' chemotype over the 'Artemisia ketone' and 'Myrox' chemotypes. The beetles gained the least weight and experienced the highest initial mortality when feeding on the 'Myrox' chemotype. Conversely, short-term weight gain and long-term performance were highest on the 'B-thujone' chemotype (Sasidharan et al., 2023a). These results highlight the importance of terpenoid composition in flower heads and pollen influencing insect preferences and performance beyond pollinators.

The effect of chemodiversity is not limited to single interactions. Plant chemotypes are crucial in structuring food webs (Bálint et al., 2016). Specific tansy chemotypes were found to attract predators probably through volatile signals, facilitating the prey's location. This study highlighted the significance of intraspecific chemical variation in understanding trophic interactions and the structure of ecological food webs, suggesting that genotypic and

phenotypic differences within *T. vulgare* explain these dynamics (Bálint et al., 2016). Chemotypes influence herbivore preference and performance, shaping associated food webs and exhibiting varied responses to herbivory. For example, different chemotypes may respond uniquely to prior aphid attacks, resulting in distinct priming effects that affect their responses to subsequent dual herbivory (Clancy et al., 2020).

To further understand the multidimensional role of chemodiversity, it is essential to explore the various components that constitute this phenomenon. One such component is the spatial variation in chemodiversity (Keefover-Ring, 2022; Hahn & Maron, 2016). Spatial variation refers to differences in chemical composition among individuals within a population or populations of the same species across different geographic locations. Spatial variation can lead to differential abiotic conditions and herbivore and competition pressures across a landscape, with some populations being more exposed to abiotic stressors and more susceptible to herbivory than others and some populations being less or more competitive than their congeners (Wolf et al., 2011). For example, the 'Thujone' and 'Carvyl-acetate' tansy chemotypes exhibited distinct responses to drought in the root/shoot ratio, with a higher sensitivity by the last chemotype (Kleine & Müller, 2014). The spatial variation and the differences in selecting pressures might drive local adaptation and potentially lead to the emergence of new chemotypes (Moore et al., 2014).

Within-population chemical diversity is common in plants. Wolf et al. (2012a) compared tansy populations across their native range, Europe, and its expanded range, North America, finding higher genetic diversity within the populations of the last continent. However, they observed no significant correlation between genetic and chemical diversity, suggesting that the genetic structure of invasive populations does not necessarily predict chemical diversity or vice versa (Wolf et al., 2012a). Volatile compound variation in Finnish tansy populations resulted in six chemotypes. The geographical distribution of the 'Camphor-containing' chemotypes differed between Central and Southern Finland, hitting at a possible link between volatile compounds and origin (Keskitalo et al., 2001). Another study examined the large-scale effects of chemodiversity on ecological interactions and geographic variation in specialized metabolites (Rahimova, Neuhaus-Harr et al., 2024). Environmental differences and geographic gradients significantly influenced the distribution of plant chemotypes and herbivores. This study highlighted the importance of understanding chemotypes' distribution and ecological roles within plant communities, demonstrating that abiotic factors can shape the ecological outcomes of chemodiversity (Rahimova, Neuhaus-Harr et al., 2024).

These studies collectively demonstrate that chemodiversity at the plant level is potentially important and can profoundly influence ecological interactions. By examining the chemical profiles of individual plants and their effects on herbivores, predators, and mutualistic species,

the mechanisms driving ecosystem dynamics and the evolutionary forces shaping plant-insect interactions might be better understood. However, while the function of specific chemical compounds in these interactions is well-documented, there is a notable gap in understanding the role of the overall diversity of these chemical profiles. Few studies have systematically linked chemodiversity to ecological interactions and their environment. This gap highlights the need for more comprehensive investigations into the role of chemical diversity in shaping ecological interactions and community dynamics, particularly within a population.

1.2.2 Plot-level Studies

While plant-level studies have provided insights into the effects of chemodiversity in *T. vulgare*, research at the plot level still needs to be explored. Plot-level studies investigate how the combined chemical diversity of plant individuals of the same species within a plot influences ecological interactions and ecosystem functioning (Raffard et al., 2019; Koricheva & Hayes, 2018; Crutsinger et al., 2006). These studies often rely on observational and correlative patterns, leaving a gap in our understanding of the role of chemotype richness in these dynamics. Controlled experiments involving the deliberate selection and manipulation of chemotype richness within plots are essential to unravel the mechanistic effects of chemodiversity on broader ecological processes, but they are scarcer. For example, two chemically distinct tomato varieties in monocultures and dicultures in a field setup were used to check the influence on a generalist herbivore and survival. Another study manipulated the frequency of three *B. oleraceae* populations of distinct foliar glucosinolate content in different plots. Both studies found that increasing intraspecific chemical diversity increased herbivore foraging and abundance but reduced feeding damage (Hauri et al., 2022; Bustos-Segura et al., 2017).

One study in *T. vulgare* explored the role of chemodiversity in plant-aphid interactions using five tansy chemotypes (Ziaja & Müller, 2023). Researchers established field plots with either homogeneous (same chemotype) or heterogeneous (different chemotypes) compositions. They monitored aphid presence and abundance weekly. Results indicated that aphid attraction was not influenced by chemotype or plot type, likely due to the complex odor environment. However, aphid abundance varied with both chemotype and plot type. Specifically, *Uroleucon tanacetii* aphids were more abundant on certain chemotypes ('Keto' and 'ABThu' chemotypes) in homogeneous plots compared with the abundance found in the same chemotypes but in heterogeneous plots, supporting the associational resistance hypothesis. In contrast, *Macrosiphoniella tanacetaria* aphids showed differing presence probabilities between plot types on one chemotype, 'ABThu'. These findings highlight the specific effects of chemodiversity on plant-herbivore interactions, varying by aphid species

and morphs. A second study, conducted in the same field setup, investigated the effects of chemodiversity on interactions between tansy plants and their floral visitors, including pollinators and folivores (Sasidharan et al., 2023b). Researchers recorded flower visits, collected seeds, and determined germination rates of tansy chemotypes growing in homogenous and heterogenous plots. The results showed that plot-level chemodiversity significantly influenced pollinator visitation, with higher visits in heterogeneous plots. Florivore visits were affected by chemotype but not plot type; one chemotype, 'Myrox', in homogeneous plots attracted more florivores. Pollinator and florivore species richness did not vary with plot type, but a negative correlation between their visits suggested competitive interactions. Germination rates correlated positively with pollinator visits and were influenced by chemotype. This study emphasizes the importance of chemodiversity at plant and plot scales in shaping plant-pollinator-florivore interactions and reproductive plant fitness.

While observational studies have provided valuable insights into the ecological roles of chemodiversity, experimental manipulations are crucial for establishing causal relationships and understanding the mechanistic effects of chemodiversity. Existing studies primarily rely on observational data, underscoring the need for more controlled experiments to directly test the impacts of chemotype richness on ecological interactions. Despite these advances, substantial gaps remain in our understanding of plot-level chemodiversity effects. My research aims to fill this gap by systematically investigating how varying levels of chemotype richness within plots influence herbivores, flower visitors, predators, and ant community dynamics and overall plant growth and fitness. By employing rigorous experimental designs and comprehensive analyses, this research will provide new insights into the ecological significance of chemodiversity, contributing to our broader understanding of plant-insect and plant-plant interactions.

1.3 Research Objectives, Questions, and Hypotheses

1.3.1 General Research Objective

To investigate the ecological implications of intraspecific chemical variation (chemodiversity) in *Tanacetum vulgare* L. (Asteraceae) communities, focusing on plant-arthropod and plant-plant interactions.

1.3.2 Research Questions and Hypotheses

In this thesis, I investigated four main questions with multiple hypotheses:

1. Variation in Intraspecific Chemodiversity in Plant Communities:

How does the leaf chemical diversity of tansy plant communities vary regarding total terpenoid concentration, terpenoid richness, terpenoid evenness, and terpenoid Shannon diversity? How does leaf chemical diversity relate to the headspace chemical diversity of those plant communities?

- Hypothesis 1.1: Increasing plot-level chemotype richness will increase the chemodiversity of the plant community in terms of terpenoid richness, terpenoid evenness, and terpenoid Shannon diversity, but not in terms of terpenoid concentration.
- Hypothesis 1.2: Higher plot-level chemotype richness will result in more chemically diverse volatile organic compound (VOCs) headspace.

2. Ecological Consequences of Intraspecific Chemodiversity on Plant-Arthropod Interactions:

How does manipulating intraspecific chemodiversity at the plot and plant level influence plant-arthropod interactions?

- Hypothesis 2.1: Higher plot-level chemotype richness will increase the occurrence of all arthropod groups.
- Hypothesis 2.2: Higher plot-level chemotype richness will decrease herbivore and ant abundances but increase predator and flower visitor abundances.
- Hypothesis 2.3: Certain chemotypes will have specific effects on the occurrence and abundance of herbivores, predators, flower visitors, and ants.
- Hypothesis 2.4: Aphid species will show species-specific attraction towards tansy chemotypes, and their attraction will be negatively correlated with increasing chemodiversity.

3. Ecological Consequences of Intraspecific Chemodiversity on Plant-Plant Interactions:

How does the chemodiversity of *T. vulgare* affect individual plant growth and reproductive traits, and how does plot-level chemical richness influence this?

- Hypothesis 3.1: At the individual plant level, *T. vulgare* chemotypes will differ in growth and reproductive traits, influenced by the plot-level chemical richness.
- Hypothesis 3.2: Plots with higher chemotype richness will exhibit increased plant growth, reflecting biodiversity's positive ecological effects.

4. Link Between Morphological and Chemical Traits:

Are morphological and chemical traits linked at the plant level?

- Hypothesis 4.1: There will be a tradeoff between growth-related traits and chemodiversity, with chemodiversity maintenance limiting resources for growth.

1.3.3 Methodological Objectives

To address these questions and test these hypotheses, the following methodological objectives will be pursued:

- Characterize and manipulate chemodiversity by identifying and selecting *T. vulgare* chemotypes, creating plant communities with different levels of chemodiversity, and developing methods for measuring chemodiversity levels.
- Evaluate ecological consequences of chemodiversity by analyzing the influence of plot chemodiversity on different arthropod groups, examining chemotype effects on herbivore attraction/repellence, and measuring plant growth and reproductive traits.
- Assess morphological and chemical trait links by investigating correlations at the community level and exploring trade-offs between maintaining chemodiversity and plant growth.

1.4 Structure of the Dissertation

The dissertation comprises several interconnected chapters that collectively advance understanding of chemodiversity dynamics within *T. vulgare* communities (Figure 2). **Chapter I** (this chapter) presents the main concepts, context, state of the art, research questions, hypotheses, and objectives. **Chapter II** provides a comprehensive overview of the general materials and methods used throughout the research. Chapter II also details the selection of chemotypes and the design of the field experiments, establishing the foundational framework for the empirical investigations conducted in subsequent chapters. **Chapter III** summarizes the three manuscripts as the completed project deliverables and indicates all relevant results.

The first manuscript (3.1) explores the effect of intraspecific plot-level chemodiversity on plant-insect interactions. This section focuses on the responses of herbivores, the dynamics of aphids' natural enemies and mutualists, and the attraction of flower visitors to varying levels of chemodiversity. Manuscript 3.2 investigates the effect of (plant-level) chemotypes on a specific ecological process, aphid preference. It delves into the mechanisms underlying aphid species-specific preferences and their relations with plant chemodiversity components. This manuscript also shows the possible tradeoff between plant growth and plant chemical defenses. The last manuscript (3.3) investigates plant-plant interactions within plots varying in chemodiversity. It examines how the intraspecific chemodiversity of *T. vulgare* influences these interactions at the plot level, providing insights into the ecological roles and competitive dynamics among plants with differing chemotypes. **Chapter IV**, the General Discussion, synthesizes the findings from the individual chapters, discusses their broader implications,

and proposes future research directions. This final chapter integrates the insights from the study, situating them within the broader context of chemodiversity dynamics.

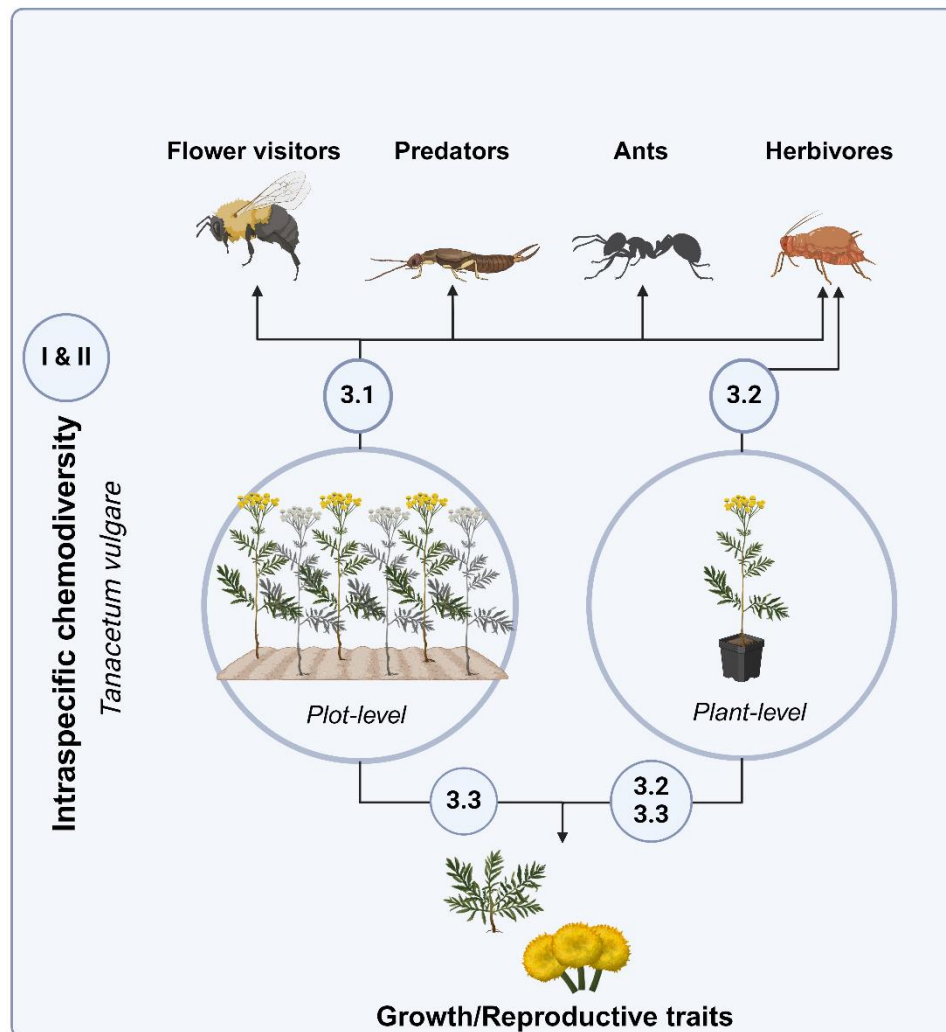


Figure 2. Dissertation overview. Effects of chemodiversity across levels, i.e., among individuals and populations, on plant traits and associated arthropod communities. This scheme shows which concepts and processes are in the scope of each chapter. Chapter I (this chapter) draws the theoretical framework by describing the intraspecific chemodiversity concept and its ecological implications. Chapter II describes the study system, including the model plant, chemotype selection, experimental approaches, data collection methods, and data analysis procedures. Chapter III summarizes the three primary manuscripts and all relevant results of the doctoral thesis: 3.1 presents the effects of plot-level chemodiversity on four arthropod groups, 3.2 explores the effects of plant-level chemodiversity on herbivore preference and the plant growth-defense tradeoffs, and 3.3 summarizes the effect of plant- and plot-level chemodiversity on plant traits. Chapter IV corresponds to the general discussion of findings and implications for future work. Created with Biorender®.

Chapter II. Study System and Methods

Lina Ojeda-Prieto

This section presents an overview of the study system and the methodologies applied in experimental work. Further descriptions of the methods are available in each relevant manuscript.

2.1 Plant Model System

2.1.1 Tansy

Tanacetum vulgare syn. *Chrysanthemum vulgare* (L.) Bernh, known as tansy, is a perennial herbaceous plant in the Asteraceae family. It typically grows between 50 to 150 centimeters in height with erect, often branched, stems (Figure 3a). The leaves are deeply divided and pinnately compound, with numerous toothed leaflets. Tansy propagates asexually by tussock-forming rhizome growth and sexually by producing small, bright yellow flower heads arranged in dense, flat-topped clusters known as corymbs (Figure 3d) (Weisser & Härr, 2005).

Tansy grows well in various habitats, including roadsides, meadows, fields, and riverbanks (Senft, 2019). It is well-suited to full sun and well-drained soils but can tolerate partial shade and less fertile soils (Tutin, 1964). This adaptability has enabled Tansy to spread widely and establish itself in many regions beyond its native range. Originally native to Europe and Asia, tansy has become naturalized in temperate regions across the globe, including North America (Wolf et al., 2012a).

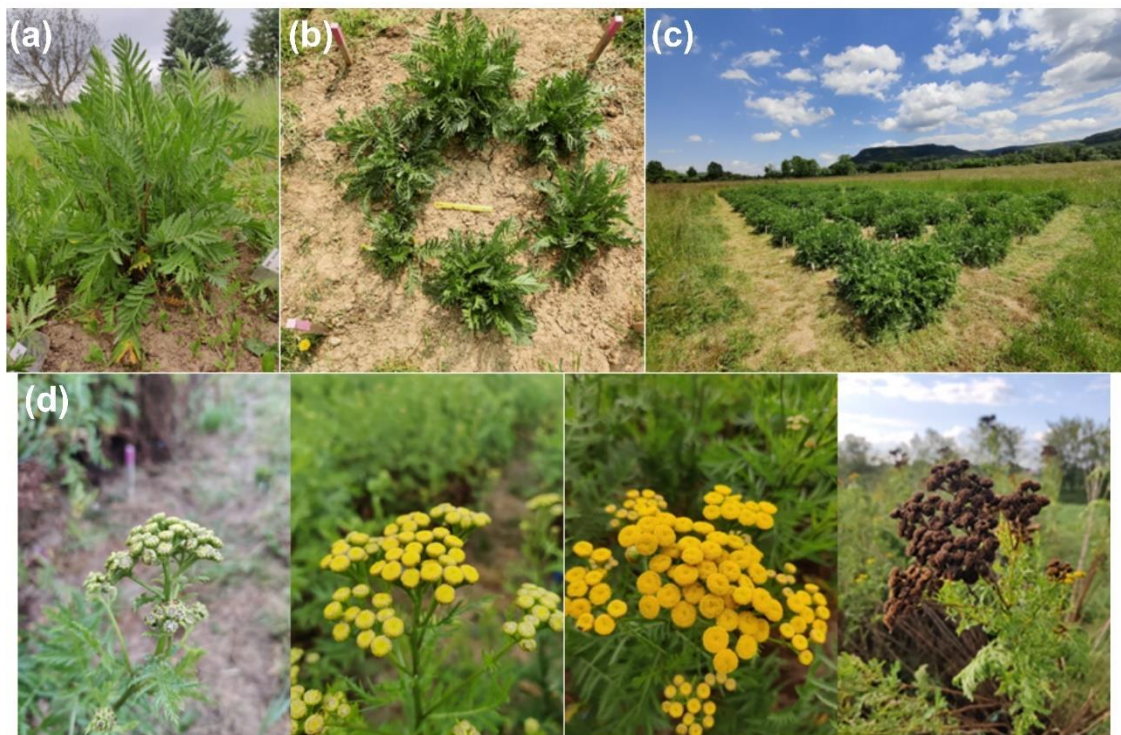


Figure 3. (a) Individual tansy plant. (b) Six distinct tansy plants arranged in a circle. (c) Tansy communities in the experimental setup in Jena, Germany. (d) Flower phenology (left-to-right): Open unripe inflorescence; Open ripe inflorescence; Mature seeds turning brown (Ojeda-Prieto, 2023).

2.1.2 Tansy-associated Arthropod Community

Tansy supports a rich and diverse community of insects and other arthropods. Among the herbivores, aphids are particularly notable, with some species exhibiting a high degree of specialization in feeding on tansy (InfluentialPoints, 2021; Hullé et al., 2020; Favret & Miller, 2012; Thieme & Müller, 2011). Generalist aphids include *Aphis fabae* and *Brachycaudus cardui*. Specialized aphids include ***Macroshiponiella tanacetaria***, typically forming colonies on the stems and undersides of leaves (Figure 4a; Kleine & Müller, 2011), ***Metopeurum fuscoviride***, whose presence can significantly influence the tansy-associated insect community, often involving mutualistic relationships with ants that protect them in exchange for honeydew (Figure 4b; Zytynska et al., 2019), ***Uroleucon tanacetii***, found on the bottom part of leaves and stems (Figure 4c; Jakobs & Müller, 2018).

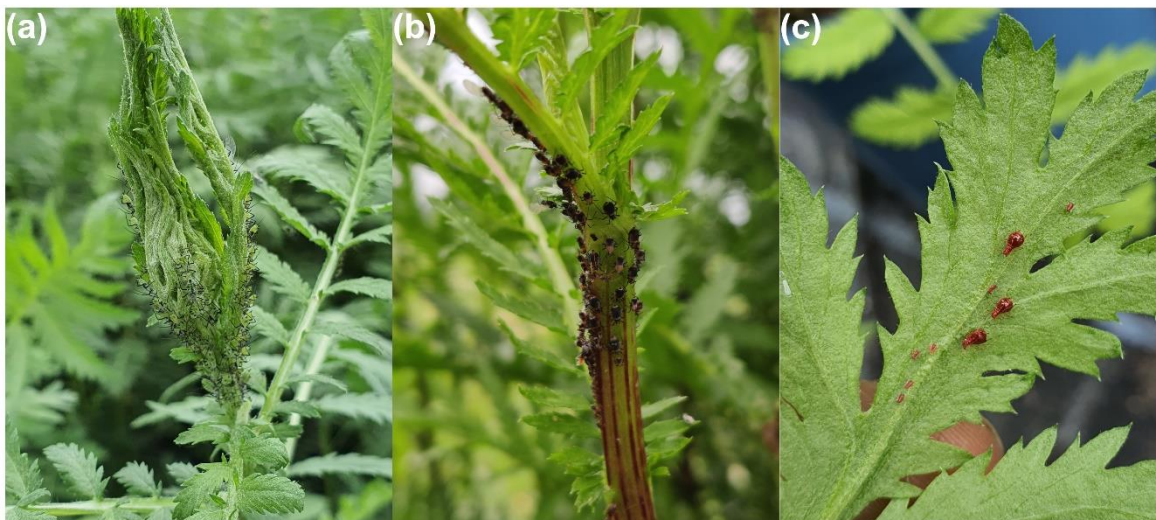


Figure 4. *Macroshiponiella tanacetaria*, *Metopeurum fuscoviride*, and *Uroleucon tanacetii* colonies on tansy plants (Ojeda-Prieto, 2023).

These aphids impact the plant directly through their feeding activities while interacting with other insects and arthropods, influencing the overall dynamics of the ecosystem (Senft et al., 2019; Benedek et al., 2015). Predators such as lady beetles and parasitic wasps often target these aphids, while mutualistic relationships with ants can alter the presence and behavior of other herbivores and predators on the plant (Sanchez et al., 2020; Mehrparvar et al., 2018; Senft et al., 2017; Züst & Agrawal, 2017).

In addition to herbivores and predators, tansy also attracts various pollinators. Bees, butterflies, and other flying insects visit tansy flowers to feed on nectar and pollen, facilitating the plant's reproduction through pollination (Sasidharan et al., 2023b; Eilers et al., 2021) (Figure 5).



Figure 5. Different arthropod groups found on tansy plants, such as **(a)** aphid predators (Syrphidae larva, mummified aphids indicating the presence of aphid parasitoids, Coccinellidae larva and adult, and Mecoptera, which occasionally predate arthropods) **(b)** aphid visiting ant (*Lasius niger*) and ant nest, and **(c)** flower visitors (such as the orders Lepidoptera, Diptera, Hemiptera, Hymenoptera (Braconidae and Apidae), and Coloptera (*Olibrus aeneu*)) (Ojeda-Prieto, 2023).

2.2 Chemical Aspects of the Study System

2.2.1 Chemotypic Characterization

Chemotypes are distinguished by the presence and concentration of specific chemical compounds produced by the plant (Thon et al., 2024; Eilers, 2021). In tansy, these compounds are often stored in specialized structures called trichomes, mainly found on the leaves (Jakobs & Müller, 2019; Clancy et al., 2016). These structures can contain a variety of secondary metabolites, with terpenoids being particularly common and diverse in tansy (Rahimova et al., 2024; Rahimova, Neuhaus-Harr et al., 2024; Kleine & Müller, 2013). Terpenoids are a large

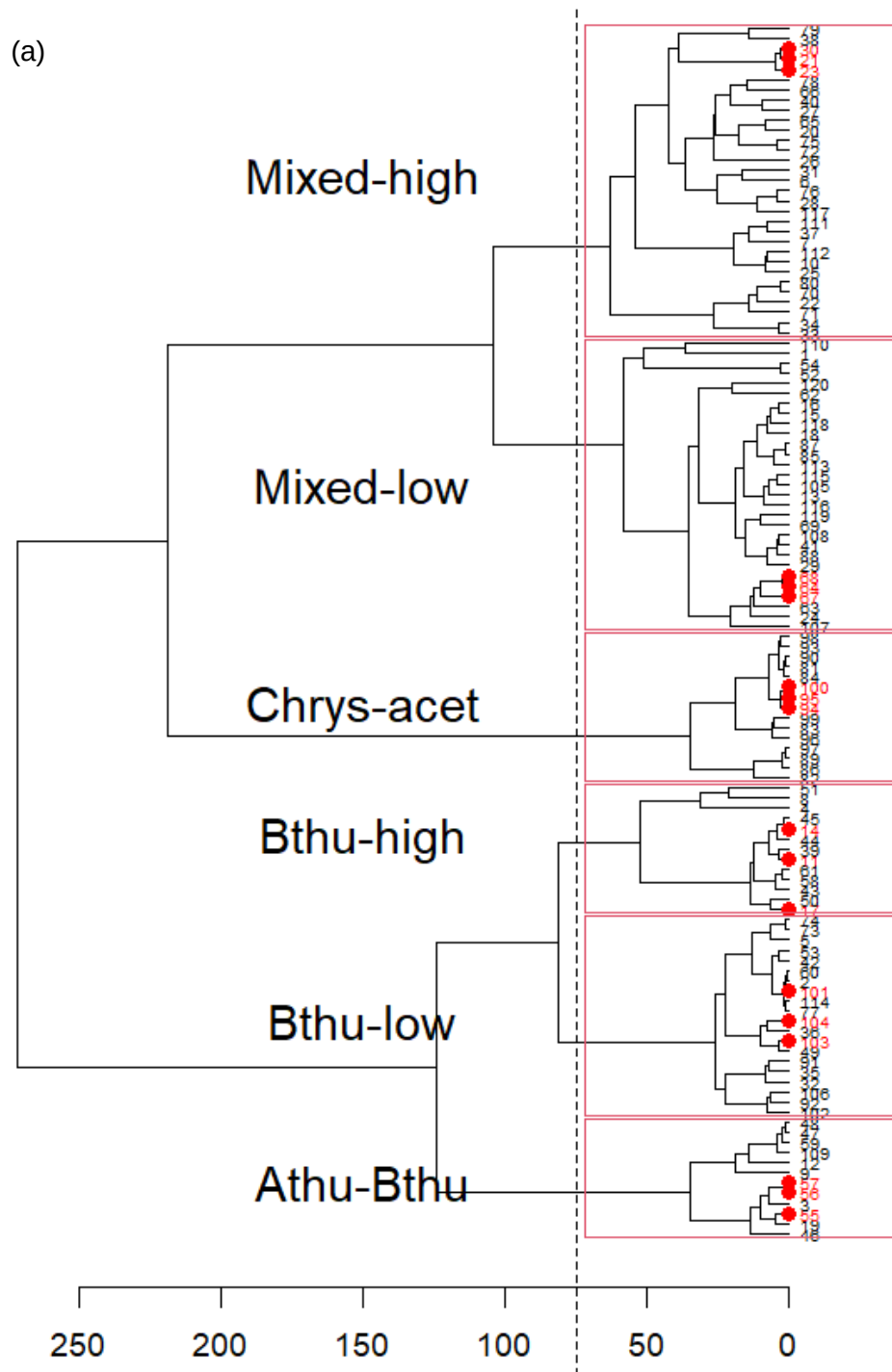
and varied class of organic compounds that play a crucial role in plant interactions with its environment, including defense against herbivores and pathogens, attraction of pollinators, and adaptation to abiotic stresses. The diversity of terpenoids in tansy can lead to the aggregation of individual plants into chemotypes (Clancy, 2021).

The chemotypic characterization of *T. vulgare* lines and their biological replicates was conducted by Dr. Elisabeth Eilers and Prof. Dr. Caroline Müller following methodologies outlined in Neuhaus-Harr, Ojeda-Prieto et al. (2024) and Ziaja & Müller (2023). Leaf and seed samples from 27 *T. vulgare* plants (referred to as mothers) were collected in Jena, Germany (50°55'48"N, 11°34'48"E) in 2019. The leaf material was subjected to terpenoid profiling by undergoing freeze-drying, homogenization, and extraction in heptane with the addition of 1-bromodecane as an internal standard. Extracts were then analyzed using gas chromatography coupled with mass spectrometry (GC-MS: GS 2010plus – MS QP2020, Shinadzu) on a semi-polar column (VF-5 MS, 30 m length, 0.2 mm ID, 10 m guard column, Varian) in electron impact ionization mode at 70 eV, with helium as carrier gas, under specific conditions: starting at 50°C, increasing to 250°C at 10°C min⁻¹, and then to a final temperature of 280°C, held for 5 min. An alkane standard mix (C7–C40, Sigma Aldrich) was measured regularly between samples. To identify and quantify terpenoids, available synthetic reference compounds library entries of the National Institute of Standards and Technology (NIST) 2014, Pherobase (El-Sayed, 2014), and mass spectra reported in Adams (2017) were used to compare retention indices (RI) and mass spectra, as well as using the peak areas of the total ion chromatograms, relative to the sample dry mass and the peak area of the internal standard.

Using unsupervised hierarchical k-means clustering (*hclust()* function), plant terpenoid profiles were organized into chemotypic clusters based on absolute values to include terpenoid composition and concentration. From the initial 27 mothers, Prof. Dr. Wolfgang W. Weisser and Dr. Robin Heinen identified seven distinct chemotypic clusters. They randomly selected six for further analyses (as the field experimental design required six chemotypes). Subsequently, two plants per cluster were randomly chosen, and seeds collected from these mothers were sown, resulting in 120 plants (10 plants from each plant, referred to as daughter plants). Seedlings were grown in controlled conditions and transplanted to a greenhouse, where leaf samples were harvested and freeze-dried for a second chemotyping process.

Hierarchical clustering of daughter terpenoid compositions revealed an optimal clustering solution of six chemotypic clusters (Figure 6a). However, the cluster differed from the one obtained based on the mother chemotyping. One reason may be that daughter plants, being products of outcrossing, demonstrated variability in chemotype expression, possibly due to variations donated by pollen donors. The six resulting clusters were characterized by dominant compounds and their relative concentrations (Figure 6b). The name was assigned after their

dominant compounds as follows: 'Athu-Bthu' chemotype had both α - and β -thujone as prevalent compounds, 'Bthu-high' and 'Bthu-low' chemotypes were dominated by β -thujone but had high or low relative levels of this terpenoid; 'Chrys-acet' chemotype was dominated by chrysanthenyl acetate, and 'Mixed-high' chemotype had three terpenoids with a high relative total concentration, whereas the 'Mixed-low' chemotype featured several terpenoids evenly. Three daughter plants from the same mother plant for each cluster were chosen, resulting in 18 daughter plants for the six chemotypes.



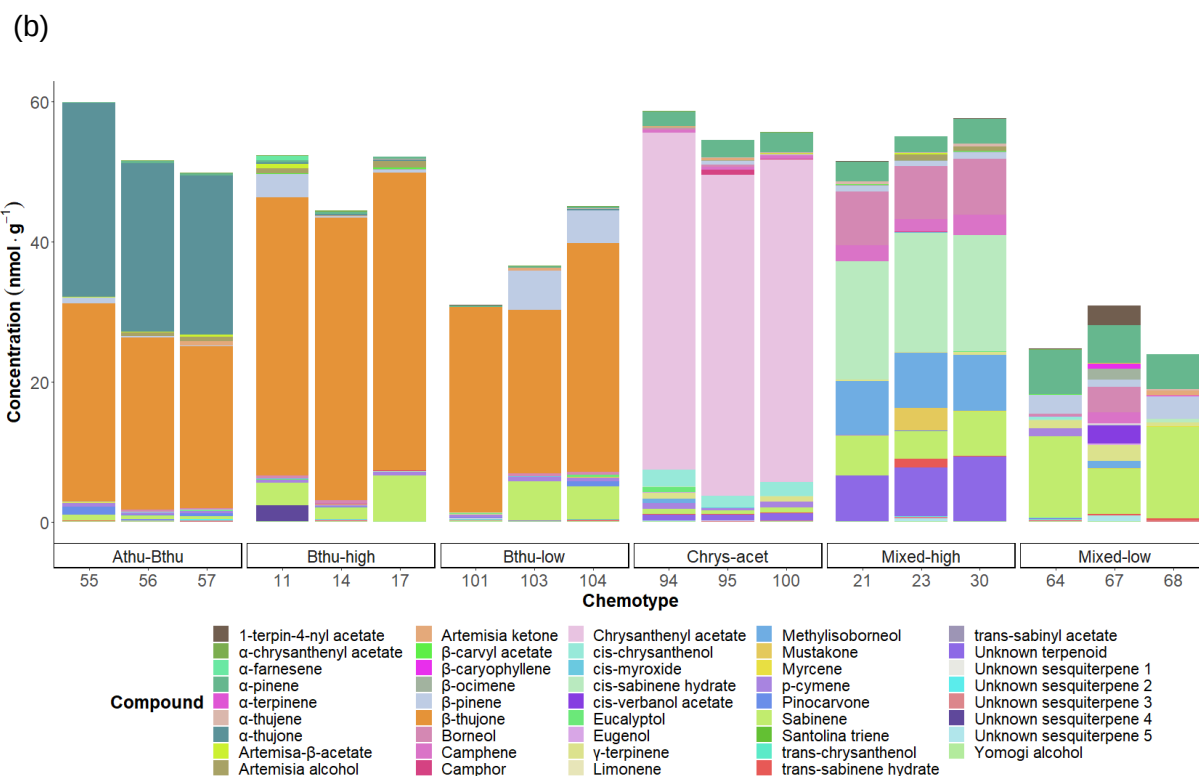


Figure 6. (a) A hierarchical clustering tree was constructed to analyze the terpenoid profiles of all 120 ‘daughter’ plants obtained from the 12 *T. vulgare* ‘mother’ plants. Red boxes visually demarcate the clusters ($k=6$). For the selection process, a distinct maternal lineage and three ‘daughter’ plants were chosen from each cluster (in red) (adapted from Neuhaus-Harr, Ojeda-Prieto et al., 2024). The name of the chemotype, displayed above each cluster, was assigned after their dominant compounds as follows: ‘Athu-Bthu’ chemotype had both α - and β -thujone as prevalent compounds, ‘Bthu-high’ and ‘Bthu-low’ chemotypes were dominated by β -thujone but had high or low relative levels of this terpenoid; ‘Chrys-acet’ chemotype was dominated by chrysanthenyl acetate, and ‘Mixed-high’ chemotype had three terpenoids with a high relative total concentration, whereas the ‘Mixed-low’ chemotype featured several terpenoids evenly. **(b)** Stacked bar charts illustrate the approximate concentration of terpenoid compounds ($\text{nmol} \cdot \text{g}^{-1}$) obtained from the 18 ‘daughter’ plant leaf samples. The offspring samples are grouped based on their chemotype (adapted from Ojeda-Prieto et al., 2024a).

2.3 Experimental Approach

2.3.1 Field Experiment

2.3.1.1 Propagation of Plant Material

In 2020, Dr. Heinen and collaborators used stem parts from the 18 selected daughters to produce 27-40 cuttings per daughter for the field experiment. Each cutting was trimmed 1-2 cm below and 4-5 cm above a leaf node, and the leaf size was reduced by 60% to minimize

evapotranspiration and enhance survival rates. These cuttings were placed into seedling trays filled with soaked potting substrate and covered with clear plastic to maintain humidity. After three weeks, when root and shoot formation occurred, the cover was opened to acclimate the cuttings. As the cuttings were established, they were transplanted into 10 cm pots and subsequently into 17 cm pots before being transplanted to the field site in May 2021.

Potted plants were automatically watered from the bottom and fertilized as needed with Universol Blue fertilizer® (18% N - 11% P - 18% K; ICL Deutschland, Nordhorn, Germany). During propagation and growth in greenhouse and field conditions, no chemical insecticides or fungicides were used; biological control measures were applied as necessary during its time in the greenhouse.

2.3.1.2 Experimental Design

I established the field experiment in the Jena Experiment site, located on the floodplain of the Saale River in Jena, Germany (50°55'N, 11°35'E, 130 m.a.s.l.) under the instructions of Prof. Dr. Weisser. In May 2021, all existing vegetation was removed, and the soil was mechanically tilled. The field was divided into 84 plots (1 x 1 m), separated by 70 cm footpaths, and distributed across six replicated blocks.

Each plot consisted of six tansy plants evenly distributed around a 70 cm diameter circle, totaling 504 plants (84 plots x 6 plants, Figure 7a). The experimental design varied the number and identity of chemotypes in each plot to study the effects of chemotype diversity. Plot-level chemotype richness ranged from 1 to 6. For example, a plot with a chemotype richness of 1 contained six plants of the same chemotype, while a plot with a richness of 6 contained one plant from each of the six different chemotypes (Figure 7b).

To ensure even representation and biological replication, daughters from each chemotype were distributed across different plots. When equal distribution was not feasible, substitutions were made with randomly selected daughters from the same chemotype. Thus, plots contained plants from multiple daughters of each chemotype.

Assignment of plants to plots was predetermined to avoid bias, with each unique chemotype combination replicated twice, except for plots with a chemotype richness of 6, which were replicated twelve times with different daughters. This configuration resulted in 12, 30, 30, and 12 (plots) replicates for chemotype richness levels 1, 2, 3, and 6 distributed across six randomized blocks. The number of chemotype combinations in the experiment for level 1 was 6 out of 6 possible chemotype combinations; for level 2, it was 15 out of 15 possible combinations; for level 3, 15 chemotype combinations out of 40 possible combinations; and level 6, 1 chemotype combination out of 1 possible combination with six chemotypes. Each block contained 14 plots: two plots of richness level 1, five plots of richness levels 2 and 3,

and two plots of richness level 6 (Figure 7c). Data collection includes the years between 2021 and 2024 (Figure 7d).

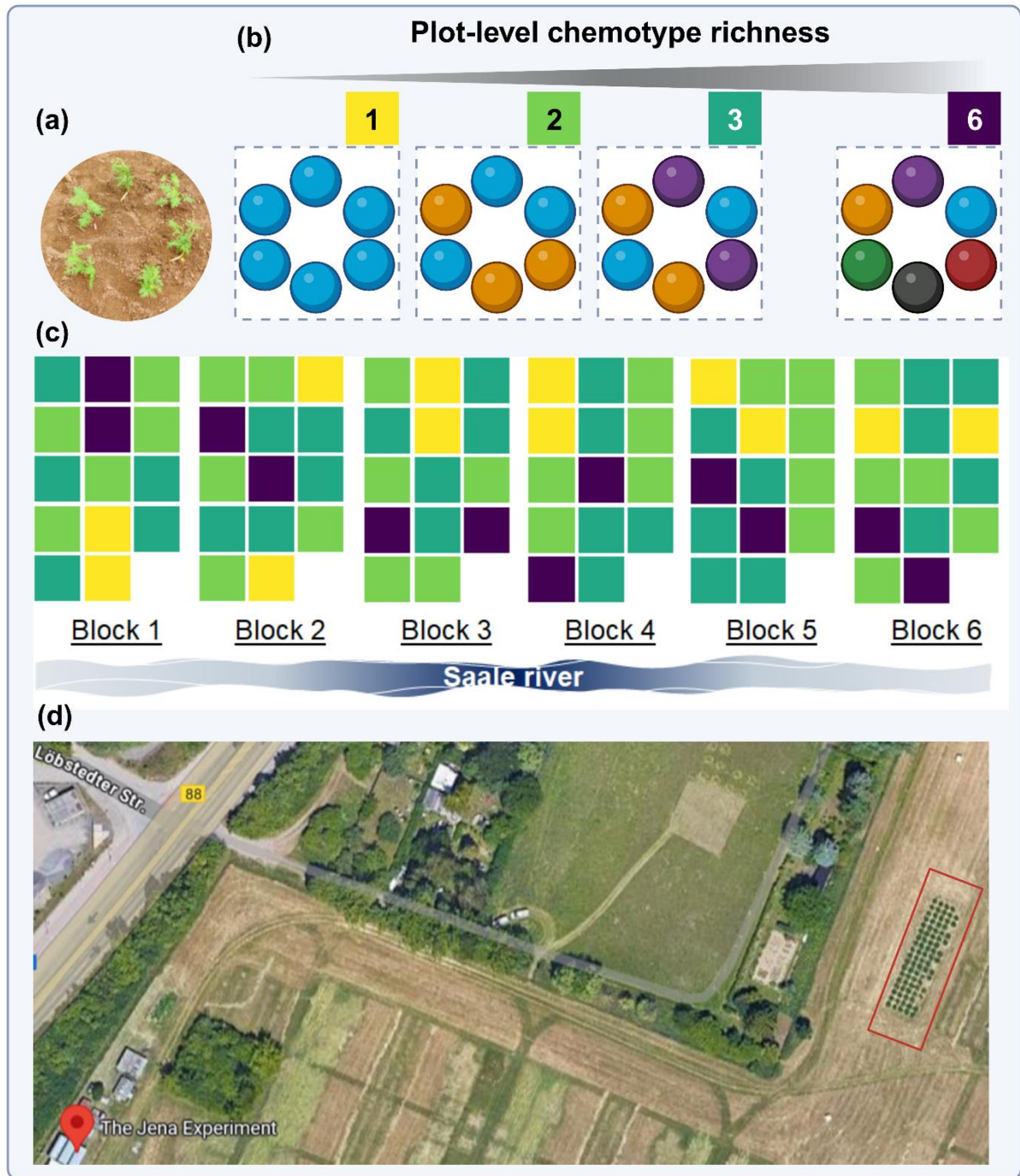


Figure 7. **(a)** Plant arrangement within the plot: Six *T. vulgare* plants distributed equidistantly around a circle with a diameter of 70 cm. The specific chemotypes in each plot were predetermined, while the positioning of the plots was random. **(b)** Plot-level chemotype richness (different colors denote different chemotypes; the number of different chemotypes per plot ranges from 1 to 6). **(c)** The experimental setup used a block design, where plots with chemotype richness levels 1, 2, 3, and 6 were represented by yellow, light green, dark green,

and purple squares, respectively. A total of 84 plots were evenly distributed across six randomized blocks. Each block contained 14 plots: two with chemotype richness level 1, five with level 2, five with level 3, and two with level 6. **(d)** Aerial image of The Jena Experiment site (GeoBasis-DE/BKG, 2024) and the location of the field experiment (indicated by the red square) (adapted from Ojeda-Prieto et al., 2024a). Created with Biorender®.

2.3.1.3 Data Collection Methods

Insect Sampling

From 2021 to 2023, insect communities associated with *T. vulgare*, including herbivores, flower visitors, predators, and ants, were assessed. Herbivore counts, predominantly aphids, were conducted 13 times in 2021, eight times in 2022, and three times in 2023. Each count involved a meticulous scan of each plant, starting from the tip of each stem and examining both sides of each leaf. Aphids were identified at the species level, and high-density populations were estimated by counting aphids on sampled stem and leaf sections and extrapolating.

Flower visitors were counted three times in July 2021 and once in August 2021. Surveys lasting three minutes per plot were conducted randomly throughout the day. Flower visitors were identified at the order level. Predatory arthropods and ants were assessed on the same dates as herbivore counts for 2021 and 2022 and the following day in 2023. Predators were classified into various taxa/feeding guilds, and mummies (parasitized aphids) were also counted.

Morphological Traits

In the field, six morphological plant traits were measured during the first three years (2021 – 2023). I included four growth traits (number of stems per plant, height of the highest stem, above-ground fresh and dry weight) and two reproductive traits (cumulative number of flower heads and flowering index). Measurements were taken thrice in 2021 (June 01, June 22, and October 28). Stems taller than 5 cm were counted, and plant height was measured from the ground to the tip of the longest stem. Ripe flower heads were counted and removed weekly from June 01 to October 28, 2021, to prevent reseeding. At the end of the first season (October 28, 2021), plants were harvested 5 cm above ground, placed in paper bags, and dried for 72 hours at 60°C to determine above-ground dry weight.

In 2022, stem counts occurred once (July 06), and plant height was measured three times (May 14, July 06, and October 05). Phenological states were recorded once (July 06) using numerical categories: [1] No inflorescence; [2] Inflorescence visible but closed; [3] Open inflorescence; [4] Beginning seed set (unripe); [5] Ripe seeds; [6] Mature seeds turning brown.

Mature seeds were collected to avoid reseeding. A flowering index was calculated for each plant by dividing the sum of all stem-level phenological stages by the number of stems. At the end of the second season (October 05, 2022), plants were harvested and immediately weighed to obtain fresh weight.

Headspace VOC Collection

Headspace volatile organic compound (VOC) emissions were collected at the plot level (including all six individual plants) from May 12 to 14, 2022. Weeds were removed ten days before measurements to reduce interference. A PET foil bag (110 cm x 110 cm x 40 cm) covered each plot, and with a closed-push-pull system, volatiles were collected for 2 hours. Air entered through an activated charcoal filter at 1.5 L/min and was pumped out through a trap containing 25 mg of Poropak-Q absorbent (Volatile Collection Trap LLC, USA) at 1 L/min (Figure 8). VOCs were collected over three days, with three rounds of ten plots per day (two blocks and two background plots per day).

After collection, traps were eluted with 200 μ l dichloromethane containing nonyl-acetate as an internal standard. VOCs were analyzed using a Hewlett Packard model 6890 gas chromatograph coupled to a 5973 mass spectrometer (GC-MS). The GC used helium as carrier gas at 1 ml/min, split-less injection at 220°C, and a DB-5MS column. The temperature program ranged from 40°C to 350°C, and the GC was coupled to a single quadrupole mass spectrometer. VOCs were identified by comparing retention times and mass spectra with commercial standards and mass spectral libraries (Wiley 275 and NIST05a). Kovats retention indices were calculated to verify VOC identity. This study reports only volatile terpenoid diversity metrics at the plot level.

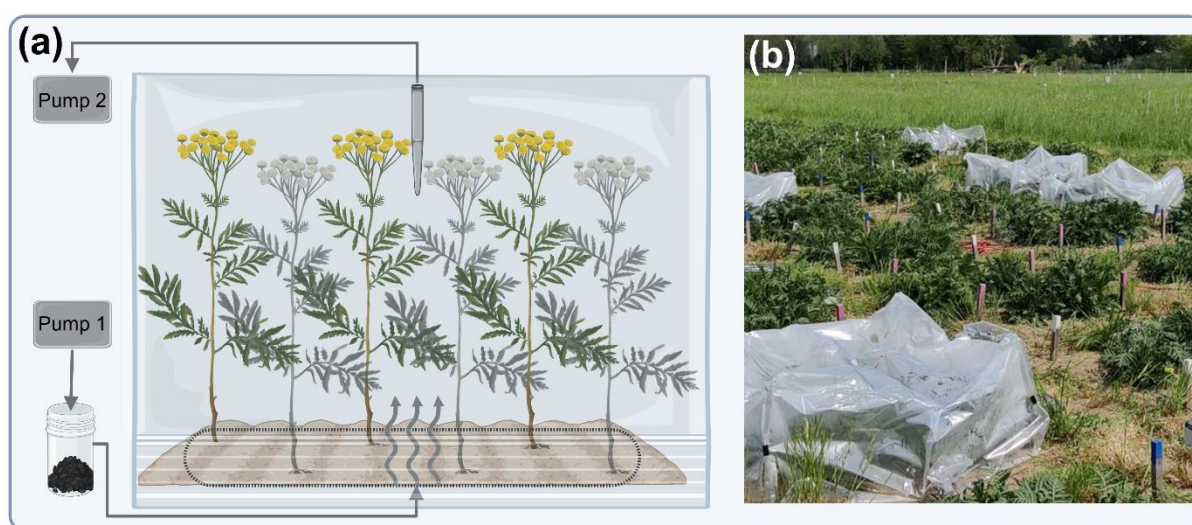


Figure 8. (a) Illustration of the enclosed push-pull headspace VOC collection apparatus. Filtered air flows from pump 1 through an activated carbon filter into the collection PET bag,

is distributed around the plants using connecting tubes, and drawn through a volatile trap positioned on top among the six plants using a second pump (adapted from Ojeda-Prieto et al., 2024). **(b)** VOC collection in May 2022 (Ojeda-Prieto, 2023). Created with Biorender®.

2.3.1.4 Data Analysis Procedures

Occurrence and Abundance of Arthropods

To examine the effects of plot-level chemotype richness and chemotype presence on the occurrence and abundance of arthropod taxa, I employed a combination of statistical models, including binomial Generalized Linear Mixed-effect Models (GLMM), Linear Mixed-Effect Models (LMM), and Zero-Inflated Negative Binomial Models (ZINB). These models were applied cumulatively for each year and sampling time, allowing us to assess the impact of chemotype diversity on arthropod communities across different time points. Data were analyzed at the arthropod group and lower taxonomic levels (when indicated).

Plot-level Chemotype Richness and Diversity Metrics

I employed a multi-step approach to assess plot-level chemotype richness and diversity metrics. Based on the cumulative terpenoid profiles of individual daughters in each plot, I calculated *theoretical leaf* diversity metrics at the plot level using the 'chemodiv' package (Petrén et al., 2023b). The *realized volatile* diversity metrics were calculated similarly using the terpenoids collected in the headspace VOC. The diversity metrics (in both calculations) included terpenoid concentration, evenness, richness, and Shannon diversity. The comparison between leaf and headspace terpenoid profiles was done by calculating Bray-Curtis dissimilarity matrices for hierarchical analyses and performing a Mantel test with 9999 permutations using the 'vegan' package (Oksanen et al., 2023).

I further investigated the relationship between theoretical leaf and realized volatile chemodiversity metrics at the plot level. Linear models were applied to analyze plot-level theoretical leaf chemodiversity metrics while incorporating plot-level chemotype richness as the independent variable. For plot-level realized volatile chemodiversity metrics based on field-collected headspace VOCs, linear models were utilized, with Block ID and Collection Day ID included as random factors to account for potential sources of variation.

Effects on Traits of Individual Plants

The effects of chemotype and plot-level chemotype richness on individual plant traits were analyzed using a combination of Generalized Linear Mixed-Effect Models (GLMM) and Linear Mixed-Effect Models (LMM). These mixed-effect models allowed us to account for the hierarchical structure of the data, with random effects such as Daughter ID and Plot ID incorporated into the models. Post hoc comparisons were conducted to further explore

significant effects, with Tukey adjustment applied to control for multiple comparisons. Additionally, I conducted supplementary analyses to investigate within- and between-chemotype differences, providing a more nuanced understanding of trait variation across different chemotype compositions.

Effects on Plot-level Means

To assess the impact of chemotype presence and plot-level chemotype richness on plot-level trait values, I employed linear models. Separate analyses were conducted for each chemotype, considering Block ID and the interaction between chemotype presence and plot-level chemotype richness as additional factors.

Overyielding Calculations

Overyielding indices were computed to compare the plot-level performance of plants growing in plots with different levels of chemotype richness compared to their performance in monocultures. The overyielding index was calculated according to the formula $OI_i = (O_{ci} - E_c) / E_c$ where OI_i is the overyielding index for plot i , O_{ci} is the observed yield of a mixture plot i , and E_c is the expected yield for the plot, calculated by averaging the yield of monocultures of each of the chemotypes present in the plot. If the overyielding index is positive, it indicates that the yield for a given chemotype in a mixture is greater than expectations from monocultures, which signifies overyielding. If the index is negative, it indicates underyielding. Linear Mixed-Effect Models (LMM) were utilized for this analysis, treating plot-level chemotype richness as a fixed factor and Block ID as a random factor.

I used R versions 4.1.2, 4.2.2, and 4.3.1, and RStudio 2022.07.2+576 and 2023.09.1. The statistical analyses contributed to a comprehensive understanding of the impact of chemotype diversity on arthropod communities, herbivore preferences, plant traits, and growth-defense tradeoffs. For data visualization, I utilized a combination of 'ggplot2', 'grid', 'gridExtra', and 'ggpubr' packages (Auguie et al., 2017; Kassambara, 2020; Wickham, 2016). These packages facilitated the creation of informative visual representations of the effect of chemodiversity, aiding in the interpretation of results.

2.3.2 Plant-level Experiment

2.3.2.1 Propagation of Plant Material

Shoot cuttings for the plant-stand experiments were prepared following the same procedure as cloning daughter plants for the field experiment. However, due to the low propagation success of the 'Bthu-low' chemotype, clones from five of the six *T. vulgare* chemotypes were used for choice assays (Section 3.2), with three replicate daughters per chemotype. Clones,

ranging from 6-10 per daughter, were grown in separate pots randomly spaced in the greenhouse, ensuring independent development for each plant.

2.3.2.2 Experimental Design

A full-factorial series of pairwise choice assays was designed, allowing aphids to choose between leaves of cloned plants of two different chemotypes. Within each replicate series, all chemotypes were tested against each other using randomly picked clones from randomly picked daughters of the mother chemotypes, maximizing the number of unique pairwise choices between chemotype-daughter pairs. Choice assays were conducted in three rounds on three different days with different aphid cohorts standardized by age (9–10 days old) within one week (9–16 December 2021). In total, 23 replicate rounds for *M. tanacetaria* and 13 for *U. tanacetii* were performed, as cohort numbers were lower for *U. tanacetii*.

The second and third youngest fully expanded leaves of a plant were selected, the first three leaflets discarded, and the following leaflets used. Two different leaflets were placed in new 14.5 cm petri dishes at equal distances from the center and 8 cm apart from each other. The sides for each replicate alternated to account for external bias. One starved aphid was placed in the center of the petri dish, and the petri dishes were sealed with parafilm to prevent the leaves from drying quickly. Petri dishes were kept in a climate chamber at the Technical University of Munich (TUM Model EcoSystem Analyzer TUMmesa). The LED lighting system in these chambers generates homogenous light conditions, reducing spatial effects. Petri dishes were left for 24 hours (16:00 : 8:00 h L, 21°C, 60% RH). Aphid preference was recorded after 2, 5, and 24 hours. However, due to decreased leaf quality after 24 hours, most aphids were not on the leaves or had died, so the 24-hour time point was excluded from all following analyses. Each aphid and leaf were only used once, and dead aphids were excluded from further analyses.

2.3.2.3 Data Collection Methods

Morphological Traits

Morphological traits of the original 120 daughter plants were measured non-destructively in February 2021. Traits assessed included the number of stems, leaves, and nodes per plant. Plant height was recorded in centimeters (cm), and internode length was calculated by dividing the height by the number of nodes. The youngest fully expanded leaf was analyzed for total number of leaflets, leaf length, and leaflet density (leaflets per petiole length). Chlorophyll content was measured using a Konica Minolta SPAD-502Plus chlorophyll meter. Leaf surface area was determined using ImageJ (Schneider et al., 2012). The leaves were dried for 72 hours at 60°C to determine dry weight and specific leaf area.

2.3.3.3 Data Analysis Procedures

In the analysis of pairwise choice assays, binomial tests assessed whether aphids preferred specific chemotypes and whether spatial or observer effects influenced these preferences. Conditional logistic regression models evaluated the attractiveness of *T. vulgare* chemotypes and daughters to aphids, with z-values indicating attractiveness levels. Plant chemodiversity metrics (Shannon diversity, terpenoid evenness, richness, and relative terpenoid concentration) were calculated using the ‘*chemodiv*’ package. The relationship between chemodiversity metrics and plant attractiveness was analyzed through models for each aphid species. Correlations between individual terpenoid concentrations and attractiveness were also examined, and a multiple regression model identified significant compounds, adjusting for multicollinearity. To test differences in plant characteristics (height, stem and leaf count, leaflet density, specific leaf area, chlorophyll content, and chemodiversity metrics) among chemotypes, I employed a one-way ANOVA.

Chapter III. Results

This thesis contains three first-author/co-first-author manuscripts. This section includes a summary of relevant results, a list of addressed questions, a detailed description of author contributions, and a graphical abstract for each manuscript. The complete manuscripts are attached in the Appendix A.

3.1 Manuscript I: Intraspecific Chemical Variation of *Tanacetum vulgare* and its Effect on Plant-insect Interactions

Ojeda-Prieto, L., Moreno, E. L., Heinen, R.* & Weisser, W. W.* (2024). Increasing intraspecific plant chemical diversity at plot and plant level affects herbivorous, predatory, and pollinating arthropod communities.

* These authors supervised the project equally and share senior authorship

Preprint available on: <https://www.biorxiv.org/content/10.1101/2024.07.10.602874v1>

3.1.1 Summary

The study focuses on the effect of intraspecific chemical variation in tansy (*Tanacetum vulgare* L., Asteraceae) on four arthropod groups (herbivores, flower visitors, predators, and ants) at the plot level (as described in Chapter II). I aim to understand how intraspecific plot-level chemical diversity affects arthropod communities in occurrence and abundance over three seasons. Furthermore, this research emphasizes the distinct effects of specific chemotypes on community assembly within arthropod groups over time, highlighting the role of plant chemical diversity in shaping insect communities.

Plot-level chemotype richness significantly influenced the overall annual abundance of insects but with contrasting effects on different functional groups. As chemotype richness increased in the plot, herbivore numbers declined (Figure 9a), while flower-visiting insects became more abundant (Figure 9b). These trends were particularly pronounced for certain species; the specialist aphid *Uroleucon tanacetii* drove the herbivore pattern (Figure 10a), while the positive effect on flower visitors was consistent across multiple insect orders, including beetles, bees, and butterflies (Figure 10b).

The presence of specific plant chemotypes within a plot had effects on the arthropod community. For herbivorous species, the effect of chemotype presence changed over time, transitioning from attractant to repellent (Table 1). In contrast, pollinators consistently responded positively to chemotype presence (Table 2). Interestingly, the study found that indirect interaction partners, such as ants and predatory insects, exhibited less clear-cut patterns in their responses to chemotype richness and chemotype identity. This suggests that additional factors beyond plant chemical diversity may influence their population dynamics.

The results emphasize the plant-centered perspective in understanding the relationships between plant chemodiversity and different types of plant-arthropod interactions. My findings

provide valuable insights into the ecological consequences of chemodiversity on arthropod communities and shed light on the evolutionary forces that have shaped intraspecific chemical diversity in plants.

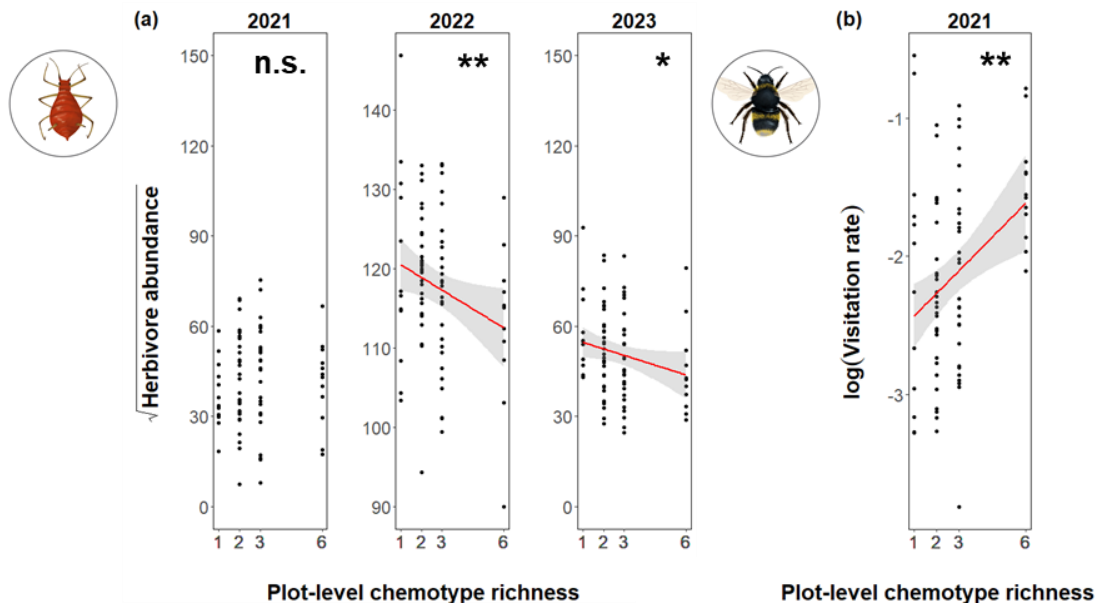


Figure 9. Effect of plot-level chemotype richness on the abundance of different arthropod communities. (a) Effect on herbivore abundance (2021 – 2023). **(b)** Effect on flower visitor abundance (i.e., visitation rate), calculated as the cumulative count of flower-visiting insects divided by the sum of flower heads counted during each assessment date (2021). Significance is indicated as follows: n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$ (adapted from Ojeda-Prieto et al., 2024b).

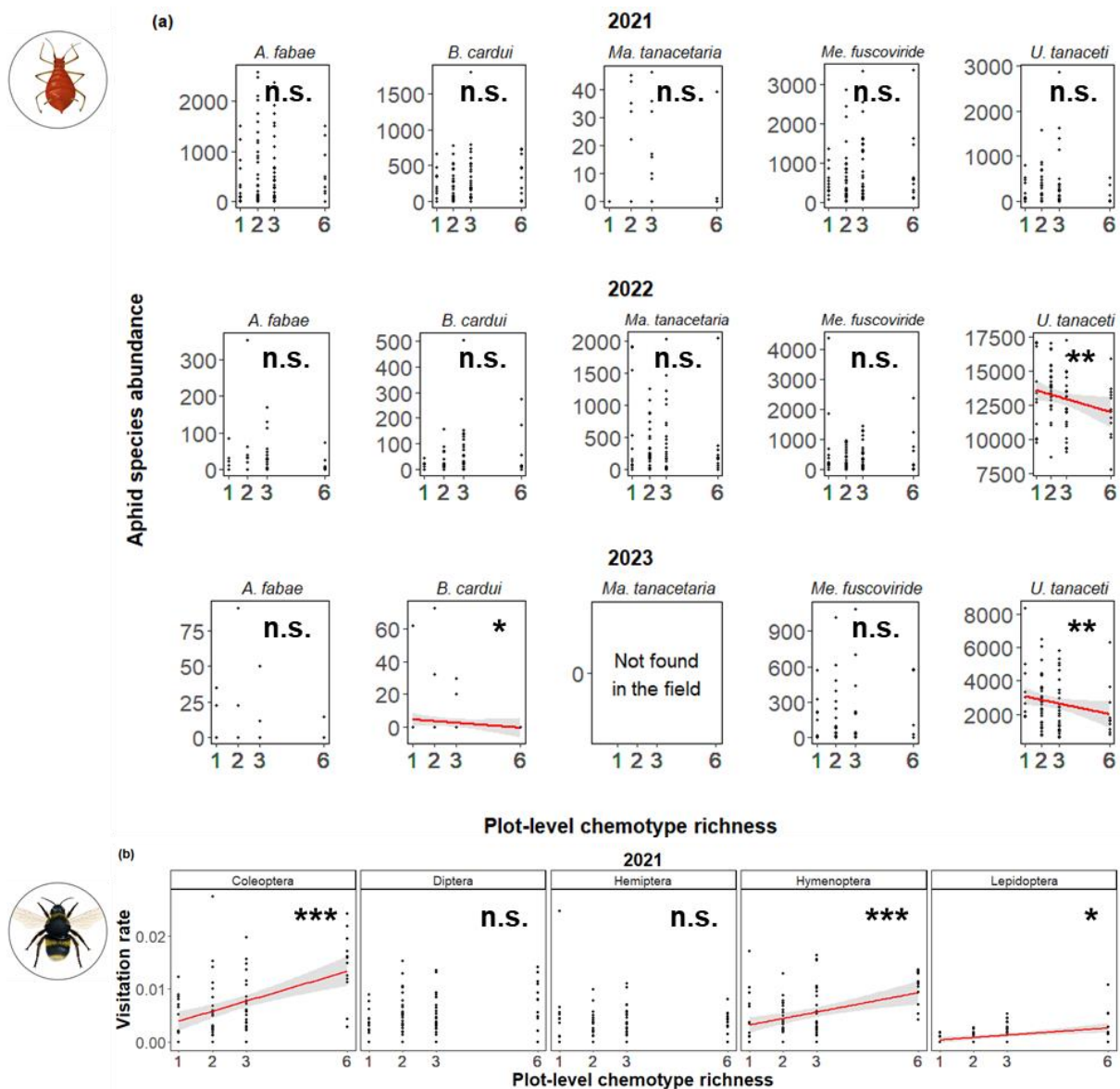


Figure 10. Effect of plot-level chemotype richness on specific group abundances within each guild of arthropod communities. (a) Effect on herbivore abundance of *Aphis fabae*, *Brachycaudus cardui*, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride*, and *Uroleucon tanacetii* each year (2021 – 2023). **(b)** Effect on flower visitor abundance of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera (2021). Significance is indicated as follows: n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$ (adapted from Ojeda-Prieto et al., 2024b).

Table 1. Significant effects of plot-level chemotype presence on herbivore species.

Relative changes were calculated by the logarithm of the ratio of mean values for the “Presence” and “Absence” groups of each chemotype (columns) for each respective herbivore response variable (rows). The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive effect of chemotype presence) to white (no effect) to red (negative effect of chemotypes), with the midpoint set to 0; stronger colors represent stronger effects of the respective chemotype on plot-level response variables (adapted from Ojeda-Prieto et al., 2024b).

		CHEMOTYPE					
		Athu-Bthu	Bthu-high	Bthu-low	Chrys-acet	Mixed-high	Mixed-low
Occupancy	2021	All species					
		<i>A. fabae</i>					
		<i>B. cardui</i>					
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>				-0.288	
	2022	All aphid species					
		<i>A. fabae</i>		0.488		0.619	-0.540
		<i>B. cardui</i>	0.330	-0.433			
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>					
	2023	All aphid species					
		<i>A. fabae</i>		-0.629		0.916	-0.097
		<i>B. cardui</i>					
		<i>Me. fuscoviride</i>	-0.410			-0.601	
		<i>U. tanaceti</i>					
Abundance	2021	All species					
		<i>A. fabae</i>				0.297	
		<i>B. cardui</i>	0.449		0.663		
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>	0.815				
	2022	All aphid species			-0.046	-0.034	
		<i>A. fabae</i>		-0.481			
		<i>B. cardui</i>					
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>		-0.341			
		<i>U. tanaceti</i>			-0.050	-0.037	
	2023	All aphid species	-0.134				-0.134
		<i>A. fabae</i>	-1.916		-0.689		
		<i>B. cardui</i>	-2.096	-0.498		-0.269	
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>	-0.133				-0.131

Table 2. Significant effects of plot-level chemotype presence on flower visitor orders.

Relative changes were calculated by the logarithm of the ratio of mean values for the “Presence” and “Absence” groups of each chemotype (columns) for each respective flower visitor response variable (rows). The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive effect of chemotype presence) to white (no effect) to red (negative effect of chemotypes), with the midpoint set to 0; stronger colors represent stronger effects of the respective chemotype on plot-level response variables.

		CHEMOTYPE					
		Athu-Bthu	Bthu-high	Bthu-low	Chrys-acet	Mixed-high	Mixed-low
Occupancy	2021	All orders					
		Coleoptera					
		Diptera					
		Hemiptera					
		Hymenoptera			0.487		
		Lepidoptera	0.730				
Abundance	2021	All orders			0.440	0.315	
		Coleoptera		0.251	0.256		
		Diptera					
		Hemiptera					
		Hymenoptera		0.332			
		Lepidoptera	0.748				

3.1.2 Addressed Questions

What is the influence of intraspecific chemodiversity on plant-arthropod interactions at the plot level?

How does increasing plot-level chemotype richness affect the occurrence and abundance of herbivores, flower visitors, predators, and ants?

What are the specific effects of individual chemotypes on herbivores, flower visitors, predators, and ants in the plot community?

3.1.3 Author Contributions

LOP participated in planting the field experiment, let the data collection efforts throughout the study period, conducted primary analysis of ecological data, wrote the first draft of the manuscript, and incorporated feedback and revisions from co-authors. ELMP participated in the arthropod surveys in the first and second year, assisted in the field experiment maintenance, contributed to the interpretation of results, and provided input on the manuscript drafting and revision. RH prepared the field experiment site, propagated the plant chemotypes,

planted the field experiment, contributed to ecological data analysis, and reviewed and provided input on the manuscript. WWW conceptualized the original research idea, designed the experimental framework, provided guidance on data analysis and interpretation, and critically reviewed the manuscript. RH and WWW share the last authorship. All authors reviewed and approved the final version of the manuscript prior to submission.

3.1.4 Graphical Abstract

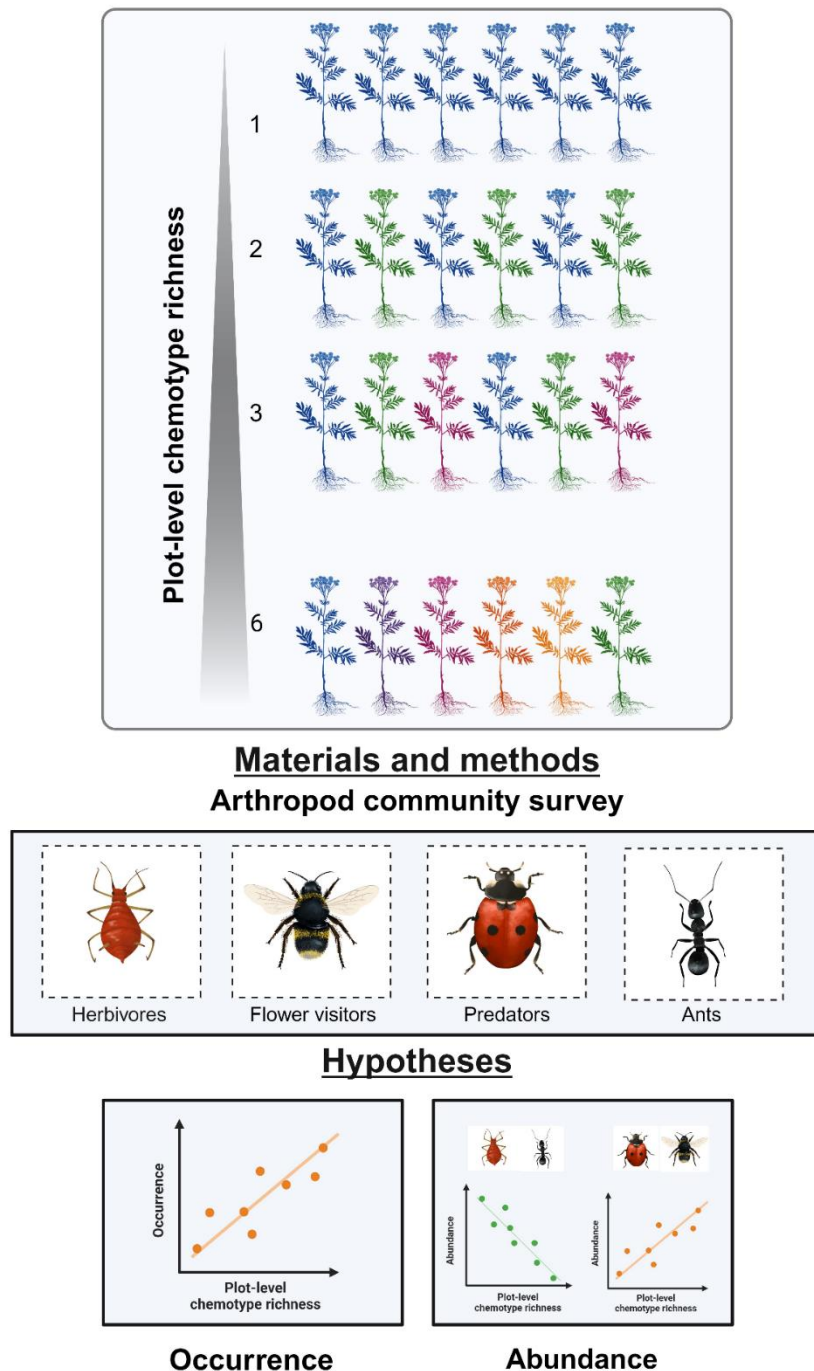


Figure 11. Section 3.1 graphical abstract created with Biorender®.

3.2 Manuscript II: Chemodiversity Affects Preference for *Tanacetum vulgare* Chemotypes in Aphid Species

Published as:

Neuhaus-Harr, A.*, **Ojeda-Prieto, L.***, Eilers, E., Müller, C., Weisser, W. W., & Heinen, R. (2023). Chemodiversity affects preference for *Tanacetum vulgare* chemotypes in two aphid species. *Oikos*, e10437.

* These authors share first authorship and contributed equally to this publication.

<https://doi.org/10.1111/oik.10437>

3.2.1 Summary

This experiment investigates the effect of chemodiversity on the preference for *Tanacetum vulgare* L. (Asteraceae) chemotypes in two aphid species. The study aimed to determine whether plants with different chemotype profiles differ in attractiveness to two specialist aphid species and how plant morphological traits relate to plant chemical traits. The study used five chemotypes of *T. vulgare* (as described in Chapter II). Each chemotype differed in terpenoid concentration, terpenoid richness, terpenoid evenness, and terpenoid Shannon diversity.

Among the five chemotypes examined, *Ma. tanacetaria* showed clear attraction to the 'Athu-Bthu' and 'Chrys-acet' chemotypes, while *U. tanaceti* did not show preference for any chemotype (Figure 12). Interestingly, plant attractiveness to aphids was marginally negatively correlated with chemodiversity in *Ma. tanacetaria*. It suggests that the interaction between compounds is responsible for preferences. The study found no clear link between individual terpenoids and their attractiveness to aphids, indicating that, instead, the blend may have a biological effect. Because plant chemical composition affects plant attractiveness to aphids, it may contribute to variations in natural aphid colonization patterns on plants of the same species. Additionally, the research showed significant positive relationships between the number of stems per *T. vulgare* chemotype and terpenoid Shannon diversity, as well as *T. vulgare* height and terpenoid Shannon diversity and relative terpenoid concentration (Figure 13).

In conclusion, I found evidence of the effect of chemodiversity on aphid preference for *T. vulgare* chemotypes. It also showed the complex interactions between plant chemical and morphological traits, and chemical traits and aphid preference. The findings underscore the consequence of intraspecific variation in plant phenotypes for structuring plant-arthropod food webs and shaping interactions with partners.

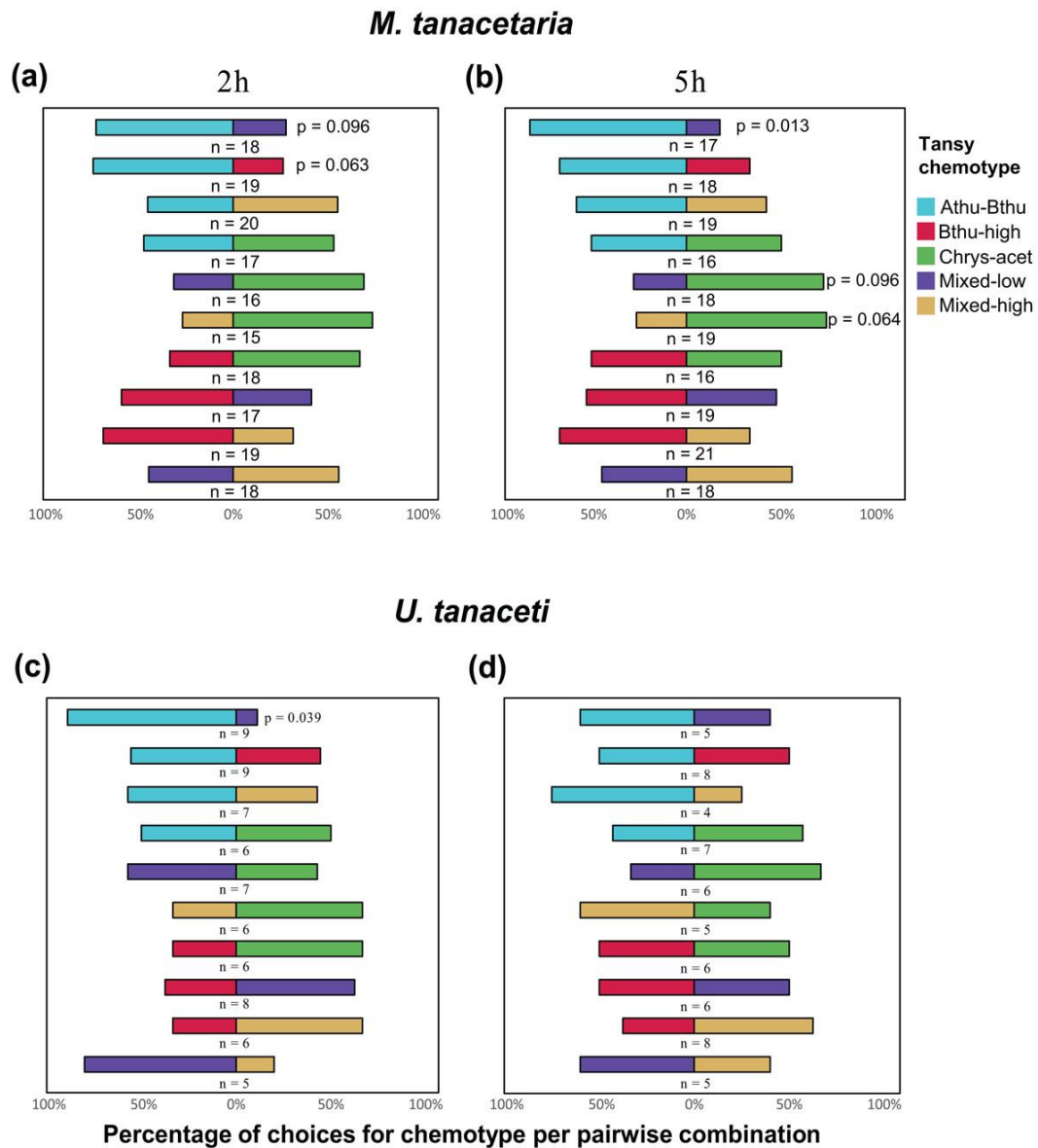


Figure 12. Chemotype effects on pair-wise choice experiments. Mean percentage of choices by *Macrosiphoniella tanacetaria* after two **(a)** and five hours **(b)**, and *Uroleucon tanacetii* after two **(c)** and five **(d)** hours. Effective sample size and P-values are also indicated (Neuhaus-Harr, Ojeda-Prieto, et al., 2024).

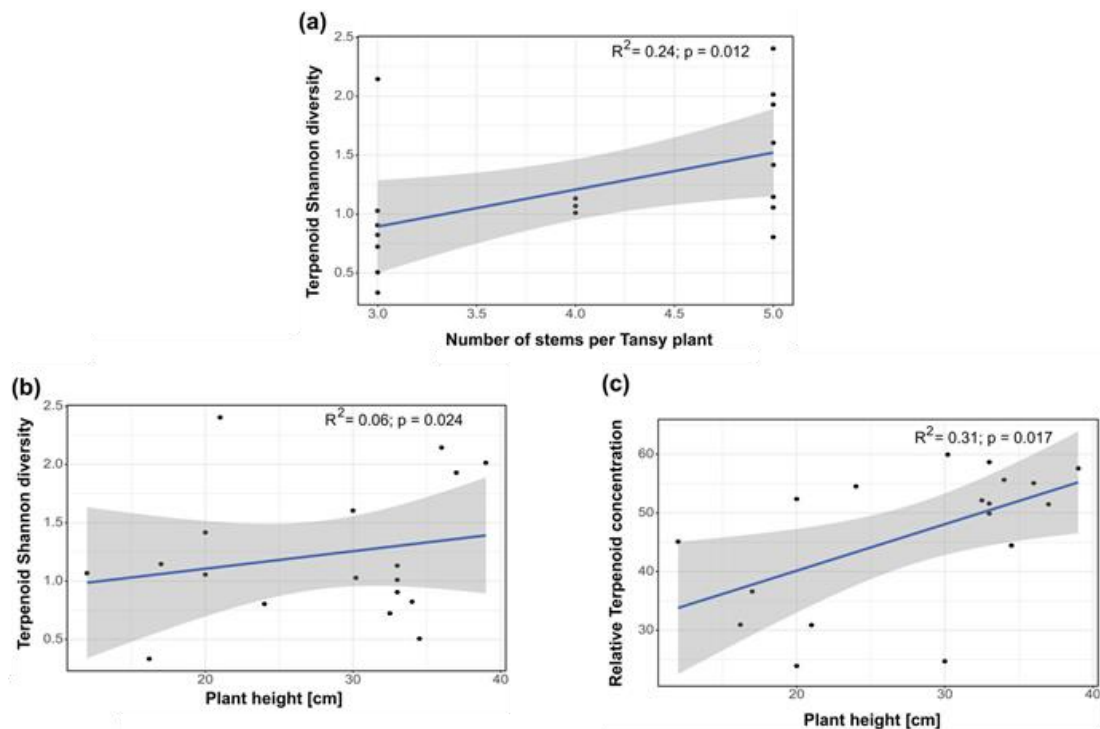


Figure 13. Correlation between chemical and morphological traits. Each of the 18 tansy daughters are shown as an individual dot in each panel (3 daughter per chemotype). The correlation coefficient (R^2) and the p-value are displayed for each relationship. **(a)** Relationship between number of stems and terpenoid Shannon diversity, and between plant height (cm) and terpenoid Shannon diversity **(b)** and relative terpenoid concentration **(c)**.

3.2.2 Addressed Questions

What are the different chemotypes of *T. vulgare*, and which is preferred by the specialist *Ma. tanacetaria* and *U. tanacetii* aphids?

How does the chemodiversity of *T. vulgare* plants influence the attractiveness of *Ma. tanacetaria* and *U. tanacetii*?

What are the relationships between morphological plant traits and chemical diversity in *T. vulgare* chemotypes?

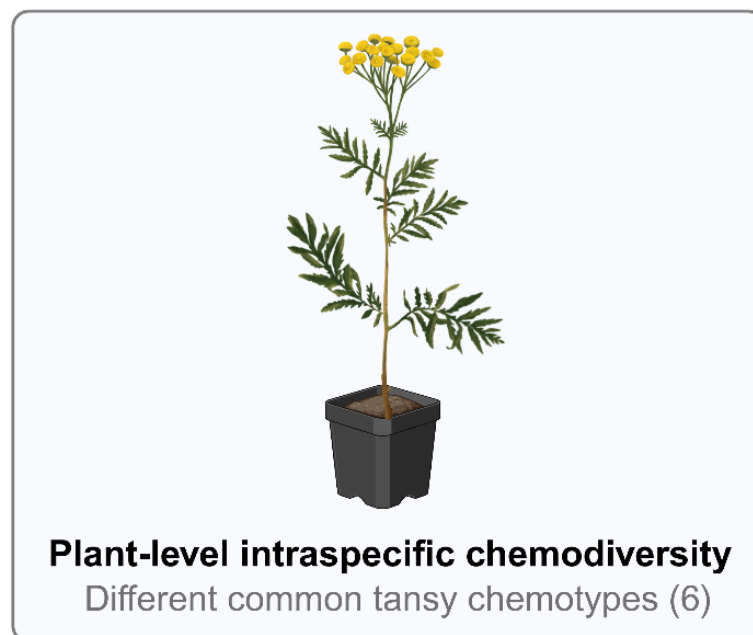
Which individual terpenoids are correlated with the attractiveness to *T. vulgare* plants by *Ma. tanacetaria* and *U. tanacetii*?

3.2.3 Author Contributions

ANH and LOP shared the first authorship and contributed equally to the publication. Their specific roles are outlined as follows: ANH co-lead conceptualization of the study, conducted primary formal analysis, contributed to data curation and visualization, wrote the original draft

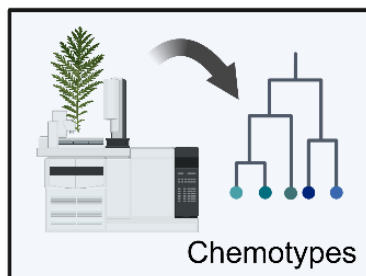
of the manuscript, and participated in manuscript review and editing. LOP co-led conceptualization of the study, played a key role in data curation and visualization, provided supporting roles in formal analysis, contributed to original draft writing, and participated in manuscript review and editing. EE provided supporting roles in formal chemical analysis, and participated in manuscript review and editing. CM contributed to formal chemical analysis, assisted with methodology development on chemical analyses, and participated in manuscript review and editing. RH supervised the project, led project administration, validated data, contributed to methodology development and visualization, and participated in manuscript drafting and editing of the final version. WW conceived the original research idea, secured funding for the project, contributed to project supervision, and participated in manuscript review and editing. All authors contributed to the final version of the manuscript, and reviewed and approved the final submission.

3.2.4 Graphical Abstract



Materials and methods

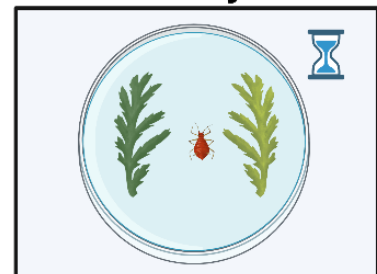
Chemotypic characterization



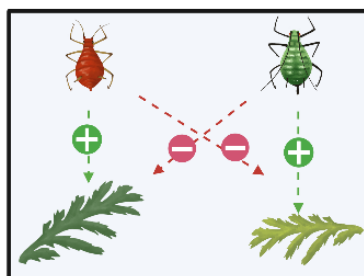
Growth traits



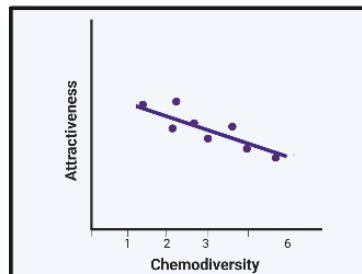
Pairwise choice assay



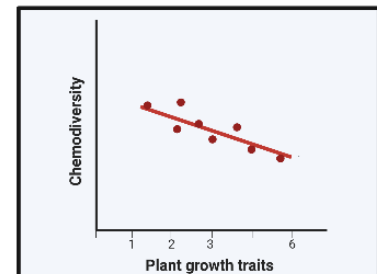
Hypotheses



Species-specific attraction



Correlation between chemodiversity and attractiveness



Trade-offs between chemodiversity and growth traits

Figure 14. Section 3.2 graphical abstract created with Biorender®.

3.3 Manuscript III: Intraspecific Chemical Variation of *Tanacetum vulgare* and its Effect on Plant-plant Interactions

Published as:

Ojeda-Prieto, L., Medina-van Berkum, P., Unsicker, S. B., Heinen, R.*, & Weisser, W. W.* (2024). Intraspecific chemical variation of *Tanacetum vulgare* affects plant growth and reproductive traits in field plant communities. *Plant Biology*, plb.13646.

* These authors supervised the project equally and share senior authorship

<https://doi.org/10.1111/plb.13646>

3.3.1 Summary

The research article discusses the effect of intraspecific plant chemodiversity on plant growth and reproductive traits in field plant communities, including the number of stems, plant height, aboveground fresh and dry weight, cumulative number of flower heads, and flowering phenology. I manipulated intraspecific plant chemodiversity at the plot level using six different chemotypes of common tansy (*Tanacetum vulgare* L., Asteraceae) (as described in Chapter II) to understand how chemodiversity affects ecosystem functioning and plant-plant interactions. The findings revealed that plant chemotypes differed in growth, but the differences did not persist through time. Chemotypes also differed in reproductive traits, and the differences were affected by the chemotype richness of the plots (Figure 15). Additionally, the study found that the presence or absence of certain chemotypes in a plot affected plot-level trait means, with the direction of the effect depending on the specific chemotype. However, it was found that the plant community chemodiversity did not lead to overyielding effects, suggesting that the relationship between chemical diversity and plant productivity is not straightforward. The mechanisms underlying these effects were discussed.

I calculated theoretical leaf plot-level diversity metrics based on the sum of individual plant leaf terpenoid contents that conformed each plot. I compared theoretical leaf-plot level diversity metrics with the realized plot-level volatile diversity metrics, which were calculated on the headspace volatile terpenoid compounds (a subset of VOCs). Plots with higher plot-level chemotype richness had higher theoretical leaf terpenoid diversity metrics, except for total terpenoid concentration, as expected by experimental design. However, the plot-level chemotype richness did not correlate with the abundance, richness, diversity, or evenness of terpenoids released as VOCs (Figure 16). A weak positive link was observed between leaf

and headspace terpenoid profiles, indicating that as plots became more dissimilar in their leaf terpenoids, they became more dissimilar in their headspace terpenoids.

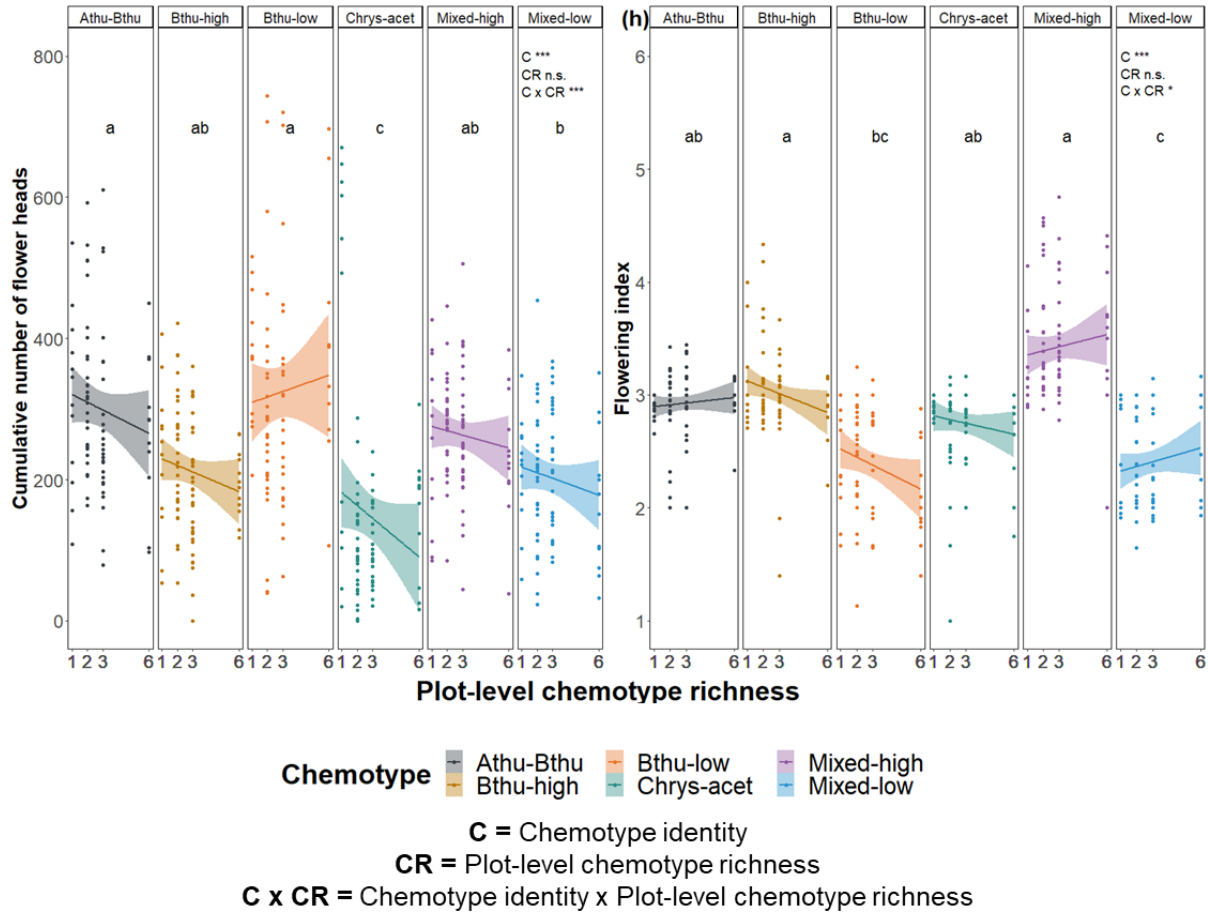


Figure 15. Effect of chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness (C × CR) on reproductive traits of *T. vulgare* plants: Cumulative number of flower heads 2021, and flowering index in 2022. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Significance is indicated as follows: n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Tukey post-hoc significant differences between chemotypes are indicated with different letters (adapted from Ojeda-Prieto et al., 2024a).

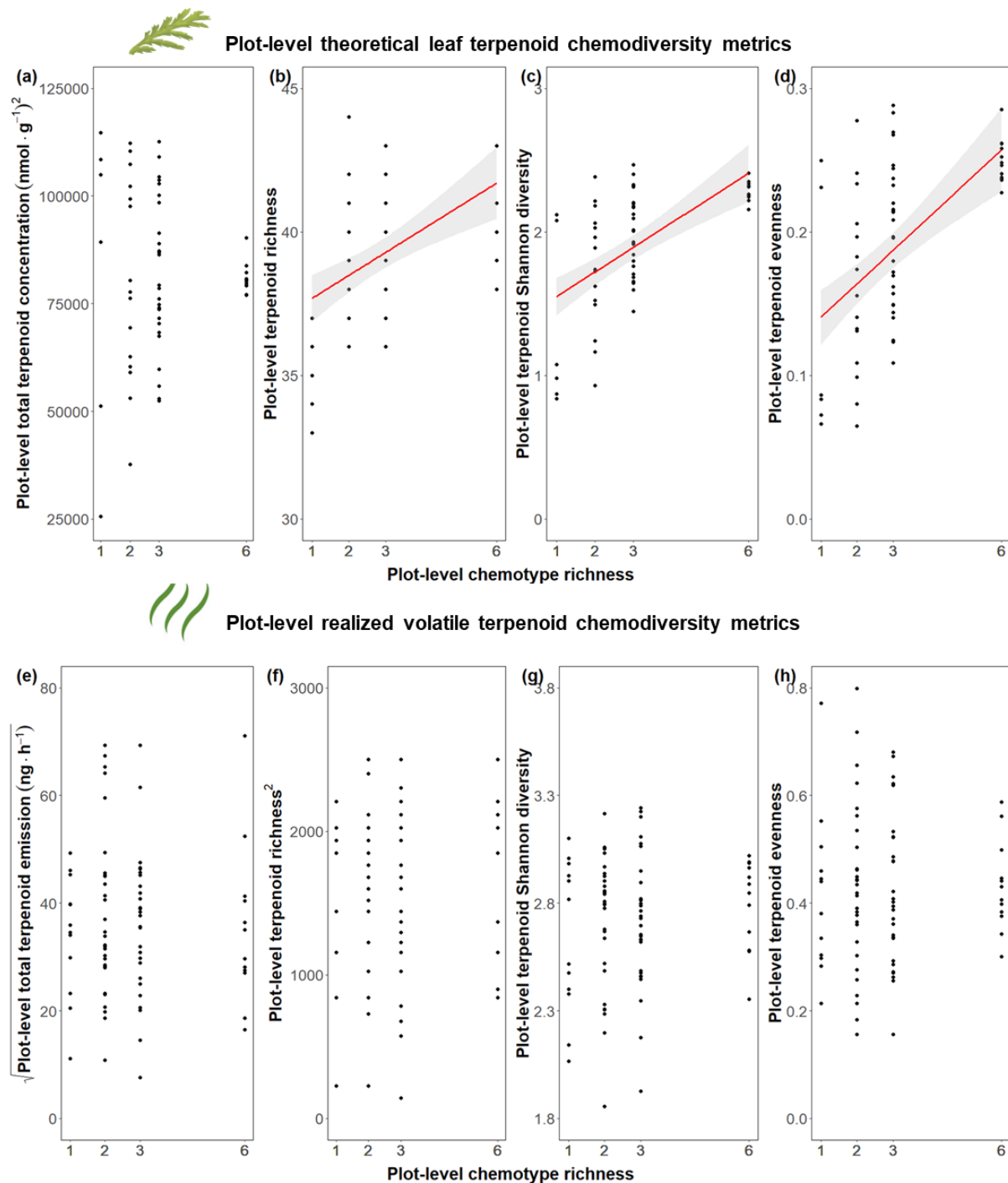


Figure 16. Effects of plot-level chemotype richness on theoretical plot-level chemodiversity metrics based on leaf terpenoid profiles (a–d) and realized plot-level volatile chemodiversity metrics (e–h). Only significant correlations are shown (adapted from Ojeda-Prieto et al., 2024a).

3.3.2 Addressed Questions

How does intraspecific plant- and plot-level chemodiversity affect the growth and reproductive traits of *T. vulgare*?

What are the effects of chemotype identity on the growth and reproductive traits of individual plants and plant communities in a field setup?

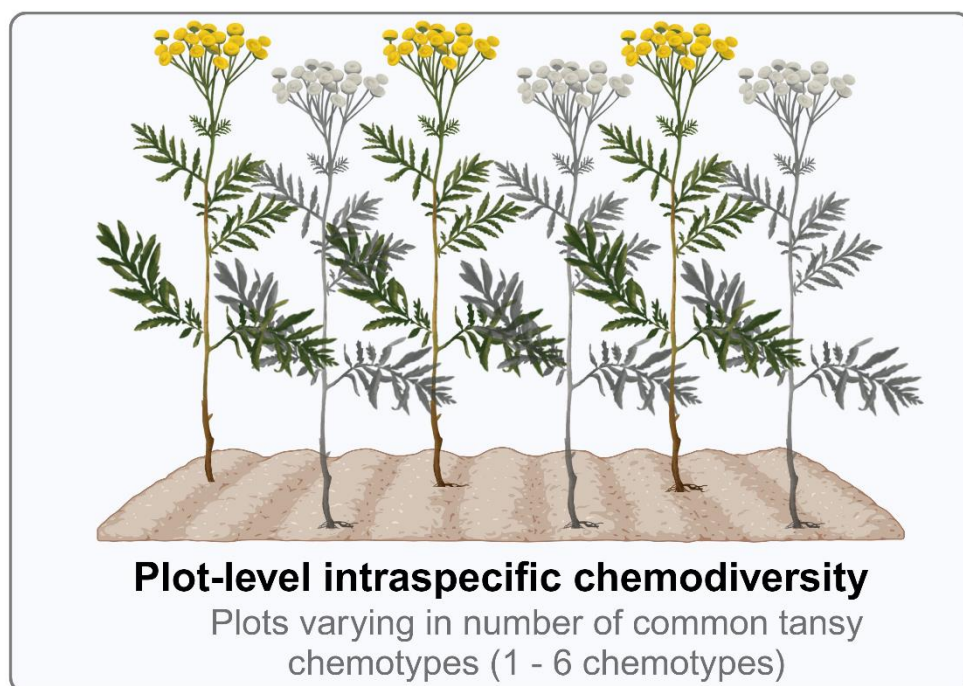
How does plot-level chemotype richness affect plot-level measurements and overyielding indices?

What are the relationships between leaf and headspace terpenoid profiles, and how does plot-level chemotype richness influence headspace terpenoid profiles?

3.3.3 Author Contributions

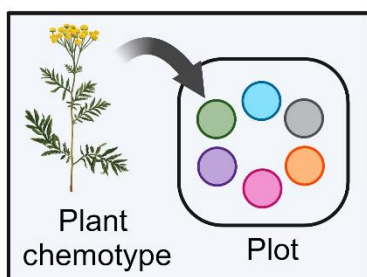
LOP participated in planting the field experiment, led data collection efforts, maintained the field experiment throughout the study period, conducted primary analysis of ecological data, conceived the volatile collection, contributed to volatile collection, authored the first draft of the manuscript, and incorporated feedback and revisions from co-authors and reviewers. PMvB contributed to preparation and execution of volatile collection, and led the chemical analysis of volatile compounds. SBU assisted in preparation and execution of volatile collection. RH prepared the field experiment site, performed plant propagation, participated in planting the field experiment, contributed to volatile collection, assisted in ecological data analyses, and provided input on manuscript drafting and revision. WWW conceived the original research idea, designed the experimental framework, provided guidance on ecological data analysis, and contributed to manuscript review. All authors reviewed and contributed to the final version of the manuscript and approved the final submission.

3.3.4 Graphical Abstract

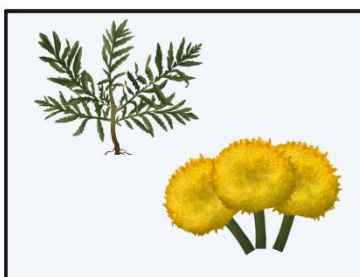


Materials and methods

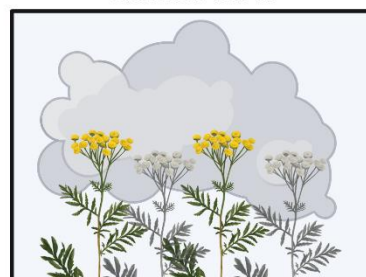
Experimental design



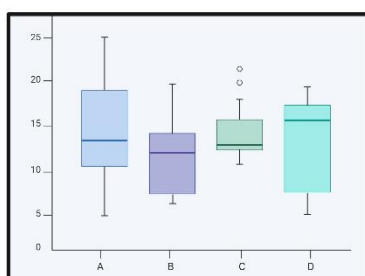
Growth/ Reproductive traits



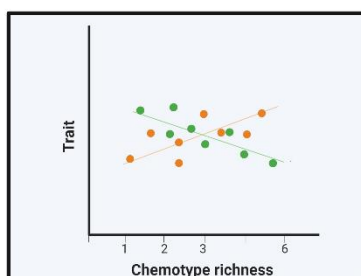
Headspace VOC collection



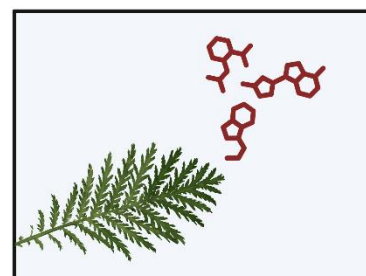
Hypotheses



**Plant-level
chemotype effects**



**Plot-level
chemotype richness
effects**



**Leaf-terpenoids vs.
Headspace terpenoids**

Figure 17. Section 3.3 graphical abstract created with Biorender®.

Chapter IV. General Discussion

Lina Ojeda-Prieto

4.1 Overview of the Main Findings

Intraspecific plant chemical diversity is increasingly acknowledged as a driver of ecological interactions (Petrén et al., 2023a; Wetzel & Whitehead, 2020; Christensen et al., 2019; Kessler & Kalske, 2018; Silva et al., 2018; Junker, 2016; Schuman et al., 2016; Meiners, 2015; Moore et al., 2014). Most of our understanding regarding these relationships comes from interpreting patterns in observational studies and correlative patterns, which have provided crucial insights into the effect of plant chemical diversity on patterns of herbivory and insect diversity (Salazar et al., 2016; Richards et al., 2015), insect performance (Neuhaus-Harr et al., in prep.; Glassmire et al., 2020), and plant evolution (Volf et al., 2018; Becerra et al., 2009).

Plant chemical diversity is challenging to manipulate because the secondary metabolite production implies complex and interconnected biosynthetic pathways, genetic regulation processes that add another layer of complexity when manipulating those pathways, pleiotropy as many genes involved in the biosynthesis affect other traits, and the influence of environmental conditions that modulate the expression of genes involved in secondary metabolism (Erb & Kliebenstein, 2020; Saito & Matsuda, 2010; D'Auria & Gershenson, 2005). However, field settings have the potential for manipulation, although controlled studies on the effects of plant chemical diversity on ecological interactions are still uncommon. The research included two experimental approaches to investigate the intricate relationships between plant chemodiversity and plant-arthropod dynamics within ecological communities. In this dissertation, I manipulated plant chemical diversity in two ways: first, by selecting plant chemotypes that differed in their chemical blends, and second, by manipulating the number of plant chemotypes growing together in a plot (i.e., plot-level chemotype richness).

This research delved into the influence of chemotype richness on arthropod occurrences and abundances within these plant communities. Contrary to initial expectations, chemotype richness showed weak evidence of affecting the presence of the different studied arthropod groups at the plot level. However, specific arthropod taxa significantly responded to varying chemotype richness, especially in abundance. Flower-visiting taxa showed positive associations, while herbivore taxa exhibited negative relationships. Arthropod taxa that interact with plants more indirectly, like aphid predators and ants, were less affected by the chemotype richness of the plant community. This study also highlights the role of individual chemotypes in driving interactions. The strong effect of plant chemistry on certain arthropod groups and the effect of specific chemotypes underscores the intricate role of chemodiversity in shaping arthropod community dynamics within plant ecosystems.

The investigation extended to the relation between plant chemodiversity and herbivore preferences. One aphid species, *Ma. tanacetaria* exhibited a distinct preference for specific

chemotypes, with chemodiversity marginally negatively correlating with attractiveness, suggesting that the diversity of terpenoid compounds affected aphid preferences. This preference pattern was absent in the other aphid species, *U. tanacetii*. The results also revealed significant relationships between plant morphological traits (like stem number and height) and terpenoid diversity and concentration, further emphasizing the complex interplay between plant chemical traits, plant morphology, and herbivore preferences.

The results show that plant chemotypes exhibited distinct growth and reproductive traits, although growth trait differences were less pronounced with time. Furthermore, the chemotype richness of the plot significantly influenced reproductive traits. Interestingly, the presence or absence of specific chemotypes in a plot had varied effects on trait means, depending on the chemotype itself. Despite these complex interactions, the overall chemotype richness did not produce overyielding effects.

My research underscores the role of chemical diversity by demonstrating how chemodiversity shapes reproductive traits, drives arthropod community assembly, and influences herbivore preferences. My findings highlight the necessity of incorporating chemodiversity into our understanding of ecological interactions, offering a more comprehensive framework for studying the complex web of relationships within plant ecosystems.

4.2 Discussion of Results in Relation to Research Questions and Hypothesis

This section aims to synthesize the study's findings in relation to the initial research questions and hypotheses, as outlined in Figure 18. The discussion will follow the structure of the hypotheses, addressing each main topic: A variation on plot-level chemodiversity, ecological consequences on arthropod community and plant responses, and the link between chemical and growth traits.

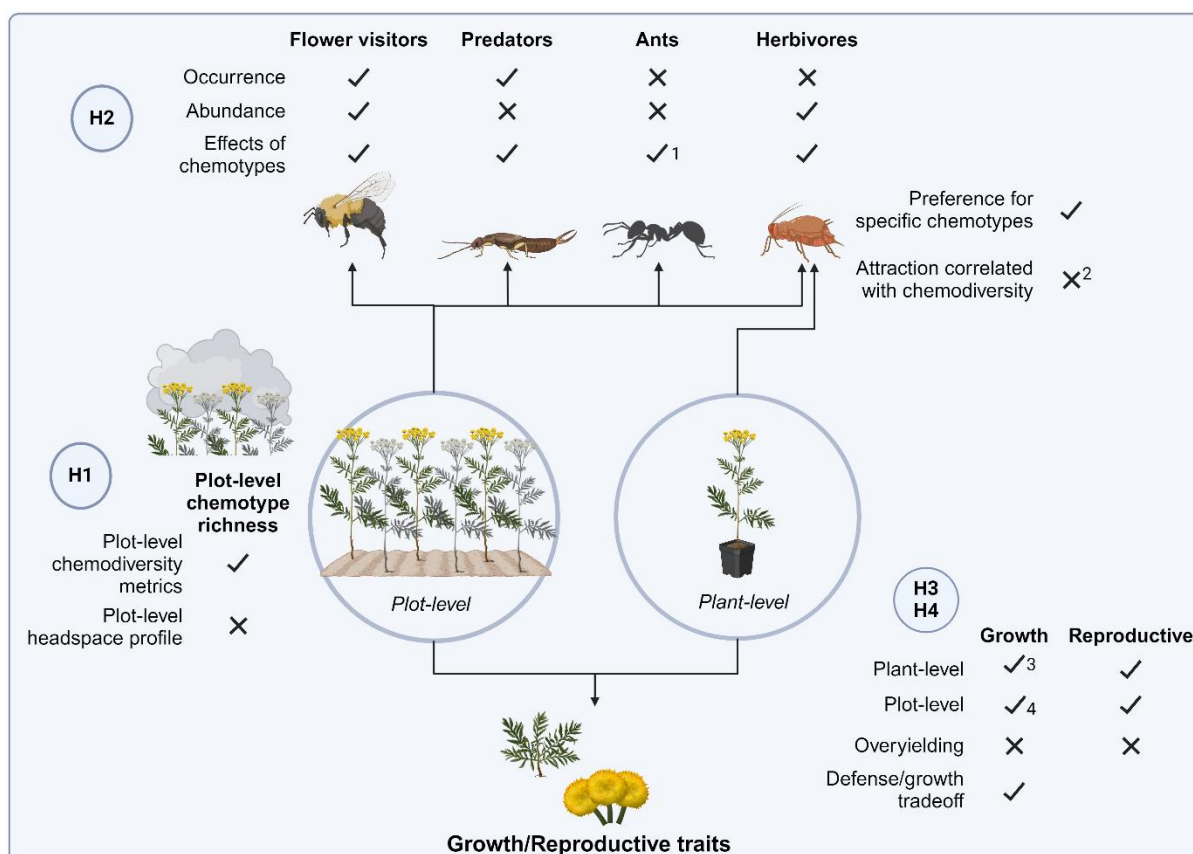


Figure 18. Hypothesis overview. Effects of chemodiversity across levels, i.e., among individuals and populations, on plant traits and associated arthropod communities. This scheme shows hypothesis confirmations (✓) and rejections (✗) icons indicating the results of each section. I hypothesized that increasing the number of different chemotypes in a plot (i.e., plot-level chemotype richness) will increase the plot-level *theoretical* leaf chemodiversity metrics (richness, evenness, Shannon diversity) and the plot-level *realized* chemodiversity metrics based on VOC headspace collection (**H1**). At the plot level, I expect that increasing plot-level chemotype richness will lead to increased occurrence of all arthropod groups, and higher predator and flower visitor abundances, while lower herbivore and ant abundances, and that certain chemotypes will have specific effects on the occurrence and abundance of those arthropod groups (**H2**). ⁽¹⁾ Specific chemotypes showed effects on the occurrence and abundance of all groups except for ants, in which the chemotypes had an effect only on ant abundance. At the plant level, I hypothesize that some chemotypes are more attractive to aphids than others and that the attractiveness is aphid-species specific and negatively correlated with increasing chemodiversity of the chemotype (**H2**). ⁽²⁾ The number of terpenoids and plant attractiveness to aphids marginally negatively correlated. At the plot level, I expect that increasing plot-level chemotype richness will result in overyielding effects, and at the plant level, chemotypes differ in growth and reproductive traits and that there is an influence of the chemical diversity of the plot (**H3**). ⁽³⁾ Chemotypes differed in growth traits at the beginning of

the first season, and the differences dissolved over time. ⁽⁴⁾ The number of stems across chemotypes was influenced by plot-level chemotype richness but only on one date at the beginning of the second sampling season (2022). Finally, I expect a tradeoff between chemical and growth traits (**H4**). Created with Biorender®.

4.2.1 Variation in Intraspecific Chemodiversity in Plant Communities

Plant chemotypes can be investigated using several methods, including hexane extraction of plant parts and volatile collection of the headspace (Section 3.1; Clancy et al., 2016). High variation has been found within tansy plant populations (Clancy et al., 2020; Kleine & Müller, 2011) and among populations (Rahimova, Neuhaus-Harr et al., 2024; Wolf et al., 2012a). My first research question aimed to understand how leaf chemical diversity of tansy plant communities varies in terms of terpenoid profiles. Based on the leaf terpenoid profiles obtained by hexane extraction, individuals of *T. vulgare* from a local population in Jena, Germany, varied in their chemical diversity in terms of total terpenoid concentration, terpenoid richness, terpenoid evenness, and terpenoid Shannon diversity. Six chemotypes were chosen to establish the experimental approaches in this dissertation (Chapter II; Neuhaus-Harr, Ojeda-Prieto et al., 2024). Plant communities were established in a field site in Jena, Germany, with varying levels of chemodiversity in terms of the number and identity of chemotypes (Ojeda-Prieto et al., 2024).

Leaf diversity metrics at the plot level are theoretical because the chemotype selection process involved the analysis of terpenoid compound profiles from leaf samples taken from plants grown under controlled greenhouse conditions before porting them into the field in May 2021. We selected 6 chemotypes using hierarchical analysis, each represented by 3 biological replicates. The field experiment was then set up by varying the number and identity of these chemotypes in each plot. Thus, the plot-level diversity metrics are theoretical because they are derived from summing the individual diversity metrics of each of the 6 plants present in the plot rather than measuring them directly in the field. In line with **H1.1**, the results showed that increasing plot-level chemotype richness led to the plant community's higher *theoretical* leaf terpenoid richness, evenness, and Shannon diversity. However, plot-level chemotype richness did not significantly affect total terpenoid concentration (Figures 16 and 18). Plot-level diversity metrics such as richness, evenness, and Shannon diversity are expected to differ, while the total terpenoid concentration does not. While individual terpenoid concentrations may vary due to environmental influences, this variability might average out when considering multiple plants within a plot. In contrast, richness is a more stable trait, as modifying the number of compounds a plant produces involves significant genetic regulation and changes in complex biosynthetic pathways. Similarly, Shannon diversity and evenness reflect the relative abundance and distribution of different terpenoids within a plant, which are

less likely to fluctuate compared with the total concentration. Thus, the observed relationships between chemotype richness and diversity metrics are logical, as increasing the number of distinct chemotypes inherently increases the terpenoid richness, evenness, and diversity but not necessarily their total concentration.

This finding supports the idea that chemical diversity can be manipulated at the community level without necessarily altering the overall concentration of chemical compounds. VOC bouquets of these *T. vulgare* communities were also collected and analyzed under field conditions. Contrary to **H1.2**, the headspace VOC profiles released from plant communities did not become richer or more diverse with increasing plot-level chemotype richness (Figures 16 and 18). However, the headspace did become more dissimilar as the leaf terpenoid profile of the plot became more dissimilar, suggesting that, in line with previous findings, community-level leaf chemical diversity may not directly straightforwardly translate to airborne chemical diversity. This unexpected result highlights the complex relationship between stored and emitted plant volatiles. Given this complexity, why is there so much noise in the relationship between leaf terpenoid diversity and headspace VOC diversity?

The volatile terpenoid profile of a plant community is influenced by the specialized metabolites of individual plants, the intrinsic chemical properties of their compounds (such as volatility and solubility), and various physiological and morphological characteristics like the presence and number of trichomes in some plant species (Aschenbrenner et al., 2013; He et al., 2011; Gershenzon & Dudareva, 2007). Biological factors, including the abundance of interacting organisms and plant age and size, also play a role (Fabisch et al., 2019; Kessler & Kalske, 2018; Clavijo McCormick et al., 2012; Takabayashi et al., 1994). Although predicting volatile production imposed many challenges (Dicke et al., 2009; Dudareva et al., 2006), it is reasonable to expect that the volatile headspace profile of *T. vulgare* would correlate with the compounds stored in its glandular trichomes. However, the hexane extraction was performed from leaves of young plants before field planting in 2021 at Bielefeld University, while the headspace terpenoids were obtained a year later, in spring 2022, under field conditions and processed at the Max Planck Institute in Jena, Germany. Both sampling and laboratory differences potentially led to mismatch variations in terpenoid diversity between leaf and headspace samples in a previous study on tansy (Eckert et al., 2023). Additionally, emitted volatile profiles may differ from stored profiles due to specific compounds produced only during attacks or under stress (Rashid & Chung, 2017; Unsicker et al., 2009). For instance, Clancy et al. (2016) found a 70% difference between emitted headspace volatiles and compounds in individual *T. vulgare* leaves, explained by the influence of environmental conditions and stressors on the headspace volatiles, while hexane extractions captured a stable profile of stored compounds.

The impact of chemotype richness and stored chemical profiles on communal headspace volatiles remains unclear. Observing how the volatile profile at the community level evolves as plants grow and competition intensifies will be interesting. Future research could focus on the effect of intraspecific volatile diversity on arthropod communities (Kessler & Kalske, 2018), but several additional factors must be considered. Soil volatiles, for instance, may significantly influence the overall volatile profiles, as soil microorganisms also produce terpenes and other compounds (Peñuelas et al., 2014; Insam & Seewald, 2010; Leff & Fierer, 2008).

The Jena Experiment is a biodiversity experiment that uses up to 60 plant species divided into four groups (grasses, small herbs, tall herbs, and legumes), varying the number of species and functional groups in each plot for its experimental design (Roscher et al., 2004). Although our field was tilled before planting, these plants were common in our plots. Even though we manually removed non-tansy plants from the plots 10 days before the volatile collection, the belowground parts that were not removed could still contribute to or alter the communal headspace.

Atmospheric conditions and airborne particles may interact with plant-produced volatiles, potentially modifying their distribution (Holopainen & Gershenzon, 2010). It is important to control for or measure these additional sources of volatiles to isolate the specific effects of chemodiversity on volatile headspace and arthropod communities (Dicke & Baldwin, 2010).

4.2.2 Ecological Consequences of Intraspecific Chemodiversity

My study's second focus was understanding how chemodiversity affects plant-arthropod and plant-plant interactions. I present the main ecological plant-arthropod interactions at the plot level, setting the stage for understanding the broader context.

The initial hypothesis (**H2.1**) aimed to explore the potential association between increasing plot-level chemotype richness and the increased occurrence of arthropod groups. The results of my first study (Section 3.1) partially supported it (Figure 18). While not all arthropod groups showed increased occurrence with higher plot-level chemotype richness, herbivores exhibited a negative correlation (which got stronger over time), and flower visitors had a positive correlation (Figure 9).

While higher chemotype richness may enhance resource availability, potentially leading to increased occurrence of certain herbivore species (Schneider et al., 2021; Herms & Mattson, 1992), the findings underscored the role of chemical-mediated deterrence mechanisms in reducing the occurrence of herbivores (Kessler & Baldwin, 2001). Upon examining the effects on individual sampling dates, a positive correlation at the onset of the first season is noted, aligning with the initial **H2.1**. However, upon considering the cumulative effect of each season

on herbivore occurrence, it becomes evident that colonization and dispersal events over time result in the eventual establishment of aphids in all available plots each year. Instead of the effect on plot occupancy in the whole season, the initial colonization processes by winged aphids are likely influenced by specific chemotypes and plot-level chemotype richness (Clancy et al., 2016, 2018; Loxdale & Balog, 2018; Williams & Avakian, 2015; Le Guigo et al., 2012). Furthermore, the weak effects found in the study (3.1) emphasize the multifaceted nature of factors shaping aphid occurrence patterns, extending beyond chemodiversity to include dispersal dynamics, microhabitat preferences, seasonal variations, and competitive interactions (Senft et al., 2017; Mehrparvar et al., 2013, 2014; Farré-Armengol et al., 2013). Moreover, the analyses in this study did not distinguish between winged and unwinged aphid morphs. Given that winged aphids likely play a dominant role in dispersal events, their movement among host plants, guided probably by chemical cues, may be significantly influenced by chemodiversity at plant and plot levels (Clancy et al., 2016).

The occurrence of flower visitors positively correlated with plot-level chemotype richness. It suggests that a diverse array of chemotypes within a plot may attract a broader range of flower visitors because as plots became more dissimilar in their leaf terpenoids, they also became more dissimilar in the blend of terpenoids in the headspace (Ojeda-Prieto et al., 2024). This diverse chemical environment can appeal to a wider variety of flower visitors, each of which may be attracted to specific volatiles or combinations. The greater the variety of chemical signals, the higher the likelihood that different flower visitor taxa will find the plot attractive, enhancing pollination opportunities and interactions within the plant community (Farré-Armengol et al., 2020; Parachnowitsch & Manson, 2015; Junker & Blüthgen, 2010). Recent studies have demonstrated significant effects of plant chemotype on reproductive traits, such as the cumulative number of flower heads and flowering phenology (Ojeda-Prieto et al., 2024; Eilers et al., 2021). Interestingly, despite a decrease in the number of flower heads with increasing plot-level chemotype richness, the observations underscored the profound influence of plant chemistry on plant-pollinator interactions, leading to alterations in the structure of flower-visitor networks (Hoffmeister et al., 2016). This emphasizes the importance of considering intraspecific variation in plant chemistry when assessing its effects on insect visitation patterns and determining chemical profiles in specific tissue locations: leaves and flowers (Eilers, 2021; Kessler & Kalske, 2018; Dudareva et al., 2013; Kessler & Halitschke, 2009; Pichersky et al., 2006).

While there are significant effects of chemodiversity on flower visitor occurrence, the findings suggest a more subtle relationship with predators and ants. The chemical diversity of tansy plants directly influences herbivores and flower visitors, probably given their close interactions with plant tissues. In contrast, predators and ants may exhibit broader dietary preferences and

be less sensitive to specific chemotypes (Smith et al., 2023; Scherer & Smee, 2016). The findings indicate that predator occurrence was positively influenced by plant communities' chemical environment, albeit only observed in 2023. On the other hand, ant occurrence remained unaffected by chemotype richness. Despite evidence of ants being impacted by interspecific diversity in experimental grasslands (Achury et al., 2022), the results suggest that intraspecific chemodiversity may not be a predominant factor shaping ant foraging in the study system.

H2.2 was partially supported, with herbivore abundance generally decreasing in plots with higher chemotype richness, although this relationship exhibited variability across aphid species and time. Flower visitor abundance increased with chemotype richness, aligning with the hypothesis. However, contrary to expectations, plot-level chemotype richness did not significantly affect predator and ant abundances (Figure 18). The first variability noted likely stems from differences in co-evolutionary histories and feeding behaviors between specialist and generalist aphid species, as suggested by previous studies (Le Guigo et al., 2012; Gripenberg et al., 2010). Generalist species, which are more adaptable to changes in resource availability and interspecific competition (Glassmire et al., 2016; Travers-Martin & Müller, 2007), initially exhibited positive responses to chemodiversity, specifically during the first sampling dates in the initial year. However, as the plants matured in the following years, a shift towards specialist aphids led to more robust and evident effects of plot-level chemotype richness on herbivore abundance. Specialist aphids might be more susceptible to chemodiversity than generalists (Benedek et al., 2015). Furthermore, specialist herbivores might be influenced by chemical defenses in plots with high chemotype richness, consistent with the neighborhood-mediated associational resistance hypothesis (Ziaja & Müller, 2023; Randlkofer et al., 2010). This hypothesis suggests that plant diversity can enhance the resistance of individual plants to herbivores as they might indirectly benefit from the defenses of neighboring plants. In high chemotype richness plots, the varied chemical landscape could enhance the overall resistance of the plant community to specialist herbivores, thus reducing their abundance.

Plots with higher intraspecific chemodiversity attracted more flower visitors (i.e., higher visitation rates), suggesting that a high diversity of chemotypes may benefit a more heterogeneous group of flower visitors (Sasidharan et al., 2023b). Additionally, the varied phenological development of different chemotypes throughout the season, influenced by plot-level chemotype richness (Ojeda-Prieto et al., 2024), suggests that more diverse chemotypes in a plot could extend the availability of flowers in that same plot over time. This extension of plot floral availability occurs because different chemotypes may bloom at different times. For example, the 'Mixed-high' chemotype might be an early bloomer (Ojeda-Prieto et al., 2024),

while others like the 'Mixed-low' and 'Bthu-low' chemotypes peak later in the flowering period. These differences create a more consistent and prolonged presence of flowers within high chemotype richer plots, enhancing the occurrence and abundance of flower visitors.

My investigations revealed that the chemodiversity of the plot did not influence predator or ant abundance. This raises the question: Why do these arthropod groups appear unresponsive to changes in plant chemical diversity? To address this, we need to consider alternative factors that might be more influential in determining the abundance and distribution of predators and ants. For example, the availability and quality of prey, which could be affected by the chemical composition of host plants (Benedek et al., 2019), might play a more significant role than overall chemodiversity. In addition, ants and predators may employ diverse foraging strategies that are not directly influenced by the plant chemical diversity (Wäschke et al., 2013). To fully understand the complex relationships between these groups, further studies should explore these potential influencing factors as indirect responses to chemodiversity.

Specific chemotypes had distinct effects on different arthropod groups, potentially influencing their abundance and occurrence patterns within plant communities, which aligns with **H2.3** (Figures 10 and 18). This hypothesis suggests that the chemical composition of individual plant chemotypes may play a crucial role in driving interactions with different arthropod groups, highlighting the complex and multifaceted nature of plant-arthropod relationships. For instance, the 'Chrys-acet' chemotype did not significantly affect the herbivore occurrence or any herbivore species. In contrast, the other chemotypes exhibited mixed effects, with outcomes varying between positive and negative depending on the species and year. This finding supports the existence of species-specific preferences among tansy aphids towards certain chemotypes (Section 3.2; Neuhaus-Harr, Ojeda-Prieto et al., 2024; Clancy et al., 2018; Kleine & Müller, 2011). Moreover, the observed differential responses of generalist and specialist aphid species to chemodiversity also highlight the intricate connection between individual chemical profiles and aphid dynamics. While some chemotypes may positively impact aphid abundance, others may have adverse effects, indicating the importance of considering species-specific interactions in predicting the outcomes of chemodiversity on aphid populations.

I observed a positive effect of the 'Bthu-high' and 'Mixed-high' chemotypes on predator occurrence across different years and groups, suggesting that food webs are chemotype-specific such as reported in other studies in tansy (Benedek et al., 2015, 2019; Bálint et al., 2016). Due to their broad dietary preferences and adaptive foraging strategies, generalist predators may exhibit limited sensitivity to chemotype richness (Van Geem et al., 2014). In contrast, specialist predators may display stronger responses driven by prey availability, prey quality, and previous adaptation to chemodiversity (Erb et al., 2021). For example, in other

studies on tansy, aphid specialist ladybug *Coccinella septempunctata* was more abundant in the 'Camphor pure' chemotype, while *Pisaura mirabilis* spiders were in the 'Borneol pure' chemotype (Benedek et al., 2019; Bálint et al., 2016). I found that the effect of specific chemotypes being present in a plot on abundance also varies among groups. For instance, the 'Chrys-acet' chemotype positively affected parasitized aphid abundance in 2021 and ant abundance in 2023 but negatively affected total predator abundance and Coleoptera abundance in 2023. Indirect effects of chemodiversity through herbivores, particularly aphids serving as hosts for parasitoids and sugar sources for ants, may influence these patterns (Senft et al., 2019). The positive effect of the 'Chrys-acet' chemotype on the abundance of *B. cardui* in 2021 aligns with the expectation of finding more parasitized aphids on plots containing this chemotype, as most of the parasitized aphids belonged to this species. Additionally, *B. cardui* can establish mutualistic relationships with ants. Differences in phloem chemistry among chemotypes could influence the honeydew produced by aphids (Jakobs et al., 2019; Stolpe et al., 2017), and that could determine the ant foraging behavior (Zytynska et al., 2019). Ant occurrence and abundance are not directly but indirectly influenced by the aphid host (Layman & Lundgren, 2015; Yao, 2014; Stadler & Dixon, 2008; Powell et al., 2006). Further research should be done on the ant-aphid mutualism/predation relationship under the context of chemodiversity. I am working with a colleague doctoral candidate (Elikplim Setordjie) to investigate these relationships in the ongoing chemodiversity field experiment.

The 'Chrys-acet' chemotype stands out among the studied chemotypes due to its lack of significant effects on both herbivore and flower visitor occurrence and flower visitor abundance. Previous studies have indicated that floral scents can have both attractive and defensive functions (Stevenson, 2020; Farré-Armengol et al., 2013). A balanced trade-off between these functions might explain the absence of effects of the 'Chrys-acet' chemotype. It is conceivable that the specific volatile compounds in this chemotype neither strongly attract nor repel herbivores and flower visitors. This balance could result from evolutionary pressure to maintain a chemical profile that does not overly negative affect pollinator attraction for increasing herbivore defense, or vice versa (Kessler et al., 2013; Theis et al., 2007). Flower visitors, being more mobile and likely to respond to volatiles from a distance, might not find the 'Chrys-acet' scent profile particularly attractive compared to other chemotypes but also not repellent enough to actively avoid.

I observed variations in visitation rates among different insect orders, suggesting differential responses to specific chemotypes (Sasidharan, 2023b). For instance, Hymenoptera and Lepidoptera exhibited positive responses to plot-level chemotype richness and specific chemotypes within the plot, consistent with other findings in the tansy pollinator web (Junker et al., 2010). In contrast, Hemiptera did not show significant responses to chemodiversity or

chemotype identity. This could be attributed to the composition of Hemiptera in my system, which is predominantly herbivorous with some omnivorous species. Although I did not separate these groups in the analysis, this distinction is important as the ecological roles within this order are diverse and this translates into differences in the response to leaf chemodiversity. This variability could potentially mask chemotype-specific responses when analyzed as a single group. Additionally, Hemiptera generally has a lower dependence on pollen and nectar compared with other orders (Wardhaugh, 2015). Similarly, Diptera exhibited less influence from the identity of chemotypes within the plot, suggesting a more generalized foraging behavior than other pollinating groups (Orford et al., 2015; Kearns, 2001; Goulson, 1999; Downes & Dahlem, 1987).

Building upon the plot-level interactions, I examined specific plant-insect interactions at the chemotype level. My second study (Section 3.2) found evidence of species-specific aphids' responses to different tansy chemotypes, largely supporting **H2.4** (Figures 12 and 18). The aphid species *Ma. tanacetaria* exhibited a distinct preference for specific chemotypes, and the attractiveness of this species negatively correlated with chemodiversity, specifically to the diversity of terpenoid compounds. However, the study revealed variability in this pattern among aphid species, as preference for any of the chemotypes was evident in *U. tanacetii*. The variation in responses between aphid species underscores the need for species-specific analyses when studying the ecological consequences of intraspecific plant chemical diversity. Besides, some studies have pointed out that the secondary metabolite concentration might not be a good predictor of resistance of herbivores, but plant traits such as genetic variation in life-history traits are more related to anti-herbivore defense of plants (Agrawal & Weber, 2015; Carmona et al., 2011; Endara & Coley, 2011).

Shifting the focus from insect interactions to plant-plant interaction within different plant and plot-level chemodiversity settings, I describe here the implications of my third study (Section 3.3). In support of **H3.1**, individual *T. vulgare* chemotypes exhibited significant differences in growth and reproductive traits, including stem number, plant height, flower head number, and flowering phenology (Figure 18). These findings are consistent with previous studies demonstrating how chemical composition can drive phenotypic variation within plant species (Chapter II and Section 3.2; Neuhaus-Harr, Ojeda-Prieto et al., 2024; Keskitalo et al., 2001). Contrary to the **H3.2**, plots with higher chemotype richness did not exhibit increased plant growth (Figure 18). This suggests that while individual chemotypes within a plot may exhibit distinct growth strategies, the overall plot-level chemical diversity did not enhance growth across *T. vulgare* communities. This finding contrasts with studies suggesting that increasing biodiversity positively affects ecosystem processes (Hughes et al., 2008; Moreira et al., 2016).

Instead, the results suggest that the relationship between chemotype richness and plant growth may be more species-specific than previously thought.

Interestingly, differences in reproductive traits of *T. vulgare* chemotypes responded to plot-level chemotype richness, demonstrating the complex interplay between individual plant chemistry and community-level diversity (Figure 15). Most chemotypes, except for the 'Bthu-low' chemotype, exhibited reduced flower head numbers in plots with higher chemotype richness. This unexpected result suggests that while some chemotypes may benefit from chemical diversity in terms of reduced herbivore pressure or enhanced pollination services (Sasidharan et al., 2023b; Ziaja & Müller, 2023), others may experience competitive disadvantages or altered flowering phenology, as observed in the study. The findings also indicate plot-level chemotype richness influenced flowering phenology across *T. vulgare* chemotypes.

To analyze phenology at the plant level, I calculated a plant flowering index by dividing the sum of all stem-level phenological stages (1 to 6, with 1 no inflorescence and 6 mature seeds) by the number of stems and obtained the plot flowering index by averaging the six plant flower indices of each plot. Chemotypes varied in their flowering index value depending on the chemical composition of their surrounding environment. For instance, chemotypes like 'Athu-Bthu' and 'Mixed-high' flowered earlier in plots with higher chemotype richness, while chemotypes like 'Bthu-low' and 'Chrys-acet' exhibited delayed flowering. This variability suggests that *T. vulgare* may exhibit phenotypic plasticity in response to neighboring plant chemotypes, potentially as an adaptive strategy. This phenological plasticity may minimize competition for pollinators (Caruso, 2000). By adjusting their flowering periods, chemotypes can potentially reduce competition by being available to different subsets of pollinator community (Elzinga et al., 2007). Secondly, the phenological shifts in tansy could indicate a broader plant-plant communication in which plants potentially use chemical cues from neighbors to adapt their growth and reproductive strategies (Karban et al., 2014; Heil & Karban, 2010). The study highlights that while chemotype-specific growth traits initially varied, these differences diminished over time. I suggest that the initial morphological differences respond to different growth strategies across chemotypes but the phenotypic plasticity of tansy allowed chemotypes to reallocate resources in response to local conditions (Miner et al., 2005; Herms & Mattson, 1992). Furthermore, as morphological differences decrease over time under field conditions, we can effectively isolate and study the effects of chemodiversity on plant-insect interactions, making long-term field studies relevant in plant chemical ecology.

4.2.3 Link Between Morphological and Chemical Traits

In addition to understanding the ecological consequences of plant chemodiversity, my research also aimed to explore the links between chemical and morphological traits in *T. vulgare*. These links provide insights into the complex interplay between plant growth strategies and defensive capabilities against herbivores. The findings reveal several significant correlations between plant morphology and chemical diversity.

Contrary to **H4.1**, which predicted a trade-off between growth-related traits and chemodiversity, the study found positive relationships between plant structural complexity (stem number and height) and chemical diversity measures (terpenoid Shannon diversity and concentration) (Figures 13 and 18). These results suggest that higher chemodiversity within plant individuals is associated with increased structural complexity but also challenges traditional growth-defense trade-off theories. I hypothesize that plants may optimize growth and defense simultaneously, possibly due to greater energy budgets in larger plants.

Traditionally, ecological theory suggests a trade-off between growth-related traits and chemical defense, where plants allocate resources either to growth or defense mechanisms (Herms & Mattson, 1992; Coley et al., 1985). However, contrary to this expectation, the study did not find evidence of such a trade-off in *T. vulgare*. Previous research indicated negative correlations between growth factors like plant height and biomass with terpenoid concentration (Moles et al., 2013; Wolf et al., 2011). In contrast, the results demonstrate a synergistic relationship between growth traits and chemical diversity. A plausible explanation for these findings could be the metabolic advantages of larger plants with higher photosynthetic capacities. Larger plants may have greater energy budgets, enabling them to invest more resources into synthesizing and storing a diverse array of terpenoids. This aligns with theories suggesting that plants optimize fitness by simultaneously growing and defending against herbivores within their dynamic environments (Huot et al., 2014).

Moreover, the influence of maternal 'chemo-genotypes' on leaf metabolic composition in *T. vulgare* underscores the complexity of chemodiversity (Dussarrat et al., 2023). The study's chemotypes, differentiated by their maternal origins, may have broader implications for understanding how maternal influences shape plant traits and subsequent interactions with herbivores. Future research should explore how these maternal effects on chemodiversity impact aphid attraction and performance and investigate how chemotype variation interacts with plant ontogeny stages. Additionally, expanding studies to assess broader metabolic profiles influenced by maternal origins could provide deeper insights into the ecological and evolutionary implications of chemodiversity in plant communities.

4.3 Limitations of the Study

Understanding the complexities of chemodiversity and its implications for plant-arthropod interactions represents a critical area of ecological research. While the published chapters of this dissertation have provided valuable insights into the relationships between plant chemical diversity and arthropod- and plant-plant interactions, several limitations warrant consideration for future investigations.

4.3.1 Effects on Processes

While the study primarily focused on elucidating the effects of chemodiversity on arthropod occurrence and abundance in field conditions, the conclusions might be challenging to draw as some critical ecological processes that underpin plant-arthropod interactions are overlooked. For instance, top-down processes like predation and bottom-up processes like aphid performance on plant hosts are fundamental to understanding ecosystem dynamics. These processes can be influenced by chemodiversity in complex ways that extend beyond simple abundance metrics. In order to further understand the dynamics between plant chemodiversity, herbivores, and their predators, together with a colleague doctoral candidate, Annika Neuhaus, we performed experiments on aphid survival and performance in controlled greenhouse conditions. A summary of the study design and results is presented here (more details are available in Neuhaus et al. (in prep)).

We conducted a study to investigate the relationships between tansy chemotypes, aphids, and their predators. The experimental design utilized 240 clonally propagated plants derived from the 18 daughter tansy plants used in the other studies included in this dissertation. We included the combinations of the 6 chemotypes and 2 aboveground treatment levels (with and without *Ma. tanacetaria* aphids) and 2 belowground treatment levels (with and without wireworms). While the study included a belowground herbivory treatment, this aspect is beyond the scope of this dissertation discussion, but it is discussed by Neuhaus et al. (in prep). Instead, my interest lay in examining predator-prey interactions and aphid performance across different tansy chemotypes.

Our study comprised two main experiments: a ‘top-down’ experiment focusing on the effects of chemotype on survival aphid rates, and a ‘bottom-up’ experiment examining aphid performance across chemotypes. In the first experiment, the aphid survival of 12 five-day-old *Ma. tanacetaria* was monitored over time (0, 2, 4, 6, 12, 24, 36, 48, and 60 starting at 6:00 h on Day 0 (one day after aphid infestation)) in the presence of naturally occurring predators. We also assessed aphid predator identity and abundance during each count. We used the Kaplan-Meier and Cox regression methods to evaluate the chemotype effect on aphid survival

times and probabilities. I also used a GLMM with Poisson distribution to check the effect of chemotype and plant dry biomass and its interaction on predator abundance. We found significant differences in aphid survival among chemotypes with a 74.3% higher risk of aphid mortality in the 'Bthu-low' chemotype compared to others (Figure 19a; $P < 0.001$). This difference could be attributed to chemical traits in this chemotype that make it less suitable as a host plant for aphids, potentially due to toxicity, reduced nutritional quality, or stronger induced plant defenses. Notably, the observed lower aphid numbers on the 'Bthu-low' chemotype are also partially explained by aphids leaving the plant rather than due to mortality. This indicates that the chemotype might be repellent (although not effects were found in our study 3.2). To further differentiate between mortality and dispersal (repellence) effects, future studies might implement tracking of aphid movement and feeding behavior. Interestingly, despite differences in aphid survival, no significant variations in predator numbers were observed across chemotypes or in relation to plant biomass (Figure 19b). This indicates that predator abundance might be influenced by ecological factors beyond chemotypic differences or plant size, which were not assessed in this study.

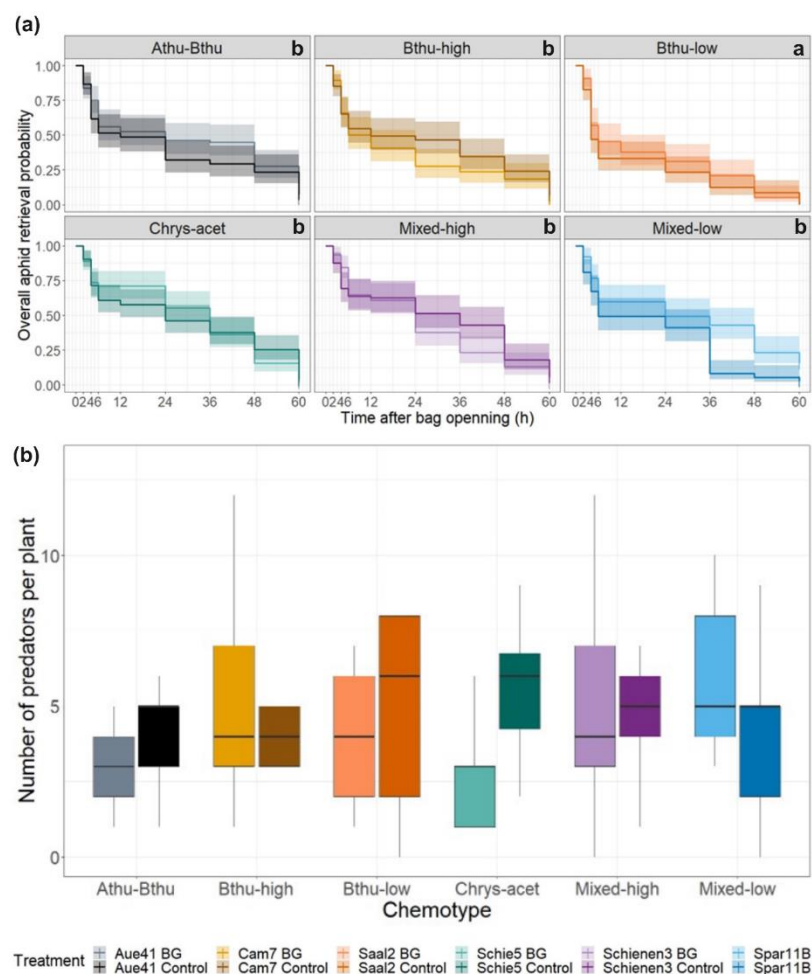


Figure 19. (a) Kaplan-Meier survival curves for aphids by chemotype and treatment. Light colors represent plants treated with below-ground herbivores (BG), while bold colors represent

control plants. Different letters next to the chemotype name indicate statistically significant differences in aphid retrieval probability among chemotypes. The 'Bthu-low' chemotype had a lower aphid retrieval probability compared with the others ($HR_{(5)} = 30.42$, $P < 0.001$). **(b)** Number of predators per plant. We found no differences in the number of predators across chemotypes ($X^2_{(5)} = 7.69$, $P = 0.174$), nor varying with the plant biomass ($X^2_{(1)} = 2.29$, $P = 0.130$), nor the interaction ($X^2_{(5)} = 8.21$, $P = 0.145$).

The 'bottom-up' experiment assessed aphid colony growth over three weeks. The final colony size analysis showed significant differences among chemotypes ($X^2_{(5)} = 12.51$, $P = 0.028$; Figure 20). The 'Bthu-low' chemotype, which had shown lower aphid retrieval in the top-down experiment, also exhibited the lowest final aphid colony size. In contrast, the 'Mixed-low' chemotype had the highest aphid colony size and growth rate ($X^2_{(5)} = 21.55$, $P < 0.001$).

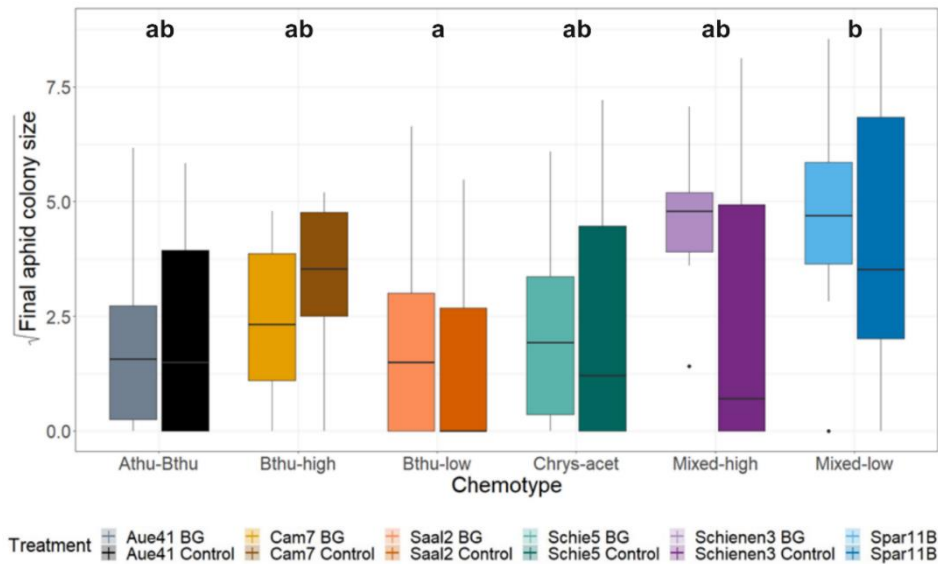


Figure 20. Final *M. tanacetaria* aphid colony size after 21 days on growth on different tansy chemotypes. Light colors represent plants treated with below-ground herbivores (BG), while bold colors represent control plants. Different letters indicate statistically significant differences across chemotypes ($P < 0.05$) based on Tukey's post hoc test.

The top-down and bottom-up experiments provide complementary insights into the complex interactions between tansy chemotypes, herbivores, and predators. The 'Bthu-low' chemotype had the lowest retrieval rate, aphid colony size, and growth rate. This suggests that 'Bthu-low' plants may be less suitable hosts for aphids, possibly due to their chemical profile. Conversely, the 'Mixed-low' chemotype exhibited the highest aphid colony size and growth rate in the bottom-up experiment, indicating it is a favorable host for aphids. However, in the top-down experiment, this chemotype showed increased aphid predation when treated with below-ground herbivores. This suggests that the presence of below-ground herbivores may induce

changes in the plant that either make aphids more vulnerable to predation or more willing to leave their host.

These results highlight the importance of considering both top-down and bottom-up processes when studying plant-arthropod interactions. The varying responses across chemotypes demonstrate that plant chemical diversity plays a crucial role in mediating these interactions, with some chemotypes favoring herbivores and others decreasing aphid survival. Moreover, the influence of below-ground herbivory on these interactions adds another layer of complexity (see Neuhaus et al., (prep)), emphasizing the need to consider multiple trophic levels and herbivory types in future studies.

4.3.2 Effects of Plot-level Chemodiversity on Volatile Composition and Insect Community Assembly

I propose further exploring the relationship between plot-level chemotype richness, emitted volatile blends, and winged aphid colonization patterns within plant communities. Plant volatiles are known to mediate a variety of ecological interactions. For instance, volatile organic compounds (VOCs) shape plant interactions with their surroundings. They can attract pollinators, repel herbivores, or serve as signals to other plants. Specific VOCs can attract beneficial insects that pollinate flowers or act as natural enemies to herbivores, providing an indirect plant defense. Conversely, some volatiles might attract herbivorous insects, leading to increased plant damage.

Contrary to expectations, increasing chemotype richness did not correlate with higher richness or diversity in emitted volatile blends in the plant system. Instead, I found that as plant communities became more dissimilar in their leaf terpenoid profiles, their emitted volatile blends also became more dissimilar (Ojeda-Prieto et al., 2024). A deeper analysis might indicate that specific terpenoid compounds significantly contribute to the dissimilarity observed in emitted volatile profiles, and those terpenoids may play crucial roles in mediating plant-insect interactions, particularly in relation to winged aphid attraction, which are particularly sensitive to plant volatiles.

The ability of winged aphids to detect and respond to plant volatiles underscores the importance of understanding how these chemicals influence insect community dynamics. Despite the recognized importance of plant chemodiversity and volatile emissions in influencing insect community assembly, few studies have explored these relationships at the plot level. Specifically, there is a lack of research linking plot-level chemotype richness to both the composition of volatile emissions and the patterns of insect colonization, particularly for winged aphids. I hypothesize that more dissimilar volatile emissions are driven by differences in specific leaf terpenoid compounds (H1) and that this dissimilarity influences the colonization

patterns of the plots by winged aphids (H2). Furthermore, it will be interesting to observe how the volatile profile at the community level evolves as plants grow and competition and facilitation processes intensify. This dynamic aspect could provide valuable insights into the ecosystem's ongoing interactions between plants and insects.

4.3.3 Temporal Dynamics of Chemodiversity

One significant limitation is the potential temporal dynamics of chemodiversity, which were not in the scope of this dissertation. The plant chemical profiles were measured from leaf samples collected when growing in greenhouse conditions before transplanting. At the same time, the long-term field experiment involved monitoring plant traits and arthropod communities over three years. This discrepancy raises essential questions about the stability and variation of chemodiversity over time and its impact on ecological interactions.

Chemodiversity is not a static trait; it encompasses changes in the chemical composition of plant tissues over time, across seasons, and in response to abiotic and biotic factors (Figure 1). The dynamic nature of chemodiversity involves the patterns and changes in chemical profiles within plant populations over time and across different ecological contexts. These temporal changes can significantly influence the interactions among plants and between plants and insect communities. One key aspect is the temporal dynamics of leaf terpenoid compounds and chemical signals emitted by *T. vulgare* within the experimental plots. Over the three years, the chemical profiles of these plants likely changed due to environmental factors. For example, seasonal changes in environmental conditions like climate, soil composition, and light availability are critical factors that can influence phytochemical production in plants. Interactions with other organisms, such as herbivores, pollinators, and pathogens, can also drive phytochemical variation. Plants may produce different compounds in response to herbivory or pollination, and these interactions can change over time as the community composition of insects and other organisms evolves. The age and developmental stage of the plants can affect their chemical profiles, as younger plants may produce different compounds compared to mature plants.

The initial chemotyping done in the greenhouse might not precisely reflect the chemical profiles of the plants in the field throughout the study duration. Thus, it is crucial to reassess the chemical profiles of the plants from the field to understand how these dynamics influence insect communities over time. Future studies should incorporate repeated chemotyping of plants in the field to capture these temporal variations and their effects. However, it is important to stress that while chemical compounds might vary across time and under different environmental conditions, plant chemotypes are limited due to specific metabolic pathways determined by the individual plant's genetics. Thus, a plant's chemodiversity is constrained by

its genetic makeup. Under this assumption, the findings of this research remain valid, providing valuable insights into the role of chemodiversity in ecological interactions.

4.4 Recommendations for Future Research

The following recommendations aim to address the limitations identified in the current study and push the boundaries of our understanding of intraspecific chemodiversity and its ecological consequences. By pursuing these research directions, we can better understand how intraspecific plant chemodiversity shapes ecosystem functioning and biodiversity.

First, future studies should incorporate repeated chemotyping of plants in the field over multiple growing seasons. Such long-term monitoring would help reveal the stability of chemotypes under field conditions by capturing temporal variations in chemical profiles and their responses to various environmental factors. It will also provide insights into how these changes impact arthropod communities over time. Second, specific ecological processes should be explored by integrating both field and greenhouse experiments. This could include investigating predation rates, aphid performance on different chemotypes, and the cascading effects of chemodiversity on multiple trophic levels. The next step could be to examine potential mediating factors influencing arthropod responses to chemodiversity, such as the nutritional quality of herbivores feeding on different chemotypes and its subsequent impact on predator abundance and performance. Additionally, investigating how chemodiversity affects plant-pollinator mutualisms and plant-aphid-ant interactions would provide valuable insights into the broader ecological consequences of intraspecific chemical variation. Research should also focus on the relationship between plot-level chemotype richness, emitted volatile blends, and patterns of insect colonization, particularly for winged aphids. This would involve collecting and analyzing volatile organic compounds (VOCs) from individual and plant communities and correlating these with insect community assembly patterns.

Given the increasing importance of understanding ecosystem responses to climate change, future research should examine how chemodiversity interacts with changing environmental conditions. This could include studying how soil nutrient content and community differences affect plant chemical profiles and subsequent arthropod interactions. Moreover, future research could also explore the potential applications of chemodiversity in agricultural settings, for instance, studying how mixed-chemotype communities affect pest control and crop yield of various farm systems.

4.4.1 Integrating Chemodiversity

4.4.1.1 Increasing Ecosystemic Services

Chemodiversity can enhance plant breeding programs by improving resistance to insect pests and strengthening ecosystem services like pollination and predation (Snyder et al., 2020; Ratnadass et al., 2012). By selecting chemotypes that produce diverse compounds deterring herbivores, breeders can use pest-resistance cultivars, reducing the need for chemical pesticides and promoting sustainable agriculture (Snyder et al., 2020; Tooker & Frank, 2012; Hajjar et al., 2008). While higher plot chemotype richness may offer some associational resistance against herbivores (Ziaja & Müller, 2023; Ida et al., 2018; Wetzal & Thaler, 2016), the specific outcomes depend on the chemical profiles of individual plant species (Silva et al., 2018; Schuman et al., 2016) as well as the specialization grade of herbivores, as they respond differently to chemodiversity (Glassmire et al., 2020).

Chemodiversity can also enhance pollination services, which is crucial for agricultural productivity, and studying its effects can reveal how plant chemical profiles have evolved in response to various ecological pressures, including interactions with pollinators (Parachnowitsch & Manson, 2015; Arimura et al., 2009; Mitchell et al., 2009). With this knowledge, researchers can develop plant varieties with enhanced pollinator appeal, potentially increasing crop yield and stability in agricultural systems.

Moreover, promoting chemically diverse plant communities that support diverse pollinator and predator assemblages, increases ecosystem resilience and indirectly reduces pest populations through natural biological control. This approach is valuable for restoring degraded habitats or designing pollinator-friendly urban green spaces.

4.4.1.2 Decline of Plant Intraspecific Chemodiversity and its Ecological Consequences

The decline in plant diversity, particularly at the interspecific level, poses significant threats to ecosystem functioning and stability (Tilman et al., 2014; Isbell et al., 2011). However, little is known about the effects of the decline of intraspecific diversity (Snyder et al., 2020; Tooker & Frank, 2012; Hajjar et al., 2008). As intraspecific chemodiversity decreases, plants may become more vulnerable to herbivory, disease, or environmental changes (Mitchell et al., 2016; War et al., 2012). Different chemotypes within a species often result from distinct selection pressures resulting in varying resistance levels. From an evolutionary perspective, the loss of intraspecific chemodiversity can reduce population-level resilience against these threats (Thon et al., 2024; Kessler & Kalske, 2018; Weng et al., 2012).

The decline in intraspecific chemodiversity can also significantly impact other taxonomic levels, influencing the composition and dynamics of the entire arthropod community associated with a plant species (Dyer, 2018; Bálint et al., 2016). As demonstrated in this study, different chemotypes can attract or repel specific insect groups. Simplifying the chemical landscape within a plant population could lead to homogenizing the associated insect community, potentially reducing overall biodiversity and ecosystem stability. Conservation efforts should focus on preserving species diversity, maintaining intraspecific chemodiversity, protecting diverse wild plant populations, and implementing breeding programs that prioritize chemical diversity.

Conclusion

This study has significantly advanced our understanding of intraspecific chemodiversity dynamics in plant communities and their ecological consequences. By characterizing and manipulating chemodiversity, evaluating its ecological impacts, and assessing links between morphological and chemical traits, we have gained valuable insights into the complex relationships between plant chemistry, community structure, and arthropod interactions.

The findings demonstrate that intraspecific chemodiversity plays a crucial role in shaping plant-arthropod interactions at both the individual plant and community levels. High chemodiversity enhances plant defense against herbivores and attracts beneficial flower visitors, possibly contributing to overall plant fitness. Specific chemotypes within a plot exert distinct effects on different arthropod groups, influencing their abundance and occurrence patterns in both temporal and species-specific ways. This aligns with evolutionary processes that may have selected patterns of chemical diversity that we see in nature. For plants, it makes sense to maintain what repels antagonists and attracts mutualists, and this relationship with direct interaction partners is evident in our data.

The research highlights the complexity of plant-arthropod relationships and emphasizes the need for further investigation into the underlying mechanisms driving these interactions. Understanding how plant chemodiversity influences predator and ant communities is critical for predicting the consequences of changing plant communities on arthropod populations. Interestingly, indirect interaction partners, including ants and predators, seem to have less straightforward patterns, other processes likely govern their dynamics. These insights might be vital for developing strategies for pest management and biodiversity conservation in agricultural and natural ecosystems.

Additionally, the study revealed the effects of chemodiversity on plant-arthropod interactions. The negative correlation between chemotype richness and herbivore abundance, particularly for specialist aphid species, suggests that chemical diversity is an effective defense mechanism. Conversely, the positive relationship with flower visitor abundance indicates that chemodiversity can enhance pollination services. The species-specific responses of aphids to different chemotypes further emphasize the importance of considering intraspecific variation in plant-insect studies.

Our research also challenged traditional growth-defense trade-off theories by showing a positive correlation between plant structural complexity and chemical diversity measures. This finding opens new avenues for researching how plants balance resource allocation between

growth and defense strategies. The discrepancy observed between leaf-level and headspace volatile terpenoid profiles highlights the complex nature of plant volatile emissions.

However, the study also reveals areas requiring further investigation. Future research should focus on long-term chemical profiling, integrating ecological processes, exploring mediating factors influencing arthropod responses, and examining the relationship between volatile emissions and insect colonization patterns in more detail.

In conclusion, this comprehensive investigation into the effects of intraspecific chemodiversity in *Tanacetum vulgare* has provided valuable insights into the complex interplay between plant chemical diversity, growth strategies, and ecological interactions with insects. By deepening our understanding of how intraspecific chemodiversity shapes ecological interactions, this study bridges the gap between chemical and community ecology, contributing significantly to both fields.

Summary

Intraspecific chemical diversity is crucial in shaping ecological interactions within plant communities. Using greenhouse experiments and a comprehensive field experimental approach in which we created plots with varying levels of chemotype richness (1 to 6 chemotypes) and specific chemotype combinations, this study investigated the effects of manipulating chemodiversity in *Tanacetum vulgare* (tansy) on plant-arthropod interactions, aphid preferences, plant growth and reproduction traits, VOC headspace emissions, and defense/growth tradeoffs.

Our results revealed that higher plot-level chemotype richness correlated negatively with herbivore abundance, particularly for specialist aphid species. Conversely, flower visitor occurrence and abundance increased with chemotype richness. Predator and ant communities showed more subtle responses to chemodiversity. Specific chemotypes had distinct effects on different arthropod groups, highlighting the complex nature of plant-insect relationships. We also found aphid-species-specific attraction towards specific chemotypes and a marginally negative correlation between attractiveness and chemotype chemodiversity.

T. vulgare chemotypes exhibited distinct growth and reproductive traits, with differences more pronounced in early developmental stages. This suggests that plots become increasingly more similar in terms of morphology over time, allowing us to explore the effects of chemodiversity on plant-insect interactions. Contrary to expectations, plot-level chemotype richness did not significantly affect plant growth traits nor lead to overyielding effects. However, it influenced reproductive traits, with most chemotypes showing reduced flower head numbers in high-diversity plots. Flowering phenology also varied among chemotypes responding to plot-level chemodiversity, suggesting adaptive strategies to optimize reproductive success. Interestingly, leaf-level terpenoid profiles showed increased diversity with higher plot-level chemotype richness, but this trend was not observed in headspace volatile profiles. This discrepancy underscores the complex relationship between stored and emitted plant volatiles.

We also found positive correlations between plant structural complexity (stem number and height) and chemical diversity measures (terpenoid Shannon diversity and concentration), challenging traditional growth-defense trade-off theories. This suggests that *T. vulgare* may optimize growth and defense simultaneously, possibly due to greater energy budgets in larger plants.

Overall, this study underscores the significant effect of intraspecific chemodiversity on plant growth, reproduction, and plant and arthropod community dynamics. These findings contribute

to understanding how chemical diversity within plant species influences ecosystem functions and highlight the importance of considering intraspecific variation in ecological studies.

Zusammenfassung

Die intraspezifische chemische Vielfalt spielt eine entscheidende Rolle für die ökologischen Interaktionen in Pflanzengemeinschaften. In dieser Doktorarbeit untersuchte ich mithilfe von Gewächshaus-Experimenten und einem umfassenden Feldexperiment, bei dem wir Parzellen mit einer unterschiedlichen Anzahl von Chemotypen (1 bis 6) und spezifischen Chemotypen-Kombinationen anlegten, die Auswirkungen von Chemodiversität auf Pflanzen-Arthropoden-Interaktionen. Die Modellpflanze war der Rainfarn, *Tanacetum vulgare*. Der Fokus war auf Blattlauspräferenzen, Pflanzenwachstums- und Reproduktionseigenschaften, VOC-Headspace-Emissionen sowie Abwehr/Wachstums-Abwägungen.

Die Ergebnisse zeigten, dass eine höhere Anzahl von Chemotypen auf Parzellenebene negativ mit der Herbivoren-Abundanz, insbesondere bei spezialisierten Blattlausarten, korrelierte. Im Gegensatz dazu nahm die Häufigkeit und Abundanz von Blütenbesuchern mit dem Chemotypen-Reichtum zu. Räuber- und Ameisengemeinschaften reagierten subtiler auf die Chemodiversität. Spezifische Chemotypen hatten unterschiedliche Auswirkungen auf verschiedene Arthropodengruppen, was die komplexe Natur der Pflanzen-Insekten-Beziehungen verdeutlicht. Wir fanden auch eine blattlausartspezifische Reaktion auf bestimmte Chemotypen und eine marginal negative Korrelation zwischen Attraktivität und Chemotypen-Chemodiversität.

T. vulgare-Chemotypen wiesen unterschiedliche Wachstums- und Reproduktionseigenschaften auf, wobei die Unterschiede in den frühen Entwicklungsstadien der Pflanzen ausgeprägter waren. Dies deutet darauf hin, dass die Pflanzen in den Parzellen im Laufe der Zeit zunehmend ähnliche morphologische Merkmale aufwiesen, was uns ermöglichte, die Auswirkungen der Chemodiversität auf Pflanzen-Insekten-Interaktionen zu untersuchen. Entgegen den Erwartungen beeinflusste der Chemotypen-Reichtum auf Parzellenebene die Pflanzenwachstumseigenschaften nicht signifikant und führte nicht zu Überertragseffekten. Er beeinflusste jedoch die Reproduktionseigenschaften, wobei die meisten Chemotypen in hochdiversen Parzellen eine reduzierte Anzahl von Blütenköpfen zeigten. Die Blühphänologie variierte ebenfalls zwischen den Chemotypen, in Abhängigkeit von der Anzahl der Chemotypen in der Parzelle, was adaptive Strategien zur Optimierung des Fortpflanzungserfolgs nahelegt. Interessanterweise zeigten die Terpenoidprofile auf Blattebene eine erhöhte Vielfalt bei einer höheren Anzahl von Chemotypen auf Parzellenebene, aber dieser Trend wurde nicht in den Headspace-Volatilprofilen beobachtet. Diese Diskrepanz unterstreicht die komplexe Beziehung zwischen gespeicherten und freigesetzten Pflanzen-Duftstoffen.

Wir fanden auch positive Korrelationen zwischen der strukturellen Komplexität der Pflanze (Stängelanzahl und -höhe) und den chemischen Diversitätsmaßen (Terpenoid-Shannon-Diversität und -Konzentration), was traditionelle Theorien zu Wachstums-Abwehr-Abwägungen in Frage stellt. Dies legt nahe, dass der Rainfarn möglicherweise Wachstum und Abwehr gleichzeitig optimieren kann, möglicherweise aufgrund eines höheren Energiebudgets bei größeren Pflanzen.

Insgesamt unterstreicht diese Studie die signifikanten Auswirkungen der intraspezifischen Chemodiversität auf Pflanzenwachstum, Reproduktion sowie auf die Pflanzen- und Arthropodengemeinschaftsdynamik. Diese Erkenntnisse tragen zum Verständnis bei, wie chemische Vielfalt innerhalb von Pflanzenarten Ökosystemfunktionen beeinflusst, und sie heben die Bedeutung der Berücksichtigung intraspezifischer Variation in ökologischen Studien hervor.

Resumen

La diversidad química intraespecífica juega un papel crucial en la configuración de las interacciones ecológicas dentro de las comunidades vegetales. Mediante experimentos de invernadero y un enfoque experimental de campo integral en el que creamos parcelas con niveles variables de riqueza de quimiotipos (1 a 6 quimiotipos) y combinaciones específicas de quimiotipos, este estudio investigó los efectos de la chemodiversidad en *Tanacetum vulgare* (tanaceto) sobre las interacciones planta-artrópodo, las preferencias de los áfidos, los rasgos de crecimiento y reproducción de las plantas, las emisiones de compuestos orgánicos volátiles de las comunidades de plantas (VOCs), y los posibles tradeoffs entre defensa y crecimiento.

Nuestros resultados revelaron que una mayor riqueza de quimiotipos en una comunidad se correlacionó negativamente con la abundancia de herbívoros, particularmente para las especies de áfidos especialistas. Por el contrario, la ocurrencia y abundancia de visitantes florales aumentó al aumentar la riqueza de quimiotipos en la parcela. Las comunidades de depredadores y hormigas mostraron respuestas más sutiles a la chemodiversidad. La presencia de ciertos quimiotipos tuvieron efectos distintos en diferentes grupos de artrópodos, destacando la naturaleza compleja de las relaciones planta-insecto. También encontramos que algunas especies de áfidos se encuentran atraídas hacia quimiotipos específicos y la atracción en esta especie marginalmente se correlaciona negativamente con el aumento en la diversidad química de los quimiotipos.

Los quimiotipos de *T. vulgare* exhibieron rasgos de crecimiento y reproducción distintos, con diferencias más pronunciadas en las etapas tempranas de desarrollo. Esto sugiere que las parcelas se vuelven cada vez más similares en términos de morfología con el tiempo, permitiéndonos explorar los efectos de la chemodiversidad en las interacciones planta-insecto. Contrario a nuestras expectativas, la riqueza de quimiotipos a nivel de parcela no afectó significativamente los rasgos de crecimiento de las plantas ni condujo a efectos de sobreproducción. Sin embargo, influyó en los rasgos reproductivos, con la mayoría de los quimiotipos mostrando una reducción en el número de cabezas florales en parcelas de alta diversidad. La fenología de la floración también varió entre quimiotipos respondiendo a la chemodiversidad a nivel de parcela, sugiriendo estrategias adaptativas para optimizar el éxito reproductivo. Por otro lado, la diversidad de la parcela, basada en la composición de terpenoides en las hojas, aumentó conforme lo hizo la diversidad de quimiotipos presentes en ella. Sin embargo, esta tendencia no se observó en los perfiles de volátiles del espacio de cabeza. Esta discrepancia subraya la compleja relación entre los volátiles almacenados y emitidos por las plantas.

También encontramos correlaciones positivas entre la complejidad estructural de la planta (número de tallos y altura) y las medidas de diversidad química (diversidad de Shannon de terpenoides y concentración), desafiando las teorías tradicionales de tradeoffs entre crecimiento y defensa. Esto sugiere que *T. vulgare* puede optimizar el crecimiento y la defensa simultáneamente, posiblemente debido a mayores presupuestos energéticos en plantas más grandes.

En general, este estudio subraya el efecto de la chemodiversidad intraespecífica en el crecimiento de las plantas, la reproducción y la dinámica de las comunidades de plantas y artrópodos. Estos hallazgos contribuyen a comprender cómo la diversidad química dentro de las especies vegetales influye en las funciones del ecosistema y destaca la importancia de considerar la variación intraespecífica en los estudios ecológicos.

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Appendix A. Manuscripts

A-I. Increasing Intraspecific Plant Chemical Diversity at Plot and Plant Level Affects Herbivorous, Predatory, and Pollinating Arthropod Communities

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Author contributions:

WWW conceived the original idea and designed the experiment. RH prepared the field experiment and propagation of plants. LOP, RH, and WWW planted the field experiment. LOP and ELM collected all data and maintained the field experiment. LOP analyzed ecological data with input from RH and WWW. LOP wrote the manuscript with input from ELM, RH, and WWW. All authors contributed to the final version and approved the final submission.

Abstract

Plant chemistry mediates interactions between plants and their environment. While intraspecific chemodiversity at the plant level is well-studied, the effects of groups of plants differing in chemistry on interactions need more attention. To test how intraspecific chemodiversity affects plant-arthropod interactions, we manipulated plots of *Tanacetum vulgare* L., differing in chemotype richness and composition. Over three seasons, we monitored four arthropod groups (herbivores, flower visitors, predators, and ants). We hypothesized that higher plot-level chemotype richness enhances occurrence across all studied arthropod groups and that the effect on abundance would be negative for herbivore and ant abundance and positive for flower visitors and predators. Mixed models revealed that with increasing plot-level chemotype richness, herbivore abundance decreased, flower visitor abundance increased, and predatory arthropods and ants remained largely unaffected. Specific chemotypes influenced community assembly within arthropod groups over time, emphasizing that plant chemical diversity shapes insect communities and contributes to ecosystem dynamics.

Introduction

Biodiversity is recognized as a driver of ecosystem functioning and stability (Espinosa-García, 2022; Mora et al., 2014). Biodiversity studies have focused on species richness, examining how increasing plant community diversity affects ecosystem-level processes (Cardinale et al., 2006; Eisenhauer et al., 2011; Schulze & Mooney, 1992; Weisser et al., 2017). Plant communities with greater species richness are linked to a more diverse community of organisms (Ebeling et al., 2018), alterations in food web structure (Giling et al., 2019), and increased ecosystem process rates (Hertzog et al., 2017; Meyer et al., 2017). While species-level diversity has been well-studied, recent research explores biodiversity within species (Crutsinger et al., 2006; Govaert et al., 2024; Konefal et al., 2024; Koricheva & Hayes, 2018; Noto & Hughes, 2020; Raffard et al., 2019; Zerebecki & Hughes, 2023).

One component of within-species diversity is chemodiversity (Müller et al., 2020; Wetzel & Whitehead, 2020). Chemodiversity refers to the variety of chemical compounds produced by organisms (Walker et al., 2022; Whitehead et al., 2021). These compounds, including terpenoids, alkaloids, and phenolics, play diverse roles in plant defense (Hare, 2011; Wetzel et al., 2023), communication, and reproduction (Hartmann, 2007; Whitehead et al., 2022), potentially altering ecosystem dynamics like herbivory rates and pollinator preferences (Eisenring et al., 2021; Müller & Junker, 2022). Chemodiversity affects ecological interactions, impacting richness, diversity, and community structure (Dyer & Jeffrey, 2021; Fernandez-

Conradi et al., 2022; Petrén et al., 2023). Studies have shown cascading chemodiversity effects within food webs (Bálint et al., 2016; Kos et al., 2011; Senft et al., 2019).

Intraspecific chemodiversity can be investigated at different scales, from individual plants to larger groups like plots or populations (Müller et al., 2020; Ojeda-Prieto et al., 2024). Research at the plant level has focused on chemodiversity effects on arthropod-plant interactions (Benedek et al., 2019; Kos et al., 2011; Senft et al., 2017). For instance, field observations show certain compounds influence herbivore preference and performance (Clancy et al., 2018; Kleine & Müller, 2011), as well as natural enemies' behavior and reproductive success (Benedek et al., 2015; Zytynska et al., 2019). Manipulative studies reveal that plants with different chemical compositions differ in attractiveness to aphids (Neuhaus-Harr et al., 2024) and herbivore performance (Jakobs & Müller, 2018), reinforcing the role of chemodiversity in plant-arthropod interactions.

Larger-scale studies in chemodiversity are scarce and predominantly correlative. Studies have examined how local chemotype richness influences arthropod communities (Espinosa-García, 2022; Hauri et al., 2021), but questions remain on the responses of different arthropod groups. Manipulative experiments, directly testing the consequences of a gradient of chemotype richness at the group level, show that increasing chemodiversity correlates with higher herbivore diversity but lower plant damage (Bustos-Segura et al., 2017). By systematically manipulating plot-level chemotype richness (CR), we aim to understand how chemodiversity at plant and plot levels shapes arthropod abundance and occurrence. Due to their distinct ecological roles, chemodiversity's effects are expected to vary among arthropod groups. This complexity has not been fully addressed, highlighting the need for comprehensive experimental approaches on arthropod groups and their interactions with plants.

Different plant-interacting groups, such as herbivores, flower visitors, predators, and ants, may share different co-evolutionary histories with – and offer different selective pressures to – the plant that have likely shaped its chemical composition by selecting chemical profiles that serve optimal plant fitness (Dyer & Jeffrey, 2021; Schneider et al., 2021; Whitehead et al., 2021, 2022). Arthropod **abundance** is influenced by plant attractiveness and resource suitability, but it is also shaped by a complex interplay of factors, including predator-prey dynamics, trophic cascades, and habitat structure. However, conceptually, these relationships are best understood from a plant-centered perspective. For herbivores, plants may benefit from having a diverse bouquet of chemicals to deter herbivores and reduce their abundance and impact on the plant (Glassmire et al., 2019; Kariñho-Betancourt, 2020; Rabelo et al., 2023; Zu et al., 2020). For predatory arthropods, plants may benefit from their presence as predators may control herbivore populations (Barbosa et al., 2009; Turlings & Erb, 2018). Therefore, it is likely that more diverse blends of compounds may have evolved in part to attract predatory

arthropods (Clavijo McCormick et al., 2012; De Boer et al., 2004, 2008). Similarly, many flower visitors play a crucial role in pollination (Dantas et al., 2020; Jacobsen & Raguso, 2018). Plants may evolve specific compounds to attract more flower visitors, and more diverse profiles attract more visitors. Ants may have positive, negative, or no effects on plants (Ramos et al., 2022; Yamawo et al., 2021). Given that many ants engage in mutualisms with herbivorous aphids, it may be beneficial for plants to evolve repellent compounds. On the other hand, if ants engage in protective mutualisms with plants, it may be beneficial for plants to evolve attractant compounds. Therefore, hypotheses regarding relationships between plant chemodiversity and ant abundance will likely depend on the role of the ants in the study system. Concerning the **occurrence** of arthropods, higher chemodiversity likely favors arthropod occurrence by increasing the likelihood that a specific compound can be used as a host recognition cue (Dyer, 2018; Jacobsen & Raguso, 2018; Lampert et al., 2010). As a chemical profile is, by definition, a result of cumulative selection processes that have taken place over evolutionary history, compounds may serve unique or dual purposes depending on the interactions. Understanding how plant chemodiversity impacts arthropod communities will provide insights into the evolutionary forces shaping it.

Despite extensive research on plant chemodiversity's effects on arthropod communities, gaps remain. Studies often test only one arthropod group, focus on short-term effects, or compare high vs. low chemodiversity without examining a gradient. Our study addresses these gaps by manipulating the chemodiversity gradient and observing the responses of different arthropod groups over several seasons.

We used *Tanacetum vulgare* L. (tansy), an herbaceous plant with high intraspecific variation in terpenoids, to investigate how variation in the number of tansy chemotypes in a plot affects associated arthropod communities. In a field experiment with 84 plots (six plants each), we manipulated plot-level chemotype richness (CR; i.e., 1, 2, 3, or 6 chemotypes present in a plot) and studied its effects on herbivores, flower visitors, predators, and ants (Fig. 1). We examined the effects of chemodiversity on arthropod occurrence and abundance at the plot level, recognizing that responses may differ across groups due to their distinct ecological roles and interactions with plants. Additionally, we investigated the effects of each of the six chemotypes on arthropod communities, anticipating differential responses based on compound attractiveness or repellence.

We specifically tested the following hypotheses:

H1: Plots with higher chemotype richness will have increased probabilities of arthropod occurrence across groups.

H2: Plots with higher chemotype richness will have decreased herbivore and ant abundances but increased predator and flower visitor abundances.

H3: The presence of certain chemotypes in a plot will have specific effects on herbivores, predators, flower visitors, and ants, potentially influencing their abundance and occurrence patterns.

Materials and methods

Experimental design

Tansy chemotypes were characterized based on their leaf terpenoid compositions. We selected six chemotypes ('Athu-Bthu', 'Bthu-high', 'Bthu-low', 'Chrys-acet', 'Mixed-high', and 'Mixed-low') with three biological replicates each (Fig. S1). These chemotypes were propagated via stem cuttings and utilized in a field experiment at the Jena Experiment site in Germany in 2021. The experiment consisted of 84 1m² plots, each containing six tansy plants. The plots were designed to vary in chemotype richness levels ranging from 1 to 6 (Fig. S2), with 12, 30, 30, and 12 replicate plots respectively for each level. Each plot's chemotype composition was pre-assigned, ensuring biological replication of each chemotype combination across the experiment. Plots were distributed equally among six randomized blocks, with specific numbers of plots allocated per chemotype richness level within each block (more detail in: Ojeda-Prieto et al., 2024).

Insect sampling

From 2021 to 2023, we assessed herbivores, flower visitors, predators, and ants. Specific sampling dates are shown in Table S1. Each year, herbivore communities were monitored by counting individual aphids on the plants from their first appearance until nearly none were found. Although the focus was on aphids, other herbivores were scarce. Therefore, the generalization to herbivores here reflects predominantly aphids. Counts were conducted 13 times from June to August 2021, eight times from May to August 2022, and three times from June to August 2023. Each count, executed within a day between 7h and 19h, involved a meticulous scan of each plant, which started from the tip of each stem and proceeded to the end, examining both sides of each leaf. Identification of aphid species followed the key provided in Supplementary Information (SI). When multiple aphid species were present on a plant, we recorded the total number of each. In cases of high aphid densities (>100), we estimated the total by counting aphids on 1 cm of stem or 1 cm² of leaf three times in different stems and leaves for each plant, then multiplying the average by the estimated lengths of stems (in cm) or the estimated areas of leaves (in cm²) colonized by the aphids. We used plot-level occupancy and cumulative plot-level number of aphids to analyze occurrence and abundance.

Flower visitors were assessed by counting the flower heads of individual plants during the flower-visiting recording. Flower visitors were counted three times in July 2021 and once in August 2021. Surveys lasted three minutes per plot and were conducted in random block order from 9h to 15h under optimal weather conditions (no gusts of wind or precipitation). Flower visitors were identified at the order level. We used presence absence data to analyze the effects of CR and chemotype presence on occurrence. However, as CR and individual chemotypes influence reproductive traits in our system (Ojeda-Prieto et al., 2024), flower visitor abundance per flower head (visitation rate) assessed effects on abundance.

Predatory arthropods and ants on individual plants were recorded during herbivore counting for 2021 and 2022 and the day after in 2023. Predators were classified into taxa/feeding guilds (Araneae, Coleoptera, Dermaptera, Diptera, Hemiptera, and Hymenoptera), specifying aphid parasitoids and parasitized aphids (counted as mummies found). Ant presence on plants, but not abundance, was noted. Predator and ant occurrences and parasitized aphid abundance were used for analyses for the three seasons. In 2023, predator and ant abundances were also analyzed.

Statistical analyses

Statistical analyses were conducted using R version 4.1.2 and RStudio 2023.09.1 (R Core Team, 2021). All statistics were performed at the plot level. The effects of chemotype presence and CR on the occurrence of herbivores, flower visitors, predators, and ants were assessed through binomial Generalized Linear Mixed-effect Models (GLMM) using the 'lme4' package (Bates et al., 2015). Linear Mixed-Effect Models (LMM) and Zero-Inflated Negative Binomial Models (ZINB), using the "glmmTMB" package (Brooks et al., 2017), modeled the effect on abundances. P-values were estimated by type II Wald-Chi-Squared tests using the Anova() function ('car' package; J. Fox & Weisberg, 2019). Data visualization used academic-licensed Biorender® and 'ggplot2' (Wickham, 2009), 'grid' (R Core Team, 2021), 'gridExtra' (Auguie et al., 2017), 'ggpubr' (Kassambara, 2020), and 'DHARMA' (Hartig, 2022) packages.

Effects of chemotype richness and chemotype presence on arthropod taxa occurrence and abundance

Binomial GLMMs assessed the effect of CR and chemotype presence on occurrence. LMMs and ZINB tested the effects on abundance. Data were analyzed at the arthropod group and lower taxonomic levels (when indicated). Data were analyzed cumulatively for each year and for each independent sampling time. Detailed model conditions and transformations for each group are given in Supplementary Information (SI).

Results

During our sampling campaigns, we registered the following arthropod numbers: For 2021, 166.630 herbivores in total for 13 sampling dates (58.550 *Aphis fabae* (Scopoli, 1763), 22.691 *Brachycaudus cardui* (Linnaeus, 1758), 382 *Macrosiphoniella tanacetaria* (Kaltenbach, 1843), 62.055 *Metopeurum fuscoviride* (Stroyan, 1950), and 22.952 *Uroleucon tanacetii* (Linnaeus, 1758)), 974 flower visitors in four sampling dates (316 Coleoptera, 236 Diptera, 134 Hemiptera, 237 Hymenoptera, and 51 Lepidoptera), and 4.233 parasitized aphids in 10 sampling dates. For nine sampling dates in 2022, 11'171.066 herbivores (1.610 *A. fabae*, 3.321 *B. cardui*, 35.902 *Ma. tanacetaria*, 37.196 *Me. fuscoviride*, and >1.1 Mio *U. tanacetii*), and 341 parasitized aphids. For three sampling dates in 2023, 234.386 herbivores (249 *A. fabae*, 217 *B. cardui*, 0 *Ma. tanacetaria*, 9.535 *Me. fuscoviride*, and 224.385 *U. tanacetii*), 9.940 predators (1.573 Araneae, 4.770 Coleoptera, 508 Dermaptera, 1.032 Diptera, 531 Hemiptera, 5.309 Hymenoptera) and 3.783 ants (*Lasius niger* (Linnaeus, 1758)).

Seasonal patterns in the herbivore community

Phloem feeders heavily dominated the free-living insect herbivore community in the tansy model system, whereas chewing herbivores were largely absent. We observed two generalist aphid species in our field study (*A. fabae* and *B. cardui*) and three tansy-specialist aphid species (*Ma. tanacetaria*, *Me. fuscoviride*, and *U. tanacetii*). Our observations revealed the species-specific seasonal pattern of aphid populations. Populations grew exponentially during the warmer months of June and July and collapsed in August each year (Fig. S2). However, the timing and height of peak abundance varied among the species. The two generalist species (*A. fabae* and *B. cardui*) exhibited a similar pattern; they were the first to colonize the tansy plants and reached peak abundance in early July 2021 (Fig. S2a). However, they were much less abundant in 2022, with a peak occurring at the end of May. Conversely, the specialist species were less abundant in 2021, reaching their peak in mid-June for *Ma. tanacetaria* and in mid-July for *Me. fuscoviride* and *U. tanacetii*. In 2022, these species were more abundant, displacing the generalist species, and reached peak abundance in mid to late June (Fig. S2b). Generalist aphid species were even less common in the field in 2023, while *U. tanacetii* dominated the plots with increased abundance in July (Fig. S2c).

Effects of chemotype richness and chemotype on herbivore occurrence and abundance

Our study first investigated the effect of CR on plot-level I) herbivore occurrence and II) herbivore abundance across samplings in each experimental year. All plots were occupied by at least one herbivore each year, but the herbivore species-specific occurrence in plots varied. For instance, *Me. fuscoviride* was present in all plots in 2021 (Table S2), for *U. tanacetii* this was the case in 2022 (Table S3) and 2023 (Table S4). The only significant effect of CR on

aphid occurrence was observed for *Me. fuscoviride* in 2023, which decreased when CR increased ($X^2_1=9.42$, $P = 0.002$).

We then examined how specific tansy chemotypes influenced herbivore occurrence at the plot level using individual models for each chemotype (S1). Certain chemotypes were associated with higher or lower likelihoods of colonization, i.e., occurrence, and higher or lower herbivore abundance, depending on the year and herbivore species (Table S11). *A. fabae* occurrence in 2022 was higher when 'Bthu-low' ($X^2_1=4.50$, $P = 0.034$) or 'Mixed-high' was in the plot ($X^2_1=6.68$, $P = 0.010$), but lower when 'Mixed-low' was in the plot ($X^2_1=4.89$, $P = 0.027$). In 2023, it was lower when 'Bthu-low' ($X^2_1=4.50$, $P = 0.034$) or 'Mixed-low' ($X^2_1=4.89$, $P = 0.027$) was present and higher when 'Mixed-high' was present ($X^2_1=6.68$, $P = 0.010$). Certain chemotypes within the plot affected *B. cardui* occurrence in 2022; 'Bthu-high' increased *B. cardui* occurrence ($X^2_1=4.16$, $P = 0.041$), while 'Bthu-low' decreased it ($X^2_1=6.42$, $P = 0.011$). *Ma. tanacetaria* occurrence was not affected by any chemotype. *Me. fuscoviride* occurrence in 2023 decreased when 'Athu-Bthu' ($X^2_1=5.23$, $P = 0.022$) or 'Mixed-high' ($X^2_1=9.42$, $P = 0.002$) was present in the plot. *U. tanacetii* occurrence in 2021 decreased when 'Mixed-high' was present ($X^2_1=7.47$, $P = 0.002$).

Concerning abundance, there was no effect of CR on cumulative aphid abundance across all species ($X^2_1 = 0.29$, $P = 0.588$) nor within each of the five species in the first year (*A. fabae*: $X^2_1 = 0.03$, $P = 0.870$; *B. cardui*: $X^2_1 = 1.51$, $P = 0.219$; *Ma. tanacetaria*: $X^2_1 = 1.13$, $P = 0.288$; *Me. fuscoviride*: $X^2_1 = 0.52$, $P = 0.471$; *U. tanacetii*: $X^2_1 = 0.38$, $P = 0.536$; Fig. 3a, Table S2). However, increasing CR negatively affected herbivore abundance in the following years (2022: $X^2_1=7.63$, $P = 0.006$; 2023: $X^2_1=4.39$, $P = 0.036$; Fig. 2a, Tables S1-3, S1-4), mainly driven by the negative effect of CR on *U. tanacetii* populations in 2022 ($X^2_1=5.93$, $P = 0.015$) and on *U. tanacetii* ($X^2_1=4.44$, $P = 0.035$) and *B. cardui* abundances in 2023 ($X^2_1=5.56$, $P = 0.018$; Fig. 3a). Notably, *Ma. tanacetaria* aphids were not observed in the field in 2023 at all. Plot-level chemotypic diversity had little effect on whether a plot was occupied by aphids during the year, mainly because all plots were occupied. However, there were negative effects on the abundance of several herbivore species.

If there was an effect of a specific chemotype present in a plot on herbivore abundance in the year 2021, it was always positive. However, all significant effects of particular chemotypes observed in 2022 or 2023 were negative (Table S11). Herbivore abundance was lower in 2022 in either 'Chrys-acet' or 'Mixed-high' presence and lower in 2023 when 'Athu-Bthu' or 'Mixed-low' was in the plot (Tables S1-3 and S1-4). When investigating species-specific effects, we found that *A. fabae* abundance in 2021 increased when 'Mixed-high' was present ($X^2_1=6.77$, $P = 0.009$), *B. cardui* when either 'Bthu-high' ($X^2_1=3.97$, $P = 0.046$) or 'Chrys-acet' were present ($X^2_1=6.16$, $P = 0.013$), and *U. tanacetii* when 'Bthu-high' was in the plot ($X^2_1=5.98$, $P =$

0.014). Lower *A. fabae* abundance was observed in 2022 when 'Bthu-low' was in the plot ($X^2_1=3.91$, $P = 0.048$) and in 2023 when 'Athu-Bthu' ($X^2_1=7.39$, $P = 0.006$) or 'Chrys-acet' ($X^2_1 = 19.14$, $P < 0.001$) were part of the community. *Me. fuscoviride* abundance in 2022 was negatively associated with 'Bthu-low' ($X^2_1=5.85$, $P = 0.016$), and *U. tanacetii* abundance in 2022 was negatively associated with either 'Chrys-acet' ($X^2_1 = 12.77$, $P < 0.001$) or 'Mixed-high' ($X^2_1=5.58$, $P = 0.018$). In 2023, *B. cardui* was lower when 'Athu-Bthu', 'Bthu-high', or 'Mixed-high' was present (Athu-Bthu: $X^2_1=4.42$, $P = 0.035$; Bthu-high: $X^2_1=40.71$, $P < 0.001$; Mixed-high: $X^2_1=79.26$, $P < 0.001$), and *U. tanacetii* abundance was negatively associated to the presence of 'Athu-Bthu' ($X^2_1=5.08$, $P = 0.024$) or 'Mixed-low' ($X^2_1=3.92$, $P = 0.048$). The effects of specific chemotypes on herbivore abundance varied across different years, with positive impacts observed in 2021 and predominantly negative impacts in 2022 and 2023.

Effects of chemotype richness and chemotype identity on flower visitors

We first analyzed the effect of CR on flower visitor occurrence. Higher CR increased the occurrence of Lepidoptera, i.e., adult butterflies ($X^2_1=3.87$, $P = 0.049$), but not other taxa. Hymenoptera and Lepidoptera flower visitor occurrences increased when 'Bthu-low' and 'Athu-Bthu' were in the plot, respectively (Tables S1-5, S1-11).

We evaluated the effect of CR on the visitation rate of flower visitors. We found a positive effect on all orders ($X^2_1 = 10.71$, $P = 0.001$, Fig. 2b), and specifically for Coleoptera ($X^2_1 = 16.78$, $P < 0.001$), Hymenoptera ($X^2_1 = 11.56$, $P < 0.001$), and Lepidoptera ($X^2_1=8.80$, $P = 0.003$, Fig. 3b). Concerning the presence of particular chemotypes within plots, 'Chrys-acet' ($X^2_1=5.98$, $P = 0.014$) and 'Mixed-high' ($X^2_1=6.95$, $P = 0.008$) positively affected the visitation rate across all the orders. While Diptera and Hemiptera abundances were not influenced by the presence/absence of any chemotypes, Coleoptera was influenced by the presence of 'Bthu-low' and 'Chrys-acet' (Table S5); Hymenoptera by 'Bthu-low' ($X^2_1=7.58$, $P = 0.006$), and Lepidoptera by 'Athu-Bthu' ($X^2_1=7.53$, $P = 0.006$, Table S12).

Analysis of the effect on the total number of individuals (not the visitation rate) is in Table S6. We found positive effects on total number of individuals of all orders ($X^2_1 = 10.71$, $P = 0.001$), Coleoptera ($X^2_1 = 16.78$, $P < 0.001$), Hymenoptera ($X^2_1 = 11.56$, $P < 0.001$), and Lepidoptera ($X^2_1=8.80$, $P = 0.003$), as found by the analysis of CR on visitation rate. However, when using the total number as the response variable, particular chemotypes had different effects on different groups. The abundance of all orders was affected by the presence of any of the chemotypes except for 'Chrys-acet', 'Athu-Bthu' affected the number of flower visitors belonging to Coleoptera and Lepidoptera, 'Bthu-low' to Coleoptera and Hemiptera, and 'Bthu-high' and 'Mixed-low' to Coleoptera (Table S6).

Effects of chemotype richness and chemotype on predators and ants

Predatory arthropods occurred in all plots in all years (Tables S1-7 to S1-9), and ants (*L. niger*) occurred in all plots in 2023 (Table S10). The only effect of CR on predator taxa/feeding guild occurrence was observed in predatory Hemiptera in 2022 ($X^2_1=6.54$, $P = 0.010$), which increased with CR. For chemotype identity effects, the occurrence of parasitized aphids in 2021 decreased when 'Mixed-low' was in the plot and in 2022 when 'Chrys-acet' was present (2021: $X^2_1=4.71$, $P = 0.030$; 2022: $X^2_1=5.55$, $P = 0.018$, Tables S1-7, S1-8).

Increasing CR did not increase predator abundance (overall -Fig. 2c- nor by taxa/feeding guild -Fig. 3c-). However, there was a positive effect of 'Chrys-acet' presence on the number of parasitized aphids in 2021 ($X^2_1=6.30$, $P = 0.012$, Table S7) and ant abundance in 2023 ($X^2_1=6.58$, $P = 0.010$, Table S8), but a negative effect on total predator abundance in 2023 ($X^2_1=4.16$, $P = 0.041$) and on abundance of predatory beetles in 2023 (Coleoptera: $X^2_1=3.85$, $P = 0.050$, Table S9). A positive effect on Dermaptera abundance in 2023 was found when 'Athu-Bthu' was present ($X^2_1=8.51$, $P = 0.004$).

Temporal effects

Analyses at independent sampling times, available in Supplementary Information (Tables S1-15 to S1-22), revealed that while relationships between chemotype richness and the occurrence of various ecological groups were generally weak, the temporal patterns in abundance were clear. Effect on abundance showed a shift in slope from positive to negative for herbivores over time (particularly in specialist aphids); while it remained mostly positive relationships for flower visitors, ants, and predators.

Discussion

Intraspecific chemodiversity is a key driver of interaction variation within plant species. Our understanding mainly comes from observational and correlative studies, with controlled studies in natural or semi-natural settings limited due to the challenges of manipulating plant chemistry. In this study, we manipulated plant chemical diversity at the plot level by selecting plant chemotypes with varying chemical blends and manipulating the number of chemotypes within plots (i.e., plot-level chemotype richness -CR-). Using tansy (*Tanacetum vulgare* L.), we explored the effect of chemodiversity on natural arthropod communities. Our study provides evidence that intraspecific chemodiversity affects processes at the plot level. We showed that CR had many negative effects on herbivores but positive effects on flower visitors, with minimal effects on predators or ants. Additionally, there were strong effects of chemotype identity, i.e., the composition of the plots, on plant-arthropod interactions at the plot level, an effect also often found in biodiversity experiments (e.g., Scherber et al., 2010). Our study thus

highlights the role of individual chemotypes in shaping interactions, contributing to our understanding of the ecological significance of chemical diversity in plants.

Effects of chemotype richness on the occurrence of arthropod groups

Contrary to our expectations, we did not find strong evidence that CR affects plot-level arthropod occurrences (**H1**). While some significant relationships between CR and specific taxa occurrence were observed, most were weak. One reason may be that many arthropod taxa occurred in all plots or were absent during certain samplings, limiting the variation needed to test hypotheses. Another reason is that specialized herbivore populations build up over the season before they decline, and in years when aphids are abundant, total population sizes are very high, and almost all plants are infested. We observed significant positive relationships for polyphagous aphid species such as *A. fabae* and *B. cardui* in the individual samplings during the first sampling year. These species only feed on tansy for several weeks. Significant negative relationships were observed for monophagous species, particularly in *Me. fuscoviride* in 2023, suggesting that polyphagous and monophagous species may respond differently to chemical cues in their host-seeking behavior (Benedek et al., 2015; Gripenberg et al., 2010; Ziaja & Müller, 2023). It also emphasizes the strong shift from polyphagous to monophagous herbivores in the system over the season. It could be that during the establishment phase, polyphagous herbivores were more abundant in the surrounding grassland and that monophagous species required time to colonize from the nearest tansy hosts. All specialized tansy aphids overwinter on or next to the host plant; hence, once the field plots are colonized, local overwintering and early colonization in the season by the specialized aphids are possible.

For flower-visiting taxa, we consistently observed positive relationships between CR and occurrence, indicating the role of specialized chemistry in these mutualists (Farré-Armengol et al., 2020; Sasidharan et al., 2023; Silva et al., 2018). In contrast, the relationship between CR and other groups' occurrence was weak. These findings suggest that plant chemistry differentially affects arthropod groups based on their interaction with the plant. While plant chemistry significantly influences directly interacting organisms like flower visitors, it does not show a similar significant impact on indirectly interacting organisms such as predators and ants (Ali et al., 2023).

Effects of chemotype richness on the abundance of arthropod taxa

We found strong support for CR affecting the abundance of herbivores and flower-visiting arthropods but not predatory arthropods and ants, partially in line with (**H2**). Higher CR plots supported fewer herbivores in 2022 and 2023, although this relationship varied between aphid species. In general, the effects of CR on herbivore abundance were driven by its effects on the dominant monophagous aphid species, *U. tanacetii*, for both years and *B. cardui* for 2023.

An interesting observation is that the slope between CR and herbivore abundance, despite the relationships not always being significant, started consistently positive in 2021 but turned increasingly negative over the first season and across the years. It might be that the shift towards monophagous aphids over time emphasized the negative effect of CR on herbivore abundance. Since *U. tanacetii* had not yet successfully colonized the experiment in the first year, and polyphagous species were more common, this may explain the lack of CR effects in the first year. Monophagous herbivores may be more strongly affected by chemical defenses in high CR (Ziaja & Müller, 2023) in concordance with the neighborhood-mediated associational resistance hypothesis (Randlkofer et al., 2010).

Higher CR plots had more flower visitors, with significant positive effects observed for Coleoptera, Hymenoptera, and Lepidoptera but not for Diptera and Hemiptera, suggesting that CR may differentially affect flower visitors (Sasidharan et al., 2023). Chemotypes exhibit variations in their phenology, influenced by the chemical diversity of their growth environment (Ojeda-Prieto et al., 2024). These variations can extend the flowering period within a plot containing a greater number of different chemotypes. Consequently, CR will affect the occurrence and abundance of flower visitors.

Our study revealed that the chemodiversity of the plot did not affect predator or ant abundance. The precise reasons underlying these findings remain unclear. However, it is plausible that additional factors, such as prey availability, which may be influenced by herbivore-host chemical composition (Benedek et al., 2019), or alternative foraging strategies (Wäschke et al., 2013), contribute to shaping these patterns. Further research is warranted to elucidate the interplay between these factors and their collective impact on predator and ant abundance in response to chemodiversity.

Effects of chemotype presence on arthropod communities

We found chemotype-specific impacts on plot-level occurrence and abundance across arthropod taxa, in line with our hypothesis **(H3)**. In herbivores, patterns were rather incongruent and differed strongly with the year of sampling. Herbivore occurrence data showed few chemotype-specific effects in 2021, the first season after establishment. Different chemotypes positively and negatively affected the species observed in the following two years. This suggests that most aphids seem to respond to plant-chemical cues as expected (Clancy et al., 2018; Mehrparvar et al., 2014). Herbivore abundance data show a clear pattern, where in 2021, chemotype effects were typically positive, which may suggest that colonizers were using specific terpenoid cues initially. Interestingly, in the subsequent years, chemotype-specific effects, when significant, were always negative. A possible scenario suggests that chemotypes may serve as a mosaic that partly regulates aphid densities, which aligns with

the idea that specialized chemistry evolved with a defensive function (Fox, 1981; Wolf et al., 2011). This idea is further reinforced by the fact that the overall effect of chemotypes on herbivore abundance tends to be neutral to negative.

For flower-visiting arthropods, chemotype-specific patterns were most common in abundance data. Most flower visitors are highly mobile and do not linger in the same plot for long (Burdon et al., 2020; Knauer et al., 2021), suggesting that specific chemotypes lead to higher abundance in certain plots. Significant chemotypes positively affected flower visitors, with low-concentration B-thujone chemotypes having the most robust and consistent effects on different taxa, aligning partially with previous results (Sasidharan et al., 2023). Mixed chemotypes had few effects, and high-concentration B-thujone chemotype did not affect flower visitors. Although B-thujone can signal nectar or pollen rewards (Metcalf & Kogan, 1987), its effects depend on the overall blend of volatile compounds and the preferences of local flower-visiting species. We found stronger effects of chemotype identity on the total number of individuals than on the visitation rate (Tables S1-5 and S1-6). CR and individual chemotypes influence reproductive traits in our system (Ojeda-Prieto et al., 2024). These effects might be confounded by the influence of CR and chemotype on reproductive traits rather than reflecting true effects on flower visitors.

Fewer and weaker chemotype-specific effects were found for predators and ants, suggesting that these groups could be influenced by different mechanisms, including modified behaviors, such as predation activity or aphid-tending in ants (Hauri et al., 2022; Mehrparvar et al., 2018; Senft et al., 2017).

Future perspectives for chemodiversity research

Exploring several key areas of chemodiversity will deepen our understanding. Scaling up experiments to entire landscapes will elucidate how chemodiversity influences ecosystems and biodiversity across diverse habitats. Assessing its effect on plant-insect interactions should include ecosystem functions like predation rates and herbivore performance. Studying how chemodiversity influences herbivore behavior, including responses from generalist and specialist species, will offer insights with potential applications in pest management. Further exploring the interplay between plant chemistry and arthropod communities will advance our understanding of ecosystem functioning and guide conservation and management practices.

Conclusion

Previous studies have focused on intraspecific variability in ecosystem functioning. Our research demonstrates that plot-level chemotypic diversity impacts arthropod colonization patterns. Our results emphasize the role of intraspecific chemodiversity in shaping arthropod communities on plants. Our work shows that plots with higher intraspecific chemodiversity

accumulate fewer herbivores and attract more flower visitors. The presence of specific chemotypes within a plot exerted highly variable impacts on abundance but also on occurrence patterns of various arthropod groups, suggesting that specific chemotypes, and potentially specific components they produce, may be a driver of the occurrence of arthropod taxa.

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Main Figures

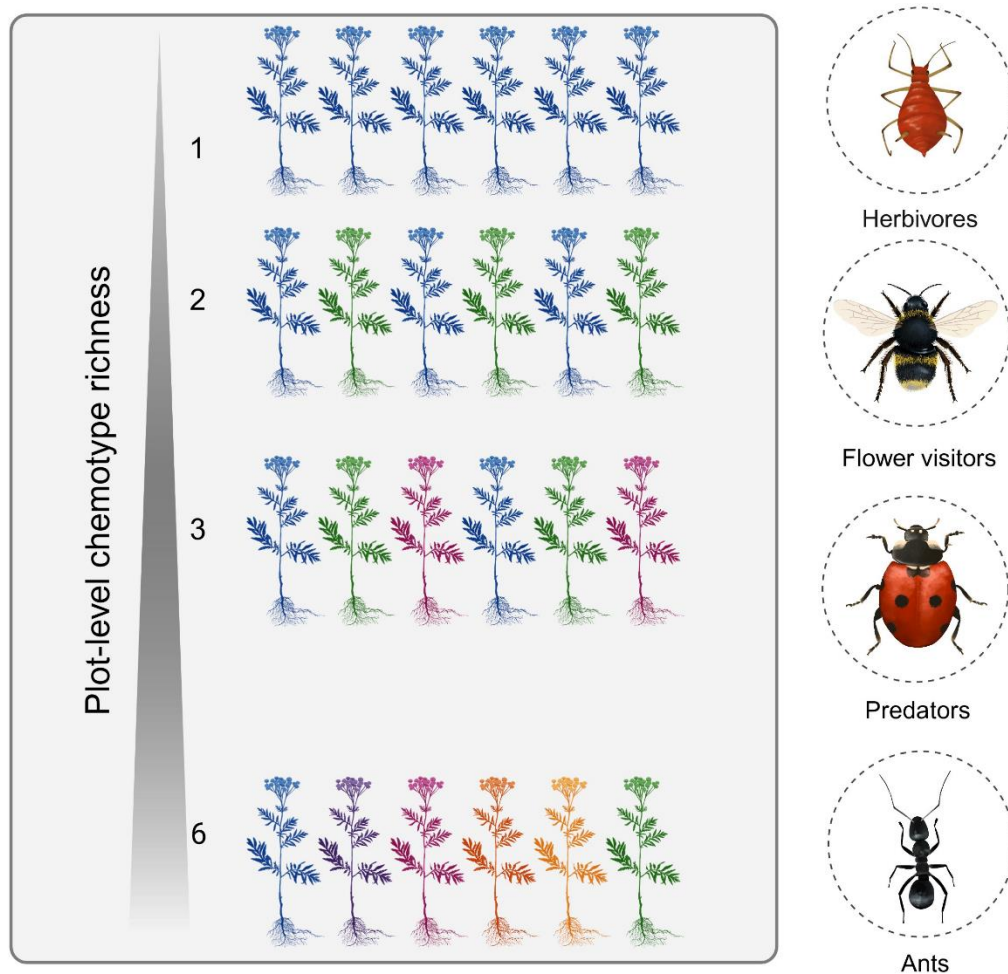


Figure 1. Influence of *Tanacetum vulgare* intraspecific chemodiversity on arthropod communities. The left panel illustrates the gradient of plot-level chemotype richness, with each color symbolizing a specific chemotype of *T. vulgare* in a six-plant community. From levels 1 to 6, the chemodiversity increases, indicating an increase in different chemotypes. The right panel presents the evaluated arthropod communities: herbivores, flower visitors, predators, and ants, which are expected to be influenced by intraspecific chemodiversity. Created with Biorender®.

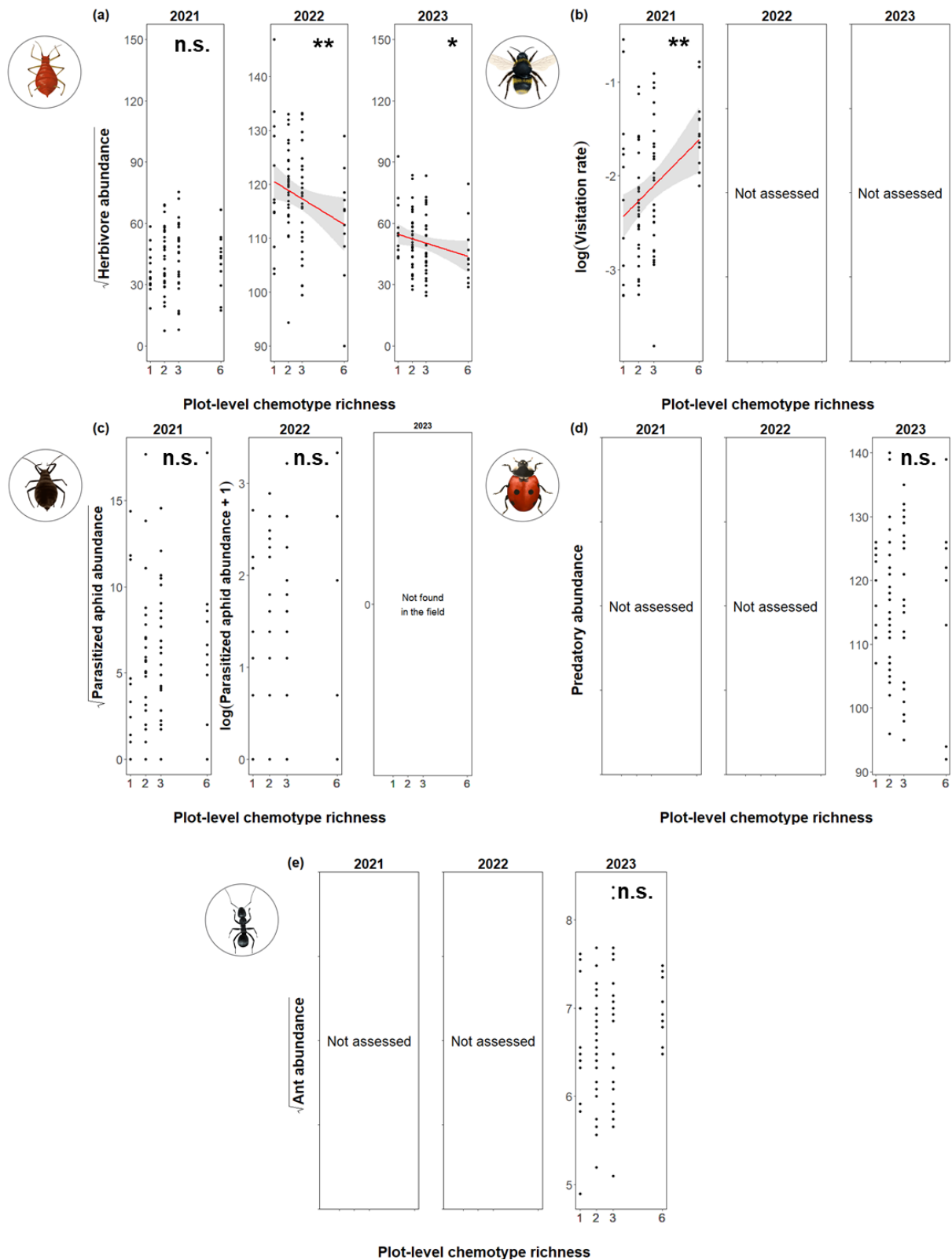


Figure 2. Effect of plot-level chemotype richness on the abundance of different arthropod communities over three years (2021–2023). (a) Effect on herbivore abundance, represented by five aphid species each year. (b) Effect on flower visitor abundance (i.e., visitation rate), calculated as the cumulative count of flower-visiting insects divided by the sum

of flower heads counted during each assessment date. **(c)** Effect on parasitized aphid abundance (aphid mummies). **(d)** Effect on predator abundance. **(e)** Effect on ant abundance. Significance is indicated as follows: n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported in Tables S1 – S8.

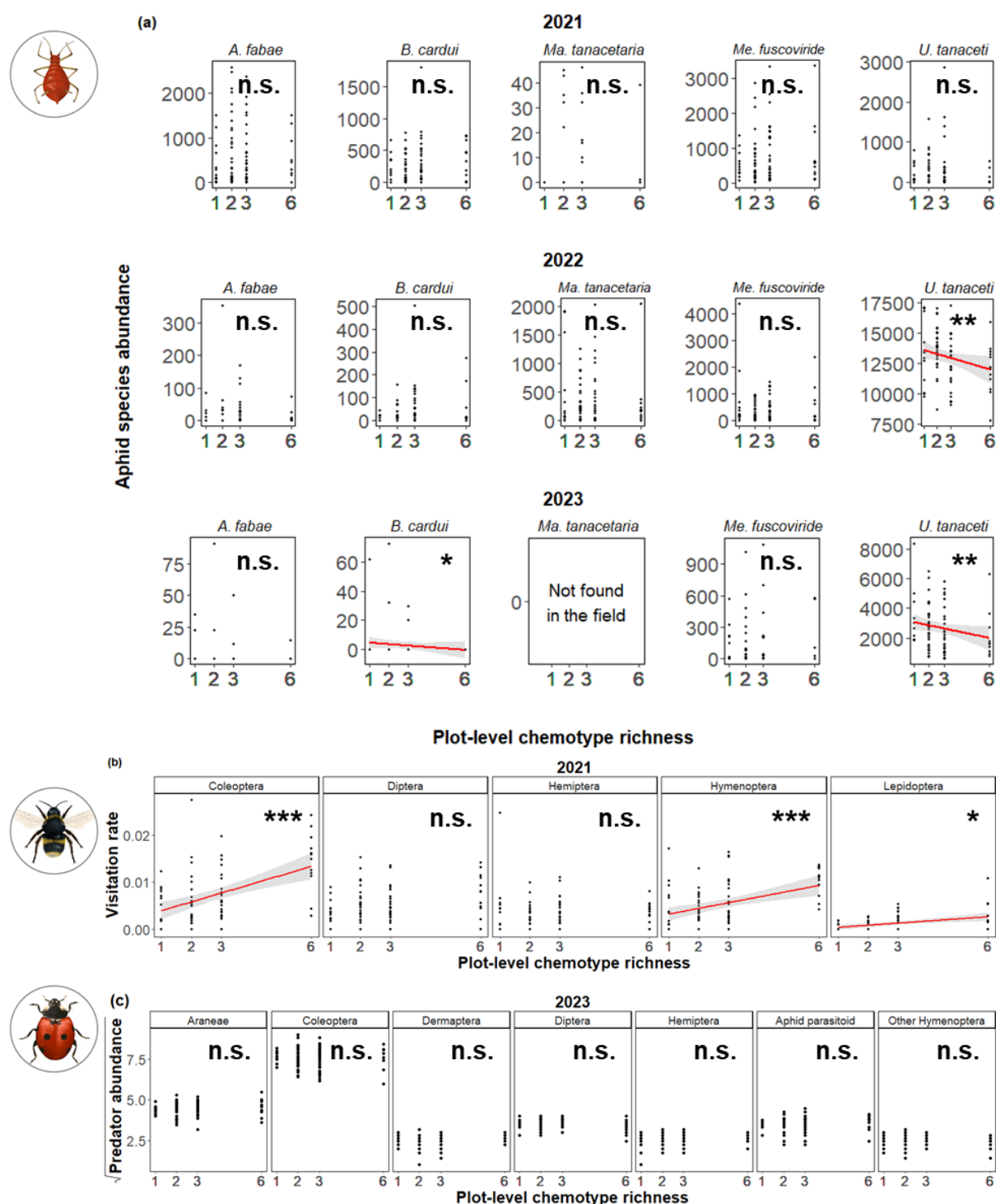


Figure 3. Effect of plot-level chemotype richness on specific group abundances within each guild of arthropod communities over three years (2021–2023). (a) Effect on herbivore abundance of *Aphis fabae*, *Brachycaudus cardui*, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride*, and *Uroleucon tanacetii* each year. (b) Effect on flower visitor abundance of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera. (c) Effect on predator abundance of Araneae, Coleoptera, Dermaptera, Diptera, Hemiptera, Aphid parasitoids, and Other Hymenoptera for 2023. Significance is indicated as follows: n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported in Tables S1 – S7.

Increasing intraspecific plant chemical diversity at plot and plant level affects herbivorous, predatory, and pollinating arthropod communities

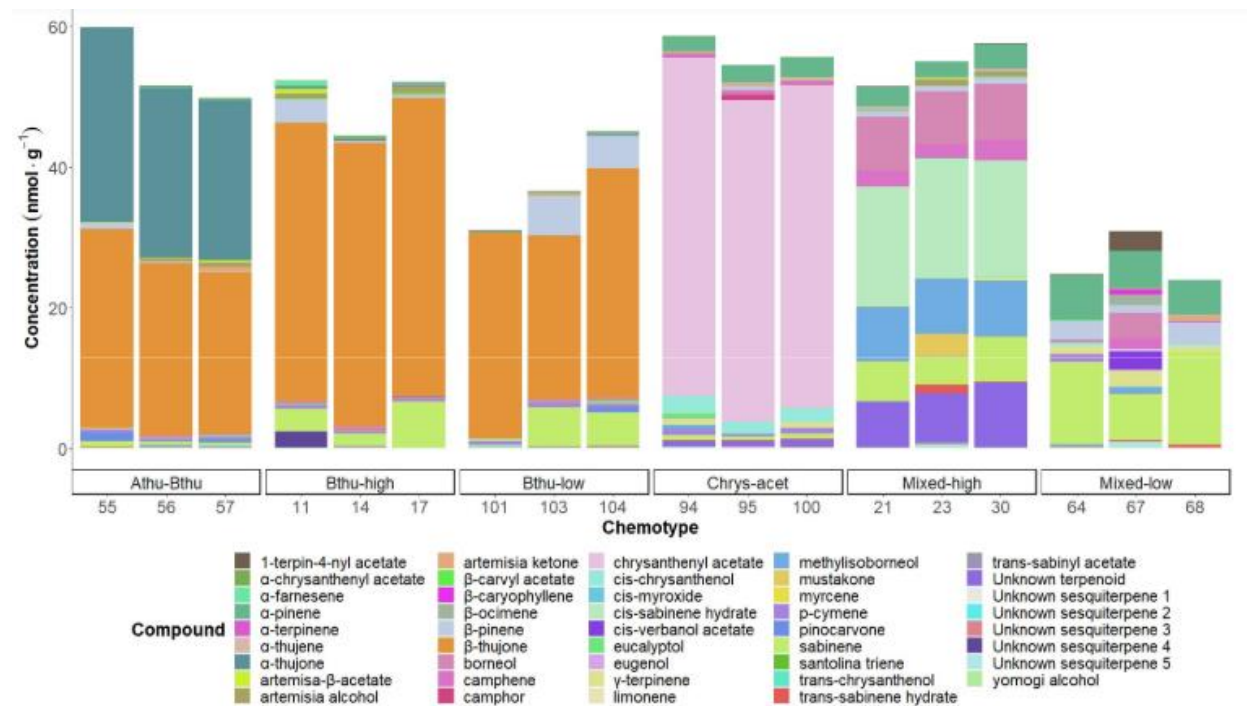
Supplementary Information (SI)

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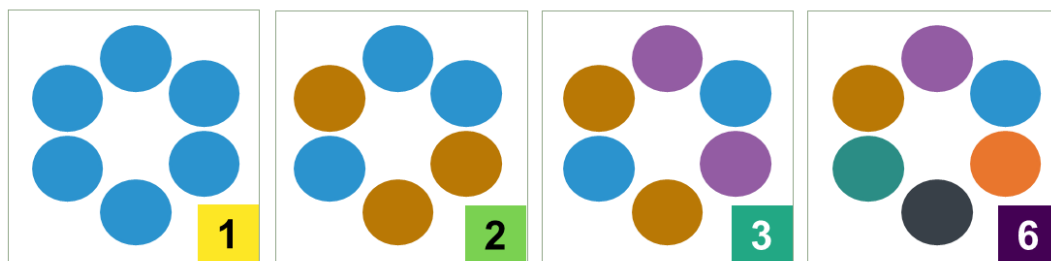
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1. Supplementary methods

1.1 Field design



a) Plot-level chemotype richness (i.e., CR)



b) Field Experimental Design

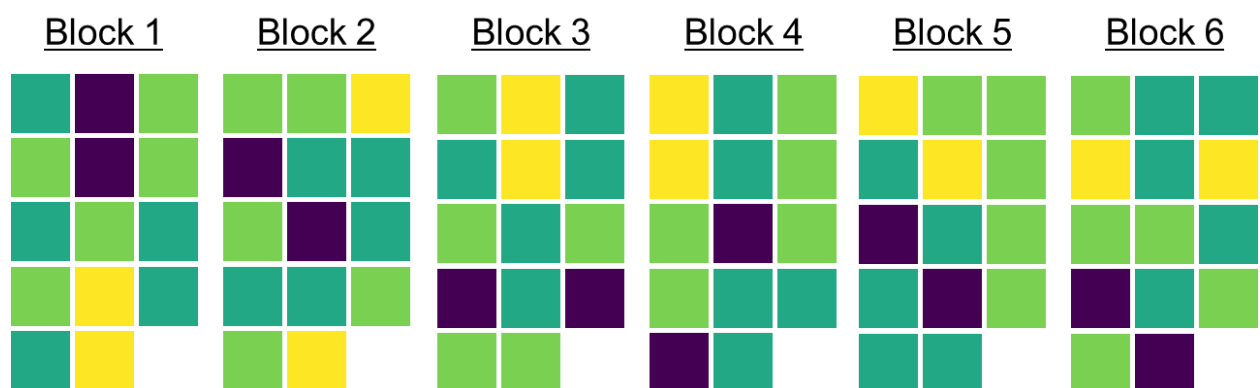


Figure S1-2. (a) Plot-level chemotype richness, which refers to the number of different chemotypes in a single plot, ranged from 1 to 6. **(b)** Block design. Section (a) displays the plot-level chemotype richness color scheme: yellow for 1, light green for 2, dark green for 3, and purple for 6. There were 84 plots in total, distributed equally across six randomized blocks. Each block contained 14 plots: two plots with chemotype richness level 1, five plots with level 2, five plots with level 3, and two plots with level 6.

1.2 Insect sampling

1.2.1 Sampling dates

Table S1-1. Sampling dates in 2021, 2022, and 2023, specifying calendar week, specific date, and sampled arthropod group (herbivore, flower visitors, predators, and ants). Total counts across the three years are 25 for herbivores, 4 for flower visitors, 21 for predators, and 20 for ants.

Year	Calendar week	Date	Sampled arthropod group
2021	24	Jun 07	Herbivores
	24	Jun 11	Herbivores
	25	Jun 14	Herbivores, Predators, Ants
	25	Jun 18	Herbivores, Predators, Ants
	26	Jun 21	Herbivores, Predators, Ants
	26	Jun 25	Herbivores, Predators, Ants
	27	Jun 28	Herbivores, Predators, Ants
	27	Jul 02	Herbivores, Predators, Ants
	27	Jul 03	Flower visitors
	28	Jul 08	Herbivores, Predators, Ants
	28	Jul 09	Flower visitors
	29	Jul 15	Herbivores, Predators, Ants
	29	Jul 16	Flower visitors
	30	Jul 22	Herbivores, Predators, Ants
	31	Jul 29	Herbivores, Predators, Ants
	32	Aug 04	Flower visitors
	33	Aug 10	Herbivores, Predators
2022	20	May 14	Herbivores, Predators, Ants
	22	May 25	Herbivores, Predators, Ants
	23	May 31	Herbivores, Predators, Ants
	24	Jun 07	Herbivores, Predators, Ants
	25	Jun 15	Herbivores, Predators, Ants
	26	Jun 21	Herbivores, Predators, Ants
	27	Jun 27	Herbivores, Predators, Ants
	29	Jul 13	Herbivores
	32	Aug 03	Herbivores
2023	26	Jun 20	Herbivores
	26	Jun 21	Predators, Ants
	31	Jul 25	Herbivores
	31	Jul 26	Predators, Ants
	36	Aug 29	Herbivores
	36	Aug 30	Predators, Ants

1.2.2 Aphid species identification key

The following aphid species identification key is an English version based on Thieme & Müller (2011). All aphid species listed here are associated with *Tanacetum vulgare* L. plants. The identification key was complemented with figures, a summary of the main characteristics of each genus, and a glossary of terms.

Common species on tansy: *Aphis fabae*, *A. vanderghooti*, *Brachycaudus cardui*, *B. helichrysi*, *Coloradoa tanacetina*, ***Uroleucon tanaceti***, ***Metopeurum fuscoviride***, ***Macrosiphonella millefolii***, ***M. tanacetaria***, *Uroleucon tanaceti*.

1. Cauda not longer than wide, semicircular, triangular or pentagonal..... ***Brachycaudus* (2)**

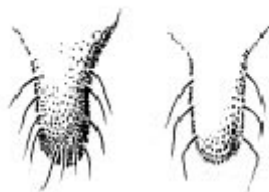
cauda stout, approximately as long as wide



(Miller & Stoetzel, 1997)

1*. Cauda longer than broad, tongue- or finger-shaped or acutely triangular.....
***Aphidinae*, *Macrosiphoninae* (3)**

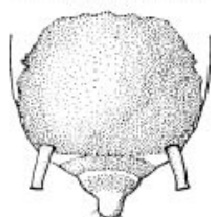
cauda elongate, longer than wide



(Miller & Stoetzel, 1997)

2. Cornicles are shorter than the distance between the bases of the antennae (the terminal process of the last antennal segment is three or more times the basal part). Tip of proboscis exceeding the coxa of the third pair. Immatures are light green, sometimes reddish or orange. Body broadly rounded. 1.6-2.5 mm. Dorsal abdomen variably pigmented (dark sclerotic shield)..... ***Brachycaudus cardui* (L.)**

abdomen with dorsal patch



cornicles $2\frac{1}{2}$ - 4 times as long as wide

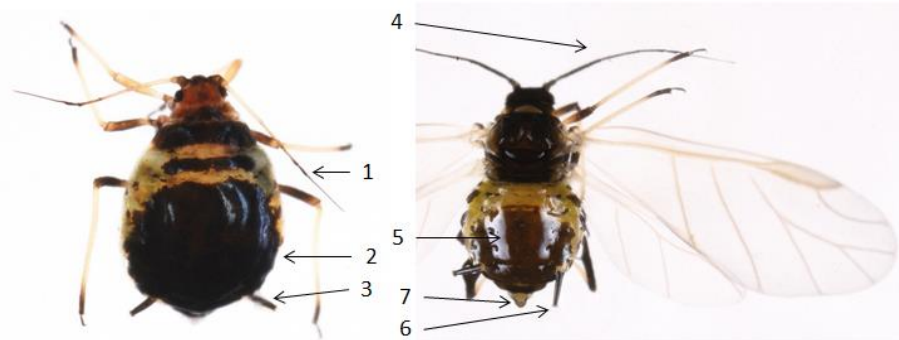


***Brachycaudus cardui* (L.)**
thistle aphid

(Miller & Stoetzel, 1997)



(InfluentialPoints, 2021)



(Hullé et al., 2020)

2*. Cornicles are as long as or slightly longer than the distance between the bases of the antennae. Cornicles of unwinged colorless or only weakly tanned. The upper side of unwinged aphids (except fundatrix) is unpigmented. Body coloration is generally light green, sometimes yellowish, pink to white (without dorsal patch). Winged: Yellowish green with a large brown dorsal patch. Antennae are shorter than the body and have dusky tips. Siphunculi are pale, tapered, and short (0.8-2.0 times the length of the cauda) 1.2-2.2 mm ... ***Brachycaudus helichrysi* (Kaltenbach)**

abdomen without dorsal patch

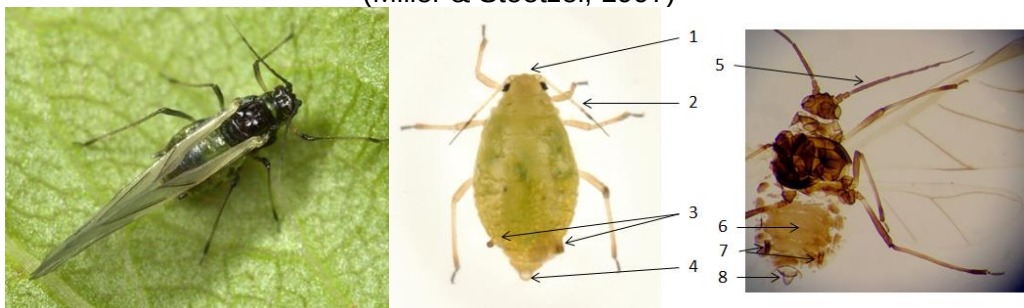


cornicles $1\frac{1}{2}$ - 2 times as long as wide



***Brachycaudus helichrysi* (Kaltenbach)**

(Miller & Stoetzel, 1997)



(Hullé et al., 2020; InfluentialPoints, 2021)

Brachycaudus

- Small to medium-sized oval aphids.
- Low lateral prominences.

- Antennae are shorter than the body.
- Siphunculi short to moderate in length.
- Cauda is short and often semicircular.
- May be attended by ants.

Aphidinae, Macrosiphoninae

3. Antennae usually longer than $\frac{3}{4}$ of body length, often longer than the body, on clearly visible antennal tubercles. If antennal tubercles are unclear, then reddish or green with black antennae. In dense colonies with ant visitation on *Tanacetum*.....**(4)**

3*. Antennae $\frac{1}{2}$ or $\frac{2}{3}$ of body length, i.e., shorter than $\frac{3}{4}$ of body length. Mostly feeding along rims of leaves. Not attended by ants. Very small (adult 1.0-1.6 mm), yellowish or greenish globe-shaped. Legs, cornicles, and Cauda are almost colorless. The antennae are hard or, at most, slightly dark towards the tip only. Length of antennae. Cauda triangularly tongue-shaped, half as long as cornicles. Frontal sinus straight...***Colorado tanacetina* WALKER**



(InfluentialPoints, 2021)

Coloradoa

- Small green or reddish globe-shaped.
- Convex frons with no antennal tubercles.
- Antennae are always shorter than the body, and the terminal process is always longer than the base of the last antennal segment.
- Short dorsal body hairs and expanded at the tip.
- Apical rostral segment with concave sides.

4. Bright red to brownish red, feeding on the underside of bottom leaves, sometimes on shoots. Leaves often turn yellow on the upper side. Cornicles are long, thin, brown, and dark only at the tip and base. Antennae are a little shorter to (usually) longer than the body. Apterous body 2.5-3.4mm, pear-shaped. Legs yellowish, and black tibia's apices never with wax powder. Cauda is yellowish white (pale), relatively short, as long as the distance between bases of antennae. Antennal bases are divergent, not with frontal cusps directed inward or forward, i.e., inner sides not parallel to the longitudinal axis. Size: 2.5 to 3.4mm..... ***Dactynotus tanaceti* (L.) (*Uroleucon tanaceti*)**



(InfluentialPoints, 2021)

Uroleucon

- Well-developed antennal tubercles with diverging sides.
- Antennae long as the body.
- Dorsal abdominal hairs are not capitated and are placed on sclerites, typically dark.

4*. Colored differently. If red or brown, then not very shiny or with wax powder..... **(5)**

5. The body is completely covered with wax powder. Cornicles are primarily black, sometimes lighter, and then darker distally. Only at Asteraceae... ***Macrosiphoniella* DEL GUERCIO (6)**

5*. Roundish body, shiny or dull, at most the larvae weakly powdered with wax. Coloration brownish red. The abdomen is often green, with a large dark spot in the center. Mostly ant-tended. In inflorescences or upper stem parts with ant visitation Size: 2.2-2.8mm. Antennae as long as body length. Cornicles 1/5-1/6 of body length..... ***Metopeurum fuscoviride* Stroyan**



(InfluentialPoints, 2021)

Metopeurum

- Medium-sized aphids.
- Adult viviparous may be winged or wingless.
- Antennal tubercles are very weakly developed.
- Siphunculi dark over at least half of the length.
- Cauda tapering, triangular.

6. (rare on tansy) Tibiae and femora are black except for the basal part of the front femur, which is brown. Virgins green to yellowish green, sometimes reddish yellow in late summer (lighter green than *M. tanacetaria*). Dorsum has numerous hair-bearing black platelets (sclerites). Brown head. Medium to large (2.5-3.6mm), oval to elongate oval. White-grey waxy powder on the back, except for a spinal stripe on the abdomen and presiphuncular spots. Eyes mostly red. Antennae 1.0-1.2 times as long as the body with the terminal process is 3.7-4.3 times the length of the basal part. Si, cauda, F u B black except for the lighter thigh bases. Si 1/8-1/7 of body length, 3/4-4/5 of caudal length. Mostly on stems, without ant visitation, some drop or play dead when disturbed. Pinkish-red male (middle picture)..... ***Macrosiphionella millefolii* (De Geer)**

Mostly on *Achillea millefolium*



(InfluentialPoints, 2021)

6*. (common) Dorsum without black sclerites. Upper stem parts. Green or pinkish-brown, transversely powdered. The antennae, legs, siphunculi, and cauda are black. 3.2-3.9mm. Cornicles 1/7 of body length, 7/8 of caudal length. Antennae 1.0-1.3 times the body length, with the terminal process 2.9-3.5 times the length of the base. Siphunculi 0.1-0.2 times the body length and 0.6-0.9 times the length of the cauda. Colonies occur on the upper parts of the stem and between the flowers. Two color forms of *Macrosiphionella tanacetaria* are green (more common) and pink. Not ant-tended (killed by ants)..... ***Macrosiphionella tanacetaria* (Kaltenbach)**



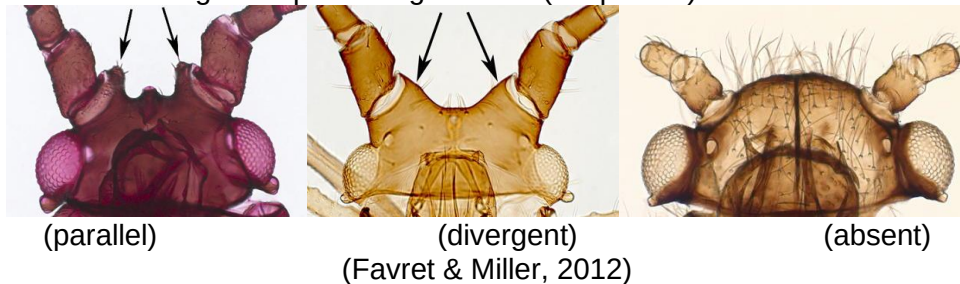
(InfluentialPoints, 2021)

Macrosiphionella

- Green to dark brown.
- Adult viviparous may be winged or wingless.
- Dorsum is not sclerotic; if pigmented, it is in small, localized hair-bearing sclerites.
- Siphunculi long, cylindrical, or with a slight taper from base to apex.
- No host alternation and no ant-attendance.

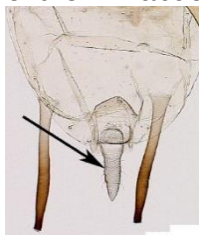
GLOSSARY

Antennal tubercles: Base of antenna. Two lumps on the head, each of which bears one antenna. Sometimes large and protruding inwards (left picture).



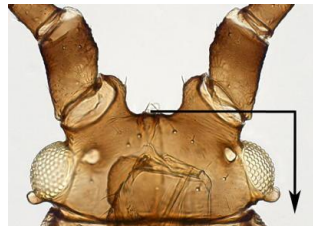
Antesiphuncular: Immediately anterior to the base of each siphunculus.

Cauda: A taillike process or extension of the VIII abdominal segment.



(Favret & Miller, 2012)

Frons: The middle part of the front of the head.



(Favret & Miller, 2012)

Scleroites: When the dorsal abdominal sclerotization consists of small sclerites at the base of the dorsal setae.



(Favret & Miller, 2012)

Siphunculi/Cornicle: Structures on the dorsum of the VI abdominal segment from which alarm pheromones are expelled.



(Favret & Miller, 2012)

Rostrum: Beak-like labium usually of 4 segments, supporting the stylets.

Terminal process: The terminal antennal segment, usually the VI but sometimes the V segment, is divided into the base and the processus terminalis (PT).



(Favret & Miller, 2012)

1.3 Statistical analysis

1.3.1 Effects of chemotype richness and chemotype presence on plot-level arthropod group occurrence

Each arthropod group occurrence indicates whether an herbivore, flower visitor, predatory arthropod, or ant was found in a plot at the group level and lower taxonomic level when indicated. The occurrence was assessed at plot level for every year. Binomial GLMMs were fitted with CR as a fixed effect and block as a random effect to test the effect of CR. Separate analyses were conducted for each chemotype to investigate the effect of specific chemotypes on occurrence. In these models, chemotype presence (indicating whether a particular chemotype is present or absent in a plot) was used as a fixed effect, with block as a random effect in binomial GLMMs.

If chemotype presence had a significant effect on the response variable, we calculated the slope (e.g., correlation coefficient) of the linear relation between occurrence and CR.

1.3.1.1 Statistical models

General models: Effect of chemotype richness on the occurrence

GLMM: `glmer(Occurrence of arthropod group or lower taxonomic level (when indicated) ~ CR + (1|Block), family = binomial)`

General models: Effect of chemotype presence on the occurrence

GLMM: `glmer(Occurrence of arthropod group or lower taxonomic level (when indicated) ~ CP + (1|Block), family = binomial)`

1.3.2 Effects of chemotype richness and chemotype presence on plot-level arthropod group abundance

Herbivore abundance refers to the total number of aphids across all species accumulated in each plot over each year and to the cumulative plot-level number of individuals of all five aphid species separately across each year. Given the skewed nature of our data and the prevalence of zero counts in the herbivore abundance, we adopted Zero-Inflated Negative Binomial (ZINB) models when data transformations failed to meet LMM assumptions. We applied both models strategically based on the distribution of each subset of data. The goodness of fit was assessed through DHARMA plots alongside tests for overdispersion and zero inflation.

To assess the effects of CR on flower visitor abundance, we used the visitation rate (flower visitor abundance divided by the sum of the plot-level number of flower heads on the days of the respective surveys) as the response variable. This approach is supported as we found a significant influence of plant chemotype and CR on flower number and phenology (Ojeda-Prieto et al., 2024).

Predator refers to the total number of predators across all taxa/feeding guilds accumulated in each plot over the year and to the cumulative plot-level number of individuals of all predator categories separately across each year. Ant abundance refers to the total number of ants in each plot over the year.

To check the effect of CR on arthropod group abundance, LMMs were fitted with CR as a fixed effect and Block ID as a random effect on the total abundance of each arthropod group and lower taxonomic level.

To meet the model assumptions, we transformed the data. For herbivores, we squared-root the total abundance in 2021, 2022, and 2023, *A. fabae* abundance in 2021, *U. tanacetii*

abundances in 2022 and 2023, and log-transformed *Me. fuscoviride* abundance in 2021. ZINB models were used for *A. fabae* abundances in 2022 and 2023, *B. cardui* abundances in the three years, *Ma. tanacetaria* abundances for 2021 and 2022, *Me. fuscoviride* abundance in 2022 and 2023, and *U. tanacetii* abundance in 2021. In the case of flower visitors, we used log-transformed flower visitor abundance across all orders and squared-transformed flower visitor abundance for each observed insect order without normalizing the number of flower heads. For predators, we squared-transformed the total number (plus one) of parasitized aphids in 2021, log-transformed the total number (plus one) of parasitized aphids in 2022, and used the untransformed predator abundances in 2023 (total predator count and by category).

We examined the effect of the presence/absence of a chemotype on each arthropod group abundance. In the case of herbivores, the same model structure, whether LMM or ZINB, was applied per chemotype, with chemotype presence (indicating whether a specific chemotype is present in the plot) and Block as fixed and random effects, respectively. We used LMMs for flower visitors, predators, and ants.

If chemotype presence had a significant effect on the abundance variable, we calculated the log-response ratio by taking the logarithm of the ratio of mean values for the “Presence” and “Absence” for each chemotype, allowing us to obtain the relative effect size for each chemotype, rather than absolute differences.

1.3.2.1 Statistical models

General models:

Effect of chemotype richness on the abundance

LMM: lmer(Abundance of arthropod group or lower taxonomic level (when indicated) ~ CR + (1|Block))

ZINB: glmmTMB(Abundance of arthropod group or lower taxonomic level (when indicated) ~ CR + (1|Block), zi = ~1, family = "nbinom2")

Effect of chemotype presence on the abundance

LMM: lmer(Abundance of arthropod group or lower taxonomic level (when indicated) ~ CP + (1|Block))

ZINB: glmmTMB(Abundance of arthropod group or lower taxonomic level (when indicated) ~ CP + (1|Block), zi = ~1, family = "nbinom2")

1.3.3 Temporal effects

Although a discussion of detailed temporal effects by sampling date is beyond the scope of this manuscript, we acknowledge that such temporal differences may occur. To visualize these temporal effects, we analyze CR's effect on the occurrence and abundance for each species, group, and order of herbivores, flower visitors, predators, and ants across the different sampling dates. Binomial GLMMs were applied to each sampling date occurrence with CR as the fixed factor and block as the random factor. Only when occurrence was higher than 60% (cut-off, otherwise indicated in grey in the table of Supplementary Information – S2) were abundance analyses made using LMMs. The choice of a 60% cut-off for occurrence when conducting abundance analyses is a strategic approach to ensure that LMM-based abundance analyses are conducted on a subset of data that aligns well with the model's assumptions. The cut-off is based on statistical considerations related to the distribution of data and the suitability of different modeling approaches.

We performed separate analyses for each sampling date, with abundance as the response variable, CR as the explanatory variable, and block as the random factor. Untransformed data were used for occurrence and abundance, except when indicated otherwise. For abundance,

we squared root-transformed herbivore abundance for *total herbivore in 2021*, *A. fabae in 2021*, and *U. tanacetii in 2022*, and predator abundance in 2023 for *Araneae*, *Coleoptera*, *Diptera*, and *Parasitoid*. Log-transformation with an added constant of 1 was applied to the herbivore abundance for *total herbivores in 2022 and 2023*, *Ma. tanacetaria in 2022*, *U. tanacetii in 2023*, and flower visitor abundance in 2021 for the *visitation rate across all orders*. The slope corresponds to the correlation coefficient of the linear relationship between group occurrence or group abundance and CR.

2. Supplementary results

2.1 Population patterns in the herbivore community

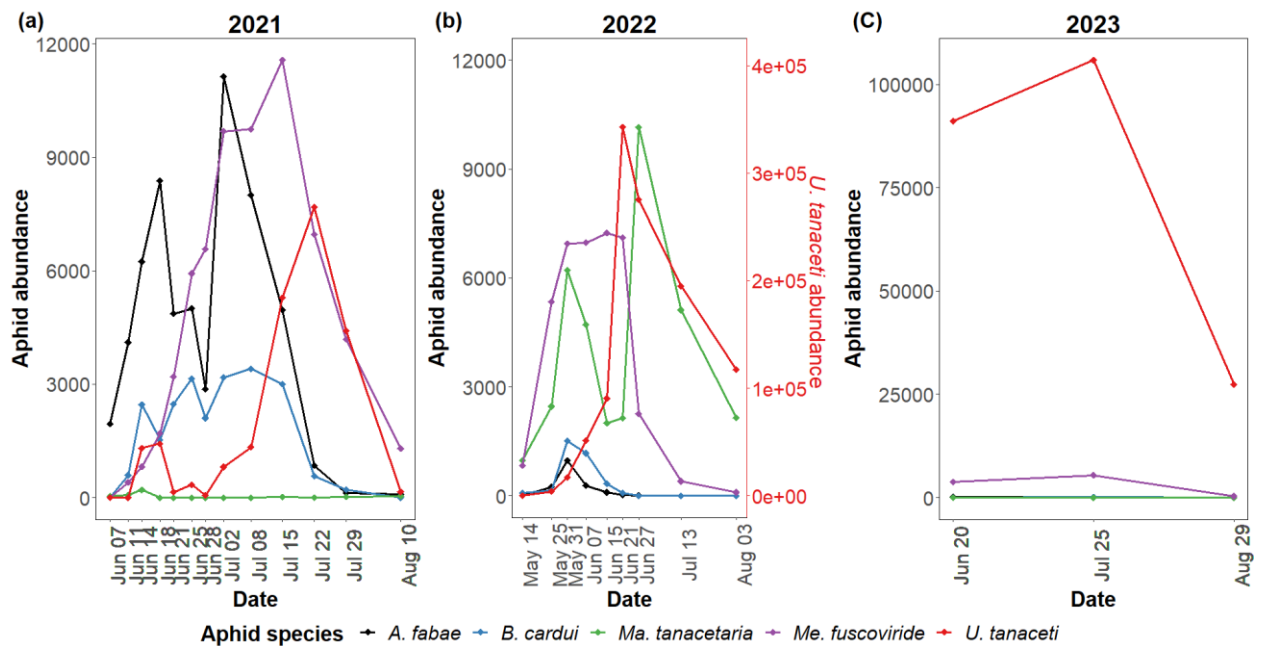


Figure S1-3. Total abundance of herbivores showing five different aphid species (*Aphis fabae*, *Brachycaudus cardui*, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride*, and *Uroleucon tanacetii*) during the observation dates in 2021 (a), 2022 (b), and 2023 (c). Each species is represented by a different color (black, blue, purple, green, and red). The points on each line represent the abundance of the corresponding aphid species on a specific date, while the lines illustrate the trend of aphid abundance over time. The dashed lines indicate the maximum abundance of each species throughout the year. The second y-axis in panel b is scaled differently for *U. tanacetii* species.

2.2 Temporal effects

Although an in-depth analysis by sampling dates will not be discussed here in detail, it is crucial to recognize temporal differences. Supplementary Information 2 (SI2) provides a detailed breakdown of the relationship between chemotype richness and the occurrence and abundance of various ecological groups across different sampling dates and years. For instance, most relationships with plot-level chemical richness in occurrence data were week, if significant. However, for abundance, these temporal patterns were sometimes very clear. Particularly for herbivore abundance, there was a positive relationship between plot-level chemodiversity in the weeks after establishing the field experiment in 2021, it changed towards a consistent negative correlation CR across all following sampling dates, particularly for specialist aphids. There was a positive correlation between flower visitor orders and ants. The effect on the abundance of different predator groups varied, but they tended to be positive when significant relationships were observed.

2.3 Supplementary tables

Table S1-2. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on herbivore occurrence, and Linear Mixed-effect Models (LMM) and Zero-Inflated Negative Binomial models (ZINB) testing herbivore abundance across all species (*All species*), as well as on each aphid species (*A. fabae*, *B. cardui*, *Ma. tanacetaria*, *Me. fuscoviride*, and *U. tanacetii*) in 2021. If all plots were occupied by at least one aphid in the year, we did not model occurrence (-), and this was the case for all species and *Me. fuscoviride*. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable	Factor	d.f.	2021					
			All species χ^2 (p-value)	<i>A. fabae</i> χ^2 (p-value)	<i>B. cardui</i> χ^2 (p-value)	<i>Ma. tanacetaria</i> χ^2 (p-value)	<i>Me. fuscoviride</i> χ^2 (p-value)	<i>U. tanacetii</i> χ^2 (p-value)
Occurrence	CR	1	-	1.04 (0.306)	0.08 (0.784)	0.62 (0.430)	-	3.38 (0.066)
	Athu-Bthu	1	-	0.55 (0.459)	0.02 (0.890)	0.15 (0.695)	-	0.68 (0.409)
	Bthu-high	1	-	0.31 (0.576)	0.06 (0.800)	1.34 (0.247)	-	0.46 (0.495)
	Bthu-low	1	-	0.57 (0.449)	0.39 (0.531)	0.35 (0.555)	-	1.35 (0.245)
	Chrys-acet	1	-	0.52 (0.470)	2.48 (0.115)	0.04 (0.845)	-	0.51 (0.476)
	Mixed-high	1	-	0.29 (0.587)	0.25 (0.615)	0.00 (1.000)	-	7.47 (0.006)
	Mixed-low	1	-	0.00 (0.998)	0.01 (0.909)	0.15 (0.695)	-	0.42 (0.515)
Abundance	CR	1	0.29 (0.588)	0.03 (0.870)	1.51 (0.219)	1.13 (0.288)	0.52 (0.471)	0.38 (0.536)
	Athu-Bthu	1	0.19 (0.665)	0.05 (0.815)	0.07 (0.793)	1.21 (0.271)	0.74 (0.390)	3.60 (0.057)
	Bthu-high	1	0.48 (0.487)	0.07 (0.791)	3.97 (0.046)	0.00 (0.990)	1.78 (0.182)	5.98 (0.014)
	Bthu-low	1	0.15 (0.699)	0.09 (0.766)	0.16 (0.688)	0.05 (0.818)	3.06 (0.080)	0.14 (0.712)
	Chrys-acet	1	0.15 (0.697)	0.98 (0.322)	6.16 (0.013)	0.28 (0.595)	0.27 (0.601)	0.12 (0.725)
	Mixed-high	1	2.24 (0.135)	6.77 (0.009)	0.01 (0.935)	0.14 (0.705)	0.03 (0.853)	0.47 (0.491)
	Mixed-low	1	0.82 (0.364)	0.61 (0.434)	0.00 (0.965)	1.14 (0.286)	0.35 (0.552)	0.33 (0.565)

Table S1-3. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on herbivore occurrence, and Linear Mixed-effect Models (LMM) and Zero-Inflated Negative Binomial models (ZINB) testing herbivore abundance across all species (*All species*), as well as on each aphid species (*A. fabae*, *B. cardui*, *Ma. tanacetaria*, *Me. fuscoviride*, and *U. tanacetii*) in 2022. If all plots were occupied by at least one aphid in the year, we did not model occurrence (-); this was the case for all species and *U. tanacetii*. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values (P <0.05) are reported in bold.

Response variable	Factor	d.f.	2022					
			All species χ^2 (p-value)	<i>A. fabae</i> χ^2 (p-value)	<i>B. cardui</i> χ^2 (p-value)	<i>Ma. tanacetaria</i> χ^2 (p-value)	<i>Me. fuscoviride</i> χ^2 (p-value)	<i>U. tanacetii</i> χ^2 (p-value)
Occurrence	CR	1	-	1.96 (0.162)	1.43 (0.231)	0.42 (0.515)	0.97 (0.325)	-
	<i>Athu-Bthu</i>	1	-	1.61 (0.204)	0.26 (0.606)	0.18 (0.669)	0.06 (0.812)	-
	<i>Bthu-high</i>	1	-	0.19 (0.662)	4.16 (0.041)	0.31 (0.576)	1.66 (0.198)	-
	<i>Bthu-low</i>	1	-	4.50 (0.034)	6.42 (0.011)	0.00 (0.953)	1.26 (0.261)	-
	<i>Chrys-acet</i>	1	-	0.00 (0.967)	0.26 (0.606)	0.52 (0.470)	1.22 (0.270)	-
	<i>Mixed-high</i>	1	-	6.68 (0.010)	2.54 (0.111)	0.40 (0.529)	1.55 (0.213)	-
	<i>Mixed-low</i>	1	-	4.89 (0.027)	2.04 (0.153)	0.14 (0.705)	0.33 (0.568)	-
Abundance	CR	1	7.63 (0.006)	1.60 (0.206)	2.57 (0.109)	2.73 (0.098)	1.10 (0.295)	5.93 (0.015)
	<i>Athu-Bthu</i>	1	3.46 (0.063)	1.70 (0.192)	0.88 (0.347)	0.02 (0.882)	0.08 (0.770)	3.30 (0.069)
	<i>Bthu-high</i>	1	0.01 (0.909)	0.79 (0.374)	0.74 (0.391)	0.09 (0.760)	0.73 (0.393)	0.02 (0.898)
	<i>Bthu-low</i>	1	0.26 (0.612)	3.91 (0.048)	3.39 (0.065)	2.19 (0.139)	5.85 (0.016)	0.13 (0.717)
	<i>Chrys-acet</i>	1	10.77 (0.001)	0.48 (0.486)	2.16 (0.142)	0.29 (0.593)	0.20 (0.654)	12.77 (<0.001)
	<i>Mixed-high</i>	1	4.81 (0.028)	2.38 (0.122)	1.01 (0.315)	2.95 (0.086)	0.32 (0.573)	5.58 (0.018)
	<i>Mixed-low</i>	1	0.18 (0.667)	2.12 (0.146)	0.00 (0.966)	0.31 (0.575)	0.53 (0.466)	0.01 (0.938)

Table S1-4. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on herbivore occurrence, and Linear Mixed-effect Models (LMM) and Zero-Inflated Negative Binomial models (ZINB) testing herbivore abundance across all species (*All species*), as well as on each aphid species (*A. fabae*, *B. cardui*, *Ma. tanacetaria*, *Me. fuscoviride*, and *U. tanacetii*) in 2023. If all plots were occupied by at least one aphid in the year, we did not model occurrence (-); this was the case for all species and *U. tanacetii*. If no aphid was observed in the field, we did not model occurrence nor abundance (-); this was the case for *Ma. tanacetaria*. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable	Factor	d.f.	2023					
			All species χ^2 (p-value)	<i>A. fabae</i> χ^2 (p-value)	<i>B. cardui</i> χ^2 (p-value)	<i>Ma. tanacetaria</i> χ^2 (p-value)	<i>Me. fuscoviride</i> χ^2 (p-value)	<i>U. tanacetii</i> χ^2 (p-value)
Occurrence	CR	1	-	0.16 (0.689)	0.81 (0.369)	-	9.24 (0.002)	-
	Athu-Bthu	1	-	1.61 (0.204)	1.22 (0.269)	-	5.23 (0.022)	-
	Bthu-high	1	-	0.19 (0.662)	0.21 (0.648)	-	1.58 (0.208)	-
	Bthu-low	1	-	4.50 (0.034)	1.10 (0.294)	-	1.11 (0.740)	-
	Chrys-acet	1	-	0.00 (0.967)	1.23 (0.267)	-	1.68 (0.194)	-
	Mixed-high	1	-	6.68 (0.010)	0.21 (0.649)	-	9.42 (0.002)	-
	Mixed-low	1	-	4.89 (0.027)	0.46 (0.497)	-	2.58 (0.108)	-
Abundance	CR	1	4.39 (0.036)	1.24 (0.265)	5.56 (0.018)	-	0.19 (0.663)	4.44 (0.035)
	Athu-Bthu	1	5.32 (0.021)	7.39 (0.006)	4.42 (0.035)	-	0.50 (0.478)	5.08 (0.024)
	Bthu-high	1	0.09 (0.761)	0.05 (0.818)	40.71 (<0.001)	-	0.21 (0.643)	0.16 (0.688)
	Bthu-low	1	0.06 (0.811)	0.05 (0.818)	0.778 (0.378)	-	0.30 (0.586)	0.13 (0.720)
	Chrys-acet	1	2.77 (0.096)	19.14 (<0.001)	3.25 (0.071)	-	1.48 (0.224)	3.59 (0.058)
	Mixed-high	1	0.65 (0.420)	1.22 (0.270)	79.26 (<0.001)	-	0.56 (0.456)	0.80 (0.372)
	Mixed-low	1	3.96 (0.046)	0.56 (0.453)	0.10 (0.748)	-	0.23 (0.631)	3.92 (0.048)

Table S1-5. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on flower visitor occurrence, and Linear Mixed-effect Models (LMM) testing on visitation rate across all orders (*All orders*), as well as on each order (Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera) in 2021. If all plots were occupied by at least one pollinator, we did not model occurrence (-); this was the case for all *orders*. Visitation rate, calculated as the cumulative plot-level number of flower-visiting insects divided by the sum of the plot-level number of flower heads on the days of the flower-visitor surveys, is used as the response variable in the models to evaluate the effect of plot-level chemotype richness on the flower visitor abundances. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable	Factor	d.f.	2021					
			All orders χ^2 (p-value)	Coleoptera χ^2 (p-value)	Diptera χ^2 (p-value)	Hemiptera χ^2 (p-value)	Hymenoptera χ^2 (p-value)	Lepidoptera χ^2 (p-value)
Occurrence	CR	1	-	0.46 (0.497)	0.16 (0.688)	0.79 (0.373)	1.10 (0.294)	3.87 (0.049)
	Athu-Bthu	1	-	0.99 (0.319)	0.43 (0.512)	2.08 (0.149)	0.28 (0.594)	5.15 (0.023)
	Bthu-high	1	-	0.26 (0.613)	0.15 (0.634)	0.24 (0.625)	0.09 (0.763)	0.44 (0.507)
	Bthu-low	1	-	2.91 (0.088)	0.62 (0.432)	1.64 (0.201)	5.30 (0.021)	1.78 (0.152)
	Chrys-acet	1	-	0.37 (0.544)	3.73 (0.053)	0.27 (0.602)	0.46 (0.499)	0.27 (0.604)
	Mixed-high	1	-	1.63 (0.202)	0.15 (0.694)	2.15 (0.143)	0.81 (0.369)	0.05 (0.825)
	Mixed-low	1	-	2.27 (0.132)	0.018 (0.895)	0.28 (0.594)	0.00 (0.942)	0.92 (0.336)
Abundance	CR	1	10.71 (0.001)	16.78 (<0.001)	2.68 (0.102)	0.54 (0.463)	11.56 (<0.001)	8.80 (0.003)
	Athu-Bthu	1	1.11 (0.293)	3.61 (0.057)	1.10 (0.293)	0.40 (0.526)	1.78 (0.182)	7.53 (0.006)
	Bthu-high	1	3.18 (0.074)	3.03 (0.082)	0.71 (0.400)	0.05 (0.826)	1.99 (0.158)	1.52 (0.217)
	Bthu-low	1	0.51 (0.474)	7.00 (0.008)	0.02 (0.894)	0.00 (0.993)	7.58 (0.006)	1.21 (0.272)
	Chrys-acet	1	5.98 (0.014)	6.38 (0.012)	0.51 (0.475)	0.61 (0.436)	2.50 (0.113)	1.65 (0.199)
	Mixed-high	1	6.95 (0.008)	0.98 (0.322)	2.71 (0.100)	1.58 (0.208)	3.12 (0.077)	0.36 (0.547)
	Mixed-low	1	0.49 (0.484)	2.95 (0.086)	0.17 (0.679)	0.06 (0.799)	0.61 (0.434)	2.39 (0.122)

Table S1-6. Summary of Linear Mixed-effect Models (LMM) testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on flower visitor abundance across all orders (*All orders*), as well as on each order (Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera) in 2021. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable	Factor	d.f.	2021					
			All orders χ^2 (p-value)	Coleoptera χ^2 (p-value)	Diptera χ^2 (p-value)	Hemiptera χ^2 (p-value)	Hymenoptera χ^2 (p-value)	Lepidoptera χ^2 (p-value)
Abundance	CR	1	43.66 (<0.001)	21.90 (<0.001)	3.83 (0.050)	1.31 (0.252)	15.21 (<0.001)	7.40 (0.006)
	Athu-Bthu	1	11.01 (<0.001)	4.63 (0.031)	1.99 (0.158)	1.11 (0.293)	2.39 (0.122)	7.47 (0.006)
	Bthu-high	1	8.26 (0.004)	5.30 (0.021)	0.85 (0.356)	0.00 (0.939)	2.47 (0.116)	0.95 (0.330)
	Bthu-low	1	31.04 (<0.001)	20.44 (<0.001)	3.26 (0.071)	1.10 (0.293)	18.88 (<0.001)	2.29 (0.130)
	Chrys-acet	1	0.16 (0.691)	0.52 (0.473)	0.98 (0.322)	0.24 (0.628)	0.38 (0.537)	0.80 (0.372)
	Mixed-high	1	7.19 (0.007)	2.01 (0.156)	2.68 (0.102)	2.05 (0.153)	3.78 (0.052)	0.10 (0.751)
	Mixed-low	1	5.66 (0.017)	4.22 (0.040)	0.95 (0.328)	0.09 (0.761)	1.22 (0.269)	2.10 (0.148)

Table S1-7. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on predator occurrence, and Linear Mixed-effect Models (LMM) testing on predator abundance across all taxa/feeding guilds (*All*), as well as on each (Araneae, Coleoptera, Dermaptera, Diptera, and Parasitized aphid) in 2021. If all plots were occupied by at least one predator, we did not model occurrence (-); this was the case for all *groups*. We did not assess abundance except for parasitized aphids. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable	Factor	d.f.	2021					
			All χ^2 (p-value)	Araneae χ^2 (p-value)	Coleoptera χ^2 (p-value)	Dermaptera χ^2 (p-value)	Diptera χ^2 (p-value)	Parasitized aphid χ^2 (p-value)
Occurrence	CR	1	-	0.28 (0.597)	3.22 (0.073)	1.14 (0.285)	1.05 (0.304)	0.02 (0.894)
	Athu-Bthu	1	-	0.00 (1.000)	2.59 (0.107)	0.04 (0.845)	1.62 (0.203)	0.30 (0.584)
	Bthu-high	1	-	0.00 (0.999)	0.00 (1.000)	0.00 (1.000)	0.40 (0.525)	2.65 (0.103)
	Bthu-low	1	-	0.00 (1.000)	1.32 (0.252)	0.09 (0.768)	1.49 (0.223)	0.17 (0.680)
	Chrys-acet	1	-	0.00 (0.971)	0.97 (0.324)	0.00 (1.000)	0.22 (0.636)	2.82 (0.093)
	Mixed-high	1	-	0.00 (1.000)	0.00 (1.000)	0.00 (1.000)	1.22 (0.269)	0.36 (0.551)
	Mixed-low	1	-	0.00 (1.000)	2.59 (0.107)	0.04 (0.845)	0.37 (0.544)	4.71 (0.030)
Abundance	CR	1	-	-	-	-	-	0.77 (0.381)
	Athu-Bthu	1	-	-	-	-	-	0.62 (0.431)
	Bthu-high	1	-	-	-	-	-	1.19 (0.275)
	Bthu-low	1	-	-	-	-	-	0.10 (0.747)
	Chrys-acet	1	-	-	-	-	-	6.30 (0.012)
	Mixed-high	1	-	-	-	-	-	0.74 (0.391)
	Mixed-low	1	-	-	-	-	-	1.75 (0.186)

Table S1-8. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on predator occurrence, and Linear Mixed-effect Models (LMM) testing on predator abundance across all taxa/feeding guilds (*All*), as well as on each (Araneae, Coleoptera, Diptera, Hemiptera, and Parasitized aphid) in 2022. If all plots were occupied by at least one predator, we did not model occurrence (-); this was the case for all taxa/feeding guilds. We did not assess abundance except for parasitized aphids. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable	Factor	d.f.	2022					Parasitized aphid χ^2 (p-value)
			All χ^2 (p-value)	Araneae χ^2 (p-value)	Coleoptera χ^2 (p-value)	Diptera χ^2 (p-value)	Hemiptera χ^2 (p-value)	
Occurrence	CR	1	-	0.02 (0.884)	0.00 (0.986)	0.13 (0.716)	6.54 (0.010)	2.69 (0.101)
	Athu-Bthu	1	-	0.00 (1.000)	0.00 (1.000)	0.03 (0.869)	0.03 (0.866)	0.12 (0.731)
	Bthu-high	1	-	0.00 (0.999)	0.00 (0.981)	0.09 (0.767)	0.66 (0.417)	0.54 (0.464)
	Bthu-low	1	-	0.00 (1.000)	0.00 (1.000)	0.02 (0.883)	0.88 (0.350)	2.47 (0.116)
	Chrys-acet	1	-	0.00 (0.974)	0.00 (1.000)	1.02 (0.313)	3.13 (0.077)	5.55 (0.018)
	Mixed-high	1	-	0.00 (0.999)	0.00 (1.000)	0.30 (0.582)	3.13 (0.077)	0.08 (0.784)
	Mixed-low	1	-	0.00 (1.000)	0.00 (1.000)	0.09 (0.763)	0.14 (0.707)	0.03 (0.870)
Abundance	CR	1	-	-	-	-	-	2.71 (0.100)
	Athu-Bthu	1	-	-	-	-	-	1.01 (0.315)
	Bthu-high	1	-	-	-	-	-	0.03 (0.859)
	Bthu-low	1	-	-	-	-	-	2.87 (0.090)
	Chrys-acet	1	-	-	-	-	-	0.87 (0.351)
	Mixed-high	1	-	-	-	-	-	0.28 (0.598)
	Mixed-low	1	-	-	-	-	-	0.32 (0.571)

Table S1-9. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on predator occurrence, and Linear Mixed-effect Models (LMM) testing on predator abundance across all taxa/feeding guild (*All*), as well as on each (Araneae, Coleoptera, Dermaptera, Diptera, Hemiptera, Parasitized aphid, Aphid parasitoid, and Other Hymenoptera) in 2023. If all plots were occupied by at least one predator, we did not model occurrence (-); this was the case for all taxa/feeding guilds and each of them. If we did not find a taxa/feeding guild in the field, we did not model occurrence nor abundance (-); this was the case for Parasitized aphids. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable	Factor	d.f.	2023								
			All χ^2 (p-value)	Araneae χ^2 (p-value)	Coleoptera χ^2 (p-value)	Dermaptera χ^2 (p-value)	Diptera χ^2 (p-value)	Hemiptera χ^2 (p-value)	Parasitized aphid χ^2 (p-value)	Aphid parasitoid χ^2 (p-value)	Other Hymenoptera χ^2 (p-value)
Occurrence	CR	1	-	-	-	-	-	-	-	-	-
	Athu-Bthu	1	-	-	-	-	-	-	-	-	-
	Bthu-high	1	-	-	-	-	-	-	-	-	-
	Bthu-low	1	-	-	-	-	-	-	-	-	-
	Chrys-acet	1	-	-	-	-	-	-	-	-	-
	Mixed-high	1	-	-	-	-	-	-	-	-	-
	Mixed-low	1	-	-	-	-	-	-	-	-	-
Abundance	CR	1	0.06 (0.800)	0.12 (0.725)	0.38 (0.538)	1.85 (0.174)	1.91 (0.167)	0.94 (0.332)	-	2.38 (0.123)	0.14 (0.706)
	Athu-Bthu	1	0.87 (0.350)	0.97 (0.324)	0.03 (0.868)	8.51 (0.004)	0.22 (0.642)	3.55 (0.060)	-	0.38 (0.535)	2.45 (0.117)
	Bthu-high	1	0.02 (0.900)	0.00 (0.951)	0.21 (0.649)	0.38 (0.539)	0.05 (0.815)	0.53 (0.465)	-	0.92 (0.338)	0.37 (0.540)
	Bthu-low	1	2.20 (0.138)	0.13 (0.720)	2.50 (0.114)	0.42 (0.517)	1.75 (0.186)	0.12 (0.730)	-	0.19 (0.666)	0.76 (0.383)
	Chrys-acet	1	4.16 (0.041)	0.47 (0.492)	3.85 (0.050)	2.95 (0.086)	3.78 (0.052)	0.52 (0.471)	-	0.49 (0.484)	0.05 (0.819)
	Mixed-high	1	0.84 (0.361)	1.62 (0.204)	0.64 (0.425)	0.20 (0.655)	1.20 (0.273)	0.02 (0.882)	-	1.65 (0.198)	0.41 (0.520)
	Mixed-low	1	2.07 (0.150)	0.12 (0.729)	0.00 (0.989)	1.43 (0.232)	0.92 (0.336)	2.39 (0.122)	-	3.83 (0.050)	0.07 (0.794)

Table S1-10. Summary of Binomial Linear Mixed-effect Models testing plot-level chemotype richness (CR) or chemotype identity (six different models, one for each chemotype: *Athu-Bthu*, *Bthu-high*, *Bthu-low*, *Chrys-acet*, *Mixed-high*, and *Mixed-low*) effects on ant occurrence, and Linear Mixed-effect Models (LMM) testing on ant abundance in 2021, 2022, and 2023. If all plots were occupied at least by one ant in the year, we did not model occurrence (-); this was the case for 2023. We assessed abundance only in 2023. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported. Significant values ($P < 0.05$) are reported in bold.

Response variable: Ants	Factor	d.f.	2021 χ^2 (p-value)	2022 χ^2 (p-value)	2023 χ^2 (p-value)
Occurrence	CR	1	0.00 (0.992)	2.13 (0.144)	-
	Athu-Bthu	1	0.00 (0.979)	0.00 (0.948)	-
	Bthu-high	1	0.00 (0.980)	0.00 (1.000)	-
	Bthu-low	1	0.00 (0.978)	0.04 (0.837)	-
	Chrys-acet	1	0.00 (0.955)	0.02 (0.891)	-
	Mixed-high	1	0.00 (0.999)	0.00 (0.957)	-
	Mixed-low	1	0.00 (0.975)	0.00 (0.946)	-
Abundance	CR	1	-	-	3.15 (0.076)
	Athu-Bthu	1	-	-	0.80 (0.370)
	Bthu-high	1	-	-	1.77 (0.183)
	Bthu-low	1	-	-	0.30 (0.584)
	Chrys-acet	1	-	-	6.58 (0.010)
	Mixed-high	1	-	-	0.33 (0.564)
	Mixed-low	1	-	-	1.36 (0.244)

Table S1-11. Significant effects of plot-level chemotype presence on herbivore species. Relative changes were calculated by the logarithm of the ratio of mean values for the “Presence” and “Absence” groups of each chemotype (columns) for each respective herbivore response variable (rows). The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive effect of chemotype presence) to white (no effect) to red (negative effect of chemotypes), with the midpoint set to 0; stronger colors represent stronger effects of the respective chemotype on plot-level response variables.

		CHEMOTYPE					
		Athu-Bthu	Bthu-high	Bthu-low	Chrys-acet	Mixed-high	Mixed-low
Occupancy	2021	All species					
		<i>A. fabae</i>					
		<i>B. cardui</i>					
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>				-0.288	
	2022	All aphid species					
		<i>A. fabae</i>		0.488		0.619	-0.540
		<i>B. cardui</i>	0.330	-0.433			
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>					
	2023	All aphid species					
		<i>A. fabae</i>		-0.629		0.916	-0.097
		<i>B. cardui</i>					
		<i>Me. fuscoviride</i>	-0.410			-0.601	
		<i>U. tanaceti</i>					
Abundance	2021	All species					
		<i>A. fabae</i>				0.297	
		<i>B. cardui</i>	0.449		0.663		
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>	0.815				
	2022	All aphid species			-0.046	-0.034	
		<i>A. fabae</i>		-0.481			
		<i>B. cardui</i>					
		<i>Ma. tanacetaria</i>					
		<i>Me. fuscoviride</i>		-0.341			
		<i>U. tanaceti</i>			-0.050	-0.037	
	2023	All aphid species	-0.134				-0.134
		<i>A. fabae</i>	-1.916		-0.689		
		<i>B. cardui</i>	-2.096	-0.498		-0.269	
		<i>Me. fuscoviride</i>					
		<i>U. tanaceti</i>	-0.133				-0.131

Table S1-12. Significant effects of plot-level chemotype presence on flower visitor orders. Relative changes were calculated by the logarithm of the ratio of mean values for the “Presence” and “Absence” groups of each chemotype (columns) for each respective flower visitor response variable (rows). The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive effect of chemotype presence) to white (no effect) to red (negative effect of chemotypes), with the midpoint set to 0; stronger colors represent stronger effects of the respective chemotype on plot-level response variables.

		CHEMOTYPE					
		Athu-Bthu	Bthu-high	Bthu-low	Chrys-acet	Mixed-high	Mixed-low
Occupancy	2021	All orders					
		Coleoptera					
		Diptera					
		Hemiptera					
		Hymenoptera			0.487		
		Lepidoptera	0.730				
Abundance	2021	All orders			0.440	0.315	
		Coleoptera		0.251	0.256		
		Diptera					
		Hemiptera					
		Hymenoptera			0.332		
		Lepidoptera	0.748				

Table S1-13. Significant effects of plot-level chemotype presence on predatory groups. Relative changes were calculated by the logarithm of the ratio of mean values for the “Presence” and “Absence” groups of each chemotype (columns) for each respective predatory response variable (rows). The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive effect of chemotype presence) to white (no effect) to red (negative effect of chemotypes), with the midpoint set to 0; stronger colors represent stronger effects of the respective chemotype on plot-level response variables.

		CHEMOTYPE					
		Athu-Bthu	Bthu-high	Bthu-low	Chrys-acet	Mixed-high	Mixed-low
Occurrence	2021	All					
		Araneae					
		Coleoptera					
		Dermaptera					
		Diptera					
		Parasitized aphid					-0.254
	2022	All					
		Araneae					
		Coleoptera					
		Diptera					
		Hemiptera					
		Parasitized aphid			-0.279		
	2023	All					
		Araneae					
		Coleoptera					
		Dermaptera					
		Diptera					
		Hemiptera					
		Aphid parasitoid					
		Other Hymenoptera					
Abundance	2021	Parasitized aphid			0.432		
	2022	Parasitized aphid					
	2023	All orders			-0.039		
		Araneae					
		Coleoptera			-0.034		
		Dermaptera	0.093				
		Diptera					
		Hemiptera					
		Parasitized aphid					
		Aphid parasitoid					
		Other Hymenoptera					

Table S1-14. Significant effects of plot-level chemotype presence on ants. Relative changes were calculated by the logarithm of the ratio of mean values for the “Presence” and “Absence” groups of each chemotype (columns) for each respective ant response variable (rows). The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive effect of chemotype presence) to white (no effect) to red (negative effect of chemotypes), with the midpoint set to 0; stronger colors represent stronger effects of the respective chemotype on plot-level response variables.

		CHEMOTYPE					
Response variable: Ants		Athu-Bthu	Bthu-high	Bthu-low	Chrys-acet	Mixed-high	Mixed-low
Occurrence	2021						
	2022						
	2023						
Abundance	2023				0.056		

Table S15. Effects of the plot-level chemotype richness on the plot-level occurrence of herbivore groups at independent sampling times and at the cumulative year. Each column represents the different groups under analysis. Herbivores: All species, *Aphis fabae*, *Bradhycaudus cardui*, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride*, and *Uroleucon tanacetii*. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group occurrence for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

OCCURRENCE		HERBIVORES																		
		All species			A. fabae			B. cardui			Ma. tanacetaria			Me. fuscoviride			U. tanacetii			
Year	Calendar week	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	
2021	24 - 1	80.95	0.020	0.45 (0.504)	80.95	0.020	0.45 (0.503)	0.00	0.000	NA	2.38	0.002	0.04 (0.835)	0.00	0.000	NA	0.00	0.000	NA	
	24 - 2	82.14	0.010	436.33 (<0.001)	80.95	0.009	0.10 (0.757)	23.81	0.062	3.64 (0.056)	2.38	0.002	0.04 (0.835)	13.10	0.018	843.64 (<0.001)	0.00	0.000	NA	
	25 - 1	90.48	0.012	0.38 (0.538)	77.38	0.038	1.78 (0.182)	46.43	-0.025	0.50 (0.482)	8.33	0.003	0.02 (0.890)	25.00	0.014	0.20 (0.657)	29.76	-0.031	0.92 (0.337)	
	25 - 2	83.33	0.016	0.43 (0.513)	66.67	0.044	1.89 (0.169)	32.14	0.021	0.36 (0.549)	0.00	0.000	NA	21.43	0.010	0.11 (0.738)	33.33	-0.049	2.03 (0.154)	
	26 - 1	84.52	0.007	0.07 (0.796)	54.76	0.005	0.02 (0.886)	55.95	0.072	3.64 (0.056)	0.00	0.000	NA	39.29	0.006	0.03 (0.871)	5.95	0.028	2.28 (0.131)	
	26 - 2	77.38	0.038	1.49 (0.222)	48.81	0.076	4.35 (0.037)	51.19	0.105	6.98 (0.008)	0.00	0.000	NA	51.19	-0.037	1.06 (0.302)	19.05	0.030	4019.3 (<0.001)	
	27 - 1	84.52	0.034	1.59 (0.206)	45.24	0.017	0.23 (0.632)	35.71	-0.003	0.01 (0.930)	0.00	0.000	NA	60.71	0.054	2.18 (0.140)	3.57	-0.018	1.95 (0.162)	
	27 - 2	91.67	-0.025	1.49 (0.221)	55.95	0.039	1.38 (0.240)	50.00	0.060	2.99 (0.084)	0.00	0.000	NA	63.10	-0.020	0.31 (0.577)	9.52	0.015	0.51 (0.474)	
	28	89.29	-0.005	0.05 (0.819)	52.38	0.024	0.62 (0.431)	45.24	0.012	0.12 (0.732)	0.00	0.000	NA	71.43	-0.023	0.49 (0.485)	9.52	0.009	0.20 (0.658)	
	29	91.67	-0.008	0.17 (0.681)	47.62	-0.008	0.06 (0.812)	40.48	-0.009	0.08 (0.781)	3.57	0.014	1.03 (0.310)	76.19	0.004	0.02 (0.896)	25.00	0.030	0.98 (0.321)	
	30	80.95	-0.030	1.40 (0.237)	15.48	-0.018	0.45 (0.500)	11.90	-0.016	0.46 (0.496)	0.00	0.000	NA	67.86	0.018	0.30 (0.587)	34.25	-0.059	4.06 (0.044)	
	31	73.81	-0.031	0.91 (0.339)	2.38	-0.003	0.08 (0.782)	3.57	-0.029	0.00 (1.000)	1.19	-0.004	0.28 (0.597)	57.14	0.018	0.24 (0.623)	27.38	-0.061	3.18 (0.074)	
	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	33	29.76	0.007	0.05 (0.822)	2.38	0.008	0.52 (0.469)	0.00	0.000	NA	2.38	-0.003	0.09 (0.766)	23.81	0.002	0.00 (0.960)	3.57	-0.013	0.85 (0.356)	
2022	20	50.00	-0.033	0.88 (0.350)	0.00	0.000	NA	14.29	-0.008	0.11 (0.744)	27.38	-0.017	0.28 (0.598)	22.62	0.006	0.04 (0.831)	0.00	0.000	NA	
	22	93.83	-0.031	2.85 (0.092)	11.11	0.03	1.66 (0.198)	11.11	0.001	0.00 (0.957)	60.49	-0.046	1.49 (0.222)	67.90	0.009	0.07 (0.796)	4.94	-0.012	0.69 (0.406)	
	23	100.00	0.000	NA	23.81	-0.009	0.09 (0.764)	52.38	0.041	1.26 (0.262)	71.43	-0.017	0.40 (0.526)	67.86	-0.026	0.58 (0.447)	64.29	0.025	0.70 (0.403)	
	24	100.00	0.000	NA	19.05	0.046	2.45 (0.117)	16.67	0.033	1.38 (0.239)	71.43	-0.006	0.04 (0.833)	71.43	0.005	0.02 (0.882)	94.05	-0.006	0.11 (0.738)	
	25	100.00	0.000	NA	5.95	-0.010	0.39 (0.532)	5.95	0.028	2.28 (0.131)	69.05	0.013	0.16 (0.686)	45.24	-0.043	1.52 (0.217)	100.00	0.000	NA	
	26	100.00	0.000	NA	1.19	0.018	0.00 (0.970)	2.38	0.019	2.13 (0.144)	79.76	-0.042	2.03 (0.154)	51.19	-0.021	0.34 (0.560)	100.00	0.000	NA	
	27	100.00	0.000	NA	3.57	0.004	0.08 (0.773)	0.00	0.000	NA	82.14	0.015	0.32 (0.572)	36.90	-0.002	0.00 (0.954)	100.00	0.000	NA	
	29	100.00	0.000	NA	0.00	0.000	NA	0.00	0.000	NA	26.19	-0.056	3.94 (0.047)	7.14	0.012	0.42 (0.514)	100.00	0.000	NA	
32	100.00	0.000	NA	0.00	0.000	NA	0.00	0.000	NA	26.20	-0.060	3.92 (0.042)	2.38	-0.020	0.00 (0.973)	100.00	0.000	NA		
2023	26	100.00	0.000	NA	8.33	-0.008	0.16 (0.689)	3.57	-0.018	1.95 (0.162)	0.00	0.000	NA	39.29	-0.044	1.75 (0.186)	100.00	0.000	NA	
	31	100.00	0.000	NA	0.00	0.000	NA	5.95	-0.016	0.81 (0.369)	0.00	0.000	NA	54.76	-0.100	6.84 (0.009)	100.00	0.000	NA	
	36	100.00	0.000	NA	0.00	0.000	NA	3.57	-0.018	1.95 (0.162)	0.00	0.000	NA	23.81	-0.086	6.31 (0.012)	100.00	0.000	NA	

Cumulative	HERBIVORES																	
	All species			<i>A. fabae</i>			<i>B. cardui</i>			<i>Ma. tanacetaria</i>			<i>Me. fuscoviride</i>			<i>U. tanaceti</i>		
Year	% occurrence	Slope	χ2 (p-value)	% occurrence	Slope	χ2 (p-value)	% occurrence	Slope	χ2 (p-value)	% occurrence	Slope	χ2 (p-value)	% occurrence	Slope	χ2 (p-value)	% occurrence	Slope	χ2 (p-value)
2021	100.00	0.000	NA	96.43	-0.014	1.04 (0.306)	89.28	0.006	0.08 (0.784)	16.67	0.022	0.62 (0.430)	100.00	0.000	NA	75.00	-0.052	3.38 (0.066)
2022	100.00	0.000	NA	47.62	0.052	1.96 (0.162)	65.48	0.043	1.43 (0.231)	96.43	-0.009	0.42 (0.515)	94.05	-0.017	0.97 (0.325)	100.00	0.000	NA
2023	100.00	0.000	NA	8.33	-0.008	0.16 (0.689)	5.95	-0.016	0.81 (0.369)	0.00	0.000	NA	57.14	-0.119	9.24 (0.002)	100.00	0.000	NA

Table S16. Effects of the plot-level chemotype richness on the plot-level abundance of herbivore groups at independent sampling times and at the cumulative year. Each column represents the different groups under analysis. Herbivores: All species, *Aphis fabae*, *Bradhycaudus cardui*, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride*, and *Uroleucon tanacetii*. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. NA indicates that the analysis is not available, usually due to low plot occupancy (<60%). Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group abundance for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

ABUNDANCE		HERBIVORES																	
		All species			A. fabae			B. cardui			Ma. tanacetaria			Me. fuscoviride			U. tanaceti		
Year	Calendar week	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)	% occurrence	Slope	χ ² (p-value)
2021	24 - 1	80.95	0.191	1.03 (0.310)	80.95	0.187	1.00 (0.317)	0.00	NA	NA	2.38	NA	NA	0.00	NA	NA	0.00	NA	NA
	24 - 2	82.14	0.327	1.25 (0.264)	80.95	0.047	0.03 (0.866)	23.81	NA	NA	2.38	NA	NA	13.10	NA	NA	0.00	NA	NA
	25 - 1	90.48	0.316	0.83 (0.362)	77.38	0.252	0.57 (0.451)	46.43	NA	NA	8.33	NA	NA	25.00	NA	NA	29.76	NA	NA
	25 - 2	83.33	0.149	0.16 (0.686)	66.67	0.165	0.16 (0.686)	32.14	NA	NA	0.00	NA	NA	21.43	NA	NA	33.33	NA	NA
	26 - 1	84.52	0.228	0.32 (0.573)	54.76	NA	NA	55.95	NA	NA	0.00	NA	NA	39.29	NA	NA	5.95	NA	NA
	26 - 2	77.38	0.540	1.06 (0.302)	48.81	NA	NA	51.19	NA	NA	0.00	NA	NA	51.19	NA	NA	19.05	NA	NA
	27 - 1	84.52	1.011	5.89 (0.015)	45.24	NA	NA	35.71	NA	NA	0.00	NA	NA	60.71	1.033	5.76 (0.016)	3.57	NA	NA
	27 - 2	91.67	0.499	0.82 (0.364)	55.95	NA	NA	50.00	NA	NA	0.00	NA	NA	63.10	0.340	0.37 (0.542)	9.52	NA	NA
	28	89.29	0.410	0.60 (0.439)	52.38	NA	NA	45.24	NA	NA	0.00	NA	NA	71.43	0.088	0.03 (0.866)	9.52	NA	NA
	29	91.67	-0.244	0.17 (0.678)	47.62	NA	NA	40.48	NA	NA	3.57	NA	NA	76.19	-0.034	0.00 (0.947)	25.00	NA	NA
	30	80.95	-0.538	1.12 (0.290)	15.48	NA	NA	11.90	NA	NA	0.00	NA	NA	67.86	0.428	1.02 (0.312)	34.25	NA	NA
	31	73.81	-0.648	1.93 (0.164)	2.38	NA	NA	3.57	NA	NA	1.19	NA	NA	57.14	NA	NA	27.38	NA	NA
	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	33	29.76	NA	NA	2.38	NA	NA	0.00	NA	NA	2.38	NA	NA	23.81	NA	NA	3.57	NA	NA
2022	20	50.00	NA	NA	0.00	NA	NA	14.29	NA	NA	27.38	NA	NA	22.62	NA	NA	0.00	NA	NA
	22	93.83	-0.207	3.81 (0.051)	11.11	NA	NA	11.11	NA	NA	60.49	-0.128	0.78 (0.378)	67.90	-0.515	1.63 (0.202)	4.94	NA	NA
	23	100.00	-0.058	0.91 (0.340)	23.81	NA	NA	52.38	NA	NA	71.43	-0.094	0.61 (0.436)	67.86	-0.232	0.30 (0.581)	64.29	-0.041	0.00 (0.949)
	24	100.00	-0.052	0.98 (0.321)	19.05	NA	NA	16.67	NA	NA	71.43	-0.120	0.83 (0.363)	71.43	-0.870	4.00 (0.045)	94.05	-0.124	0.03 (0.863)
	25	100.00	-0.050	1.32 (0.251)	5.95	NA	NA	5.95	NA	NA	69.05	0.049	0.19 (0.662)	45.24	NA	NA	100.00	-0.951	1.71 (0.191)
	26	100.00	-0.026	1.00 (0.317)	1.19	NA	NA	2.38	NA	NA	79.76	-0.088	0.64 (0.422)	51.19	NA	NA	100.00	-0.823	1.42 (0.234)
	27	100.00	-0.010	1.05 (0.304)	3.57	NA	NA	0.00	NA	NA	82.14	-0.050	0.13 (0.720)	36.90	NA	NA	100.00	-0.184	0.59 (0.441)
	29	100.00	-0.024	3.04 (0.081)	0.00	NA	NA	0.00	NA	NA	26.19	NA	NA	7.14	NA	NA	100.00	-0.504	2.96 (0.086)
32	100.00	-0.023	2.50 (0.114)	0.00	NA	NA	0.00	NA	NA	26.20	NA	NA	2.38	NA	NA	100.00	-0.410	2.97 (0.085)	
2023	26	100.00	-0.019	0.17 (0.682)	8.33	NA	NA	3.57	NA	NA	0.00	NA	NA	39.29	NA	NA	100.00	-0.017	0.13 (0.719)
	31	100.00	-0.084	4.79 (0.028)	0.00	NA	NA	5.95	NA	NA	0.00	NA	NA	54.76	NA	NA	100.00	-0.083	4.76 (0.029)
	36	100.00	-0.444	93.19 (<0.001)	0.00	NA	NA	3.57	NA	NA	0.00	NA	NA	23.81	NA	NA	100.00	-0.444	92.30 (<0.001)

Cumulative Year	HERBIVORES																	
	All species			A. fabae			B. cardui			Ma. tanacetaria			Me. fuscoviride			U. tanacetii		
	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)
2021	100.00	0.482	0.29 (0.588)	96.43	0.140	0.03 (0.870)	89.28	0.761	1.51 (0.219)	16.67	0.025	1.13 (0.288)	100.00	0.054	0.52 (0.471)	75.00	-1.104	0.38 (0.536)
2022	100.00	-1.596	7.63 (0.006)	47.62	0.057	1.96 (0.162)	65.48	0.179	2.57 (0.109)	96.43	-0.897	2.73 (0.098)	94.05	-1.026	1.10 (0.295)	100.00	-1.402	5.93 (0.015)
2023	100.00	-2.176	4.39 (0.036)	8.33	-0.086	1.24 (0.265)	5.95	-0.127	5.56 (0.018)	0.00	NA	NA	57.14	-0.641	0.19 (0.663)	100.00	-2.148	4.44 (0.035)

Table S17. Effects of the plot-level chemotype richness on the plot-level occurrence of flower visitor groups at independent sampling times and at the cumulative year. Each column represents the different groups under analysis. Flower visitors: All orders, Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group occurrence for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

OCCURRENCE		FLOWER VISITORS																	
		All orders			Coleoptera			Diptera			Hemiptera			Hymenoptera			Lepidoptera		
Year	Calendar week	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)
2021	24 - 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	24 - 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	25 - 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	25 - 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	26 - 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	26 - 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	27 - 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	27 - 2	79.76	0.007	0.07 (0.795)	57.14	0.084	4.87 (0.027)	48.81	0.054	2.03 (0.154)	22.62	0.061	3.63 (0.057)	33.33	0.066	3.51 (0.061)	0.00	0.000	NA
	28	98.81	-0.001	0.02 (0.884)	35.71	0.008	0.05 (0.820)	63.10	-0.009	0.06 (0.801)	48.81	-0.007	0.04 (0.847)	23.81	0.051	2.52 (0.112)	11.90	0.056	4.87 (0.027)
	29	97.62	0.020	0.00 (0.984)	45.24	0.05	1.84 (0.175)	34.52	0.023	0.43 (0.513)	26.19	0.004	0.014 (0.904)	47.62	0.030	0.68 (0.409)	23.81	0.018	0.32 (0.569)
	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	32	72.15	0.061	3.20 (0.074)	36.71	0.076	4.13 (0.042)	17.72	0.065	4.79 (0.028)	10.13	-0.008	0.16 (0.692)	54.43	0.080	4.20 (0.040)	10.13	0.036	2.44 (0.118)
	33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2022	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2023	26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Cumulative	FLOWER VISITORS																		
	All orders			Coleoptera			Diptera			Hemiptera			Hymenoptera			Lepidoptera			
	Year	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)
2021	100.00	0.000	NA	91.67	0.014	0.46 (0.497)	91.67	-0.008	0.16 (0.688)	73.81	0.029	0.79 (0.373)	84.52	0.029	1.10 (0.294)	41.67	0.074	3.87 (0.049)	
2022	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2023	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table S18. Effects at independent sampling times of the plot-level chemotype richness on the plot-level abundance of flower visitor groups. Each column represents the different groups under analysis. Flower visitors: All orders, Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. NA indicates that the analysis is not available, usually due to low plot occupancy (<60%). Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group abundance for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

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Table S19. Effects of the plot-level chemotype richness on the plot-level occurrence of predator groups at independent sampling times and at the cumulative year. Each column represents the different groups under analysis. Predators: All groups, Araneae, Coleoptera, Dermaptera, Diptera, Hemiptera, Parasitized aphids, Parasitoids, Other Hymenoptera. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group occurrence for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

OCCURRENCE		PREDATORS																											
Year	Calendar week	All groups			Araneae			Coleoptera			Dermaptera			Diptera			Hemiptera			Parasitized aphids			Aphid parasitoid			Other Hymenoptera			
		% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	
2021	24 - 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	24 - 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	25 - 1	6.55	0.012	2.75 (0.097)	5.95	0.010	1.95 (0.163)	1.19	0.001	0.13 (0.720)	0.00	0.000	NA	0.00	0.000	NA	-	-	-	0.00	0.000	NA	-	-	-	-	-	-	
	25 - 2	9.33	0.007	0.82 (0.366)	5.16	0.002	0.14 (0.708)	1.59	0.007	3.19 (0.074)	0.00	0.000	NA	0.99	-0.002	0.34 (0.560)	-	-	-	1.79	-0.001	0.06 (0.806)	-	-	-	-	-	-	
	26 - 1	24.80	-0.012	0.85 (0.355)	9.92	-0.009	1.08 (0.299)	7.14	-0.006	0.55 (0.459)	0.40	-0.001	0.56 (0.456)	2.38	0.000	0.01 (0.932)	-	-	-	7.74	0.007	0.73 (0.394)	-	-	-	-	-	-	
	26 - 2	9.92	0.005	0.36 (0.550)	0.00	0.000	NA	0.00	0.000	NA	0.00	0.000	NA	0.00	0.000	NA	-	-	-	9.92	0.006	0.49 (0.483)	-	-	-	-	-	-	
	27 - 1	16.47	0.015	1.95 (0.163)	7.74	0.015	3.46 (0.063)	7.74	-0.002	0.04 (0.851)	0.00	0.000	NA	0.99	0.002	0.39 (0.530)	-	-	-	-	-	-	-	-	-	-	-	-	
	27 - 2	22.02	-0.01	0.68 (0.408)	9.13	0.004	0.26 (0.610)	6.15	-0.005	0.47 (0.494)	0.00	0.000	NA	0.20	-0.001	0.28 (0.598)	-	-	-	7.34	0.001	0.01 (0.911)	-	-	-	-	-	-	
	28	23.81	-0.003	0.06 (0.810)	10.12	-0.01	1.27 (0.259)	6.75	0.004	0.27 (0.603)	0.00	0.000	NA	0.60	-0.001	0.28 (0.597)	-	-	-	8.73	0.002	0.07 (0.790)	-	-	-	-	-	-	
	29	31.15	-0.003	0.05 (0.825)	11.90	0.008	0.68 (0.409)	13.29	-0.002	0.06 (0.814)	0.20	0.000	0.02 (0.884)	0.20	0.000	0.02 (0.884)	-	-	-	9.52	-0.001	0.00 (0.941)	-	-	-	-	-	-	
	30	29.37	0.000	0.00 (0.984)	15.28	0.017	2.41 (0.120)	10.52	-0.011	1.37 (0.241)	0.20	-0.002	0.00 (0.974)	0.00	0.000	NA	-	-	-	6.94	-0.002	0.09 (0.766)	-	-	-	-	-	-	
	31	22.22	0.003	0.05 (0.826)	11.90	0.012	1.47 (0.225)	5.95	-0.004	0.34 (0.559)	0.00	0.000	NA	0.00	0.000	NA	-	-	-	0.00	0.000	NA	-	-	-	-	-	-	
	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	33	23.41	-0.007	0.30 (0.582)	15.08	-0.009	0.67 (0.412)	7.14	0.005	0.45 (0.503)	0.00	0.000	NA	0.00	0.000	NA	-	-	-	3.37	-0.007	1.48 (0.223)	-	-	-	-	-	-	-
2022	20	11.51	-0.005	0.28 (0.596)	9.52	-0.011	1.47 (0.225)	0.20	0.003	0.02 (0.887)	-	-	-	0.00	0.000	NA	1.59	0.003	0.79 (0.374)	0.40	-0.001	0.56 (0.456)	-	-	-	-	-	-	-
	22	8.53	0.015	3.14 (0.076)	3.82	0.010	8670.50 (<0.001)	2.41	-0.005	1.10 (0.295)	-	-	-	1.61	0.003	0.45 (0.504)	0.60	0.005	3.62 (0.057)	0.40	0.002	1.22 (0.269)	-	-	-	-	-	-	-
	23	30.56	-0.008	0.35 (0.555)	20.63	-0.010	0.66 (0.417)	4.37	0.006	3389.20 (<0.001)	-	-	-	1.98	0.004	0.80 (0.371)	0.20	-0.001	0.28 (0.598)	6.15	-0.009	1.67 (0.196)	-	-	-	-	-	-	-
	24	52.98	-0.025	2.93 (0.087)	31.62	-0.007	0.19 (0.665)	19.30	-0.016	1.83 (0.176)	-	-	-	6.98	-0.006	0.65 (0.420)	0.41	-0.001	0.55 (0.457)	13.35	-0.002	0.06 (0.802)	-	-	-	-	-	-	-
	25	55.75	0.000	0.00 (0.990)	41.32	0.015	0.93 (0.335)	18.80	0.004	0.18 (0.676)	-	-	-	4.13	-0.009	2.18 (0.140)	0.83	0.006	3.29 (0.070)	3.93	-0.015	6.16 (0.013)	-	-	-	-	-	-	-
	26	56.75	0.009	0.41 (0.521)	21.65	0.006	0.20 (0.651)	41.86	0.004	0.15 (0.695)	-	-	-	0.62	0.000	0.02 (0.894)	0.41	0.002	1.20 (0.273)	3.09	0.005	0.81 (0.368)	-	-	-	-	-	-	-
	27	59.13	0.004	0.10 (0.757)	0.62	-0.001	0.27 (0.605)	59.75	0.003	0.07 (0.791)	-	-	-	2.90	0.004	0.61 (0.436)	4.98	-0.010	2.75 (0.097)	1.24	0.001	0.13 (0.715)	-	-	-	-	-	-	-
	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	2023	26	42.26	0.010	0.46 (0.497)	4.96	-0.004	0.42 (0.519)	33.53	-0.002	0.03 (0.853)	0.40	-0.001	0.56 (0.456)	5.56	0.01	2.08 (0.149)	0.20	0.003	0.02 (0.880)	0.00	0.000	NA	3.57	0.001	0.02 (0.889)	0.79	-0.004	2.10 (0.148)
31		99.80	0.000	0.02 (0.884)	79.56	0.006	0.27 (0.603)	95.63	-0.002	0.06 (0.800)	48.02	0.013	0.70 (0.402)	74.40	0.005	0.14 (0.710)	54.76	0.011	0.54 (0.461)	0.00	0.000	NA	63.89	0.026	3.14 (0.076)	50.40	0.017	1.11 (0.292)	
36		100.00	0.000	NA	72.22	-0.010	0.46 (0.500)	95.44	0.010	2.50 (0.114)	52.38	0.018	1.40 (0.237)	76.98	-0.022	2.91 (0.088)	50.40	0.005	0.11 (0.742)	0.00	0.000	NA	68.06	0.000	0.00 (0.974)	50.20	-0.021	1.89 (0.169)	

Cumulative		PREDATORS																													
Year		All groups			Araneae			Coleoptera			Dermaptera			Diptera			Hemiptera			Parasitized aphids			Parasitoids			Other Hymenoptera					
		% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)	% occurrence	Slope	χ^2 (p-value)			
2021		100.00	0.000	NA	98.81	0.004	0.28 (0.597)	88.10	-0.045	3.22 (0.073)	4.76	-0.017	1.14 (0.285)	21.43	-0.028	1.05 (0.304)	-	-	-	76.19	0.004	0.02 (0.894)	-	-	-	-	-	-	-		
2022		100.00	0.000	NA	98.81	-0.001	0.02 (0.884)	98.81	0.010	0.00 (0.986)	-	-	-	53.57	-0.013	0.13 (0.716)	20.24	0.080	6.54 (0.010)	77.38	-0.050	2.69 (0.101)	-	-	-	-	-	-	-		
2023		100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA	100.00	0.000	NA

Table S20. Effects of the plot-level chemotype richness on the plot-level abundance of predator groups at independent sampling times and at the cumulative year. Each column represents the different groups under analysis. Predators: All groups, Araneae, Coleoptera, Dermaptera, Diptera, Hemiptera, Parasitized aphids, Parasitoids, Other Hymenoptera. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. NA indicates that the analysis is not available, usually due to low plot occupancy (<60%). Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group abundance for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

ABUNDANCE		PREDATORS																										
Year	Calendar week	All groups			Araneae			Coleoptera			Dermaptera			Diptera			Hemiptera			Parasitized aphid			Aphid parasitoid			Other Hymenoptera		
		% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)
2021	24 - 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	24 - 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	25 - 1	6.55	-	-	5.95	-	-	-	-	0.00	-	-	0.00	-	-	-	-	-	0.00	NA	NA	-	-	-	-	-	-	-
	25 - 2	9.33	-	-	5.16	-	-	-	-	0.00	-	-	0.99	-	-	-	-	-	1.79	NA	NA	-	-	-	-	-	-	-
	26 - 1	24.80	-	-	9.92	-	-	-	-	0.40	-	-	2.38	-	-	-	-	-	7.74	NA	NA	-	-	-	-	-	-	-
	26 - 2	9.92	-	-	0.00	-	-	-	-	0.00	-	-	0.00	-	-	-	-	-	9.92	NA	NA	-	-	-	-	-	-	-
	27 - 1	16.47	-	-	7.74	-	-	-	-	0.00	-	-	0.99	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	27 - 2	22.02	-	-	9.13	-	-	-	-	0.00	-	-	0.20	-	-	-	-	-	7.34	NA	NA	-	-	-	-	-	-	-
	28	23.81	-	-	10.12	-	-	-	-	0.00	-	-	0.60	-	-	-	-	-	8.73	NA	NA	-	-	-	-	-	-	-
	29	31.15	-	-	11.90	-	-	-	-	0.20	-	-	0.20	-	-	-	-	-	9.52	NA	NA	-	-	-	-	-	-	-
	30	29.37	-	-	15.28	-	-	-	-	0.20	-	-	0.00	-	-	-	-	-	6.94	NA	NA	-	-	-	-	-	-	-
	31	22.22	-	-	11.90	-	-	-	-	0.00	-	-	0.00	-	-	-	-	-	0.00	NA	NA	-	-	-	-	-	-	-
	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	33	23.41	-	-	15.08	-	-	-	-	0.00	-	-	0.00	-	-	-	-	-	3.37	NA	NA	-	-	-	-	-	-	-
2022	20	11.51	-	-	9.52	-	-	0.20	-	-	-	0.00	-	-	1.59	-	-	0.40	NA	NA	-	-	-	-	-	-	-	-
	22	8.53	-	-	3.82	-	-	2.41	-	-	-	1.61	-	-	0.60	-	-	0.40	NA	NA	-	-	-	-	-	-	-	-
	23	30.56	-	-	20.63	-	-	4.37	-	-	-	1.98	-	-	0.20	-	-	6.15	NA	NA	-	-	-	-	-	-	-	-
	24	52.98	-	-	31.62	-	-	19.30	-	-	-	6.98	-	-	0.41	-	-	13.35	NA	NA	-	-	-	-	-	-	-	-
	25	55.75	-	-	41.32	-	-	18.80	-	-	-	4.13	-	-	0.83	-	-	3.93	NA	NA	-	-	-	-	-	-	-	-
	26	56.75	-	-	21.65	-	-	41.86	-	-	-	0.62	-	-	0.41	-	-	3.09	NA	NA	-	-	-	-	-	-	-	-
	27	59.13	-	-	0.62	-	-	59.75	-	-	-	2.90	-	-	4.98	-	-	1.24	NA	NA	-	-	-	-	-	-	-	-
	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	2023	26	42.26	NA	NA	4.96	NA	NA	33.53	NA	NA	0.40	NA	NA	5.56	NA	NA	0.20	NA	NA	0.00	NA	NA	3.57	NA	NA	0.79	NA
31		99.80	0.011	0.01 (0.906)	79.56	0.014	0.53 (0.465)	95.63	-0.031	2.15 (0.142)	48.02	NA	NA	74.40	0.000	0.00 (1.000)	54.76	NA	NA	0.00	NA	NA	63.89	0.039	4.77 (0.029)	50.40	NA	NA
36		100.00	0.038	0.17 (0.678)	72.22	-0.006	0.10 (0.746)	95.44	0.028	1.74 (0.188)	52.38	NA	NA	76.98	-0.029	3.73 (0.053)	50.40	NA	NA	0.00	NA	NA	68.06	0.003	0.04 (0.850)	50.20	NA	NA

Cumulative		PREDATORS																										
Year		All groups			Araneae			Coleoptera			Dermaptera			Diptera			Hemiptera			Parasitized aphids			Parasitoids			Other Hymenoptera		
		% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)	% occurrence	Slope	x2 (p-value)
2021		100.00	-	-	98.81	-	-	88.10	-	-	4.76	-	-	21.43	-	-	-	-	76.19	0.269	0.77 (0.381)	-	-	-	-	-	-	-
2022		100.00	-	-	98.81	-	-	98.81	-	-	-	-	-	53.57	-	-	20.24	-	-	77.38	-0.098	2.71 (0.100)	-	-	-	-	-	-
2023		100.00	0.203	0.06 (0.800)	100.00	0.011	0.12 (0.725)	100.00	-0.028	0.38 (0.538)	100.00	0.037	1.85 (0.174)	100.00	-0.034	1.91 (0.167)	100.00	0.028	0.94 (0.332)	0.00	0.000	NA	100.00	0.000	2.38 (0.123)	100.00	-0.010	0.14 (0.706)

Table S21. Effects of the plot-level chemotype richness on the plot-level occurrence of ants at independent sampling times and at the cumulative year. Each column represents the different groups under analysis. Ants: *Lasius niger*. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group occurrence for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

OCCURRENCE		ANTS		
Year	Calendar week	% occurrence	Slope	χ^2 (p-value)
2021	24 - 1	-	-	-
	24 - 2	-	-	-
	25 - 1	47.22	0.012	0.71 (0.398)
	25 - 2	30.75	0.008	0.38 (0.538)
	26 - 1	39.29	0.007	0.24 (0.625)
	26 - 2	38.29	0.025	3.35 (0.067)
	27 - 1	32.54	0.038	7.35 (0.007)
	27 - 2	50.60	0.034	6.06 (0.014)
	28	44.84	0.002	0.02 (0.876)
	29	39.88	0.009	0.42 (0.519)
	30	19.64	0.007	0.34 (0.563)
	31	12.90	-0.012	1.39 (0.239)
	32	-	-	-
	33	-	-	-
2022	20	12.70	-0.012	1.44 (0.229)
	22	13.65	0.015	2.07 (0.150)
	23	31.75	-0.024	3.07 (0.080)
	24	33.88	0.004	0.10 (0.755)
	25	16.32	0.018	2.59 (0.107)
	26	18.97	0.013	1.10 (0.295)
	27	14.52	0.006	0.33 (0.565)
	29	-	-	-
	32	-	-	-
2023	26	16.07	0.001	0.01 (0.907)
	31	88.10	-0.002	0.03 (0.862)
	36	85.91	0.005	0.25 (0.615)

Cumulative		ANTS		
Year		% occurrence	Slope	χ^2 (p-value)
2021		98.81	-0.018	0.00 (0.992)
2022		97.62	-0.019	2.13 (0.144)
2023		100.00	0.000	NA

Table S22. Effects of the plot-level chemotype richness on the plot-level abundance of ants at independent sampling times and at the cumulative year. Each column represents the different groups under analysis. Ants: *Lasius niger*. % occurrence represents the percentage of plots that were occupied by the group under analysis for the specific sampling date or the cumulative over the year. Wald's Chi-square statistics and corresponding p-values of the LMM are presented (χ^2 (p-value)). Significant values ($P < 0.05$) are reported in bold font. Rows are: Calendar week of the survey, the specific sampling dates are found in Table S1. NA indicates that the analysis is not available, usually due to low plot occupancy (<60%). Hyphens ("-") denote instances where survey assessment is not conducted. The slope of the linear relationship between plot-level chemotype richness and group abundance for each sampling date is available inside each tile. If the slope is statistically significant ($P < 0.05$), it is presented in bold font and the tile is colored. The fill color of each tile represents the slope value for the corresponding group and date. The color scale ranges from blue (positive slopes) to white (neutral slopes) to red (negative slopes), with the midpoint set to 0.

ABUNDANCE		ANTS		
Year	Calendar week	% occurrence	Slope	χ^2 (p-value)
2021	24 - 1	-	-	-
	24 - 2	-	-	-
	25 - 1	47.22	-	-
	25 - 2	30.75	-	-
	26 - 1	39.29	-	-
	26 - 2	38.29	-	-
	27 - 1	32.54	-	-
	27 - 2	50.60	-	-
	28	44.84	-	-
	29	39.88	-	-
	30	19.64	-	-
	31	12.90	-	-
	32	-	-	-
	33	-	-	-
2022	20	12.70	-	-
	22	13.65	-	-
	23	31.75	-	-
	24	33.88	-	-
	25	16.32	-	-
	26	18.97	-	-
	27	14.52	-	-
	29	-	-	-
2023	32	-	-	-
	26	16.07	NA	NA
	31	88.10	0.006	0.07 (0.789)
	36	85.91	0.040	2.48 (0.115)

Cumulative		ANTS		
Year		% occurrence	Slope	χ^2 (p-value)
2021		98.81	-	-
2022		97.62	-	-
2023		100.00	0.089	3.15 (0.076)

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A-II. Chemodiversity Affects Preference for *Tanacetum vulgare* Chemotypes in Two Aphid Species

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Research article

Chemodiversity affects preference for *Tanacetum vulgare* chemotypes in two aphid species

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Plants of the same species can strongly differ in their specialized metabolite profiles, which can affect insect presence and abundance in the field. However, how specialized chemistry shapes plant attractiveness to herbivorous insects is not fully understood. Here, we used common tansy *Tanacetum vulgare*, Asteraceae) – a perennial plant that is highly diverse in terpenoid composition and is known to have variable chemotypes – to test whether 1) plants with different chemotype profiles differ in attractiveness to two specialist aphid species, *Macrosiphoniella tanacetaria* and *Uroleucon tanacetii*, in pairwise choice assays; 2) the diversity of the terpenoid blend affects plant attractiveness to aphids; 3) how plant chemical traits relate to plant morphological traits and which traits best explain aphid preference. We found that *M. tanacetaria* preferred two out of five chemotypes, dominated by α -thujone/ β -thujone and β -trans-chrysanthenyl acetate, while avoiding a chemotype dominated by α -pinene/sabinene. *Uroleucon tanacetii* showed no clear preference towards chemotypes, but when given a choice between chemotypes dominated by α -thujone/ β -thujone and by α -pinene/sabinene, they preferred the former. Importantly, plant attractiveness to aphids was marginally negatively correlated with chemodiversity, i.e. the number of terpenoid compounds, in *M. tanacetaria*, but not in *U. tanacetii*. Interestingly, the relative concentration and number of terpenoids were generally higher in larger and bushier plants. Hence, we did not observe a tradeoff between plant growth and defence. We conclude that plant chemical composition affects plant attractiveness to aphids and hence may contribute to variation in natural aphid colonization patterns on plants of the same species.

Keywords: aphids, attractiveness, choice assays, genotypic variation, intraspecific phytochemical diversity, plant diversity, terpenoids

Introduction

Understanding relationships between plants and herbivores is an important goal in ecology. How variation in plant diversity shapes herbivory has been a subject of study

for many decades (Scherber et al. 2010, Weisser et al. 2017). For a long time, between-species diversity was believed to be more important than within-species diversity as a driver of ecosystem processes (Des Roches et al. 2018). Intraspecific diversity, which includes the variation between individuals and the richness and abundance of genotypes and phenotypes within a population, recently gained more attention as an important driver of ecological processes (Raffard et al. 2019). It has been shown that intraspecific variation in plant genotype and phenotypes can structure plant–arthropod food webs (Crutsinger et al. 2006, Poelman et al. 2008, Bálint et al. 2016). As plants of the same species can differ strongly in various traits, understanding how this variation contributes to shaping interactions between plants and interaction partners is currently an important goal in plant ecology.

One important dimension of intraspecific variation in plants is chemodiversity, the variation in chemical composition between different plant individuals of the same species (Wetzel and Whitehead 2020). Primary metabolites are important regulators of basic physiological processes in plants, including growth, development and reproduction, and primary compounds are relatively similar across the plant kingdom (Weng et al. 2012). Specialized metabolites, on the other hand, play critical roles as mediators of interactions, and plants have evolved a much larger diversity in these specialized metabolites, both inter- and intraspecifically (Pichersky and Gang 2000, Iason et al. 2012). Intraspecific variation in specialized metabolite profiles is known to affect the structure of associated herbivore communities, including phloem-feeding insects such as aphids (Poelman et al. 2008, Bustos-Segura et al. 2017, Volf et al. 2019, Singh et al. 2021, Whitehead et al. 2021), but few studies have shown how chemodiversity structures herbivore abundance by affecting herbivore preference for plants (Ziaja and Müller 2023).

Chemodiversity may mediate the presence and abundance of insect herbivores on a plant growing in natural conditions. Natural patterns of insect herbivores are likely shaped by a combination of 1) direct attractiveness of the host plant to the insect herbivore, 2) direct effects via host plant resource quality (i.e. bottom-up effects) and 3) indirect effects, via the plant's attractiveness to natural enemies of the insect herbivore (i.e. top-down effects). Many specialized compounds likely evolved to deter and repel herbivores (Herms and Mattson 1992, Kessler and Baldwin 2001, Whitehead et al. 2021). However, some specialist herbivore species may also use these compounds to find their host (Nishida 2014, Wink 2018). As such, insects can be repelled or attracted by volatile organic compounds (VOCs) emitted into the headspace of a plant (Clancy et al. 2016, Jakobs and Müller 2019). Once an insect herbivore has arrived on the plant, stored and emitted compounds can then affect herbivore performance. For instance, stored compounds can act as feeding deterrents or influence the metabolism of the herbivores (Mithöfer and Boland 2012). But how these compounds act largely depends on the specific compound and the life history of the insect herbivore (Unsicker et al. 2009, McCormick et al. 2012, Jakobs et al. 2019).

Individual plants of the same species not only differ in their specialized metabolites, but often also differ pronouncedly in the expression of morphological traits. Various studies point out that traits related to growth or to structural defences may play an important role in driving interactions between plants and insects (Herms and Mattson 1992, Agrawal and Fischbein 2006). For instance, in a study on wheat plants, Batyrshina et al. (2020) found higher numbers of aphids on fast-maturing than on slow-maturing wheat plants. Indeed, tradeoffs between plant growth and defence are thought to be common in nature (Coley et al. 1985, Herms and Mattson 1992). Furthermore, plants with more pronounced mechanical defence traits, including stronger and tougher leaf tissues, tend to be better defended against insect herbivory (Caldwell et al. 2016). It is possible that at least some chemical traits are linked to morphological traits, together driving insect preference. For instance, Hayashi et al. (2005) found that trichome density and leaf mass per area differed between the two chemotypes of *Salix sachalinensis* (Salicaceae). Another striking example of differences in expression of chemical and morphological traits can be found in common tansy, *Tanacetum vulgare* (Asteraceae). In this species, plants with a higher storage of the terpenoid camphor were found to have taller shoots than those with lower camphor amounts, while plants containing davanone-D or artemisia ketone developed more flower heads, taller corymbs, and delayed flowering compared to plants with a lower content of these terpenoids (Keskitalo et al. 2001). Furthermore, *T. vulgare* from different origins (e.g. North America and Europe) have been found to differ in both morphological and chemical traits and exhibit negative correlations between reproductive biomass and terpenoid concentrations (Wolf et al. 2011). *Tanacetum vulgare* is a perennial, aromatic plant that has a large geographic distribution and is associated with a complex herbivore community including mono-, oligo- and polyphagous aphids (Schmitz 1998, Keskitalo et al. 2001, Kleine and Müller 2011). *Tanacetum vulgare* is rich in different mono- and sesquiterpenoids and plants can be divided into chemotypes based on the composition of leaf terpenoids (Keskitalo et al. 2001, Kleine and Müller 2011). Previous studies and breeding experiments showed that terpenoid composition has a genetic basis in *T. vulgare* (Keskitalo et al. 2001). Specialized aphids are thought to be adapted to the metabolites in *T. vulgare* and to use these for finding host plants (Schoonhoven et al. 2005, Jakobs and Müller 2019). Aphid colonization, growth rate and survival, and even the genotypic structure of aphid colonies were found to be affected by *T. vulgare* chemotypes under natural colonization in the field (Senft et al. 2017, 2019, Clancy et al. 2018, Zytynska et al. 2019). Specialized aphids show preferences towards specific chemotypes that differ between species (Jakobs and Müller 2018), but which characteristics of *T. vulgare* chemotypes (e.g. diversity, relative concentrations, individual compounds) drive these preferences needs further investigation.

Here, we used six *T. vulgare* chemotypes to investigate how intraspecific differences in chemical profiles shape

attractiveness to the specialized aphids *Macrosiphoniella tanacetaria* (Hemiptera, Aphididae) and *Uroleucon tanacetii* (Hemiptera, Aphididae). We tested the following hypotheses: (H1) two aphid species will show species-specific attraction to distinct *T. vulgare* chemotypes, as previously shown by [Jakobs and Müller \(2018, 2019\)](#); (H2) chemodiversity negatively correlates with attractiveness, under the assumption that most specialized metabolites repel antagonistic organisms; and (H3) growth-related traits will tradeoff with chemodiversity, under the assumption that maintaining chemodiversity is costly and limits available resources for growth. Specifically, we investigated whether chemical composition relates to morphological traits, whether chemical or morphological traits are more important in driving aphid preference towards specific plant chemotypes, and whether the quantity or quality of terpenoids contribute to plant attractiveness to aphids.

Material and methods

Chemotypic characterization of *T. vulgare* lines

In 2019, leaf and seed samples of 27 *T. vulgare* plants (hereafter: mothers) were collected in Jena, Germany (50°55'48"N, 11°34'48"E), and chemotyped based on their terpenoid profiles. Terpenoids were analyzed as in [Ziaja and Müller \(2023\)](#). The leaf material was freeze-dried, homogenized, weighed and extracted in heptane, adding one-bromodecane as internal standard. Extracts were centrifuged and the supernatants analyzed using gas chromatography coupled with mass spectrometry (GC-MS; GC 2010plus – MS QP2020, Shimadzu) on a semi-polar column (VF-5 MS, 30 m length, 0.2 mm ID, 10 m guard column, Varian) in electron impact ionization mode at 70 eV, with helium as carrier gas. Samples were injected at 240°C with a 1:10 split. A starting temperature of 50°C was kept for 5 min, ramping up to 250°C at 10°C min⁻¹, then increasing with 30°C min⁻¹ to a final temperature of 280°C, hold for 5 min. An alkane standard mix (C7–C40, Sigma Aldrich) was measured regularly between samples. For identifying the terpenoids, retention indices (RI) and mass spectra were compared with available synthetic reference compounds library entries of the National Institute of Standards and Technology (NIST) 2014, Pherobase ([El-Sayed 2014](#)) and mass spectra reported in [Adams \(2017\)](#). Terpenoids were semi-quantified using the peak areas of the total ion chromatograms, relative to the sample dry mass and the peak area of the internal standard.

Plant terpenoid profiles were clustered using unsupervised hierarchical k-means clustering with the *hclust()* function. A dissimilarity matrix was calculated based on the terpenoid concentrations using the *dist()* function. We used absolute values for this, as differentiation between chemical profiles (chemotypes) is likely to be the result of both the terpenoid composition and terpenoid concentration, and both aspects are considered to be ecologically meaningful in terms of mediating plant attractiveness to herbivores. The number

of clusters, *k*, was obtained using the elbow method. We selected a *k*=7 for mothers and used mothers from six clusters for further chemotype selection.

Two mothers per cluster were then randomly selected and the collected seeds were mass-sown in seedling trays in November 2020. Ten healthy seedlings were selected from each of 12 mother plants (6 clusters × 2 mothers), resulting in a total of 120 plants grown from seeds (hereafter: daughters). Seedlings were transplanted to 10 cm pots filled with standard potting substrate (Stender potting substrate C 700 coarse structure, 1 kg NPK minerals m⁻³, pH 5.5–6.0) and transferred to a greenhouse compartment at the Plant Technology Centre of the Technical University of Munich. Plants received supplemental lighting (standard Sylvania neon tube, 58W/125, universal white light) with 16:00:8:00 h L:D which was turned off when outdoor light was > 40 klx. After seven weeks, the ultimate 3–4 leaflets from the youngest fully expanded pinnate leaf of each plant were harvested. Samples were flash-frozen in liquid nitrogen, and subsequently freeze-dried for chemotyping. All daughters were transplanted to a common garden on-site in July 2021 and watered well until fully established.

As *T. vulgare* is outcrossing, daughter plants from the same mother can express different chemotypes in dependence of the pollen donors ([Lokki et al. 1973](#), [Holopainen et al. 1997](#), [Dussarrat et al. 2023](#)). Therefore, we conducted a second unsupervised hierarchical clustering on the daughter terpenoid composition as described above for mothers. For the daughter profile clustering, the elbow *k* was at 5–7 clusters, which is why *k*=6 clusters was used for daughter clustering. Clusters were based on the dominant compound(s) and their relative terpenoid concentration, for example 'Athu-Bthu' with α-thujone and β-thujone as dominant compounds.

Propagation of plant material for aphid choice assays

Based on the results of the daughter cluster analysis, we selected three daughters per mother plant for further experimentation. In August 2021, fresh plant material was taken from the 18 selected daughters (6 mothers × 3 daughters), and shoot cuttings were prepared by cutting stem parts 1–2 cm below and 4–5 cm above a leaf node. Leaves were clipped in half to reduce evapotranspiration and the risk of mold. The stem cuttings were pressed in seedling trays filled with the same substrate as used for the mother plants. Cuttings were immediately covered by a transparent plastic hood which was gradually opened after three weeks, as the plants established roots and shoots. After acclimatizing the cuttings for two weeks, they were repotted to 10 cm pots and later to 17 cm pots to avoid pot limitation before their use in choice assays in December 2021. Plants were bottom-watered automatically and fertilized with Universol Blue fertilizer (18% N – 11% P – 18% K; ICL Deutschland), to maintain a target electrical conductivity of 1.0. No chemical insecticides or fungicides were used during plant propagation. Due to low propagation success of the Bthu-low chemotype, only the

remaining five chemotypes (with the respective 15 daughters) were used in pairwise aphid choice assays, and between 6–10 clones of the daughters were used in the experiment. Note that clones from the same daughter were grown in different pots randomly spaced in the greenhouse, thus resulting in independent development of each of the plants.

Morphological traits

Morphological traits were measured non-destructively for each of the original 120 daughter plants in February 2021. The number of stems, leaves, and total number of nodes per plant were counted, height was recorded in cm, and internode length was derived by dividing height (in cm) by the number of nodes. From the youngest fully expanded leaf, the total number of leaflets from one leaf, leaf length, and leaflet density (number of leaflets/petiole length) were assessed, and chlorophyll content was measured using a chlorophyll meter (Konica Minolta SPAD-502Plus). The leaf was then harvested and leaf surface area was determined using ImageJ (Schneider et al. 2012). The leaves were then dried for 72 h at 60°C to determine dry weight, specific leaf area.

Aphid rearing

Adults and nymphs of *M. tanacetaria* and *U. tanacetii* were collected in August 2021 from *T. vulgare* plants in a field near Freising, Germany (48°24'17.7228"N, 11°41'23.50968"E) and kept in plastic cages at room temperature with supplemental light at long day regimes (16:00:8:00 h L:D). Plants for feeding the aphid colonies were unrelated to the used chemotypes for this study to avoid an induction of preferences in the aphid colonies. For each testing round, roughly 100 unwinged adult aphids of each species were placed on individual fresh plants. After 48 h, all adult aphids were removed, and all nymphs were left on the plants. Subsequently, the cohorts were kept in a Fitotron standard growth chamber 120 (21/16°C, 60% RH, Weiss Technik) for eight days. Before the start of the choice assays, the aphids were starved in a petri dish with a small piece of wet tissue for 24 h to ensure immediate feeding, as has been done in other insect species (Minoretti and Weisser 2000, Bustos-Segura and Foley 2018, Clancy et al. 2020).

Pairwise choice assays

For choice assays, we used clones from five out of the six *T. vulgare* maternal chemotypes with their respective three replicate daughters per chemotype. A priori, a full-factorial series of pairwise choice assays were designed, in which aphids could choose between cloned plants of two different chemotypes (Supporting information). Within each replicate series, all chemotypes were tested against each other using randomly picked clones from randomly picked daughters of the mother chemotypes, maximizing the number of unique pairwise choices between chemotype-daughter pairs. Choice assays were conducted in three rounds on three different days with different aphid cohorts that were standardized by age (9–10

days old), all executed within one week (9–16 December 2021). In total, we performed $n = 23$ replicate rounds for *M. tanacetaria*, and $n = 13$ for *U. tanacetii*, as their cohort numbers were substantially lower. The specific assignment of combinations of *T. vulgare* daughters for both aphid species can be found in the supplement (Supporting information).

For the choice assays, the second and third youngest fully expanded leaf of a plant were selected, the first three leaflets discarded, and the following leaflets used in assays. Two different leaflets were placed in new 14.5 cm petri dishes at equal distances from the centre, and 8 cm apart from each other. The sides for each replicate alternated between replicate rounds to account for external bias. One starved aphid was placed in the centre of the petri dish, and the petri dishes were sealed with parafilm, to prevent the leaves from drying quickly. Petri dishes were kept in a climate chamber at Technical University of Munich (TUM Model EcoSystem Analyzer TUMmesa). The LED lighting system in these chambers generates homogenous light conditions, aimed at reducing spatial effects. Petri dishes were left for 24 h (16:00:8:00 h L:D photoperiod, 21°C, 60% RH). Aphid preference was recorded after two, five and 24 h. However, as leaf quality visibly decreased after 24 h, but as aphids rely on leaf turgor for feeding, most were not on the leaves, or had died. Therefore, we excluded the 24 h time point from all following analyses. Each aphid and leaf were only used once. Dead aphids were excluded from further analyses.

Statistical analysis

All statistical analyses were performed in R (www.r-project.org). All used R code can be found in the Supporting information.

To address H1, we conducted binomial tests to test if aphids preferred one chemotype over another for each pairwise combination. We tested whether the number of choices made for one chemotype in a specific combination was significantly different from what would be expected in a random choice. Binomial tests were also used to check whether spatial (left/right side of the petri dish) effects on aphid preference occurred, using all observations per species ($n = 360$ for *M. tanacetaria*, $n = 130$ for *U. tanacetii*) as well as observer effects, using all observations ($n = 690$). Four separate logit models were used, to determine the attractiveness of specific *T. vulgare* chemotypes for each aphid species, and the attractiveness of specific *T. vulgare* daughters for each aphid species, across all combined pairwise tests, using the R 'survival' package (Therneau 2021). Z-values were obtained from the models for each *T. vulgare* chemotype and for each *T. vulgare* daughter as a proxy for attractiveness, with plants with more positive z-values being more and negative z-values being less attractive to aphids.

To test H2, we calculated plant chemodiversity metrics for each daughter plant (Shannon diversity, terpenoid evenness, terpenoid richness and relative total terpenoid concentration) from the absolute terpenoid profiles, using the 'vegan' package (Oksanen et al. 2020). In four separate models for

each aphid species, we tested for relationships between plant attractiveness (z-value, response variable) and 1) Shannon diversity; 2) terpenoid evenness; 3) terpenoid richness; and 4) relative total terpenoid concentration (1–4 explanatory variables). These models were replicated at the *T. vulgare* daughter level ($n=15$). We further tested for correlations between the relative concentrations of individual compounds in a plant and the attractiveness of the plant separately for each of the two aphid species. We used unadjusted correlation plots and Holm-adjusted plots for multiple correlations, using the 'RcmdrMisc' package (Fox 2022) and present both for visualization purposes. For verification purposes, we ran a multiple regression model testing the effect of all compounds on attractiveness. As there was a substantial number of compounds (46), our models were limited by available degrees of freedom ($n=15$). Therefore, we removed all compounds that were measured in less than two-thirds of all samples. Using step() in combination with variance inflation factors to address multicollinearity, we reduced the model to the minimum adequate version, which only included individual compounds, which did not have significant effects on plant attractiveness to aphids.

To address H3, we tested for differences among chemotypes in plant height, number of stems, number of leaves, leaflets density, specific leaf area and chlorophyll, Shannon diversity, terpenoid evenness, terpenoid richness and relative total terpenoid concentration, by using one-way ANOVA with chemotype as a fixed factor ($n=18$ replicates in total for chemotypes).

Results

Chemical profile of chemotypes

Hierarchical k-means clustering of terpenoid profiles resulted in six large daughter clusters, without any small outlier clusters driven by strongly deviating individual profiles (Fig. 1). Daughter lineages did not typically resemble their mother lineages in their terpenoid profiles or their clustering and, therefore, the observed daughter clusters typically included daughters from multiple mother lineages (Fig. 1). From each cluster, we selected three daughters from the same mother lineage. When more than three daughters were available from a mother in a cluster, we selected the three daughters clustering closest together. Our chemotype selection resulted in six maternal chemotype lines with three genetically different daughter replicates for each cluster (Fig. 1) that were used for preparing plants for the preference experiment.

Selected chemotypes showed a high diversity of compounds (Fig. 2a), and significantly differed in their Shannon diversity, terpenoid evenness and relative total terpenoid concentration, but not in their terpenoid richness (Fig. 2b–e). Specifically, the chemotype 'Athu-Bthu' had both α - and β -thujone as prevalent compounds. The chemotypes 'Bthu-low' and 'Bthu-high' were both dominated by β -thujone but characterized by a low or high relative total terpenoid concentration, respectively. The

chemotype 'Chrys-acet' was strongly dominated by β -trans-chrysantenyl acetate. In the chemotype 'Mixed-low' several terpenoids contributed more evenly to the total profile, and had overall a low relative total terpenoid concentration. In the chemotype 'Mixed-high', terpenoids had overall a higher relative total terpenoid concentration. The chemotypes Mixed-high and Mixed-low showed a significantly higher terpenoid Shannon diversity and terpenoid evenness than the other four chemotypes (Fig. 2b–c). The six selected chemotypes did not significantly differ in terpenoid richness (Fig. 2d), but did differ in their relative total terpenoid concentrations, with the chemotypes Mixed-low and Bthu-low expressing significantly lower concentrations compared to the other chemotypes (Fig. 2e). Every chemotype consisted of three daughters (biological replicates) which were number coded e.g. Mixed_high_21, Mixed_high_23 and Mixed_high_30.

Aphid preference for chemotypes (H1)

After two hours, seven *M. tanacetaria* and five *U. tanacetii* individuals were found dead and were excluded from the analyses. In total, 178 *M. tanacetaria* and 69 *U. tanacetii* had chosen the leaflet of one chemotype. A binomial test showed that *M. tanacetaria* aphids tended to marginally prefer leaflets from Athu-Bthu over leaflets from the chemotypes Mixed-low and Bthu-high (Table 1, Fig. 3a). After five hours of observation, *M. tanacetaria* showed a significant preference for chemotype Athu-Bthu over chemotype Mixed-low ($p=0.013$) and tended to prefer Chrys-acet over the chemotypes Mixed-low and Mixed-high (Table 1, Fig. 3b). *Uroleucon tanacetii* aphids significantly preferred the Athu-Bthu over the Mixed-low chemotype after two hours ($p=0.039$; Table 1, Fig. 3c), but after five hours no more significant preferences were observed for this species (Table 1, Fig. 3d).

Considering all aphid choices made across all pairwise comparisons in a clogit model, *M. tanacetaria* aphids showed a significant attraction to Chrys-acet ($z=2.331$, $p=0.020$) and a marginally significant attraction to the Athu-Bthu chemotype (Table 2, Fig. 4a), while *U. tanacetii* aphids did not show a clear preference for any chemotype (Table 2, Fig. 4b). However, we found that aphids also exhibited preferences at the individual plant daughter level, with *M. tanacetaria* showing significant preferences for the daughters Chrys-acet_95, Chrys-acet_100, Athu-Bthu_55 and Athu-Bthu_56, whereas *U. tanacetii* did not show significant preferences to any *T. vulgare* daughters (Table 3).

Aphid preference to plant chemodiversity (H2)

For *M. tanacetaria*, we observed a non-significant trend of decreasing attraction to plants with higher terpenoid Shannon diversity (Fig. 4c) and higher terpenoid evenness (Fig. 4d), when testing independent variables separately in linear regression models, but a non-significant trend of increased attraction to plants with a higher relative total terpenoid concentration (Fig. 4e). For *U. tanacetii*, we observed no significant relationships between attractiveness and chemodiversity indices.

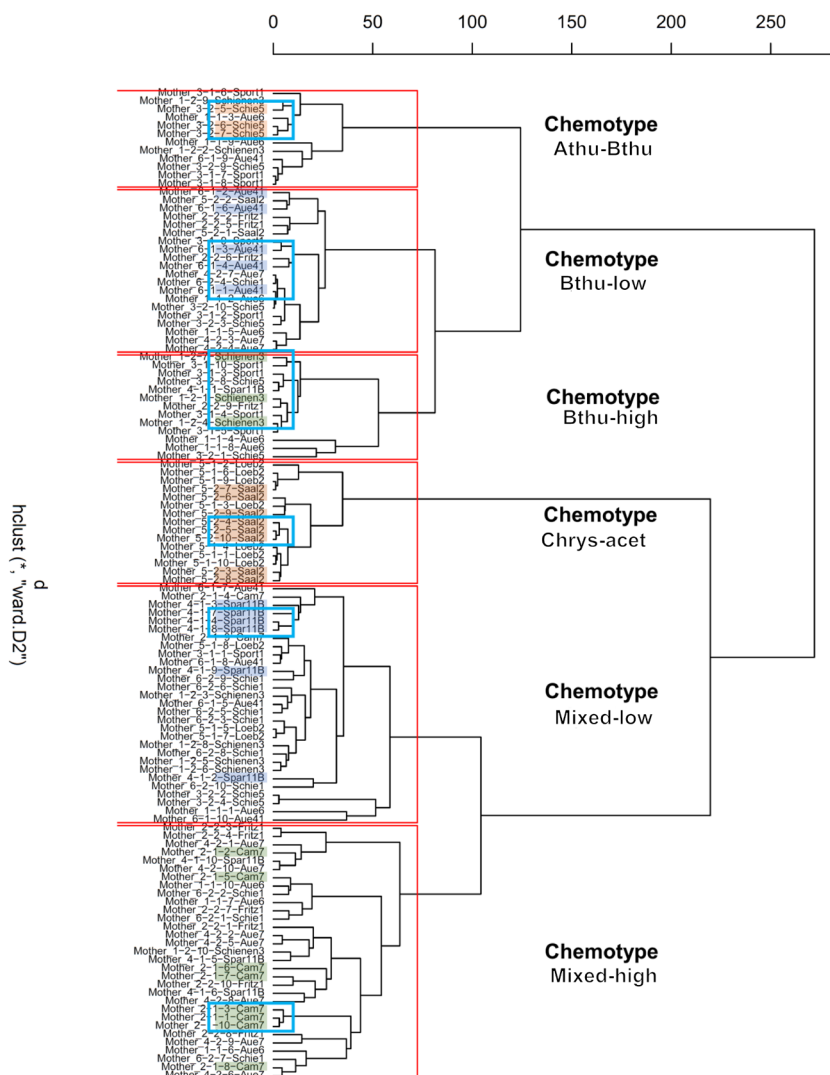


Figure 1. Hierarchical clustering tree for terpenoid profiles of all 120 daughter plants from *Tanacetum vulgare*. Clusters ($k=6$) are indicated in red boxes. For the selection, in each cluster a different mother lineage was chosen, and three daughters were manually selected and highlighted. The final selection of daughters of each cluster is indicated in blue boxes.

Unadjusted correlation plots of individual terpenoids revealed that various relationships existed between individual terpenoids and the attractiveness to aphid species, but when Holm-adjusted for multiple correlations were applied, this reduced the relationships between attractiveness and individual terpenoids to only a single weak negative relationship between 1-terpinen-4-yl acetate and plant attractiveness to *M. tanacetaria* (Fig. 4f). This was further verified with simplified multiple regression models corrected for collinearity, which reduced the models to single terpenoid compounds as factors, which did not significantly affect plant attractiveness.

Relationships between chemical diversity and morphological plant traits (H3)

Significant positive relationships were observed between the number of stems per *T. vulgare* daughter and terpenoid Shannon diversity ($n=120$ daughter plants, Table 4, Fig. 5a),

T. vulgare daughter height and terpenoid Shannon diversity (Fig. 5b), and *T. vulgare* daughter height and relative terpenoid concentration (Fig. 5c).

Discussion

In this study, we found that the investigated *T. vulgare* plants clustered into six distinct chemotypes that differed in their terpenoid Shannon diversity, terpenoid evenness and relative total terpenoid concentration. We used five of these chemotype lines to test how leaf chemical profiles affected aphid preference in pairwise choice assays and found that two specialist aphid species showed species-specific preferences to specific chemotypes. Across all pairwise combinations *M. tanacetaria* showed stronger preferences and patterns of attraction than *U. tanacetii*. In line with our expectations, we observed a trend of higher attractiveness of plants with a higher relative total

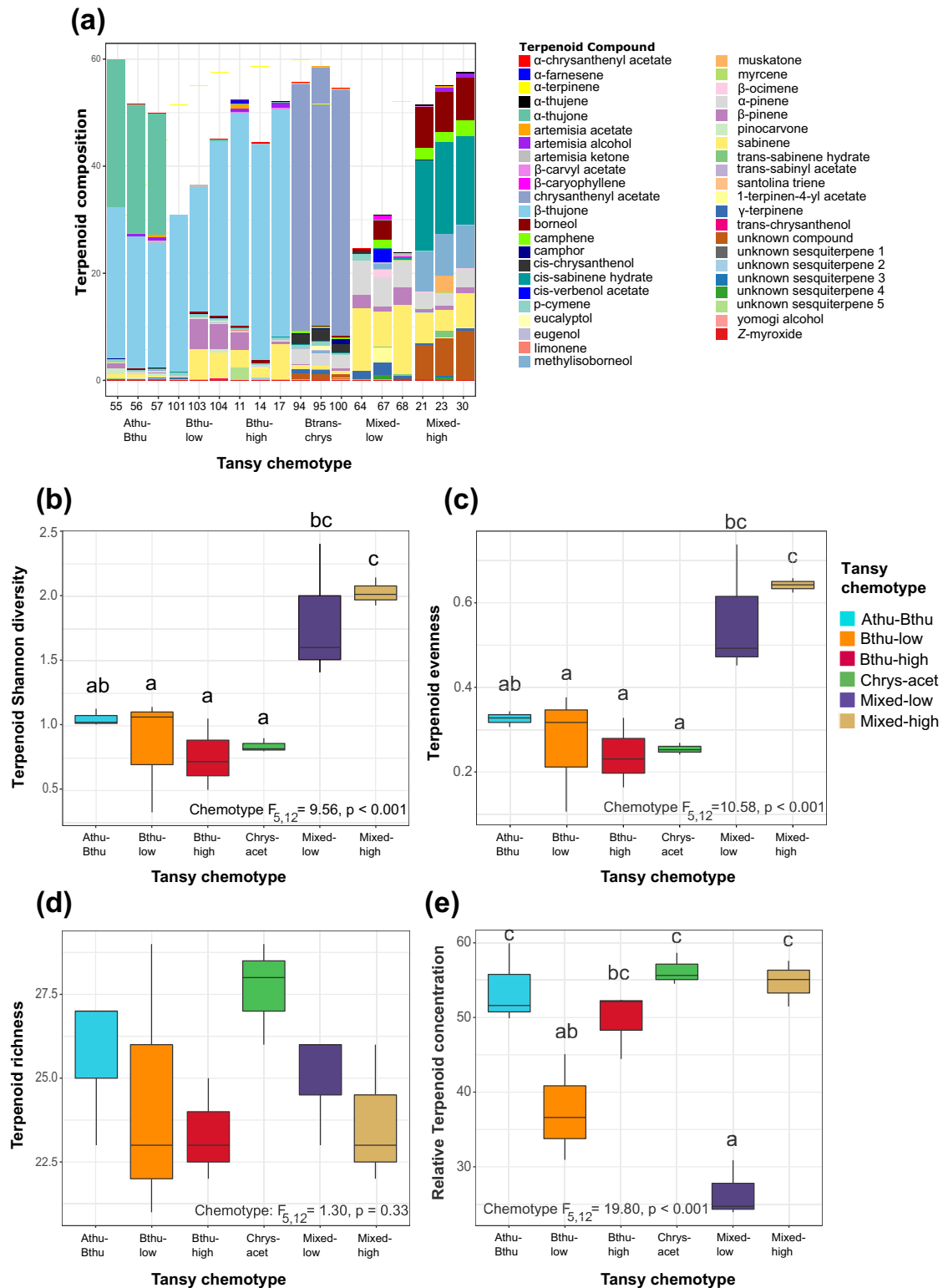


Figure 2. Differences in chemical composition of leaves of different *T. vulgare* chemotypes. (a) Stacked bar chart showing the composition of the chemical profiles of each of the three daughters of the selected six maternal chemotypes. Box plots (b–e) show differences among chemotypes as interquartile ranges of (b) terpenoid Shannon diversity, (c) terpenoid evenness, (d) terpenoid richness, and (e) relative total terpenoid concentration for each chemotype. The lower hinge corresponds to the first quartile (25th percentile) and the upper hinge depicts the third quartile (75th percentile). Whiskers extend to the 5 and 95% percentiles; solid lines represent the medians. Chemotype effect is indicated in panels, letters above bars indicate significant differences ($p < 0.05$) between chemotypes based on post hoc Tukey tests. Boxplots represent $n = 3$ daughters per chemotype.

Table 1. Effects of five *Tanacetum vulgare* chemotypes on their attractiveness to *Macrosiphoniella tanacetaria* and *Uroleucon tanacetii*, when offered in pairwise choices. A binomial test was used to obtain credible intervals and p-values. Significant values are highlighted in bold, marginally significant values in italics.

Time (h)	Chemotype 1	Chemotype 2	<i>Macrosiphoniella tanacetaria</i>			<i>Uroleucon tanacetii</i>		
			n	95% CI	p-value	N	95% CI	p-value
2	Athu-Bthu	Mixed-low	18	<i>0.465, 0.903</i>	<i>0.096</i>	9	0.518, 0.997	0.039
2	Athu-Bthu	Bthu-high	19	<i>0.488, 0.909</i>	<i>0.064</i>	9	0.212, 0.863	1
2	Athu-Bthu	Mixed-high	20	0.231, 0.685	0.824	7	0.184, 0.901	1
2	Athu-Bthu	Chrys-acet	17	0.230, 0.722	1	6	0.118, 0.882	1
2	Mixed-low	Chrys-acet	16	0.110, 0.587	0.210	7	0.184, 0.901	1
2	Mixed-high	Chrys-acet	15	0.078, 0.51	0.119	6	0.043, 0.778	0.688
2	Bthu-high	Chrys-acet	18	0.133, 0.590	0.238	6	0.043, 0.778	0.688
2	Bthu-high	Mixed-low	17	0.330, 0.816	0.629	8	0.085, 0.755	0.727
2	Bthu-high	Mixed-high	19	0.435, 0.874	0.167	6	0.043, 0.778	0.688
2	Mixed-low	Mixed-high	18	0.215, 0.692	0.815	5	0.284, 0.995	0.375
5	Athu-Bthu	Mixed-low	17	0.566, 0.962	0.013	5	0.147, 0.947	1
5	Athu-Bthu	Bthu-high	18	0.410, 0.867	0.238	8	0.157, 0.843	1
5	Athu-Bthu	Mixed-high	19	0.335, 0.798	0.648	4	0.194, 0.994	0.625
5	Athu-Bthu	Chrys-acet	16	0.247, 0.754	1	7	0.099, 0.816	1
5	Mixed-low	Chrys-acet	18	<i>0.097, 0.535</i>	<i>0.096</i>	6	0.043, 0.778	0.688
5	Mixed-high	Chrys-acet	19	<i>0.092, 0.512</i>	<i>0.064</i>	5	0.147, 0.947	1
5	Bthu-high	Chrys-acet	16	0.247, 0.754	1	6	0.118, 0.882	1
5	Bthu-high	Mixed-low	19	0.289, 0.756	1	6	0.118, 0.882	1
5	Bthu-high	Mixed-high	21	0.430, 0.854	0.189	8	0.085, 0.755	0.727
5	Mixed-low	Mixed-high	18	0.215, 0.692	0.815	5	0.147, 0.947	1

terpenoid concentration and lower terpenoid Shannon diversity and evenness, despite our low power to detect these relationships, and only for *M. tanacetaria*. Remarkably, although characteristics of the chemical blend correlated with plant attractiveness to aphids, it could not be clearly linked to individual terpenoids, suggesting that the interaction between compounds is responsible for preferences.

In line with our first hypothesis, we found that aphids preferred different chemotypes in pairwise choice assays. *Macrosiphoniella tanacetaria* preferred leaves from plants of Athu-Bthu and Chrys-acet chemotypes, with preference patterns becoming more pronounced at later time points of the assay. Previous studies found higher numbers of *M. tanacetaria* present on plants dominated by β -thujone compared to those dominated by trans-caryyl acetate in a climate chamber experiment (Jakobs and Müller 2018) but a higher abundance of *M. tanacetaria* on plants with camphor compared

to those with β -thujone as the dominant terpenoid in a field study (Benedek et al. 2019a). We also observed that *U. tanacetii* was significantly attracted towards plants of the Athu-Bthu chemotype, with the preference becoming less pronounced over time. This is interesting, as previously negative effects of β -thujone on *U. tanacetii* numbers have been found in the field (Benedek et al. 2019b), though *U. tanacetii* were attracted to plants with high relative levels of α -thujone and β -thujone growing in homogenous plant patches in

Table 3. Effects of *T. vulgare* daughters on their attractiveness to *M. tanacetaria* and *U. tanacetii* based on all pairwise combinations in the choice assays after two hours of observation. A c-logit model, including effects of daughter (five chemotypes $\times$ three daughters) on aphid choices, was used to obtain z- and p-values. Significant values are highlighted in bold, marginally significant values in italics.

Daughter	<i>Macrosiphoniella tanacetaria</i>		<i>Uroleucon tanacetii</i>	
	z-value	p-value	z-value	p-value
Mixed-high_21	-0.792	0.429	-1.203	0.229
Mixed-high_23	1.064	0.288	-1.447	0.148
Mixed-high_30	1.602	0.110	0.506	0.613
Chrys-acet_100	2.171	0.030	0.302	0.762
Chrys-acet_94	1.589	0.112	-0.659	0.510
Chrys-acet_95	2.439	0.015	0.442	0.658
Athu-Bthu_55	2.183	0.029	-0.207	0.836
Athu-Bthu_56	1.983	0.047	0.100	0.921
Athu-Bthu_57	1.119	0.263	0.467	0.640
Bthu-high_11	1.058	0.290	-1.597	0.110
Bthu-high_14	1.451	0.147	-1.103	0.270
Bthu-high_17	0.858	0.391	0.434	0.664
Mixed-low_64	-0.246	0.806	-0.292	0.770
Mixed-low_67	0.666	0.505	-0.446	0.656
Mixed-low_68	1.075	0.283	-0.297	0.766

Table 2. Effects of five *T. vulgare* chemotypes on their attractiveness to *M. tanacetaria* and *Uroleucon tanacetii* based on all pairwise combinations of the choice assays after two hours of observation. A c-logit model was used to obtain z- and p-values (for visualization see Fig. 4). Significant values are highlighted in bold, marginally significant values in italics.

Chemotype	<i>Macrosiphoniella tanacetaria</i>		<i>Uroleucon tanacetii</i>	
	z-value	p-value	z-value	p-value
Mixed-high	-0.669	0.503	-1.226	0.220
Chrys-acet	2.331	0.020	0.783	0.434
Athu-Bthu	<i>1.730</i>	<i>0.084</i>	1.206	0.228
Bthu-high	0.340	0.734	-0.448	0.654
Mixed-low	-0.752	0.452	0.404	0.686

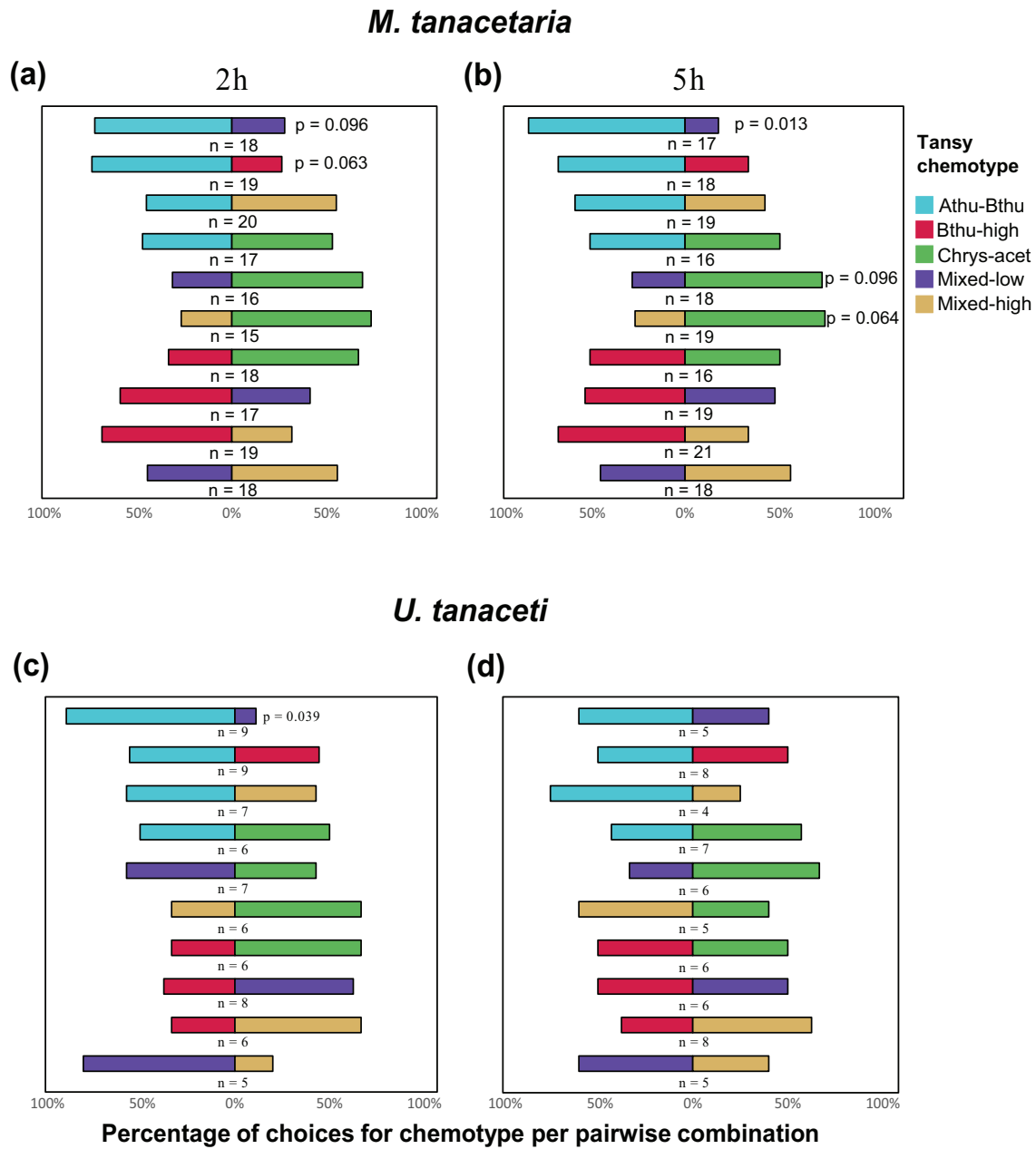


Figure 3. Chemotype effects on pair wise choices by aphids. Depicted are mean percentage of choices by *Macrosiphoniella tanacetaria* after two (a) and five hours (b), and *Uroleucon tanacetii* after two (c) and five (d) hours, for all possible pairwise combinations of chemotypes. Effective sample size is indicated for each pairwise comparison, and no-choice replicates were excluded. Note that chemotype Bthu-low was not included in pairwise comparisons due to propagation difficulties. p-values next to bars indicate (marginally) significant preferences (for test statistics see Table 1). No-choice replicates were removed from the analyzes. Realized replication levels for the choice assays ranged between n = 15–21 per chemotype pair for *M. tanacetaria*, and between 4–9 for *U. tanacetii*.

another study (Ziaja and Müller 2023). However, in another common garden study no clear preference was observed towards chemotypes for this aphid species (Kleine and Müller 2011). Under field conditions, different factors (including insect preference, bottom-up and top-down processes) affect observed aphid numbers, which may explain some discrepancies between field observations and choice assays. In ‘snapshot’ field observations, these independent factors can be hard to disentangle. In addition, concentrating only on

the dominant compounds may be misleading, as minor compounds or the blend itself can result in the biological effect (Unsicker et al. 2009). Therefore, studies under laboratory conditions are necessary to understand the influence of these individual factors on aphid behavior and performance. Our results suggest that aphid preference for plants might not always reflect how they perform on plants.

In our experiment, 70–91% of *M. tanacetaria* individuals made a choice after five hours for one chemotype in each

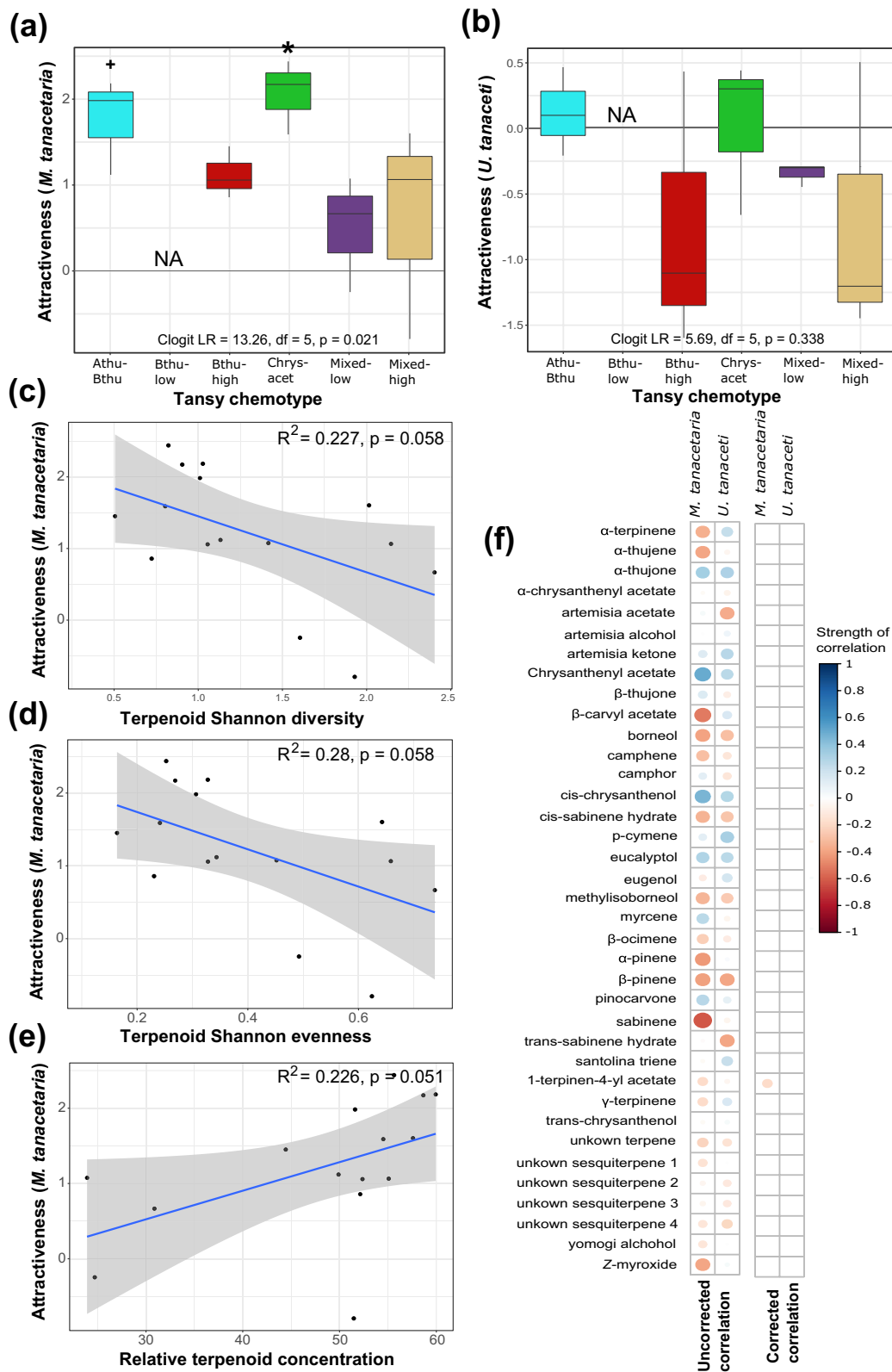


Figure 4. Relationships between *T. vulgare* attractiveness and chemodiversity for both aphid species. Attractiveness (reflected by the z-value) was computed by summarizing all decisions made towards a specific chemotype over all combinations after two hours and using a clogit model to test whether a certain chemotype was chosen more often than expected compared to a random choice. (a) Mean attractiveness per chemotype for *M. tanacetaria* after two hours. (b) Mean attractiveness per chemotype for *U. tanacetii* after two hours. Symbols indicate

Figure 4. (Continued)

significance levels (* $p < 0.05$; + $0.05 < p < 0.10$). For detailed model output for (a) and (b) Table 3. (c) Relationship between *T. vulgare* terpenoid Shannon diversity and attractiveness to *M. tanacetaria*. (d) Relationship between *T. vulgare* terpenoid evenness and attractiveness to *M. tanacetaria*. (e) Relationship between *T. vulgare* terpenoid abundance and attractiveness to *M. tanacetaria*; in (c–e) dots represent the mean z-value (attractiveness) for each of the 15 daughters (5 chemotypes $\times$ 3 daughters). (f) Correlation plots showing relationship between individual terpenoid compounds and attractiveness to both aphid species. The size of the dot depicts the strength of the correlation. Blue colors indicate positive and red colors indicate negative correlations. The left correlation plot shows all unadjusted correlations with a significant p-value. The right correlation plot shows all correlations with a significant p-value after using Holm-adjusted for multiple correlations.

combination, compared to only 30–61% of *U. tanacetii* individuals. These species-specific differences between the aphids may be explained by differences in their life histories and preferred niches (Jakobs et al. 2019). In various field and greenhouse experiments, we observed that these aphid species showed different behaviors on and off the plant. For instance, *M. tanacetaria* tends to be more mobile than *U. tanacetii*, and readily searches for new host plants when its current host deteriorates. *Uroleucon tanacetii* typically remains on leaves until yellowing, and then move to the next upper non-infested leaf. We found more deaths and fewer choices made at later time points (i.e. after 24 h), which could be because individual leaflets do dry out after some time. However, as individual choices were already apparent and similar after two and five hours, we believe that deteriorating leaf quality did not affect choices made after two hours.

Across all experimental choice combinations, we found significant effects of chemotype on the attractiveness of those chemotypes for *M. tanacetaria*, but not for *U. tanacetii*. This is in line with previous research from Kleine and Müller (2011), who found that *M. tanacetaria*, but not *U. tanacetii* exhibited distinct preferences towards specific chemotypes. To understand what may drive the attractiveness of a plant to *M. tanacetaria*, we investigated relationships between *T. vulgare* individual chemical properties and their level of attractiveness to aphids. We observed that terpenoid Shannon diversity negatively correlated with attractiveness to *M. tanacetaria* aphids. This is consistent with the hypothesis on the evolution of chemodiversity in plants, and particularly the evolution of a breadth of specialized compounds to repel antagonists (Wetzel and Whitehead 2020). Furthermore, we found that terpenoid evenness marginally negatively correlated with attractiveness to *M. tanacetaria*, indicating that blends that were more evenly distributed in terpenoid composition were

less attractive to aphids than those dominated by one or several compounds. A plausible explanation might be that having some highly dominant compounds could serve as strong cues for plant recognition (Kleine and Müller 2011). However, once an aphid has arrived on a plant, subsequent aphid performance on *T. vulgare* is likely affected more pronouncedly by the phloem sap composition (Jakobs and Müller 2019). We also found a positive effect of relative total terpenoid concentration on attractiveness to *M. tanacetaria*. This might be an indication that although Shannon diversity can have a deterrent effect (Whitehead et al. 2021), the relative total terpenoid concentration (as a proxy for potential emission) can also be an important cue for host finding. A role of specialized metabolite concentrations in herbivore attraction and repellence has been found in numerous studies (reviewed by Macel 2011). For instance, contrasting effects have been observed in the specialized aphid *Aphis jacobaea* (Hemiptera, Aphididae) on *Jacobaea vulgaris* (Asteraceae), where plants high in pyrrolizidine alkaloids hosted fewer aphids than plants with low concentrations, although this could not be related to aphid preference behavior alone (Vrieling et al. 1991). Our results align with those from a recent study that shows that chemodiversity is an important driver of dietary specialization in insects (Leong et al. 2022). The relationships between *M. tanacetaria* and terpenoid Shannon diversity, evenness and relative total terpenoid concentration were only marginally significant, which may have been a result of the limiting number of chemotype lines ($n = 15$) included in our current study. Our study was limited by the poor propagation success of one of the chemotype lines, and the low number of daughters selected for choice assays. Future studies on a range of terpenoid diversity profiles should be performed to strengthen the empirical evidence for chemodiversity as driver of herbivore preference.

Table 4. Model output of multiple linear regression models testing the effects of plant morphological characteristics on plant attractiveness for *M. tanacetaria* and *U. tanacetii*, and on plant chemodiversity characteristics. Models were checked for collinearity by variance inflation factors and simplified via stepwise model selection. Dashes indicate variables were removed from the model.

Explanatory variable	Attractiveness <i>Macrosiphoniella tanacetaria</i> F (p-value)	Attractiveness <i>Uroleucon tanacetii</i> F (p-value)	Terpenoid richness F (p-value)	Terpenoid Shannon diversity F (p-value)	Terpenoid Shannon evenness F (p-value)	Terpenoid concentration (relative) F (p-value)
Height	–	–	0.20 (0.665)	6.03 (0.028)	6.44 (0.024)	7.05 (0.017)
No. of stems	10.20 (0.010)	–	0.11 (0.741)	8.33 (0.012)	9.12 (0.009)	–
No. of leaves	5.02 (0.049)	–	0.07 (0.801)	–	–	–
Leaflets density	3.14 (0.107)	1.85 (0.199)	–	–	–	–
SLA	–	–	–	–	–	–
Chlorophyll	6.94 (0.0250)	2.42 (0.146)	–	2.55 (0.133)	2.54 (0.133)	–

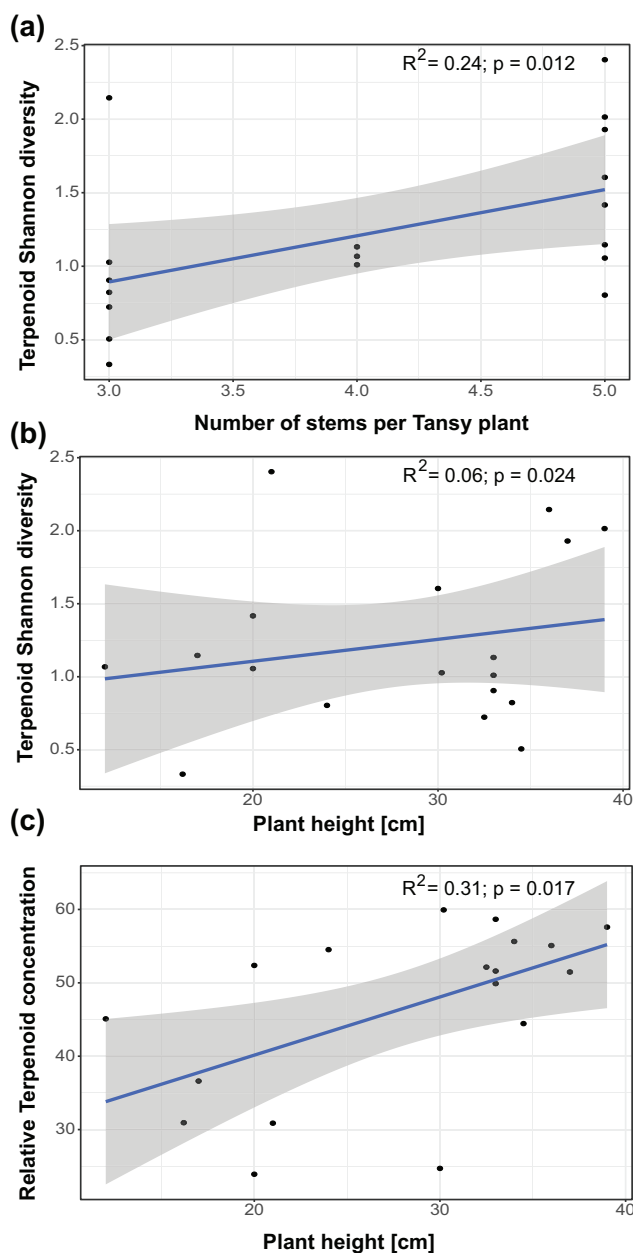


Figure 5. Relationships between chemical and morphological parameters. Each dot represents one of the 18 daughters (6 chemotypes $\times$ 3 daughters). (a) Relationship between the number of stems per *T. vulgare* plant and terpenoid Shannon diversity. (b) Relationship between *T. vulgare* height and terpenoid Shannon diversity. (c) Relationship between *T. vulgare* height and relative total terpenoid concentration. Values represent single measurements on individual daughters for each chemotype, which were used in the correlations (six chemotypes, three daughters, $n = 18$ total).

Our analyses of the role of individual compounds in influencing attractiveness indicated that the effect of individual terpenoids of *T. vulgare* attractiveness to aphids is minimal. After corrections for multiple correlations, we observed a weak negative effect of 1-terpinen-4-yl acetate on *T. vulgare* attractiveness to *M. tanacetaria*. Several studies have shown

relationships between chemotypes, or dominant compounds and aphid abundance in the field. For instance, β -thujone has been related to decreased colony distribution and colony numbers in *U. tanacetii* and abundances in *M. tanacetaria* in field studies (Bálint et al. 2016, Benedek et al. 2019b). Other studies have found an increased density of *Metopeurum fuscoviride* (Hemiptera, Aphididae) on chemotypes with high concentrations of borneol or camphor (Bálint et al. 2016, Senft et al. 2019), while plants with high amounts of α -thujone, (*E*)-dihydrocarvone, α -copaene and β -cubebene were colonized earlier (Clancy et al. 2016). Although we found only limited evidence that individual compounds impact aphid attractiveness, it cannot be ruled out that these compounds play a role in feeding deterrence once aphids have settled on the plant or in the attraction of natural enemies of herbivores. Importantly, our study included terpenoids only, but other compounds, such as, for example flavonoids that were not measured here, may also affect the preference behavior of the aphids. This calls for future studies disentangling the role of broader metabolome-wide chemodiversity in driving aphid and natural enemy dynamics on the plant.

It is important to disentangle the relation between chemical and growth traits, as both traits have been shown to influence plant–insect interactions, including preference behavior. While growth–defence tradeoffs are a fundamental principle in plant ecology (Herms and Mattson 1992, Karasov et al. 2017), we did not observe such a tradeoff in *T. vulgare*. In a previous study only inflorescence biomass but not other growth factors (e.g. plant height, total biomass, no. of stems) were significantly negatively correlated to terpenoid concentration (Wolf et al. 2011). However, instead we found a synergistic effect between variables associated with plant growth and terpenoid Shannon diversity and relative total terpenoid concentration in our plants. It is commonly assumed that plants have to partition their resources between growth and defence traits, leading to either smaller and better defended plants, or vice versa (Coley et al. 1985, Herms and Mattson 1992, He et al. 2022). Terpenoids are more expensive to produce than many other metabolites, as they require a wide array of different enzymes, posing substantial production and storage costs (Gershenzon 1994). However, contrary to these hypotheses, we found that larger and bushier plants had a higher relative total terpenoid concentration and terpenoid Shannon diversity. Similarly, positive relationships between growth and defence have been found in two *Plantago* species (Barton 2007, Plantaginaceae). One plausible explanation for our findings may be that larger plants photosynthesize more and have a larger energy budget, which can be used for elevated and diversified local terpenoid synthesis. Furthermore, it is vital for plants to grow and defend to optimize their fitness within a dynamic environment (Huot et al. 2014), and tradeoff patterns might also change with different plant ontogeny stages (Boege and Marquis 2005). Recent work has shown strong effects of maternal ‘chemo-genotypes’ on leaf metabolic composition in *T. vulgare* (Dussarrat et al. 2023). Given that our chemotypes were confounded by their maternal origin (chemo-genotypes), this may also affect broader

metabolic profiles, and future work should investigate to what extent the maternal fingerprint on chemo-genotypes also influences aphid attraction and performance.

In this study, we used unwinged (apterae) aphids. Although in early colonization in the field, host plant selection is more likely to occur by winged (alate) aphids (Mehrpavar et al. 2014), the dispersal to other plants is also commonly observed by non-winged (apterae) aphids, both in experimental colonies and the field (the authors pers. obs.). Although performing choice assays with winged early colonizers may be an important next step to understand seasonal colonization dynamics, obtaining such early-season alates from eggs is experimentally challenging. However, choice assays with asexual alates would also be interesting to investigate aphid colonization dynamics later in the season, as these often display clear preferences. For instance, in a choice assay study, Mehrparvar et al. (2014) found that alate dispersal morphs of *M. tanacetaria* displayed preferences for plants with specific herbivore infestation history, while unwinged aphids did not show any such host plant preferences. Our results indicate that preferences and choices in unwinged morphs do occur at the chemotype level, which likely represents a stronger chemical contrast for aphids than the herbivory history studied in previous work.

Conclusion

We found that terpenoid chemodiversity characteristics are one potential driver for aphid host plant preference in *T. vulgare*, which contributes to our mechanistic understanding of the link between chemodiversity in plants and insect communities that interact with them. We found that different chemotypes have distinct attraction patterns, which can be partly explained by diversity metrics of the terpenoid blend and the relative total terpenoid concentration. Insects use chemical cues, including host plant metabolites, to inform their decisions. It is eminent that we develop a better understanding of how intraspecific plant chemodiversity shapes the various aspects of the (herbivorous) insect life cycle, including development, survival, defence and overall fitness.

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Author contributions

Annika Neuhaus-Harr and **Lina Ojeda-Prieto** share first authorship and contributed equally to this publication.
Annika Neuhaus-Harr: Conceptualization (supporting);

Data curation (equal); Formal analysis (lead); Investigation (lead); Visualization (equal); Writing – original draft (lead).
Lina Ojeda-Prieto: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Visualization (equal); Writing – original draft (equal); Writing – review and editing (supporting).
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Wolfgang W. Weisser: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (equal); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – review and editing (supporting).
Robin Heinen: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (lead); Validation (supporting); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vhhmgp1k> (Neuhaus-Harr et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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Chemodiversity affects preference for *Tanacetum vulgare* chemotypes in two aphid species

Supplementary Information (SI)

1. R-code of statistical models used

1.1 Clustering of plants into chemotypes

```
D <- vegdist(data, method = "Euclidean")
```

```
Hclust(D, method = "ward.D2")
```

1.2 Binomial tests for aphid preference towards in pairwise choice assay

```
Binom.test(chosen, not chosen, P = 0.5, alternative = "two-sided", confidence level = 0.95)
```

1.3 Attractiveness towards chemotypes and daughters overall

```
clogit(Chosen(yes, no) ~ Daughter + Side (left, right) + strata(ID of aphid), data = decisions of M. tanacetaria/U. tanaceti after 2 hours)
```

1.4 Plant diversity metrics

```
Shannon diversity: H <- diversity(data)
```

```
Compound richness: S <- specnumber(data)
```

```
Evenness: J <- H/log(S)
```

```
Anova(lm(preference~shannon + evenness + richness))
```

1.5 Correlation of single compounds and aphid preference

```
Data_cor <- Cor(data terpenoids, data z-value preference for each species, use = "pairwise complete observations")
```

Corrected p-value: using RcmdrMisc package (Fox 2022)

```
rcorr.adjust(Data_cor, type = "spearman", use = "pairwise complete observations") (Holm correction by default)
```

1.6 Multiple regression for verification

```
Model <- lm(attractiveness ~all terpenoid compounds found in 10 out of 15 daughters (>66%))
```

```
vif(Model) #calculates the variation inflation factors. Terms with >1.5 exhibit multicollinearity and therefore are removed from the model
```

```
step(Model) #chooses stepwise the best model
```

1.7 One-way ANOVA for correlation of plant growth and chemodiversity

```
Model <- (lm(shannon diversity ~ height + number stems + number leaves + pinnae
density + specific leaf area + chlorophyll))
```

```
Vif(model)
```

```
Step(model)
```

```
Anova(lm(shannon diversity ~ height + number stems + chlorophyll))
```

Table S1. The number of replicates for the combinations of daughters used in the experiment, both for *M. tanacetaria* and *U. tanacetii*.

Replicates for <i>M. tanacetaria</i>	Replicates for <i>U. tanacetii</i>	Daughter 1	Daughter 2
3	3	Bthu-high_11	Mixed-high_21
2	2	Bthu-high_11	Mixed-high_23
2	0	Bthu-high_11	Mixed-high_30
3	3	Bthu-high_11	Athu-Bthu_55
2	2	Bthu-high_11	Athu-Bthu_56
2	0	Bthu-high_11	Athu-Bthu_57
3	3	Bthu-high_11	Mixed-low_64
2	2	Bthu-high_11	Mixed-low_67
2	0	Bthu-high_11	Mixed-low_68
3	3	Bthu-high_11	Chrys-acet_94
2	2	Bthu-high_11	Chrys-acet_95
2	0	Bthu-high_11	Chrys-acet_100
2	2	Bthu-high_14	Mixed-high_21
3	1	Bthu-high_14	Mixed-high_23
3	1	Bthu-high_14	Mixed-high_30
2	2	Bthu-high_14	Athu-Bthu_55
3	1	Bthu-high_14	Athu-Bthu_56
3	1	Bthu-high_14	Athu-Bthu_57
2	2	Bthu-high_14	Mixed-low_64
3	1	Bthu-high_14	Mixed-low_67
3	1	Bthu-high_14	Mixed-low_68
2	2	Bthu-high_14	Chrys-acet_94
3	1	Bthu-high_14	Chrys-acet_95
3	1	Bthu-high_14	Chrys-acet_100
2	0	Bthu-high_17	Mixed-high_21
3	1	Bthu-high_17	Mixed-high_23
3	3	Bthu-high_17	Mixed-high_30
2	0	Bthu-high_17	Athu-Bthu_55
3	1	Bthu-high_17	Athu-Bthu_56
3	3	Bthu-high_17	Athu-Bthu_57

2	0	Bthu-high_17	Mixed-low_64
3	1	Bthu-high_17	Mixed-low_67
3	3	Bthu-high_17	Mixed-low_68
3	1	Bthu-high_17	Chrys-acet_94
3	1	Bthu-high_17	Chrys-acet_95
2	2	Bthu-high_17	Chrys-acet_100
5	3	Mixed-high_21	Athu-Bthu_55
2	2	Mixed-high_21	Athu-Bthu_56
2	0	Mixed-high_21	Athu-Bthu_57
5	3	Mixed-high_21	Mixed-low_64
2	2	Mixed-high_21	Mixed-low_67
2	0	Mixed-high_21	Mixed-low_68
5	3	Mixed-high_21	Chrys-acet_94
2	2	Mixed-high_21	Chrys-acet_95
2	0	Mixed-high_21	Chrys-acet_100
2	2	Mixed-high_23	Athu-Bthu_55
3	2	Mixed-high_23	Athu-Bthu_56
3	1	Mixed-high_23	Athu-Bthu_57
2	2	Mixed-high_23	Mixed-low_64
3	1	Mixed-high_23	Mixed-low_67
3	1	Mixed-high_23	Mixed-low_68
2	2	Mixed-high_23	Chrys-acet_94
3	1	Mixed-high_23	Chrys-acet_95
3	1	Mixed-high_23	Chrys-acet_100
0	0	Mixed-high_30	Athu-Bthu_55
3	1	Mixed-high_30	Athu-Bthu_56
3	2	Mixed-high_30	Athu-Bthu_57
0	0	Mixed-high_30	Mixed-low_64
3	1	Mixed-high_30	Mixed-low_67
3	3	Mixed-high_30	Mixed-low_68
1	1	Mixed-high_30	Chrys-acet_94
3	1	Mixed-high_30	Chrys-acet_95
2	2	Mixed-high_30	Chrys-acet_100
5	3	Athu-Bthu_55	Mixed-low_64
2	2	Athu-Bthu_55	Mixed-low_67
2	0	Athu-Bthu_55	Mixed-low_68
5	3	Athu-Bthu_55	Chrys-acet_94
2	2	Athu-Bthu_55	Chrys-acet_95
2	0	Athu-Bthu_55	Chrys-acet_100
2	2	Athu-Bthu_56	Mixed-low_64
3	1	Athu-Bthu_56	Mixed-low_67
3	1	Athu-Bthu_56	Mixed-low_68
2	2	Athu-Bthu_56	Chrys-acet_94
3	1	Athu-Bthu_56	Chrys-acet_95

3	1	Athu-Bthu_56	Chrys-acet_100
0	0	Athu-Bthu_57	Mixed-low_64
3	1	Athu-Bthu_57	Mixed-low_67
3	3	Athu-Bthu_57	Mixed-low_68
1	1	Athu-Bthu_57	Chrys-acet_94
3	1	Athu-Bthu_57	Chrys-acet_95
2	2	Athu-Bthu_57	Chrys-acet_100
5	3	Mixed-low_64	Chrys-acet_94
2	2	Mixed-low_64	Chrys-acet_95
2	0	Mixed-low_64	Chrys-acet_100
2	2	Mixed-low_67	Chrys-acet_94
3	1	Mixed-low_67	Chrys-acet_95
3	1	Mixed-low_67	Chrys-acet_100
1	1	Mixed-low_68	Chrys-acet_94
3	1	Mixed-low_68	Chrys-acet_95
2	2	Mixed-low_68	Chrys-acet_100

A-III. Intraspecific Chemical Variation of *Tanacetum vulgare* Affects Plant Growth and Reproductive Traits in Field Plant Communities

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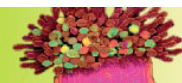
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Author contributions:

WWW conceived the original idea and designed the experiment. RH prepared the field experiment and propagated plants. LOP, RH, and WWW planted the field experiment. LOP collected all data and maintained the field experiment. LOP analyzed ecological data with input from RH and WWW. PMvB, SBU, RH, and LOP prepared and executed volatile collections. PMvB chemically analyzed volatiles. LOP wrote the manuscript with input from RH and WWW. All authors contributed to the final version and approved the final submission.



RESEARCH ARTICLE

Intraspecific chemical variation of *Tanacetum vulgare* affects plant growth and reproductive traits in field plant communities

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Keywords

Chemodiversity; complementarity; functional traits; plant–plant competition; tansy; terpenoid; volatile organic compound (VOC).

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ABSTRACT

- The study investigated the impact of intraspecific plant chemodiversity on plant growth and reproductive traits at both the plant and plot levels. It also aimed to understand how chemodiversity at stand level affects ecosystem functioning and plant–plant interactions.
- We describe a biodiversity experiment in which we manipulated intraspecific plant chemodiversity at the plot level using six different chemotypes of common tansy (*Tanacetum vulgare* L., Asteraceae). We tested the effects of chemotype identity and plot-level chemotype richness on plant growth and reproductive traits and plot-level headspace emissions.
- The study found that plant chemotypes differed in growth and reproductive traits and that traits were affected by the chemotype richness of the plots. Although morphological differences among chemotypes became less pronounced over time, reproductive phenology patterns persisted. Plot-level trait means were also affected by the presence or absence of certain chemotypes in a plot, and the direction of the effect depended on the specific chemotype. However, chemotype richness did not lead to overyielding effects. Lastly, chemotype blends released from plant communities were neither richer nor more diverse with increasing plot-level chemotype richness, but became more dissimilar as they became more dissimilar in their leaf terpenoid profiles.
- We found that intraspecific plant chemodiversity is crucial in plant–plant interactions. We also found that the effects of chemodiversity on plant growth and reproductive traits were complex and varied depending on the chemotype richness of the plots. This long-term field experiment will allow further investigation into plant–insect interactions and insect community assembly in response to intraspecific chemodiversity.

INTRODUCTION

Individuals of the same plant species can exhibit varying phenotypes, which reflect variation in growth, reproductive, physiological, and other traits (Raffard *et al.*, 2019; Siefert *et al.* 2015; De Bello *et al.* 2011; Fridley & Grime 2010; Bolnick *et al.* 2003). This variation within plant species is a major element in individual performance and population-, community- and ecosystem-scale processes (Violle *et al.* 2012; Siefert *et al.* 2015; Guisan *et al.* 2019; Westerband *et al.* 2021). Functional traits are attributes of species that can be measured at the individual level, and are related to the individual's response to environmental conditions and which impact ecosystem properties and ecosystem functioning (Isbell *et al.* 2011). In addition to visible morphology-related functional traits, plants can vary intraspecifically in less apparent traits, such as chemical composition (Wetzel & Whitehead 2020). For instance, many plant species show pronounced intraspecific variation in specialized metabolites along environmental gradients (Moore

et al. 2014; Bakhtiari *et al.* 2019), or even at finer spatial scales, such as plant patches located in areas of less than a few square kilometers (Kleine & Müller 2011). Variation in chemodiversity has recently gained increased attention in ecology as it might structure community assembly or community composition, as well as species interactions, and fulfil ecosystem functions, including structuring plant-associated food webs and biodiversity (Bálint *et al.* 2016; Erb & Kliebenstein 2020; Müller *et al.* 2020; Wetzel & Whitehead 2020).

Individuals of a plant species can be clustered into distinct groups – also called chemotypes – by their dominant compounds, the composition of volatile and non-volatile compound blends, or by comparisons of specific specialized metabolites produced by individuals (Eilers 2021). The consequences of specialized metabolites for intra- and interspecific interactions have been studied in various herbaceous plant model systems (Moore *et al.* 2014), including *Tanacetum vulgare* (Kleine & Müller 2011; Clancy *et al.* 2016; Eilers *et al.* 2021; Neuhaus-Harr *et al.* 2023), *Jacobaea vulgaris*

(Macel 2011; Kostenko & Bezemer 2013; Carvalho *et al.* 2014), *Plantago lanceolata* (Harvey *et al.* 2005; Wurst *et al.* 2008), *Senecio inaequidens* (Cano *et al.* 2009; Macel & Klinkhamer 2010), and *Brassica oleracea* (Gols *et al.* 2008; Gols *et al.* 2009; Poelman *et al.* 2009; Kabouw *et al.* 2010; Kos *et al.* 2011; Bustos-Segura *et al.* 2017). Specialized metabolites can be stored in specialized structures, such as glandular trichomes in *T. vulgare*, and in the headspace when released into the environment as volatiles. Conversely, some compounds are only produced *de novo* and released immediately, for instance, in plants without storage structures. These volatile organic compounds (VOCs) and other compounds found in leaves shape the assemblage and interaction within the plant-associated insect community (Ponzio *et al.* 2013). Although ecologists are beginning to understand the consequences of plant chemodiversity for plant–insect interactions, much less is known about how it affects plant–plant interactions (Thorpe *et al.* 2011).

Plants can display intraspecific chemodiversity at different levels. Through variations in chemical composition at a small scale, groups of plants in a natural stand may differ in their chemotypes (Senft *et al.* 2017; Clancy *et al.* 2018; Müller *et al.* 2020; Clancy 2021; Eilers 2021). In such scenarios, intraspecific chemodiversity can be described by the richness (i.e., the number of chemotypes) and relative abundance of different chemotypes at the stand level. So far, the ecological consequences of variation in chemodiversity at the stand level have rarely been investigated (but see Glassmire *et al.* 2020).

The effects of increasing plant diversity on processes at the ecosystem level have been intensively studied in the framework of biodiversity–ecosystem functioning research (Chapin III *et al.* 1992; Weisser *et al.* 2017). In most empirical work, plant diversity was manipulated by creating plant communities that differed in the number of plant species they contained. In contrast to the wealth of studies manipulating plant community diversity at the plant species level, there are far fewer studies where plant community diversity is manipulated at the within-species level, i.e., by creating plant communities with the same number of plant species, but with different extent of intraspecific variation. In a seminal study, Crutsinger *et al.* (2006) showed that in *Solidago altissima* communities that differed in the number of *Solidago* genotypes they contained, increasing genotypic diversity enlarged arthropod community species richness and increased plant community biomass. The number of studies manipulating the intraspecific diversity of plant communities has been increasing in the past years (Genung *et al.* 2012; Koricheva & Hayes 2018; Raffard *et al.* 2019). However, the detailed results differ among studies and taxa, even when only considering research conducted on the effects on herbivores (Barton *et al.* 2015; Bustos-Segura *et al.* 2017; Fernandez-Conradi *et al.* 2022; Hauri *et al.* 2022). A general trend is that increased intraspecific genotypic diversity of the plant community increases the diversity of the associated arthropod community and that these diversity effects on natural enemies of herbivores are generally higher than effects on the herbivores themselves, suggesting changes in top-down control (see meta-analysis in Koricheva & Hayes 2018; Wetzel *et al.* 2018; Hauri *et al.* 2021). The mechanisms underlying these effects are still being discussed.

Plants in intraspecifically diverse communities may compete with their neighbouring conspecifics, resulting in changes in trait expression, such as growth (Viola *et al.* 2010; Genung

2012; Bustos-Segura *et al.* 2017; Ziaja & Mueller 2023). On the other hand, plants may also experience reduced competition through niche partitioning because of *a priori* differences in functional traits, such as phenology (Kuppler *et al.* 2016; Gallien 2017). Little is known about how the chemotypes of plants differ in other traits and how intraspecific chemotype richness at the stand level affects individual plant performance.

Here, we designed a field experiment using *Tanacetum vulgare* L. (Asteraceae), in which we manipulated plot-level chemotype richness and the presence of specific plant chemotypes within the plots, to test the effects on plant growth and volatile emission. *T. vulgare* exhibits high intraspecific variation in specialized metabolites (Rohloff *et al.* 2004; Bálint *et al.* 2016), mainly mono- and sesquiterpenes (Keskitalo *et al.* 2001; Ziaja & Mueller 2023), and is easy to propagate clonally (Bálint *et al.* 2016). Moreover, variation in *T. vulgare* in terpenoid profiles has been documented to differ strongly among different geographic regions and even among individuals within populations, meaning that plant–plant interactions of distinct chemotypes often occur in close proximity in nature (Kleine & Müller 2011; Clancy *et al.* 2016).

We measured growth and reproductive traits over two growing seasons and sampled headspace volatiles to test the following hypotheses:

- 1 At the individual plant level, chemotypes will differ in growth and reproductive traits, which will be affected by the plot-level chemical richness of the plots in which they grow.
- 2 At the plot level, higher plot-level chemotype richness will increase plant growth, in line with biodiversity's generally observed positive effects described in the ecological literature.
- 3 Individual chemotypes will differ in their effect on plot-level effects.
- 4 Plant communities with higher plot-level chemotype richness will emit a more chemically diverse headspace of VOCs than plots with lower plot-level chemotype richness.

MATERIAL AND METHODS

Chemotypic characterization of *T. vulgare* lines and biological replicates

Plant chemotyping and chemotype selection are described in detail in Data S1 and in Neuhaus-Harr *et al.* (2023). The leaf terpenoid composition of the *T. vulgare* chemotypes used is shown in Fig. 1a and Table S1-1. We named the chemotypes according to their dominant compounds as follows. The 'A-Bth' chemotype had both α - and β -thujone as prevalent compounds. The 'Bth-high' and 'Bth-low' chemotypes were dominated by β -thujone but had high or low relative levels of this terpenoid. There was a strong dominance of chrysanthemyl acetate in the 'Chrys-acet' chemotype. The 'Mixed-high' chemotype featured three terpenoids with a high relative total concentration, whereas the 'Mixed-low' chemotype featured several terpenoids evenly contributing to the total profile.

Propagation of plant material for the field experiment

Plants were propagated via stem cuttings. A detailed description can be found in Data S1.

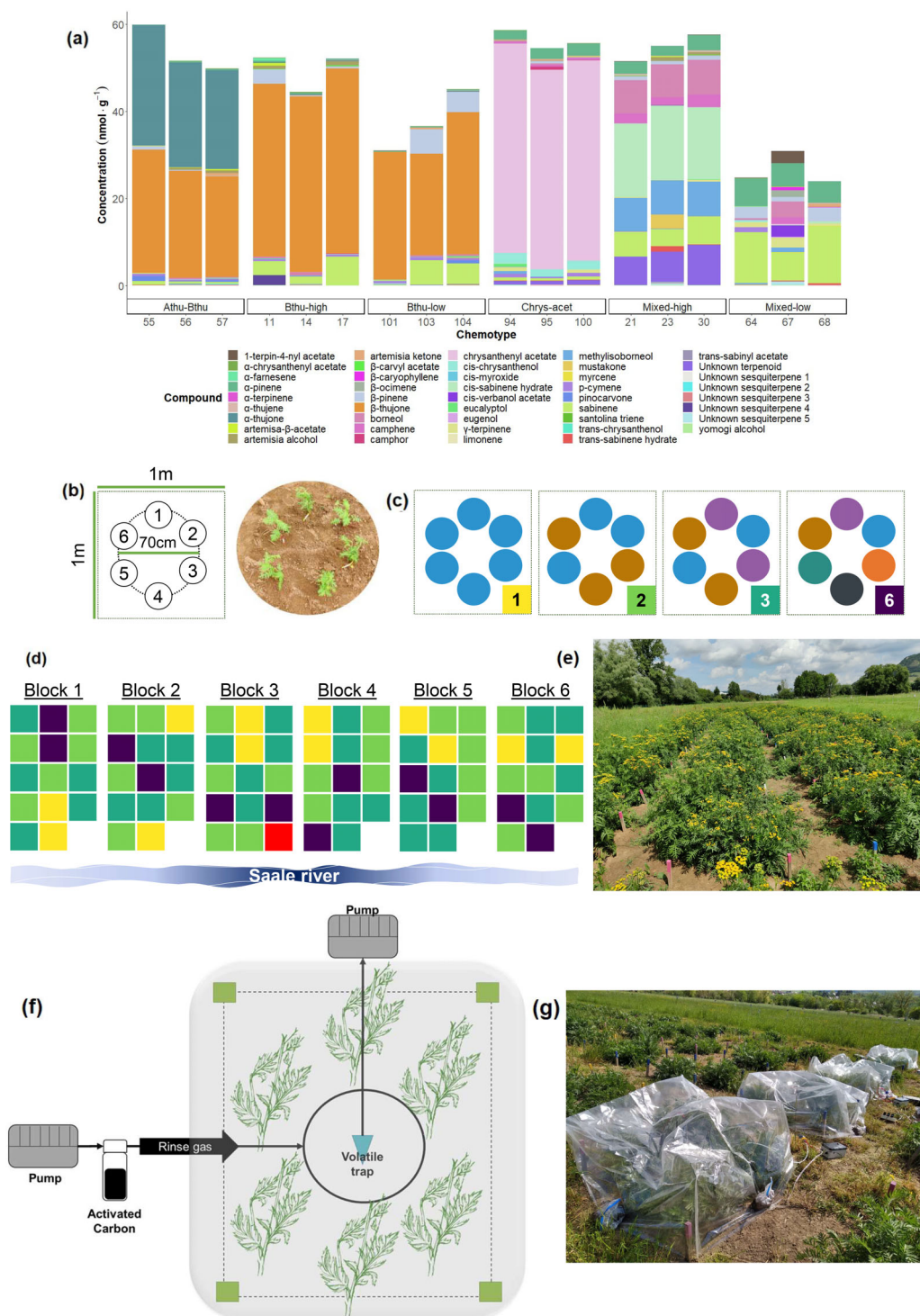


Fig. 1. Field experiment design. (a) Stacked bars modified from Neuhaus-Harr *et al.* (2023) show approximate concentrations of terpenoid compounds (nmol·g⁻¹) extracted from leaf samples of the 18 selected daughters (exact values are reported in Table S1-1). Daughter replicates are clustered by their chemotype. (b) Plant arrangement within the plot: six *T. vulgare* plants were evenly distributed around a 70-cm diameter circle. The identity of tansy chemotypes in each plot was assigned to plots *a priori*, and plot position was assigned randomly. (c) Plot-level chemotype richness: Number of different chemotypes in one plot ranged from 1, 2, 3, to 6. (d) Block design showing plot-level chemotype richness 1, 2, 3, and 6 as yellow, light green, dark green, and purple squares, respectively. N = 84 plots were distributed equally in six randomized blocks. Each block consisted of 14 plots: two plots of chemotype richness level 1, five plots of chemotype richness level 2, five plots of chemotype richness level 3, and two plots with chemotype richness level 6. The red plot indicates the location of the background volatile profile plot used only for VOC analysis. (e) Picture of the field in June 2021. (f) Diagram of the closed push-pull headspace VOC collection system. Purified air enters the collection PET bag and is pulled through a volatile trap located in the middle of the six plants at the higher side of the bag. (g) VOC collection setup in May 2022.

Experimental design

The field experiment took place in the Jena Experiment site, located on the floodplain of the Saale River in Jena, Germany (50°55' N, 11°35' E, 130 m a.s.l.; Weisser *et al.* 2017). In May 2021, all vegetation was removed, and the soil was mechanically tilled. No fertilizer, chemical insecticides, or fungicides were used, and weeds were removed by hand every 2 weeks during the growing season.

We created plots of six tansy plants that were evenly distributed around a 70-cm diameter circle (84 plots × 6 plants = 504 plants total; Fig. 1b). The design followed suggestions of the design for biodiversity experiments: each plot type differed in the number and identity of tansy chemotypes assigned to it. The number of different chemotypes in one plot (hereafter: plot-level chemotype richness) ranged from 1, 2, 3, to 6 (Fig. 1c). A plot with a plot-level chemotype richness of 1 was assigned six plants of the same chemotype. Within the plot, we maximized the number of daughters per chemotype. For example, we used the three *Athu-Bthu* chemotype daughters (56, 57, and 58) for plot-level chemotype richness of 1 of *Athu-Bthu*. Daughters from each chemotype were equally distributed over the different treatment plots where possible or structurally assigned where an equal division was not possible (e.g., in the case of a shortage of plants of one daughter, they were replaced with a randomly picked daughter from the remaining two daughters of the same chemotype). So, a plot with plot-level chemotype richness 1 was assigned two clones from each of the three daughters of the plot chemotype. For plot-level chemotype richness 2, there was one clonal plant of each of the three daughters of each of the two chemotypes in the plot, etc. Lastly, a plot with plot-level chemotype richness 6 was assigned one clonal plant from one daughter of each of the six different chemotypes. Varying the daughter identities per chemotype in each plot allowed all level chemotype plots to be biologically replicated.

Prior to an in-depth analysis of the terpenoid composition, the composition of chemotype richness at the plot level was pre-assigned for each plot. Each chemotype combination was thus replicated twice, except for plot-level chemotype richness level 6, which was replicated 12 times but with different daughters. Hence, our field experiment contained 12, 30, 30, and 12 replicate plots for plot-level chemotype richness levels 1, 2, 3, and 6, respectively. Plots were distributed equally in six randomized blocks. The field was divided into 84 plots (1 × 1 m) separated from each other by 70-cm footpaths and distributed in six replicated blocks (Fig. 1d). Each block consisted of 14 plots: two plots of chemotype richness level 1, five plots of chemotype richness level 2 and 3, and two plots with chemotype richness level 6 (Fig. 1d, e). The exact assignment of plants to plots is given in Table S1-2.

Plant morphological trait measurements

We measured six morphological plant traits for individual plants, including four growth traits (number of stems per plant, height of the highest stem, and aboveground fresh and dry weight) and two reproductive traits (cumulative number of flower heads and flowering index). A more detailed description of each variable and time points used can be found in Data S1.

Headspace VOC collection

Headspace VOC emissions were collected at the plot level. A detailed description of the process is available in Data S1.

Statistical analysis

All analyses were performed in R version 4.2.2 and RStudio 2022.07.2 + 576 (R Core Team 2021). A description of all models is provided in Data S1.

To analyse plot-level chemotype richness, we calculated plot-level diversity metrics using the '*chemodiv*' package (Petrén *et al.* 2023). Note that we calculated theoretical chemotype diversity metrics based on the cumulative leaf terpenoid profiles of each respected daughter present in a plot. Calculated realized volatile diversity metrics were based on our headspace VOC collection at the plot level. Data were visualized using the '*ggplot2*', '*grid*', '*gridExtra*', and '*ggpubr*' packages (Wickham 2016; Auguie 2017; Kassambara 2020; R Core Team 2021).

We distinguished between plant-level and plot-level analyses, whereby plant-level analyses focused on the performance of the individual plants growing in the different diversity plots, controlling for the plot in which they grow. Plot-level analyses focused on plot-level measures of plant performance calculated by averaging over all plants in a plot. All analyses of the effects of chemodiversity on plant traits were done with mixed-effect models using the '*lme4*' package (Bates *et al.* 2015). All variables were analysed separately for each time point. For evaluating the effects on traits of individual plants, *P*-values were estimated by type II Wald-Chi-Square tests using the *Anova()* function in the '*car*' package (Fox & Weisberg 2019) and by type I Wald-Chi-Square tests using the *anova()* function in base R for evaluating the effects of chemotype presence on plot-level measurements and overyielding indices. After fitting a model, *post-hoc* pair-wise comparisons among factor levels (i.e., chemotypes) were assessed with the '*emmeans*' package with Tukey adjustment (Russell 2021). All plant- and plot-level model assumptions were met in all models, except for the model covering plant-level height on 28 October 2021, in which the residuals were not normally distributed, and transformations did not improve normality of model residuals. Despite the non-normal distribution of the data, we chose to keep all measurements untransformed, including outliers, as we found no ecological justification for their exclusion, and decided to maintain consistency with models at other time points to facilitate meaningful comparisons.

Effects of chemotype and plot-level chemotype richness on traits of individual plants

To test the effects of chemotype and plot-level chemotype richness on traits of individual plants growing in the different plots with six plants each, both factors (chemotype, plot-level chemotype richness) and their interaction were included as fixed factors in Generalized Linear Mixed-Effect Models (GLMM), with Poisson distribution for counting data (number of stems for both years and the cumulative number of flower heads), and with Linear Mixed-Effect Models (LMM) for the other individual plant traits (plant height, flowering index, and square root-transformed aboveground dry weight and square

root-transformed aboveground fresh weight). We treated chemotype richness as a continuous variable with one degree of freedom. In the main analysis, random effects were Daughter ID (to account for technical replication of each daughter via cuttings) and Plot ID (84 in total) nested in Block ID (R scripts are provided as S3). In some variables, the random effect structure of the model led to singularity. We performed a second model excluding Plot ID since it had the lowest explanatory power of all random effects. We then chose the higher-quality statistical model using the estimator of prediction error AIC.

If the main effect of a factor was significant, *post-hoc* pairwise comparisons with Tukey adjustment were conducted to assess significant differences between factor levels. While this is the most correct analysis from the point of daughter distribution within chemotypes, it results in a low degree of freedom. Hence, we carried out additional analyses to complement our understanding of within- and between-chemotype differences.

Effects of daughter and plot-level chemotype richness on traits of individual plants

We performed separate analyses per chemotype with Daughter, plot-level chemotype richness, and their interaction as fixed factors, and Plot ID nested in Block ID as a random factor. For count data, we used a GLMM with Poisson distribution and Nelder Mead optimizer and, for the other assessed variables, LMM models.

In a final analysis, we directly compared daughters' performance, using Daughter ID (with 18 levels) and plot-level chemotype richness as independent variables, and Plot ID and Block ID as random factors.

Effects of chemotype and plot-level chemotype richness on plot-level means

We first averaged each plant trait at the plot level to test the effects of chemotype and chemotype richness on plot-level plant traits. To test the effect of the presence/absence of a chemotype on plot-level trait values, we carried out a separate analysis per chemotype. This was done by running a linear model with Block ID, chemotype presence (indicating whether a specific chemotype is present in the plot), plot-level chemotype richness, and the interaction between chemotype presence and plot-level chemotype richness, separately for each chemotype.

Overyielding calculations

We assessed the plot-level performance (i.e., the plot-level mean yield of the measured trait) of plants growing in plots of different chemotype richness levels (plot-level chemotype richness = 2, 3, and 6) and compared this to their performance in a monoculture (i.e., the respective chemotype-specific plots in plot-level chemotype richness = 1). This was done by calculating the overyielding index (OI) according to Hector *et al.* (2002) and Hooper *et al.* (2004). Overyielding indices are positive when the yield for a given chemotype in a mixture is greater than expectations from monocultures and indicates overyielding (Loreau 1998). Overyielding indices for each plot-level chemotype richness ($i = 1, 2, 3$, or 6) were obtained for aboveground dry weight, aboveground fresh weight, the

cumulative number of flower heads, and the flowering index for each plot. Mathematically, we calculated $OI_i = (Oc_i - Ec) \times Ec^{-1}$, where Oc_i is the observed yield of a mixture plot i obtained by means of yields of the plants in the mixture, and Ec is the expected yield for the plot. Ec was calculated by averaging the yield of monoculture of each of the chemotypes present in the plot (Table S2-11).

In separate analyses per trait, we carried out LMM models with the calculated overyielding indices for all plot-level chemotype richness levels, with plot-level chemotype richness as a fixed factor and Block ID as a random factor.

Plot-level theoretical leaf and plot-level realized volatile chemodiversity metrics

We calculated chemodiversity metrics at the plot level based on the leaf terpenoid profiles of individual chemotypes before planting (plot-level *theoretical* leaf chemodiversity) and on the headspace VOC measurements in the field (plot-level *realized* volatile chemodiversity). Plot-level theoretical leaf chemodiversity metrics were calculated by summing the absolute leaf terpenoid concentrations ($\text{nmol}\cdot\text{g}^{-1}$) produced by each of the six specific daughters present in each plot (Fig. 1a). Those absolute leaf terpenoid profiles were obtained from the chemical analysis performed on leaves from greenhouse plants in 2020, before making the cuttings and planting them in the field. Based on the individual values of each plant present in a plot, we calculated plot-level theoretical leaf terpenoid richness, concentration, Hill Shannon index, and Hill evenness (Petrén *et al.* 2023). Plot-level realized volatile chemodiversity metrics were calculated based on the plot-level absolute terpenoid emissions ($\text{ng}\cdot\text{h}^{-1}$) detected by headspace VOC collection.

As plants were chemotyped *a priori* (in Neuhaus-Harr *et al.* 2023) before transplanting them to the field, and chemotyping was hence not affected by field conditions, plot-level theoretical leaf chemodiversity was analysed by linear models with plot-level chemotype richness as the independent variable, without putting block as a random factor into the model. Plot-level realized volatile chemodiversity metrics based on field-collected headspace VOCs were analysed by linear models with plot-level chemotype richness as the independent variable and Block ID (6 blocks) and Collection Day ID (3 days) as random factors.

We also analysed the correlation between leaf and headspace terpenoid profiles by calculating Bray–Curtis dissimilarity matrices for hierarchical analyses and performing a Mantel test by specifying 9999 permutations using the 'vegan' package (Oksanen *et al.* 2022).

RESULTS

Field establishment

The establishment of the field experiment was successful; all 504 plants survived until the first seasonal harvest date (28 October 2021). By early May of the second year (2 May 2022), 96.6% of the plants (487 of 504 plants) showed shoot regrowth. Of these 487 plants, 4 more plants, which had shown some aboveground growth, naturally died and were not present at the harvest date of the second year (05 October 2022). Missing

data were excluded from analyses of plant traits at the plant level, with 17 plants missing for the first (May), 20 missing for the second (July), and 21 missing for the final measurements (October). Because of regrowth and mortality, the missing plants between time points only partially overlap. Plot-level averages were calculated according to the number of plants recorded in the plot at the measurement date, but we retained the original plot chemotype richness level for the statistical analysis as this was the treatment variable.

At the point of planting in May 2021, the plants were visually very similar. First trait measurements were conducted 2 weeks post-planting (Figure S2-2), and at various intervals leading up to the annual harvest. Notably, uniform height was observed among all plants during these assessments. Additionally, the number of stems per plant was recorded (see Figure S2-1). While all plants initially possessed a single main stem at planting, subsequent rhizome growth resulted in the rapid emergence of new stems.

Effects of chemotype and plot-level chemotype richness on traits of individual plants

To test hypothesis (i), we used analyses separated for each time point to assess the effect of chemotype and plot-level chemotype richness across and between seasons.

The number of stems of a plant was significantly affected by plant chemotype identity on 01 June ($\chi^2_5 = 24.99$, $P < 0.001$; Figure S2-1) and 22 June 2021 ($\chi^2_5 = 21.49$, $P < 0.001$; Fig. 2a), but not at the other time points ($P > 0.05$; Table S2-2). *Post-hoc* analyses revealed that in the 2021 season, the Mixed-high chemotype had the highest number of stems compared with all other five chemotypes. However, the effects of chemotype on the number of stems across chemotypes were not stable across nor between growing seasons (Figure S2-1, Table S2-2). Differences in the number of stems across chemotypes were less pronounced towards the end of the first season (Figure S2-1a–c) and even became indistinct for 2022 ($\chi^2_5 = 3.28$, $P = 0.657$; Fig. 2d).

For plant height, chemotypes were marginally different on 22 June 2021 ($\chi^2_5 = 10.54$, $P = 0.061$; Fig. 2b) and strongly different when harvested on 28 October 2021 ($\chi^2_5 = 12.26$, $P = 0.031$; Figure S2-2c). At this time point, several outliers caused deviation from a normal distribution that could not be solved with transformation. Therefore, for this time point, the chemotype effect must be interpreted cautiously. For instance, even though the chemotype had a significant effect, a *post-hoc* test for 28 October 2021, did not reveal differences in height across chemotypes. Moreover, no effect of chemotype on height was retained in 2022 (Fig. 2e, Figure S2d–f, Table S2-3).

For plant biomass, the aboveground weight of the Bthu-low chemotype was slightly higher in both growing seasons, although the effect of the chemotype was not significant (aboveground dry weight 2021: $\chi^2_5 = 9.35$, $P = 0.096$; Fig. 2c; aboveground fresh weight 2022: $\chi^2_5 = 2.65$, $P = 0.753$; Fig. 2f, Table S2-4).

There was no significant effect of plot-level chemotype richness, nor the interaction between chemotype and plot-level chemotype richness, for any of the growth traits measured on individual plants, except for a slight negative effect of plot-level chemotype richness on the number of stems in 2022 ($\chi^2_1 = 4.67$, $P = 0.031$; Fig. 2d).

Both reproductive plant traits were significantly affected by plant chemotype: the cumulative number of flower heads ($\chi^2_5 = 55.08$, $P < 0.001$) and the flowering phenology ($\chi^2_5 = 51.07$, $P < 0.001$). Interestingly, reproductive plant traits depended on both chemotype and the plot-level chemotype richness, as indicated by an interaction between these two factors (cumulative number of flower heads: $\chi^2_5 = 779.33$, $P < 0.001$; flowering index: $\chi^2_5 = 14.93$, $P = 0.011$). For example, the Bthu-low chemotype produced more flower heads in plots with higher plot-level chemotype richness in the first growing season. The other five chemotypes produced fewer flower heads in plots with higher plot-level chemotype richness (Fig. 2g). The Mixed-high, Mixed-low, and Athu-Bthu chemotypes showed more advanced flowering phenology (i.e., higher flowering index) in plots with higher plot-level chemotype richness. In contrast, the Bthu-low, Chrys-acet, and Bthu-high chemotypes showed more advanced phenology in plots with lower plot-level chemotype richness (Fig. 2h).

We found strong variation among daughters – across all chemotypes and within individual chemotypes. More detailed results of the effect of daughter and plot-level chemotype richness on plant traits can be found in Data S2.

Chemotype presence and plot-level chemotype richness effects on plot-level measurements

Related to hypothesis (iii), the presence or absence of certain chemotypes in a plot affected plot-level variables related to plant growth: number of stems, plant height, aboveground dry weight, and reproduction: the cumulative number of flower heads and flowering phenology. However, the effects of specific chemotypes were variable and differed with time in the growing season. Effects on the number of stems, number of flower heads, and flowering phenology are described and presented below, and additional effects on plant height and biomass are described in Data S2 and Figures S2-8–S2-10.

With respect to the mean number of stems per plot, three chemotypes significantly affected these in 2021, i.e., Bthu-low, Mixed-high, and Athu-Bthu on 01 July, and two on 22 July, i.e., Mixed-high and Bthu-high (Fig. 3a), but not on the other time point in 2022. The number of stems at the plot level significantly increased when Mixed-high was present in both time points (01 July: $F_{1,75} = 12.85$, $P < 0.001$; 22 July: $F_{1,75} = 10.35$, $P = 0.002$; Figure S2-7). The Mixed-high chemotype was also the one with the highest number of stems in 2021 for both dates. The presence of the Bthu-high chemotype lowered the number of stems at the plot level on 22 June 2021 ($F_{1,75} = 8.10$, $P = 0.006$; Fig. 3a). The effect of the presence/absence of the Mixed-high or Bthu-high chemotypes did not differ across chemotype richness levels, as indicated by the absence of interactions (Table S2-7). In 2022, chemotype presence/absence patterns on the number of stems differed slightly. Although we did not find a significant main effect of the plot-level chemotype richness of any of the chemotypes on the number of stems in any of the six separated models, we did observe an interaction between plot-level chemotype richness and the chemotype presence for the Mixed-high model ($F_{1,75} = 4.29$, $P = 0.042$; Fig. 3b). In plots where the Mixed-high chemotype was present, the number of stems did not differ, whereas in its absence, the number of stems decreased sharply with increasing plot-level chemotype richness. Across

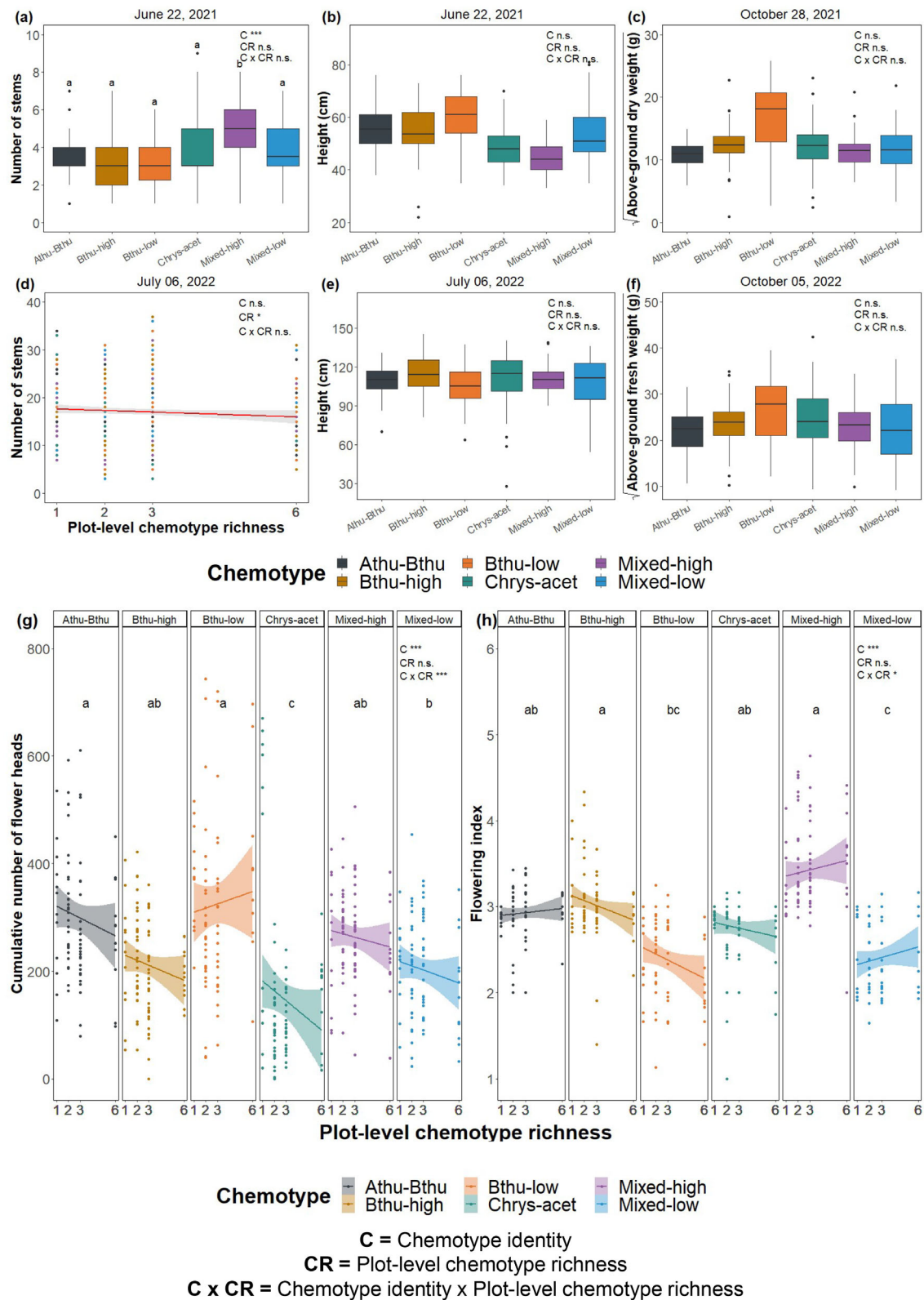


Fig. 2. Effect of chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness (C × CR) on growth traits of individual plants of *T. vulgare*. (a) Number of stems 2021, (b) height (cm) 2021, (c) square-root aboveground dry weight (g) 2021, (d) number of stems 2022, (e) height (cm) 2022, (f) square-root aboveground fresh weight (g) 2022, (g) cumulative number of flower heads 2021, and (h) flowering index in 2022. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Degrees of freedom, Wald's Chi-square statistics, and P -values are reported in Tables S2-2–S2-5. Tukey *post-hoc* significant differences between chemotypes are indicated with different letters.

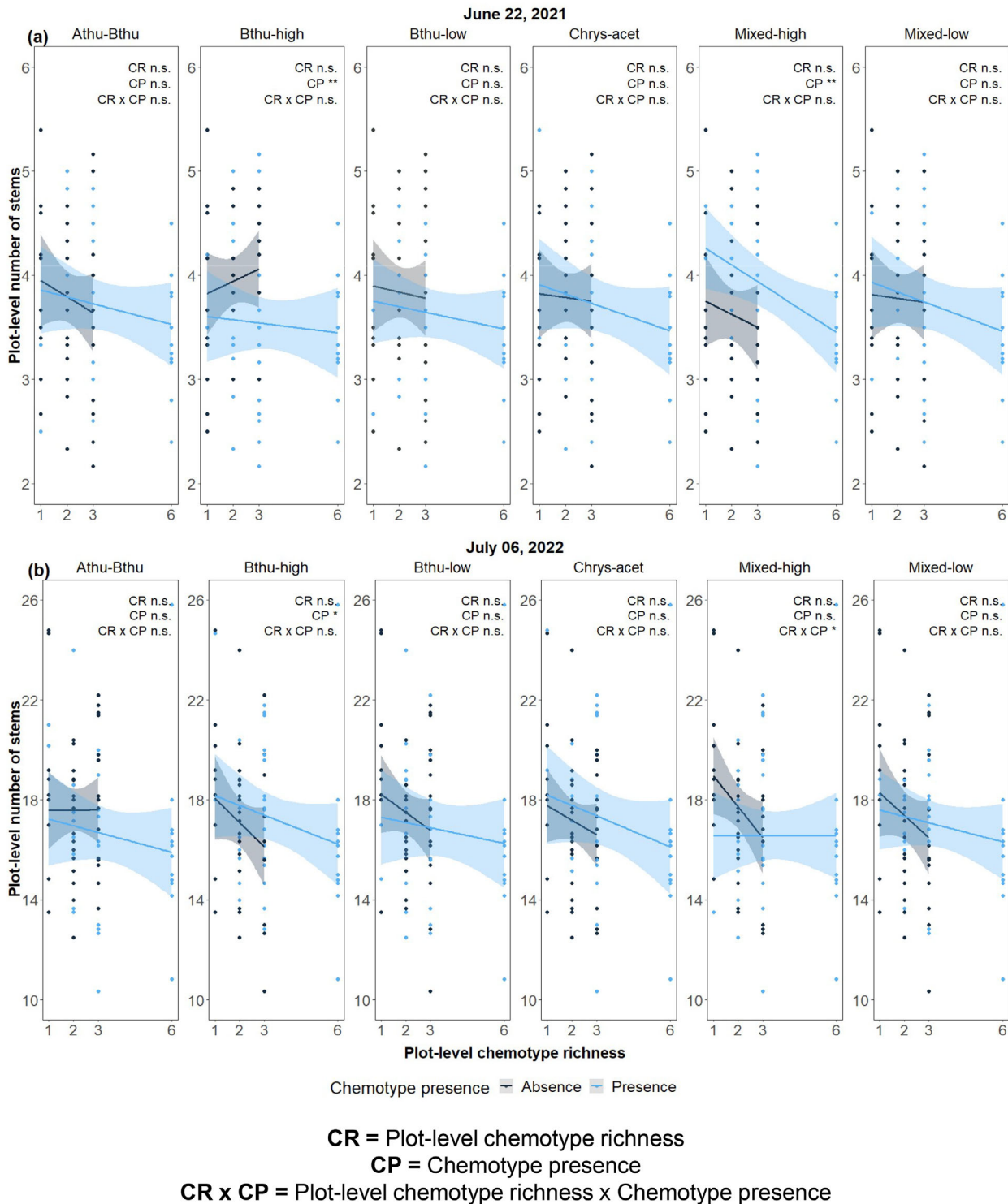


Fig. 3. Effect of chemotype presence (CP), plot-level chemotype richness (CR), and interaction between chemotype presence and plot-level chemotype richness (CP $\times$ CR) on average plot-level number of stems of *T. vulgare* in (a) 2021 and (b) 2022. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Degrees of freedom, Wald's Chi-square statistics, and P -values are reported in Table S2-7.

all six chemotype-specific models and at all time points in both years, plot-level chemotype richness had marginally significant negative effects on the mean number of stems per plot.

The number of flower heads per plot was affected positively by the presence of the Bthu-low chemotype in 2021

($F_{1,75} = 13.08$, $P < 0.001$; Fig. 4a), probably because the Bthu-low chemotype produced the highest number of flower heads among the chemotypes (Fig. 2g). In contrast, the presence of the Chrys-acet chemotype negatively affected the number of flower heads ($F_{1,75} = 12.12$, $P < 0.001$). We also observed an

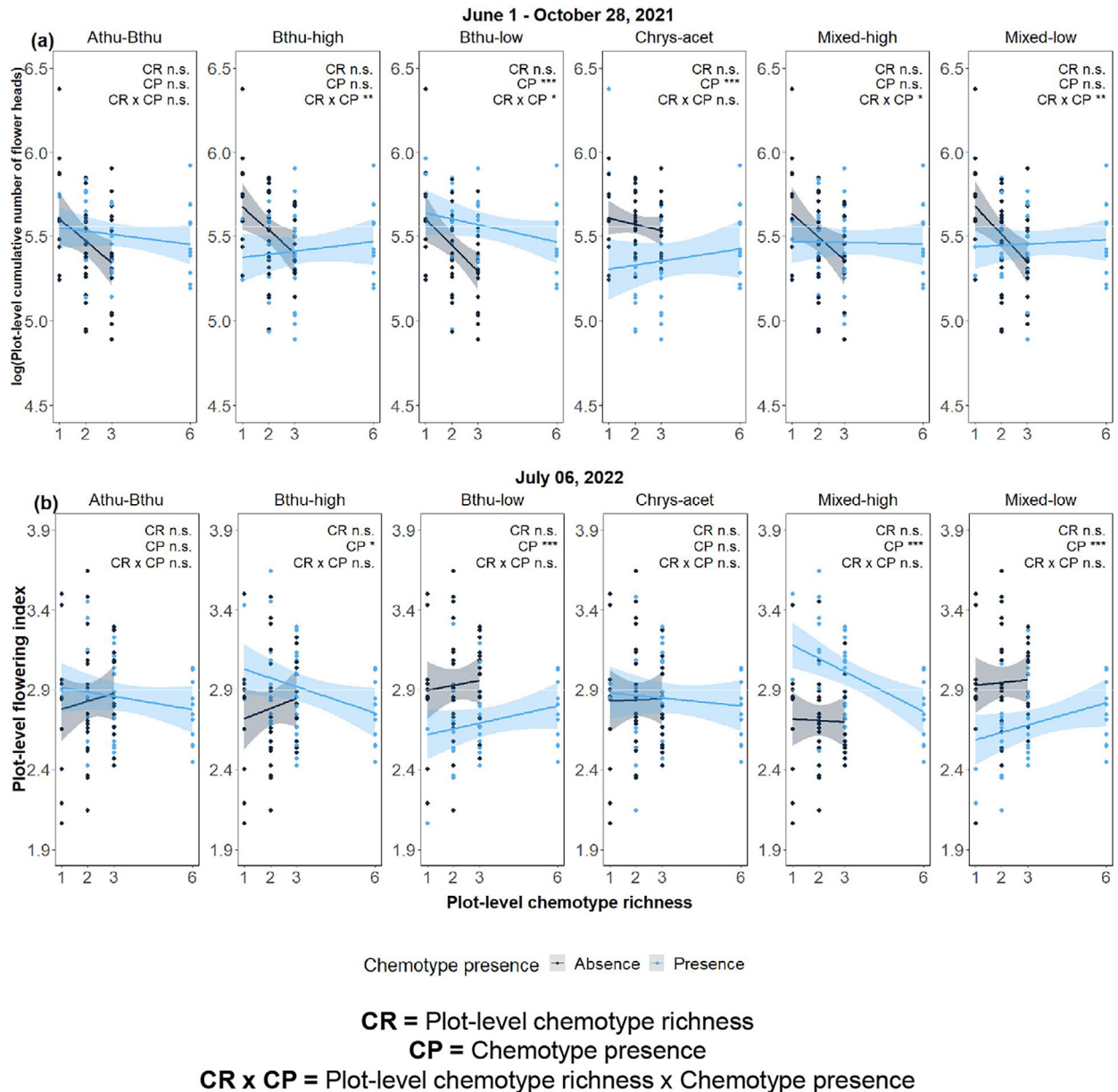


Fig. 4. Effect of chemotype presence (CP), plot-level chemotype richness (CR), and interaction between chemotype presence and plot-level chemotype richness (CP $\times$ CR) on reproductive traits of *T. vulgare* at plot level: (a) logarithm of cumulative number of flower heads in 2021, (b) flowering index in 2022. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Degrees of freedom, F -statistics, and P -values are reported in Table S2-10.

interactive effect between the presence of the Bthu-low chemotype and plot-level chemotype richness ($F_{1,75} = 5.25$, $P = 0.025$), between the presence of the Mixed-high chemotype and plot-level chemotype richness ($F_{1,75} = 4.98$, $P = 0.029$), between the presence of the Bthu-high chemotype and plot-level chemotype richness ($F_{1,75} = 7.08$, $P = 0.010$), and between the presence of the Mixed-low chemotype and plot-level chemotype richness ($F_{1,75} = 9.60$, $P = 0.003$). In all the interactions, plot-level chemotype richness negatively affected flower number when the chemotypes were absent but not when they were present (Fig. 4a, Table S2-10).

For the second growing season (2022), the presence/absence of certain chemotypes also strongly affected the flowering

phenology of plots. This was true for the Bthu-high, Bthu-low, Mixed-low, and Mixed-high chemotypes (Fig. 4b, Table S2-10). The presence of the Bthu-high or Mixed-high chemotype resulted in a higher flowering index, i.e., advancing flowering phenology compared to the plots where they were not present (Bthu-high chemotype presence: $F_{1,75} = 5.88$, $P = 0.018$; Mixed-high chemotype presence: $F_{1,75} = 37.90$, $P < 0.001$). Conversely, plot-level flowering phenology was retarded (i.e., less advanced flowering phenology) when the Bthu-low or Mixed-low chemotype was present than when it was not (Bthu-low chemotype presence: $F_{1,75} = 16.27$, $P < 0.001$; Mixed-low chemotype presence: $F_{1,75} = 22.42$, $P < 0.001$). All other models of the presence/absence of other chemotypes were non-significant.

Overyielding calculations

Regarding our hypothesis (ii), we did not observe an overyielding effect in plot-level plant performance on plots with higher chemotype richness for any plot-level plant traits (plot-level chemotype richness always $P > 0.05$; Table S2-12). However, we observed a weak negative tendency towards plants producing fewer flower heads ($\chi^2 = 2.57$, $P = 0.109$) when they were associated with more chemotypes (chemotype richness 2, 3, 6) compared to their performance in monocultures (Figure S2-11).

Headspace VOC analysis

The *T. vulgare* headspace VOC collections led to the identification of 60 compounds (Table S2-1). Classification of VOCs and a comparison between plot-level headspace VOC profiles and plot-level chemotype richness are available in Data S2.

Plot-level theoretical leaf and plot-level realized volatile chemodiversity metrics

Our results confirmed that plots that had a higher plot-level-chemotype richness (i.e., the number of different chemotypes present in the plot) also had higher *theoretical* leaf terpeneoid richness ($F_{1,82} = 20.48$, $R^2 = 0.20$, $P < 0.001$), diversity ($F_{1,82} = 37.25$, $R^2 = 0.31$, $P < 0.001$), and evenness ($F_{1,82} = 31.78$, $R^2 = 0.28$, $P < 0.001$) at the plot level (Fig. 5b–d). However, the theoretical leaf terpeneoid concentration did not show any relationship with plot-level chemotype richness ($F_{1,82} = 0.00$, $R^2 = 0.00$, $P = 0.967$; Fig. 5a). For the terpenoids in the headspace VOC profiles, plot-level chemotype richness had no significant effect on the abundance, richness, diversity, or evenness of terpenoids released as VOCs (Fig. 5e–h, Table S2-15). This rejects our hypothesis (iv) since plant communities with higher plot-level chemotype richness did not emit a more chemically diverse headspace of VOCs than plots with lower plot-level chemotype richness.

Plots that were more diverse in terms of their leaf terpenoids were not necessarily more diverse in their plot-level headspace terpeneoid profile. However, there was a weak positive correlation between leaf and headspace terpeneoid profiles (Mantel statistic $R^2 = 0.05$, $P < 0.001$). As plots became more dissimilar in terms of their leaf terpenoids, they also became more dissimilar in terms of their headspace terpenoids.

DISCUSSION

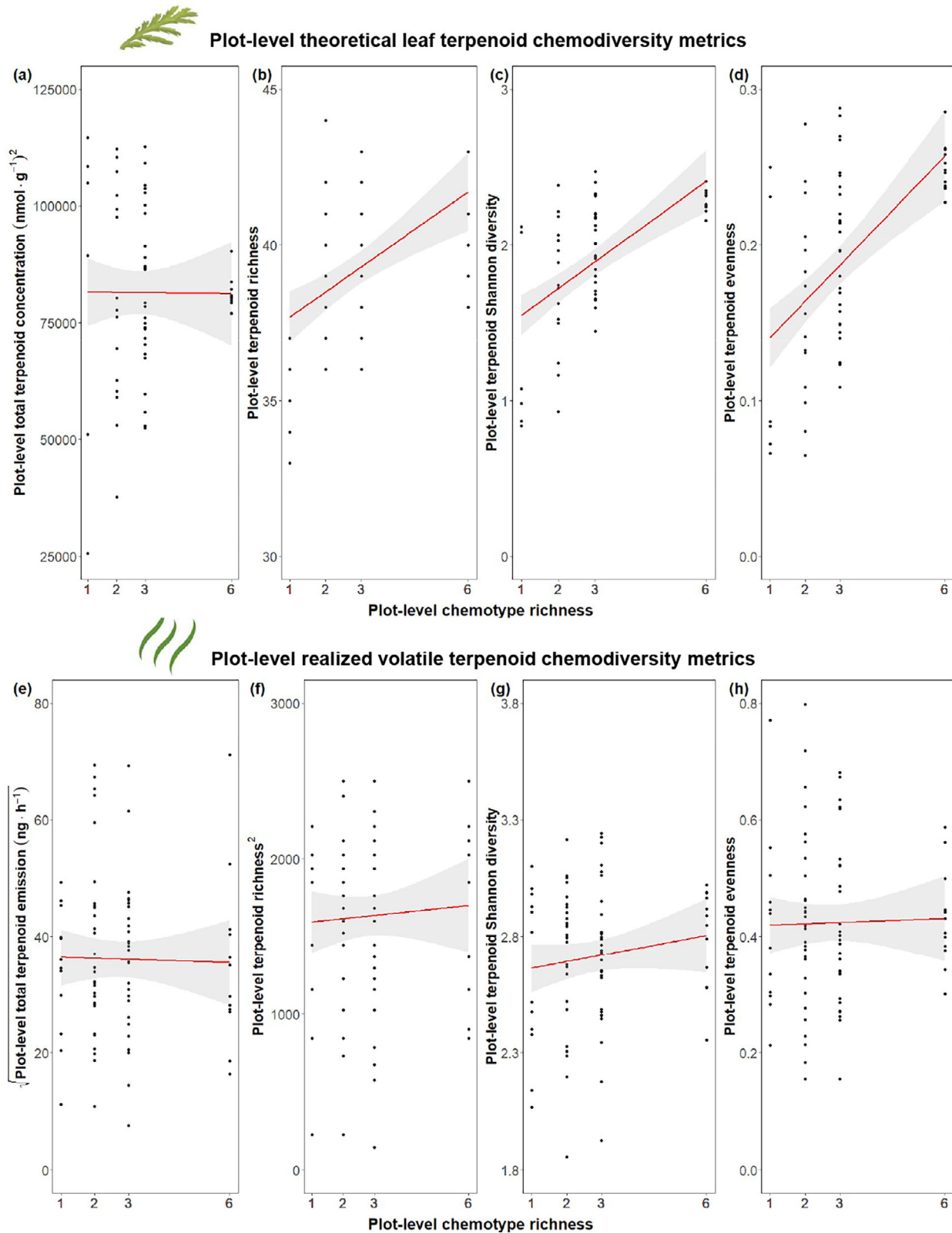
Here, we designed a biodiversity field experiment in which we manipulated the number of chemotypes of *Tanacetum vulgare*

plants at plot level to study how surrounding chemodiversity affects plant performance in the first 2 years after establishment. Our study showed that chemotypes initially differed in the studied morphological traits, confirming our first hypothesis (i). Concerning our second hypothesis (ii), the effects of plot-level chemodiversity on plot-level traits were only found for plot-level averages of reproductive traits, but not for growth-related traits. The third (iii) was also confirmed, i.e., the presence or absence of certain chemotypes and the plot-level chemotype richness influenced plot-level trait means. Importantly, the relationships between chemotypes, plot-level chemotype richness, and traits decreased over time in our 2-year study. Lastly, we found that the theoretical plot-level leaf terpeneoid profiles significantly predicted the plot-level headspace terpeneoid profiles, but the variance explained was low. However, plots that are chemically more diverse in terms of leaf terpenoids are not necessarily more diverse in their terpeneoid headspace profile (hypothesis iv).

Our results show that tansy chemotypes vary in their chemical profiles and growth-related (number of stems and height) and reproductive traits (number of flower heads and flowering phenology) under field conditions. These findings broadly support the results of previous studies that used the same plant model system and found links between plant chemotypes and plant traits (Keskitalo *et al.* 2001; Neuhaus-Harr *et al.* 2023). For instance, in a previous study, tansy chemotypes with a high concentration of camphor were taller compared to other chemotypes rich in trans-thujone, artemisia ketone, 1,8-cineole, or davadone-D, and chemotypes rich in artemisia ketone or davadone-D produced more flower heads and flowered later compared with the other four chemotypes (Keskitalo *et al.* 2001). However, since Keskitalo *et al.* (2001) analysed the effect of chemical composition on certain traits at a broader geographic scale, and the chemotypes used by them and those used here are very different in their chemical composition, the current study's findings are – although conceptually similar – hard to directly compare. In an earlier study using the same chemotype lineages used here, the chemotypes showed similar growth patterns (Neuhaus-Harr *et al.* 2023). This is not entirely surprising but reveals that clonally-produced chemotypes show a high degree of consistency in phenotypes, at least in the early weeks of growth. As chemotypes in this study are maternally related, this seems a plausible reason why chemotypes may differ in some of their traits. However, daughter lines often differed more strongly within chemotypes than between chemotypes for many traits, making it unlikely that a maternal effect is the sole explanation (Figures S2-3–S2-6).

Variability in growth traits across chemotypes may enable individuals to partition local resources into different growth strategies and thus avoid intraspecific competition (Messier

Fig. 5. Effects of plot-level chemotype richness on theoretical plot-level chemodiversity metrics based on leaf terpeneoid profiles (a–d) and realized plot-level volatile chemodiversity metrics (e–h). *Theoretical plot-level leaf* terpeneoid diversity metrics were calculated by summing absolute leaf terpeneoid concentrations ($\text{nmol}\cdot\text{g}^{-1}$) of each chemotype/daughter present in each plot based on the analysis of leaves from greenhouse plants in 2020 (Neuhaus-Harr *et al.* 2023). Realized plot-level volatile chemodiversity was based on terpenoids collected in the headspace ($\text{ng}\cdot\text{h}^{-1}$) in May 2022. Diversity metrics were calculated using the 'chemodiv' package (Pétren *et al.* 2022). Plot-level chemotype richness effects on *theoretical plot-level leaf* (a) squared total terpeneoid concentration ($\text{nmol}\cdot\text{g}^{-1}$), (b) terpeneoid richness, (c) terpeneoid Shannon diversity, and (d) terpeneoid evenness (summary of linear models in Table S5-13). Plot-level chemotype richness effects on *realized plot-level volatiles*, (e) square-root of total terpeneoid emissions ($\text{ng}\cdot\text{h}^{-1}$), (f) squared terpeneoid richness, (g) terpeneoid Shannon diversity, and (h) terpeneoid evenness (summary of linear mixed-models in Tables S2-14 and S2-15).



et al. 2010; Gallien 2017). For instance, the Bthu-low chemotype developed large biomass and typically few but taller and thicker stems compared with other chemotypes, such as Mixed-high, which developed more stems but these were

shorter and thinner. Interestingly, however, the morphological differences between the chemotypes diminished over time. Only the Bthu-low chemotype remained quite distinct in both years, possibly because of its pronounced strategy of growth:

tall and thick stems and high biomass. A likely explanation is the tendency for different daughters, even within chemotypes, to diverge in their trait expression over time, introducing enough variation to diminish chemotype-specific trait expression. This emphasizes the role of different growth strategies for individual survival, particularly during early establishment, and suggests that intraspecific chemodiversity might mediate niche realization processes (Müller & Junker 2022).

Contrary to our hypothesis, no differences were observed in plant growth parameters when plants grew in plots that differed in plot-level chemotype richness, indicating that the morphology of each chemotype is consistent across the environments in which they grow. Various possible explanations exist for why plant growth did not respond to plot-level chemotype richness. For instance, genotypes of *T. vulgare* can differ in their competitive ability in response to the presence of other plant species (Tse 2014), but little is known about the response to the presence of conspecifics. Although intra- or interspecific competition is expected to affect plant growth, differences between *T. vulgare* plants might be strongly determined by the genotype, especially in the early growth stage, so that intraspecific competition does not affect growth traits. It may very well be that growth responses to plot-level chemotype richness are not adaptive in *T. vulgare*, but as discussed below, responses do occur in other traits.

The measured *T. vulgare* reproductive traits also pronouncedly differed between chemotypes, but in contrast to what was observed for growth traits, plant-level reproductive traits responded to plot-level chemotype richness. Although Moreira *et al.* (2016) and Hughes *et al.* (2008) suggested that plants growing in plots that contained more chemotypes express higher individual plant fitness, in our study, all studied chemotypes, except for the Bthu-low chemotype, were inhibited (i.e., had lower flower head numbers) in plots with high plot-level chemotype richness compared to low-chemotype richness plots. This suggests that growth strategies that made the Bthu-low chemotype very dominant in height and weight in the first year might also bring some fitness advantages to this Bthu-low chemotype in highly diverse plant communities. It also suggests that most *T. vulgare* chemotypes might be negatively affected in more chemically diverse environments. This sharply contrasts with our expectations that chemically diverse environments would benefit plants. Our interpretation is based on the effect of chemodiversity on plant traits. Chemically diverse environments might still benefit plants by affecting plant interaction partners, as found by Ziaja & Müller (2023), who reported that some *T. vulgare* chemotypes benefit from neighbours that differ in chemotype in terms of lower herbivore load of *Uroleucon tanacetii* and *Macrosiphoniella tanacetaria* aphids. However, these authors did not report any plant performance parameters, and therefore, a direct comparison between their and our studies investigating plot-level chemotype richness effects is currently not possible.

Another key finding was that plot-level chemotype richness influenced flowering phenology in *T. vulgare*. In the case of the Bthu-low chemotype, the effect of plot-level chemotype richness was positive on the number of flower heads, but negative for the flowering index value, indicating a delayed onset of flowering. It appears that in different chemical environments, the flowering strategy differs across *T. vulgare* chemotypes. For instance, the Mixed-high, Athu-Bthu, and Mixed-low

chemotypes had a more advanced flowering status at the time of assessment (high flowering index value) in plots with higher plot-level chemotype richness, while the Bthu-low, Chrys-acet, and Bthu-high chemotypes had more delayed phenology (low flowering index value) in such plots. We speculate that *T. vulgare* might be able to sense their neighbouring plants, either through direct competition (e.g., for space and nutrients), via the perception of volatiles (Heil & Karban 2010; Karban *et al.* 2014; Kessler & Kalske 2018; Ninkovic *et al.* 2019; Ninkovic *et al.* 2021), or absorption of semi-volatile compounds emitted by neighbouring plants (Himanen *et al.* 2010). As a result, *T. vulgare* may avoid competition by being reproductively active at different times, thereby optimizing their fitness. Variations in flowering phenology may also correlate with variations in interacting arthropod communities, which could affect reproductive success (Kuppler *et al.* 2016). Moreover, differences in flowering phenology across chemotypes might constitute a strategy to avoid cross-pollination between certain tansy chemotypes that could result in poor seed production (Keskitalo *et al.* 1998).

As predicted, plot-level average trait values were, in 2021, higher in mixture plots containing certain chemotypes that had either more stems, were taller, had larger aboveground dry weight, or produced more flower heads. In the same line, plot-level trait values decreased when chemotypes with fewer stems, smaller, lighter, or producing fewer flower heads were present. Several types of interaction can be observed, ranging from adverse effects related to competition, possibly for a limiting resource, to positive effects through facilitation, for instance, through increased resource availability or decreased herbivory (Roscher *et al.* 2005; Marquard *et al.* 2009; Ziaja & Müller 2023). In our study, the influence of a highly chemically diverse environment led to higher performance of the Bthu-low chemotype (i.e., a higher cumulative number of flower heads). At the plot level, individual chemotype contributions appear to become less pronounced over time, suggesting that the plots became more similar as they age, at least in terms of their morphological structure. Furthermore, we found no overyielding effects in our system, but instead, found a tendency towards lower plot-level plant trait values when increasing chemotype richness. This is important for future and ongoing work in this field experiment, which will investigate the role of chemodiversity on insect community assembly. A reduction of the plant- and plot-level differences in growth traits reduces the strength of potential confounding effects of plant growth on insect community assembly and will, therefore, help us to draw more robust conclusions and deepen our understanding of the consequences of chemodiversity. Moreover, chemotypes of tansy plants have been studied regionally in their distribution ranges (Wolf *et al.* 2012; Clancy 2021; Rahimova *et al.* 2023), and little attention has been paid to the implications of naturally co-occurring neighbouring chemotypes.

In line with our predictions, most diversity metrics based on theoretical plot-level leaf terpenoid profiles increased with increasing plot-level chemotype richness. We observed no differences between plot types for the total approximate terpenoid concentration. In contrast to what we hypothesized, we found no effect of plot-level chemotype richness on diversity metrics calculated based on headspace terpenoids. More diverse plots based on the theoretical leaf terpenoid of each chemotype were not necessarily more diverse in their plot-level headspace terpenoid

profile. The headspace volatile terpenoid of a plant community is strongly dependent not only on the constitutive specialized metabolite profile of their individual plants, but also on the intrinsic chemical properties of their compounds (e.g., volatility and solubility), and on physiological and morphological plant features (such as the presence of trichomes; see Gershenzon & Dudareva (2007), He *et al.* (2011), Aschenbrenner *et al.* (2013)), and biological characteristics, such as the abundance and interacting organisms above- and belowground, plant age, and plant size (Takabayashi *et al.* 1994; McCormick *et al.* 2012; Kessler & Kalske 2018; Fabisch *et al.* 2019). Although volatile production is hard to accurately predict (Dudareva *et al.* 2006; Dicke *et al.* 2009), it is plausible that the volatile headspace profile will be related to the compounds found and stored in glandular trichomes in leaves of *T. vulgare*, since this plant has the capacity to store VOCs. However, while the hexane extraction was performed from the leaves of young plants before planting them in the field in 2021, the headspace terpenoids were obtained in the spring season 1 year after planting (2022) under field conditions (where the plants interacted with each other and other organisms) and analysed in a different lab. This could have led to changes in terpenoid diversity that may be reflected in our analysis (Eckert *et al.* 2023). Moreover, emitted volatile profiles might also differ from the stored profiles because some specific volatile organic compounds are produced only upon attack or under abiotic stress (e.g., green leaf volatiles, benzenoids, and terpenoids known as the herbivore-induced plant volatiles – HIPV; Rashid & Chung 2017; Unsicker *et al.* 2009). For example, Clancy *et al.* (2016) found that emitted *T. vulgare* headspace volatiles differed from compounds found in leaves at the individual level by 82%. However, the extent to which the chemotype richness and stored chemical profiles of a group of plants affect the volatiles in their communal headspace remains poorly understood. It will be interesting to see how the community-level volatile profile will develop over time when plants continue to grow and competition intensifies.

Further research should be undertaken to investigate the qualitative changes in plot-level volatile composition and how they correspond to plot-level cumulative leaf terpenoid profiles, but this was beyond the scope of the present study. Future investigations of leaf terpenoids and headspace terpenoids under field conditions over time, within and across growing seasons, upon induction, in response to environmental stresses, and including soil VOC from roots would help us to understand the temporal dynamics of plant terpenoid composition and volatile emission, and their effects on shaping plant–plant interactions. Furthermore, research on the mechanistic understanding of different defence strategies, such as the storage of defence metabolites and emission of volatiles, might help us understand these observed divergent patterns.

A mechanistic understanding of biodiversity–ecosystem functioning requires analysing the role of not only species number and functional groups, but also phylogenetic diversity and within-group variation in functional traits (Tilman *et al.* 1997). Our results provide insights into the underlying processes through which intraspecific chemodiversity acts on plant growth and reproductive traits. Although this study focuses on plant traits, this established field experiment also raises the possibility of further studying the role of intraspecific chemodiversity in interactions between plants and associated interaction partners, such as herbivorous insects, natural

enemies, and pollinators. Insect diversity and abundance are typically positively correlated with plant species diversity and interspecific diversity of functional traits (Junker *et al.* 2015). However, the effect of intraspecific plant chemodiversity on shaping such interactions in the field has received limited attention to date (but see Bustos-Segura *et al.* 2017). The findings of this study suggest that intraspecific chemodiversity might influence ecosystem properties, such as primary productivity, resource use efficiency, ecosystem stability, and resilience. Given the degradation of morphological trait differences over time, this field experiment offers a unique opportunity to study the effect of chemodiversity by means of the constitutive plant terpenoid profiles in nature.

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AUTHOR CONTRIBUTIONS

WWW conceived the original idea and designed the experiment. RH prepared the field experiment and propagated plants. LOP, RH, and WWW planted the field experiment. LOP collected all data and maintained the field experiment. LOP analysed ecological data with input from RH and WWW. PMvB, SBU, RH, and LOP prepared and executed volatile collections. PMvB chemically analysed volatiles. LOP wrote the manuscript with input from RH and WWW. All authors contributed to the final version and approved the final submission.

DATA AVAILABILITY STATEMENT

Data are available on request.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1-1. Leaf terpenoid composition (nmol/g) of chemotypes of *T. vulgare* plants.

Table S1-2. Assignment of plants to plots.

Figure S1-1. Stem phenology (*left-to-right then top-to-bottom*): [1] No inflorescence; [2] Inflorescence visible but closed;

[3] Open inflorescence; [4] Beginning seed set (unripe); [5] Ripe seeds; [6] Mature seeds turning brown.

Table S2-1. Volatile organic compounds (VOCs) of *Tanacetum vulgare* at plot level collected by headspace push-pull system in the field.

Table S2-2. Summary of generalized linear mixed-effect models (GLMM) testing chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness ($CP \times CR$) effects on the number of stems of *T. vulgare* plants at different time points in 2021 and 2022.

Table S2-3. Summary of linear mixed-effect models (LMM) testing chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness ($CP \times CR$) effects on the height (cm) of *T. vulgare* plants at different time points in 2021 and 2022.

Table S2-4. Summary of linear mixed-effect models (LMM) testing chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness ($CP \times CR$) effects on the square root above-ground dry weight (g) in 2021, and the square root above-ground fresh weight (g) in 2022 of *T. vulgare* plants.

Table S2-5. Summary of generalized linear mixed-effect models (GLMM) and linear mixed-effect models (LMM) testing chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness ($CP \times CR$) effects on the cumulative number of flower heads in 2021 and the flowering index in 2022 of *T. vulgare* plants, respectively.

Table S2-6. Summary of generalized linear mixed-effect models (GLMM) testing daughter identity (D), plot-level chemotype richness (CR), and the interaction between daughter identity and plot-level chemotype richness ($D \times CR$) effects on the number of stems, and summary of linear mixed-effect models (LMM) on the effects on height (cm), the squared root above-ground dry weight (g), and the cumulative number of flower heads of *T. vulgare* plants in 2021.

Table S2-7. Summary of linear models (LM) testing Block (B), chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between chemotype presence and plot-level chemotype richness ($CP \times CR$) effects on averaged number of stems of *T. vulgare* plants at plot level at different time points in 2021 and 2022.

Table S2-8. Summary of linear models (LM) testing Block (B), chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between chemotype presence and plot-level chemotype richness ($CP \times CR$) effects on averaged height (cm) of *T. vulgare* plants at plot level at different time points in 2021 and 2022.

Table S2-9. Summary of linear models (LM) testing Block (B), chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between chemotype presence and plot-level chemotype richness ($CP \times CR$) effects on the logarithm of averaged above-ground dry weight (g) in 2021, and the logarithm of averaged above-ground fresh weight (g) in 2022 of *T. vulgare* plants at plot level.

Table S2-10. Summary of linear models (LM) testing Block (B), chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between chemotype presence and plot-level chemotype richness ($CP \times CR$) effects on the

logarithm of the cumulative number of flower heads in 2021 and flowering index in 2022 of *T. vulgare* plants at plot level.

Table S2-11. Overyielding indices (OI) were calculated for each plant trait at plot-level (above-ground dry weight (g) – 2021, above-ground fresh weight (g) – 2022, the cumulative number of flower heads – 2021, and flowering index – 2022 of *T. vulgare* plants).

Table S2-12. Summary of linear mixed-effect models (LMM) testing plot-level chemotype richness (CR) effect on overyielding indices (OI).

Table S2-13. List of leaf terpenoids identified only by hexane extraction (16), headspace terpenoids identified only in VOC collection (21), and terpenoids identified by both methods (28).

Table S2-14. Summary of linear models (LM) testing plot-level chemotype richness (CR) effect on theoretical plot-level leaf terpene diversity metrics.

Table S2-15. Summary of linear mixed-effect models (LMM) testing plot-level chemotype richness (CR) effect on realized plot-level volatile diversity metrics.

Figure S2-1. Effect of chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness ($C \times CR$) on the number of stems of *T. vulgare* plants. (a) June 01, 2021, (b) June 22, 2021, (c) October 28, 2021, and (d) July 06, 2022.

Figure S2-2. Effect of chemotype identity (C), plot-level chemotype richness (CR), and the interaction between chemotype identity and plot-level chemotype richness ($C \times CR$) on height (cm) of *T. vulgare* plants. (a) June 01, 2021, (b) June 22, 2021, (c) October 28, 2021, (d) May 14, 2022, (e) July 06, 2022, and (f) October 05, 2022.

Figure S2-3. Effect of daughter identity (D), plot-level chemotype richness (CR), and the interaction between daughter identity and plot-level chemotype richness ($D \times CR$) on the number of stems of *T. vulgare* plants on October 28, 2021.

Figure S2-4. Effect of daughter identity (D), plot-level chemotype richness (CR), and the interaction between daughter identity and plot-level chemotype richness ($D \times CR$) on height (cm) of *T. vulgare* plants on October 28, 2021.

Figure S2-5. Effect of daughter identity (D), plot-level chemotype richness (CR), and the interaction between daughter identity and plot-level chemotype richness ($D \times CR$) on the squared root of dry above-ground biomass (g) of *T. vulgare* plants on October 28, 2021.

Figure S2-6. Effect of daughter identity (D), plot-level chemotype richness (CR), and the interaction between daughter identity and plot-level chemotype richness ($D \times CR$) on the cumulative number of flower heads of *T. vulgare* plants in 2021.

Figure S2-7. Effect of chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between chemotype presence and plot-level chemotype richness ($CP \times CR$) on plot-level number of stems of *T. vulgare* plants in 2021: (a) June 01, 2021, (b) June 22, 2021, and (c) October 28, 2021.

Figure S2-8. Effect of chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between chemotype presence and plot-level chemotype richness ($CP \times CR$) on plot-level height (cm) of *T. vulgare* plants in 2021: (a) June 01, 2021, (b) June 22, 2021, and (c) October 28, 2021.

Figure S2-9. Effect of chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between

chemotype presence and plot-level chemotype richness (CP $\times$ CR) on plot-level height (cm) of *T. vulgare* plants in 2022: (a) May 14, 2022, (b) July 06, 2022, and (c) October 05, 2022.

Figure S2-10. Effect of chemotype presence (CP), plot-level chemotype richness (CR), and the interaction between chemotype presence and plot-level chemotype richness (CP $\times$ CR) on (a) the logarithm of the plot-level above-ground dry weight (g) and (b) above-ground fresh weight (g) of *T. vulgare* plants.

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Intraspecific chemical variation of *Tanacetum vulgare* affects plant growth and reproductive traits in field plant communities

Supplementary Information 1 (S1): Supplementary Methods

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1.1. Detailed description of methods

1.1.1. Chemotypic characterization of *T. vulgare* lines and biological replicates

We used six *T. vulgare* chemotypes that were also used in Neuhaus-Harr *et al.* (2023). Based on an unsupervised hierarchical k-means clustering calculated on a dissimilarity matrix of the terpenoid profile obtained from hexane extraction of leaves of 27 *T. vulgare* plants found in Jena, Germany (50.93°N, 11.58°E), we randomly chose two plants from each of 6 of the resulting 7 clusters (hereafter 'mother' plant) and mass-sown their seeds. We selected ten healthy seedlings from each mother plant (120 plants, hereafter 'daughter' plant) and chemotyped those plants. Based on another unsupervised hierarchical clustering calculated on the terpenoid profile from hexane extraction of those 120 daughter plants in 2021, we obtained 6 clusters. We chose three daughter plants from the same mother for each cluster, resulting in 6 chemotypes and 18 daughter plants. It is essential to note that, despite being daughters of the same mother plant, the chemotypes among offspring are not guaranteed to be identical, as elucidated in Neuhaus-Harr *et al.* (2024). In this related work, a hierarchical clustering analysis involving 120 daughters from twelve mothers, which encompassed the six maternal chemotypes utilized in both studies, demonstrated that daughters from the same mother may exhibit distinct chemotypic clustering patterns.

1.1.2. Propagation of plant material for the field experiment

Stem parts from the 18 selected daughters were trimmed and used to produce 27-40 cuttings per daughter. Individual cuttings were cut 1-2 cm below and 4-5 cm above a leaf node. The leaf size was reduced by 60% to reduce evapotranspiration and improve the survival rate by shortening and trimming the leaflet. Stem cuttings were placed into seedling trays with soaked potting substrate and protected with a clear plastic propagation cover. After three weeks and root and shoot formation, the cover was gradually opened to allow the cuttings to acclimate. As the cuttings grew, they were transplanted into 10 cm pots and later into 17 cm pots before transplanting in the field site in May 2021. Potted plants were automatically watered from the bottom and fertilized as needed with Universol Blue fertilizer ® (18%N - 11%P - 18%K; ICL Deutschland, Nordhorn, Germany). During propagation and growth, plants were not treated with chemical insecticides or fungicides, but we applied biological control when needed. At the end of the growing period, there were multiple cloned plants from each of the 18 daughters. Cloned plants from each of the three daughters of each chemotype were used in the experimental design.

1.1.3. Plant morphological trait measurements

We measured six morphological plant traits for individual plants, including four growth traits (the number of stems per plant, the height of the highest stem, and above-ground fresh and dry weight) and two reproductive traits (the cumulative number of flower heads and the flowering index).

Three times in 2021 (June 01, June 22, and October 28), we counted the number of stems larger than 5 centimeters and measured plant height as the distance between the ground and the longest stem without stretching out leaves.

As a measure of reproductive success, we counted and cut off all ripe flower heads weekly during the 2021 season (from June 01 to October 28). Flower heads were cut off to avoid re-seeding plots with new plants. We thus refer to the total number of flower heads collected as the cumulative number of flower heads. At the end of the season (October 28, 2021), we obtained the above-ground dry weight of each plant; plants were cut off 5 cm above the ground, placed in single paper bags, and dried for 72 hours at 60°C in a drying room (Thermo-Scientific) of the University of Jena facilities.

In 2022, we counted the number of stems once (July 06) and measured plant height three times (May 14, July 06, and October 05). The phenological state of each stem of each plant was determined once (on July 06) using numerical categories: [1] No inflorescence; [2] Inflorescence visible but closed; [3] Open inflorescence; [4] Beginning seed set (unripe); [5] Ripe seeds; [6] Mature seeds turning brown (Fig. S1-1). To analyze phenology at the plant level, we calculated a flowering index for each plant by dividing the sum of all stem-level phenological stages by the number of stems (between 1 = all stems without inflorescence and 6 = all stems with mature seeds). We averaged plant-level flower indices per plot to obtain a measurement at the plot level.

At the end of the second season, all plants were again cut off 5 cm above ground but immediately weighted in the field to obtain fresh weight (October 05, 2022). From this, we calculated both plant-level and plot-level weights.

1.1.4. Headspace VOC collection

Headspace volatile organic compound (VOC) emissions were collected at the plot level (including all six individual plants) between May 12 and 14, 2022, using a closed-push-pull system for 2 hours (Fig. 1f-g). Weeds were removed by hand from the plots ten days before the measurements

to reduce the collection of volatiles from plants different from tansy. In addition, one extra new plot was prepared by thoroughly cleaning out the plant material ten days before and used as a volatile background profile (red plot in Fig. 1d).

A squared bag made from Polyethylene terephthalate PET (110 cm x 110 cm x 40 cm) foil was installed for VOC collections, covering the whole plot. Air entered the system after passing through an activated charcoal filter at a flow rate of 1.5 L/min and was pumped out through a trap at 1 L/min. The trap contained 25 mg of Poropak-Q absorbent (Volatile Collection Trap (VCT) LLC, USA) (Fig. 1f). VOCs were collected over a period of three days with three rounds of ten plots per day (two entire blocks + two background plots = 30 plots per day). Plots were assigned beforehand to ensure each plot-level chemotype richness level were included in each round.

After VOC collection, the traps were eluted with 200 μ l dichloromethane containing nonyl-acetate as an internal standard (Sigma-Aldrich, 10 ng $\times$ μ l⁻¹). VOCs were analyzed using a Hewlett-Packard model 6890 gas chromatograph coupled to a Hewlett-Packard model 5973 mass spectrometer (GC-MS). The GC was operated with helium as carrier gas at 1 ml/min, split-less injection (injection temperature: 220 °C, injection volume: 1 μ l), a DB-5MS column (30 m $\times$ 0.25 mm, 0.25 μ m film, J & W Scientific, Folsom, CA, USA), and a temperature program from 40 °C (2 min hold) to 350 °C (2 min hold) with a first gradient of 7 °C min⁻¹ to 155 °C, and a second gradient of 60 °C min⁻¹ to 300 °C. The GC was coupled to a single quadrupole mass spectrometer (Hewlett-Packard model 5973) operated in electron impact ionization mode. The transfer line temperature was 270 °C, the ionization potential was 70 eV, and a scan range of m/z 40–350 was employed.

VOCs were identified by comparing retention times and mass spectra with commercial standards (when available) and by comparison to the mass spectral libraries Wiley 275 (Wiley and National Institute of Standards) and NIST05a (National Institute of Standards and Technology, Gaithersburg, MD). We verified the VOC identity by calculating Kovats retention indices. The qualitative and quantitative analysis of the volatile data is beyond the scope of this study; here, we report only on volatile terpenoid diversity metrics at the plot level.

1.2. Design of the field experiment

1.2.1. Leaf terpenoid composition of chemotypes

Table S1-1: Leaf terpenoid composition (nmol/g) of chemotypes of *T. vulgare* plants. The table is partitioned into three sections showing different terpenoids in alphabetic order. Each section lists the chemotypes tested (6), the three daughter plants chosen for each chemotype (18), and the concentration of each terpenoid found in each daughter after hexane extraction of leaf material. Chemotypes are named after their dominant compounds, and numbers identify daughters. Plant chemotyping and chemotype selection are described in more detail in Neuhaus-Harr *et al.* (2023).

Chemotype	Daughter	1-terpin-4-nyl acetate	α -chrysanthenyl acetate	α -farnesene	α -pinene	α -terpinene	α -thujene	α -thujone	artemisia- β -acetate	artemisia alcohol	artemisia ketone	β -carvyl acetate	β -caryophyllene	β -ocimene	β -pinene	β -thujone	borneol	camphene	camphor
Athu-Bthu	55	0.01	0.00	0.00	0.17	0.01	0.00	27.66	0.05	0.00	0.00	0.00	0.00	0.05	0.85	28.25	0.00	0.00	0.01
Athu-Bthu	56	0.01	0.07	0.00	0.34	0.00	0.00	24.05	0.13	0.52	0.00	0.00	0.00	0.01	0.11	24.67	0.30	0.00	0.01
Athu-Bthu	57	0.02	0.12	0.00	0.34	0.00	0.00	22.70	0.32	0.62	0.60	0.00	0.00	0.02	0.10	23.10	0.26	0.00	0.01
Bthu-high	11	0.02	0.08	0.70	0.29	0.00	0.00	0.20	0.64	0.69	0.00	0.06	0.00	0.05	3.28	39.76	0.43	0.00	0.01
Bthu-high	14	0.01	0.16	0.00	0.37	0.00	0.00	0.19	0.00	0.00	0.05	0.00	0.00	0.00	0.24	40.37	0.54	0.00	0.01
Bthu-high	17	0.02	0.00	0.00	0.33	0.01	0.11	0.20	0.00	0.94	0.00	0.20	0.00	0.04	0.45	42.55	0.00	0.00	0.01
Bthu-low	101	0.02	0.00	0.00	0.20	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	29.33	0.00	0.02	0.01
Bthu-low	103	0.02	0.10	0.00	0.22	0.01	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.03	5.59	23.29	0.41	0.01	0.01
Bthu-low	104	0.01	0.12	0.00	0.18	0.01	0.11	0.18	0.00	0.00	0.05	0.00	0.00	0.02	4.66	32.59	0.41	0.01	0.01
Chrys-acet	94	0.01	0.05	0.00	2.09	0.00	0.00	0.00	0.03	0.00	0.25	0.00	0.00	0.02	0.07	0.00	0.18	0.42	0.02
Chrys-acet	95	0.01	0.02	0.00	2.51	0.00	0.07	0.00	0.03	0.00	0.29	0.00	0.00	0.07	0.49	0.00	0.31	0.40	0.79
Chrys-acet	100	0.01	0.04	0.00	2.86	0.01	0.05	0.00	0.08	0.00	0.15	0.00	0.00	0.02	0.12	0.00	0.00	0.51	0.02
Mixed-high	21	0.03	0.00	0.00	2.87	0.01	0.33	0.00	0.00	0.00	0.00	0.11	0.00	0.18	0.83	0.00	7.59	2.32	0.01
Mixed-high	23	0.01	0.00	0.00	2.30	0.01	0.16	0.00	0.20	0.78	0.00	0.00	0.00	0.08	0.73	0.00	7.63	1.80	0.01
Mixed-high	30	0.02	0.00	0.00	3.58	0.00	0.36	0.00	0.00	0.66	0.00	0.14	0.00	0.03	1.00	0.00	7.96	2.91	0.01
Mixed-low	64	0.03	0.12	0.00	6.30	0.01	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.02	2.63	0.00	0.37	0.06	0.02
Mixed-low	67	2.80	0.00	0.00	5.35	0.01	0.07	0.00	0.09	0.00	0.00	0.00	0.75	1.55	1.04	0.00	3.63	1.50	0.05
Mixed-low	68	0.02	0.00	0.00	4.96	0.00	0.16	0.00	0.00	0.00	0.72	0.00	0.09	0.01	3.25	0.00	0.00	0.01	0.01

Table S1-1 (continued): This section shows the results for the second part of Table S1-1, partitioned by terpenoid.

Chemotype	Daughter	chrysanthenyl acetate	cis-chrysanthenol	cis-miroxide	cis-sabinene hydrate	cis-verbanol acetate	eucalyptol	eugenol	γ-terpinene	limonene	methyloisoborneol	mustakone	myrcene	p-cymene	pinocarvone	sabinene	santolina triene	trans-chrysanthenol	trans-sabinene hydrate
Athu-Bthu	55	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.10	0.51	1.09	0.85	0.01	0.00	0.10
Athu-Bthu	56	0.00	0.00	0.01	0.00	0.00	0.01	0.02	0.06	0.00	0.00	0.00	0.00	0.32	0.01	0.51	0.00	0.09	0.00
Athu-Bthu	57	0.00	0.02	0.01	0.07	0.00	0.02	0.01	0.03	0.00	0.05	0.00	0.00	0.24	0.46	0.42	0.01	0.00	0.00
Bthu-high	11	0.00	0.01	0.01	0.08	0.00	0.02	0.00	0.01	0.09	0.00	0.00	0.00	0.33	0.06	3.22	0.00	0.00	0.00
Bthu-high	14	0.00	0.00	0.02	0.07	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.06	0.21	0.06	1.60	0.00	0.03	0.00
Bthu-high	17	0.00	0.01	0.05	0.07	0.00	0.02	0.04	0.01	0.00	0.00	0.00	0.00	0.43	0.00	6.52	0.00	0.00	0.00
Bthu-low	101	0.00	0.01	0.02	0.10	0.00	0.12	0.03	0.02	0.00	0.00	0.00	0.06	0.43	0.03	0.04	0.01	0.00	0.00
Bthu-low	103	0.00	0.07	0.01	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.66	0.01	5.59	0.01	0.00	0.00
Bthu-low	104	0.00	0.00	0.01	0.06	0.00	0.24	0.03	0.01	0.00	0.02	0.00	0.10	0.45	0.76	4.68	0.01	0.05	0.12
Chrys-acet	94	48.13	2.32	0.02	0.08	0.00	0.78	0.05	0.85	0.00	0.58	0.00	0.02	0.84	0.01	0.73	0.01	0.00	0.10
Chrys-acet	95	45.84	1.68	0.01	0.04	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.30	0.01	0.49	0.01	0.02	0.07
Chrys-acet	100	46.13	1.95	0.01	0.08	0.00	0.00	0.02	0.70	0.00	0.00	0.00	0.02	0.75	0.00	0.80	0.00	0.00	0.04
Mixed-high	21	0.00	0.00	0.03	16.90	0.00	0.00	0.00	0.18	0.00	7.64	0.00	0.00	0.09	0.01	5.70	0.00	0.00	0.00
Mixed-high	23	0.00	0.08	0.02	17.07	0.00	0.00	0.00	0.11	0.00	7.84	3.19	0.03	0.00	0.07	3.95	0.00	0.00	1.29
Mixed-high	30	0.00	0.01	0.01	16.57	0.00	0.04	0.01	0.45	0.00	8.03	0.00	0.03	0.00	0.00	6.41	0.00	0.00	0.10
Mixed-low	64	0.00	0.43	0.02	0.03	0.00	0.00	0.03	1.13	0.00	0.00	0.00	0.00	1.18	0.01	11.62	0.01	0.06	0.03
Mixed-low	67	0.15	0.03	0.02	0.07	2.56	0.04	0.16	2.33	0.00	1.07	0.00	0.03	0.00	0.01	6.45	0.00	0.00	0.18
Mixed-low	68	0.00	0.01	0.02	0.42	0.00	0.03	0.00	0.51	0.00	0.00	0.00	0.11	0.04	0.01	13.04	0.01	0.00	0.26

Table S1-1 (continued): This section shows the results for the third and final part of Table S1-1, partitioned by terpenoid.

Chemotype	Daughter	trans-sabinyl acetate	Unknown terpenoid	Unknown sesquiterpene 1	Unknown sesquiterpene 2	Unknown sesquiterpene 3	Unknown sesquiterpene 4	Unknown sesquiterpene 5	yomogi alcohol
Athu-Bthu	55	0.00	0.01	0.00	0.00	0.07	0.00	0.00	0.03
Athu-Bthu	56	0.00	0.02	0.09	0.06	0.09	0.00	0.01	0.08
Athu-Bthu	57	0.00	0.01	0.00	0.13	0.22	0.00	0.00	0.00
Bthu-high	11	0.00	0.02	0.00	0.00	0.00	2.26	0.00	0.06
Bthu-high	14	0.00	0.01	0.00	0.16	0.15	0.00	0.00	0.09
Bthu-high	17	0.01	0.01	0.03	0.00	0.00	0.00	0.00	0.08
Bthu-low	101	0.00	0.01	0.09	0.05	0.17	0.00	0.00	0.16
Bthu-low	103	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.13
Bthu-low	104	0.00	0.01	0.00	0.00	0.10	0.00	0.00	0.08
Chrys-acet	94	0.00	0.81	0.02	0.00	0.00	0.00	0.13	0.05
Chrys-acet	95	0.00	0.79	0.12	0.05	0.06	0.00	0.00	0.00
Chrys-acet	100	0.00	1.07	0.00	0.01	0.09	0.00	0.00	0.09
Mixed-high	21	0.01	6.53	0.05	0.00	0.00	0.00	0.00	0.06
Mixed-high	23	0.00	6.92	0.00	0.06	0.25	0.00	0.44	0.06
Mixed-high	30	0.00	9.19	0.00	0.00	0.00	0.00	0.00	0.08
Mixed-low	64	0.00	0.02	0.06	0.09	0.19	0.00	0.00	0.10
Mixed-low	67	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.09
Mixed-low	68	0.00	0.02	0.03	0.00	0.18	0.00	0.00	0.00

1.2.2. Assignment of plants to plots

Table S1-2: Assignment of plants to plots. The table is partitioned into 11 sections, showing the plant identity in order. The field experiment contained 84 plots: 12, 30, 30, and 12 replicate plots for plot-level chemotype richness levels 1, 2, 3, and 6, respectively. Plots were distributed equally in six randomized blocks. Each block consisted of 14 plots: two plots of chemotype richness level 1, five plots of chemotype richness level 2, five plots of chemotype richness level 3, and two plots with chemotype richness level 6. Each plot consisted of 6 plants, which position within the plot was randomly assigned (Plot position), and which chemotype and daughter identities are listed here.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
1	1	1	1	3	Athu-Bthu	57
1	1	2	2	3	Chrys-acet	100
1	1	3	3	3	Chrys-acet	94
1	1	4	4	3	Athu-Bthu	55
1	1	5	5	3	Bthu-low	103
1	1	6	6	3	Bthu-low	101
1	2	7	1	2	Mixed-low	68
1	2	8	2	2	Mixed-low	67
1	2	9	3	2	Athu-Bthu	55
1	2	10	4	2	Athu-Bthu	57
1	2	11	5	2	Athu-Bthu	56
1	2	12	6	2	Mixed-low	64
1	3	13	1	3	Mixed-high	30
1	3	14	2	3	Mixed-high	21
1	3	15	3	3	Chrys-acet	94
1	3	16	4	3	Chrys-acet	100
1	3	17	5	3	Bthu-low	101
1	3	18	6	3	Bthu-low	104
1	4	19	1	2	Athu-Bthu	56
1	4	20	2	2	Athu-Bthu	57
1	4	21	3	2	Bthu-low	101
1	4	22	4	2	Bthu-low	104
1	4	23	5	2	Athu-Bthu	55
1	4	24	6	2	Bthu-low	103
1	5	25	1	3	Chrys-acet	95
1	5	26	2	3	Bthu-high	14
1	5	27	3	3	Bthu-high	11
1	5	28	4	3	Mixed-high	21
1	5	29	5	3	Chrys-acet	94
1	5	30	6	3	Mixed-high	30
1	6	31	1	6	Mixed-low	68
1	6	32	2	6	Bthu-low	104
1	6	33	3	6	Bthu-high	11
1	6	34	4	6	Mixed-high	30
1	6	35	5	6	Chrys-acet	100
1	6	36	6	6	Athu-Bthu	55

Table S1-2 (continued): This section shows the results for the second part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
1	7	37	1	6	Athu-Bthu	55
1	7	38	2	6	Bthu-low	101
1	7	39	3	6	Bthu-high	17
1	7	40	4	6	Mixed-low	64
1	7	41	5	6	Mixed-high	21
1	7	42	6	6	Chrys-acet	94
1	8	43	1	2	Chrys-acet	94
1	8	44	2	2	Bthu-low	101
1	8	45	3	2	Chrys-acet	100
1	8	46	4	2	Chrys-acet	95
1	8	47	5	2	Bthu-low	103
1	8	48	6	2	Bthu-low	104
1	9	49	1	1	Mixed-high	21
1	9	50	2	1	Mixed-high	30
1	9	51	3	1	Mixed-high	21
1	9	52	4	1	Mixed-high	30
1	9	53	5	1	Mixed-high	23
1	9	54	6	1	Mixed-high	23
1	10	55	1	1	Bthu-high	11
1	10	56	2	1	Bthu-high	17
1	10	57	3	1	Bthu-high	14
1	10	58	4	1	Bthu-high	14
1	10	59	5	1	Bthu-high	11
1	10	60	6	1	Bthu-high	17
1	11	61	1	2	Bthu-high	17
1	11	62	2	2	Bthu-high	11
1	11	63	3	2	Chrys-acet	94
1	11	64	4	2	Chrys-acet	95
1	11	65	5	2	Chrys-acet	100
1	11	66	6	2	Bthu-high	14
1	12	67	1	2	Bthu-low	103
1	12	68	2	2	Bthu-low	101
1	12	69	3	2	Mixed-high	23
1	12	70	4	2	Bthu-low	104
1	12	71	5	2	Mixed-high	21
1	12	72	6	2	Mixed-high	30
1	13	73	1	3	Bthu-low	104
1	13	74	2	3	Mixed-low	68
1	13	75	3	3	Mixed-low	64
1	13	76	4	3	Bthu-low	101
1	13	77	5	3	Athu-Bthu	56
1	13	78	6	3	Athu-Bthu	57
1	14	79	1	3	Athu-Bthu	55
1	14	80	2	3	Mixed-low	64
1	14	81	3	3	Bthu-high	11
1	14	82	4	3	Athu-Bthu	56
1	14	83	5	3	Mixed-low	68
1	14	84	6	3	Bthu-high	17

Table S1-2 (continued): This section shows the results for the third part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
2	15	85	1	2	Bthu-low	101
2	15	86	2	2	Mixed-low	64
2	15	87	3	2	Mixed-low	67
2	15	88	4	2	Mixed-low	68
2	15	89	5	2	Bthu-low	104
2	15	90	6	2	Bthu-low	103
2	16	91	1	6	Athu-Bthu	57
2	16	92	2	6	Chrys-acet	95
2	16	93	3	6	Bthu-low	103
2	16	94	4	6	Bthu-high	14
2	16	95	5	6	Mixed-low	67
2	16	96	6	6	Mixed-high	23
2	17	97	1	2	Mixed-high	21
2	17	98	2	2	Bthu-high	14
2	17	99	3	2	Mixed-high	23
2	17	100	4	2	Mixed-high	30
2	17	101	5	2	Bthu-high	17
2	17	102	6	2	Bthu-high	11
2	18	103	1	3	Bthu-high	17
2	18	104	2	3	Mixed-high	23
2	18	105	3	3	Athu-Bthu	57
2	18	106	4	3	Bthu-high	14
2	18	107	5	3	Mixed-high	30
2	18	108	6	3	Athu-Bthu	55
2	19	109	1	2	Mixed-low	68
2	19	110	2	2	Mixed-low	64
2	19	111	3	2	Chrys-acet	95
2	19	112	4	2	Mixed-low	67
2	19	113	5	2	Chrys-acet	100
2	19	114	6	2	Chrys-acet	94
2	20	115	1	2	Bthu-high	17
2	20	116	2	2	Athu-Bthu	56
2	20	117	3	2	Bthu-high	14
2	20	118	4	2	Athu-Bthu	57
2	20	119	5	2	Bthu-high	11
2	20	120	6	2	Athu-Bthu	55
2	21	121	1	3	Mixed-high	23
2	21	122	2	3	Mixed-high	30
2	21	123	3	3	Athu-Bthu	55
2	21	124	4	3	Chrys-acet	95
2	21	125	5	3	Athu-Bthu	57
2	21	126	6	3	Chrys-acet	100
2	22	127	1	6	Athu-Bthu	56
2	22	128	2	6	Mixed-high	23
2	22	129	3	6	Bthu-high	14
2	22	130	4	6	Bthu-low	104
2	22	131	5	6	Mixed-low	64
2	22	132	6	6	Chrys-acet	95

Table S1-2 (continued): This section shows the results for the fourth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
2	23	133	1	3	Bthu-high	14
2	23	134	2	3	Mixed-low	67
2	23	135	3	3	Bthu-high	11
2	23	136	4	3	Mixed-low	68
2	23	137	5	3	Bthu-low	104
2	23	138	6	3	Bthu-low	103
2	24	139	1	1	Bthu-low	104
2	24	140	2	1	Bthu-low	104
2	24	141	3	1	Bthu-low	101
2	24	142	4	1	Bthu-low	101
2	24	143	5	1	Bthu-low	103
2	24	144	6	1	Bthu-low	103
2	25	145	1	1	Mixed-low	67
2	25	146	2	1	Mixed-low	64
2	25	147	3	1	Mixed-low	68
2	25	148	4	1	Mixed-low	67
2	25	149	5	1	Mixed-low	68
2	25	150	6	1	Mixed-low	64
2	26	151	1	3	Bthu-high	14
2	26	152	2	3	Bthu-high	17
2	26	153	3	3	Mixed-low	67
2	26	154	4	3	Chrys-acet	95
2	26	155	5	3	Mixed-low	64
2	26	156	6	3	Chrys-acet	100
2	27	157	1	3	Bthu-high	14
2	27	158	2	3	Bthu-high	17
2	27	159	3	3	Bthu-low	104
2	27	160	4	3	Mixed-high	23
2	27	161	5	3	Mixed-high	30
2	27	162	6	3	Bthu-low	103
2	28	163	1	2	Mixed-high	23
2	28	164	2	2	Chrys-acet	95
2	28	165	3	2	Chrys-acet	94
2	28	166	4	2	Chrys-acet	100
2	28	167	5	2	Mixed-high	21
2	28	168	6	2	Mixed-high	30
3	29	169	1	2	Bthu-low	104
3	29	170	2	2	Bthu-high	14
3	29	171	3	2	Bthu-low	103
3	29	172	4	2	Bthu-high	17
3	29	173	5	2	Bthu-low	101
3	29	174	6	2	Bthu-high	11
3	30	175	1	3	Mixed-high	23
3	30	176	2	3	Mixed-high	21
3	30	177	3	3	Bthu-high	11
3	30	178	4	3	Bthu-low	101
3	30	179	5	3	Bthu-high	17
3	30	180	6	3	Bthu-low	103

Table S1-2 (continued): This section shows the results for the fifth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
3	31	181	1	2	Mixed-low	68
3	31	182	2	2	Mixed-high	21
3	31	183	3	2	Mixed-high	30
3	31	184	4	2	Mixed-low	67
3	31	185	5	2	Mixed-high	23
3	31	186	6	2	Mixed-low	64
3	32	187	1	6	Bthu-low	103
3	32	188	2	6	Mixed-low	68
3	32	189	3	6	Chrys-acet	94
3	32	190	4	6	Mixed-high	23
3	32	191	5	6	Athu-Bthu	56
3	32	192	6	6	Bthu-high	11
3	33	193	1	2	Athu-Bthu	56
3	33	194	2	2	Athu-Bthu	55
3	33	195	3	2	Chrys-acet	100
3	33	196	4	2	Chrys-acet	95
3	33	197	5	2	Chrys-acet	94
3	33	198	6	2	Athu-Bthu	57
3	34	199	1	1	Athu-Bthu	56
3	34	200	2	1	Athu-Bthu	55
3	34	201	3	1	Athu-Bthu	57
3	34	202	4	1	Athu-Bthu	56
3	34	203	5	1	Athu-Bthu	57
3	34	204	6	1	Athu-Bthu	55
3	35	205	1	1	Chrys-acet	94
3	35	206	2	1	Chrys-acet	100
3	35	207	3	1	Chrys-acet	100
3	35	208	4	1	Chrys-acet	95
3	35	209	5	1	Chrys-acet	95
3	35	210	6	1	Chrys-acet	94
3	36	211	1	3	Chrys-acet	100
3	36	212	2	3	Mixed-high	21
3	36	213	3	3	Bthu-high	11
3	36	214	4	3	Bthu-high	14
3	36	215	5	3	Chrys-acet	94
3	36	216	6	3	Mixed-high	23
3	37	217	1	3	Athu-Bthu	56
3	37	218	2	3	Mixed-low	67
3	37	219	3	3	Chrys-acet	94
3	37	220	4	3	Athu-Bthu	57
3	37	221	5	3	Chrys-acet	100
3	37	222	6	3	Mixed-low	68
3	38	223	1	2	Mixed-high	30
3	38	224	2	2	Mixed-high	21
3	38	225	3	2	Athu-Bthu	56
3	38	226	4	2	Mixed-high	23
3	38	227	5	2	Athu-Bthu	57
3	38	228	6	2	Athu-Bthu	55

Table S1-2 (continued): This section shows the results for the sixth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
3	39	229	1	3	Mixed-low	67
3	39	230	2	3	Mixed-low	64
3	39	231	3	3	Mixed-high	21
3	39	232	4	3	Bthu-high	17
3	39	233	5	3	Bthu-high	11
3	39	234	6	3	Mixed-high	30
3	40	235	1	3	Mixed-low	68
3	40	236	2	3	Mixed-high	21
3	40	237	3	3	Athu-Bthu	57
3	40	238	4	3	Athu-Bthu	56
3	40	239	5	3	Mixed-high	23
3	40	240	6	3	Mixed-low	64
3	41	241	1	2	Bthu-high	11
3	41	242	2	2	Bthu-high	14
3	41	243	3	2	Mixed-low	67
3	41	244	4	2	Mixed-low	64
3	41	245	5	2	Mixed-low	68
3	41	246	6	2	Bthu-high	17
3	42	247	1	6	Chrys-acet	100
3	42	248	2	6	Bthu-low	103
3	42	249	3	6	Mixed-low	64
3	42	250	4	6	Mixed-high	21
3	42	251	5	6	Bthu-high	11
3	42	252	6	6	Athu-Bthu	55
4	43	253	1	1	Chrys-acet	100
4	43	254	2	1	Chrys-acet	95
4	43	255	3	1	Chrys-acet	95
4	43	256	4	1	Chrys-acet	94
4	43	257	5	1	Chrys-acet	94
4	43	258	6	1	Chrys-acet	100
4	44	259	1	1	Athu-Bthu	57
4	44	260	2	1	Athu-Bthu	55
4	44	261	3	1	Athu-Bthu	56
4	44	262	4	1	Athu-Bthu	55
4	44	263	5	1	Athu-Bthu	56
4	44	264	6	1	Athu-Bthu	57
4	45	265	1	2	Athu-Bthu	55
4	45	266	2	2	Athu-Bthu	57
4	45	267	3	2	Athu-Bthu	56
4	45	268	4	2	Chrys-acet	94
4	45	269	5	2	Chrys-acet	100
4	45	270	6	2	Chrys-acet	95
4	46	271	1	2	Bthu-high	17
4	46	272	2	2	Bthu-high	14
4	46	273	3	2	Mixed-low	64
4	46	274	4	2	Mixed-low	68
4	46	275	5	2	Bthu-high	11
4	46	276	6	2	Mixed-low	67

Table S1-2 (continued): This section shows the results for the seventh part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
4	47	277	1	6	Athu-Bthu	57
4	47	278	2	6	Mixed-low	67
4	47	279	3	6	Mixed-high	21
4	47	280	4	6	Bthu-low	104
4	47	281	5	6	Chrys-acet	100
4	47	282	6	6	Bthu-high	14
4	48	283	1	3	Bthu-low	101
4	48	284	2	3	Bthu-high	11
4	48	285	3	3	Mixed-high	21
4	48	286	4	3	Bthu-low	103
4	48	287	5	3	Bthu-high	17
4	48	288	6	3	Mixed-high	23
4	49	289	1	3	Mixed-low	67
4	49	290	2	3	Mixed-high	21
4	49	291	3	3	Mixed-high	30
4	49	292	4	3	Bthu-high	11
4	49	293	5	3	Mixed-low	68
4	49	294	6	3	Bthu-high	17
4	50	295	1	6	Mixed-high	23
4	50	296	2	6	Bthu-high	14
4	50	297	3	6	Bthu-low	101
4	50	298	4	6	Mixed-low	67
4	50	299	5	6	Athu-Bthu	56
4	50	300	6	6	Chrys-acet	94
4	51	301	1	3	Bthu-high	14
4	51	302	2	3	Bthu-high	11
4	51	303	3	3	Chrys-acet	95
4	51	304	4	3	Chrys-acet	100
4	51	305	5	3	Mixed-high	21
4	51	306	6	3	Mixed-high	23
4	52	307	1	3	Athu-Bthu	56
4	52	308	2	3	Chrys-acet	100
4	52	309	3	3	Athu-Bthu	55
4	52	310	4	3	Mixed-low	64
4	52	311	5	3	Mixed-low	67
4	52	312	6	3	Chrys-acet	95
4	53	313	1	2	Mixed-low	68
4	53	314	2	2	Mixed-high	23
4	53	315	3	2	Mixed-low	64
4	53	316	4	2	Mixed-high	21
4	53	317	5	2	Mixed-low	67
4	53	318	6	2	Mixed-high	30
4	54	319	1	2	Bthu-high	11
4	54	320	2	2	Bthu-high	14
4	54	321	3	2	Bthu-low	104
4	54	322	4	2	Bthu-high	17
4	54	323	5	2	Bthu-low	101
4	54	324	6	2	Bthu-low	103

Table S1-2 (continued): This section shows the results for the eighth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
4	55	325	1	2	Athu-Bthu	56
4	55	326	2	2	Athu-Bthu	57
4	55	327	3	2	Mixed-high	30
4	55	328	4	2	Athu-Bthu	55
4	55	329	5	2	Mixed-high	21
4	55	330	6	2	Mixed-high	23
4	56	331	1	3	Mixed-low	68
4	56	332	2	3	Athu-Bthu	56
4	56	333	3	3	Mixed-low	67
4	56	334	4	3	Athu-Bthu	55
4	56	335	5	3	Mixed-high	23
4	56	336	6	3	Mixed-high	21
5	57	337	1	1	Mixed-low	67
5	57	338	2	1	Mixed-low	64
5	57	339	3	1	Mixed-low	68
5	57	340	4	1	Mixed-low	64
5	57	341	5	1	Mixed-low	68
5	57	342	6	1	Mixed-low	67
5	58	343	1	3	Bthu-high	17
5	58	344	2	3	Mixed-low	64
5	58	345	3	3	Bthu-high	14
5	58	346	4	3	Chrys-acet	94
5	58	347	5	3	Mixed-low	68
5	58	348	6	3	Chrys-acet	95
5	59	349	1	6	Athu-Bthu	57
5	59	350	2	6	Mixed-low	67
5	59	351	3	6	Bthu-high	17
5	59	352	4	6	Bthu-low	103
5	59	353	5	6	Chrys-acet	95
5	59	354	6	6	Mixed-high	21
5	60	355	1	3	Bthu-high	14
5	60	356	2	3	Bthu-low	103
5	60	357	3	3	Bthu-low	104
5	60	358	4	3	Mixed-high	23
5	60	359	5	3	Bthu-high	17
5	60	360	6	3	Mixed-high	30
5	61	361	1	3	Mixed-high	23
5	61	362	2	3	Mixed-high	30
5	61	363	3	3	Athu-Bthu	57
5	61	364	4	3	Athu-Bthu	56
5	61	365	5	3	Bthu-high	17
5	61	366	6	3	Bthu-high	14
5	62	367	1	2	Mixed-high	21
5	62	368	2	2	Chrys-acet	95
5	62	369	3	2	Chrys-acet	100
5	62	370	4	2	Mixed-high	30
5	62	371	5	2	Chrys-acet	94
5	62	372	6	2	Mixed-high	23

Table S1-2 (continued): This section shows the results for the ninth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
5	63	373	1	1	Bthu-low	101
5	63	374	2	1	Bthu-low	104
5	63	375	3	1	Bthu-low	103
5	63	376	4	1	Bthu-low	104
5	63	377	5	1	Bthu-low	101
5	63	378	6	1	Bthu-low	103
5	64	379	1	3	Mixed-high	30
5	64	380	2	3	Athu-Bthu	57
5	64	381	3	3	Mixed-high	23
5	64	382	4	3	Athu-Bthu	56
5	64	383	5	3	Chrys-acet	94
5	64	384	6	3	Chrys-acet	95
5	65	385	1	6	Bthu-high	17
5	65	386	2	6	Mixed-high	30
5	65	387	3	6	Mixed-low	68
5	65	388	4	6	Athu-Bthu	56
5	65	389	5	6	Chrys-acet	95
5	65	390	6	6	Bthu-low	103
5	66	391	1	3	Bthu-high	11
5	66	392	2	3	Bthu-low	103
5	66	393	3	3	Mixed-low	64
5	66	394	4	3	Bthu-low	104
5	66	395	5	3	Bthu-high	14
5	66	396	6	3	Mixed-low	68
5	67	397	1	2	Mixed-high	30
5	67	398	2	2	Mixed-high	23
5	67	399	3	2	Bthu-high	11
5	67	400	4	2	Bthu-high	14
5	67	401	5	2	Bthu-high	17
5	67	402	6	2	Mixed-high	21
5	68	403	1	2	Mixed-low	67
5	68	404	2	2	Mixed-low	68
5	68	405	3	2	Chrys-acet	94
5	68	406	4	2	Chrys-acet	100
5	68	407	5	2	Chrys-acet	95
5	68	408	6	2	Mixed-low	64
5	69	409	1	2	Athu-Bthu	56
5	69	410	2	2	Bthu-high	11
5	69	411	3	2	Bthu-high	17
5	69	412	4	2	Bthu-high	14
5	69	413	5	2	Athu-Bthu	55
5	69	414	6	2	Athu-Bthu	57
5	70	415	1	2	Mixed-low	68
5	70	416	2	2	Mixed-low	64
5	70	417	3	2	Mixed-low	67
5	70	418	4	2	Bthu-low	104
5	70	419	5	2	Bthu-low	103
5	70	420	6	2	Bthu-low	101

Table S1-2 (continued): This section shows the results for the tenth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
6	71	421	1	2	Bthu-low	101
6	71	422	2	2	Athu-Bthu	57
6	71	423	3	2	Athu-Bthu	56
6	71	424	4	2	Bthu-low	103
6	71	425	5	2	Athu-Bthu	55
6	71	426	6	2	Bthu-low	104
6	72	427	1	1	Bthu-high	14
6	72	428	2	1	Bthu-high	17
6	72	429	3	1	Bthu-high	11
6	72	430	4	1	Bthu-high	11
6	72	431	5	1	Bthu-high	17
6	72	432	6	1	Bthu-high	14
6	73	433	1	2	Chrys-acet	94
6	73	434	2	2	Bthu-low	103
6	73	435	3	2	Chrys-acet	95
6	73	436	4	2	Bthu-low	104
6	73	437	5	2	Chrys-acet	100
6	73	438	6	2	Bthu-low	101
6	74	439	1	6	Athu-Bthu	55
6	74	440	2	6	Mixed-low	68
6	74	441	3	6	Bthu-low	101
6	74	442	4	6	Bthu-high	11
6	74	443	5	6	Mixed-high	30
6	74	444	6	6	Chrys-acet	94
6	75	445	1	2	Mixed-high	30
6	75	446	2	2	Bthu-low	104
6	75	447	3	2	Mixed-high	21
6	75	448	4	2	Bthu-low	103
6	75	449	5	2	Mixed-high	23
6	75	450	6	2	Bthu-low	101
6	76	451	1	3	Bthu-low	101
6	76	452	2	3	Chrys-acet	100
6	76	453	3	3	Mixed-high	30
6	76	454	4	3	Bthu-low	104
6	76	455	5	3	Mixed-high	21
6	76	456	6	3	Chrys-acet	95
6	77	457	1	3	Athu-Bthu	55
6	77	458	2	3	Bthu-low	104
6	77	459	3	3	Mixed-low	64
6	77	460	4	3	Athu-Bthu	57
6	77	461	5	3	Bthu-low	101
6	77	462	6	3	Mixed-low	67
6	78	463	1	2	Athu-Bthu	56
6	78	464	2	2	Athu-Bthu	55
6	78	465	3	2	Mixed-low	67
6	78	466	4	2	Mixed-low	64
6	78	467	5	2	Athu-Bthu	57
6	78	468	6	2	Mixed-low	68

Table S1-2 (continued): This section shows the results for the eleventh part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
6	79	469	1	3	Bthu-high	14
6	79	470	2	3	Mixed-high	30
6	79	471	3	3	Mixed-high	21
6	79	472	4	3	Chrys-acet	100
6	79	473	5	3	Bthu-high	11
6	79	474	6	3	Chrys-acet	94
6	80	475	1	6	Bthu-low	103
6	80	476	2	6	Mixed-low	64
6	80	477	3	6	Chrys-acet	100
6	80	478	4	6	Mixed-high	30
6	80	479	5	6	Athu-Bthu	57
6	80	480	6	6	Bthu-high	17
6	81	481	1	3	Athu-Bthu	55
6	81	482	2	3	Chrys-acet	95
6	81	483	3	3	Bthu-low	101
6	81	484	4	3	Bthu-low	103
6	81	485	5	3	Chrys-acet	94
6	81	486	6	3	Athu-Bthu	56
6	82	487	1	1	Mixed-high	23
6	82	488	2	1	Mixed-high	21
6	82	489	3	1	Mixed-high	30
6	82	490	4	1	Mixed-high	23
6	82	491	5	1	Mixed-high	30
6	82	492	6	1	Mixed-high	21
6	83	493	1	3	Mixed-low	67
6	83	494	2	3	Athu-Bthu	57
6	83	495	3	3	Mixed-low	68
6	83	496	4	3	Bthu-high	17
6	83	497	5	3	Athu-Bthu	55
6	83	498	6	3	Bthu-high	11
6	84	499	1	2	Chrys-acet	94
6	84	500	2	2	Chrys-acet	100
6	84	501	3	2	Bthu-high	14
6	84	502	4	2	Chrys-acet	95
6	84	503	5	2	Bthu-high	11
6	84	504	6	2	Bthu-high	17

1.2.3. Stem phenology

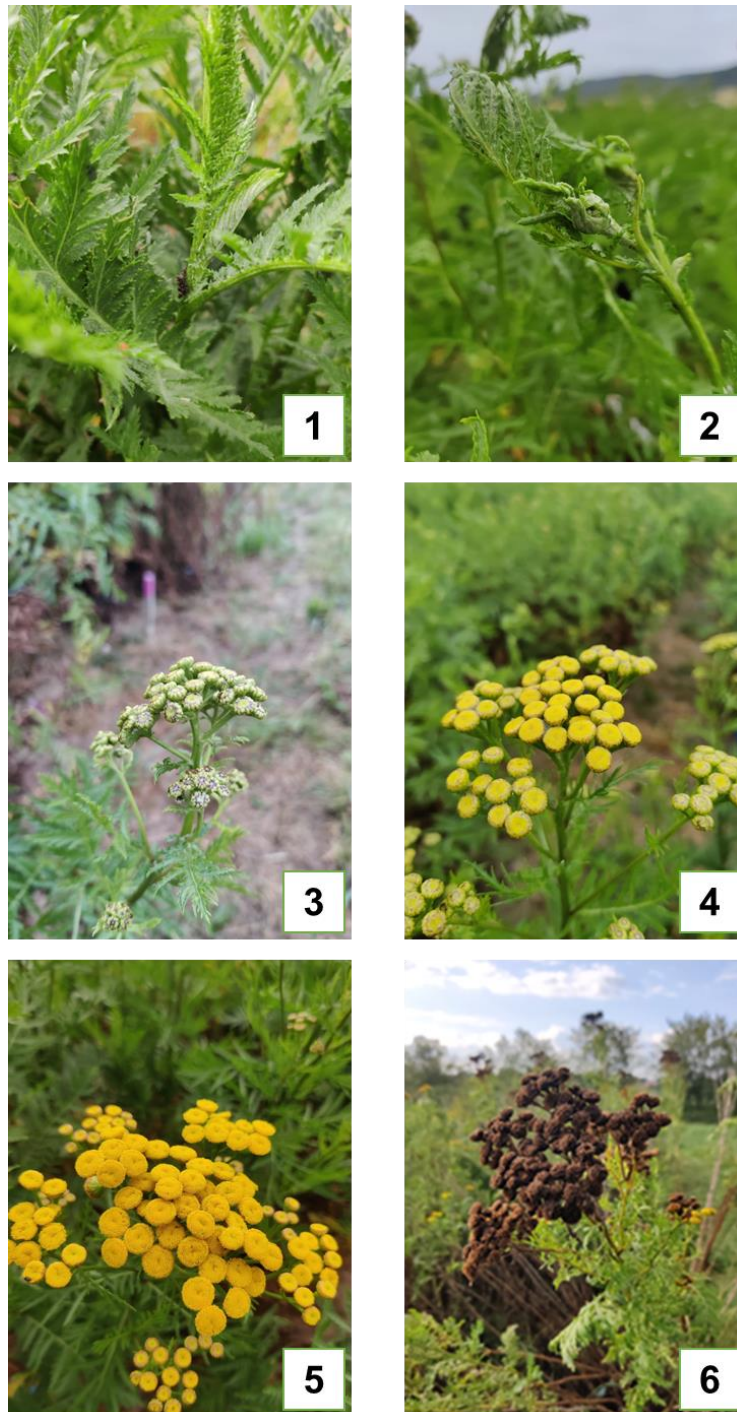


Figure S1-1: Stem phenology (*left-to-right then top-to-bottom*): [1] No inflorescence; [2] Inflorescence visible but closed; [3] Open inflorescence; [4] Beginning seed set (unripe); [5] Ripe seeds; [6] Mature seeds turning brown.

1.3. Details of the statistical analyses

1.3.1. Variables used in the analyses

Variable name	Description	Variable type	Factor levels
B	Experimental block	Factor	1 to 6
P	Experimental plot	Factor	1 to 84
CR	Plot-level chemotype richness	Integer	1, 2, 3, 6
C	Chemotype identity	Factor	Athu-Bthu, Bthu-high, Bthu-low, Chrys-acet, Mixed-high, Mixed-low
D	Daughter identity	Factor	Daughter ID of a particular chemotype
D: Athu-Bthu	Daughter identity	Factor	55, 56, 57
D: Bthu-high	Daughter identity	Factor	11, 14, 17
D: Bthu-low	Daughter identity	Factor	101, 103, 104
D: Chrys-acet	Daughter identity	Factor	94, 95, 100
D: Mixed-high	Daughter identity	Factor	21, 23, 30
D: Mixed-low	Daughter identity	Factor	64, 67, 68
CP	Chemotype presence	Factor, binary	Presence/absence (1/0) of a particular chemotype
CP: Athu-Bthu	Particular chemotype	Factor, binary	Athu-Bthu presence/absence (1/0) at plot level
CP: Bthu-high	Particular chemotype	Factor, binary	Bthu-high presence/absence (1/0) at plot level
CP: Bthu-low	Particular chemotype	Factor, binary	Bthu-low presence/absence (1/0) at plot level
CP: Chrys-acet	Particular chemotype	Factor, binary	Chrys-acet presence/absence (1/0) at plot level
CP: Mixed-high	Particular chemotype	Factor, binary	Mixed-high presence/absence (1/0) at plot level
CP: Mixed-low	Particular chemotype	Factor, binary	Mixed-low presence/absence (1/0) at plot level
Day	Day of headspace VOC collection	Factor	1 to 3

1.3.2. Models of effects on plant traits

For each analysis, we give the model run in R.

Plant-level traits

1.3.2.1. Effects of chemotype, plot-level chemotype richness, and the interaction between chemotype and plot-level chemotype richness on plant-level traits

We first analyzed the effect of chemotype identity and plot-level chemotype richness on the performance of individual plants within the plots.

Growth traits

Number of stems: We analyzed four measurements of the number of stems per plant separately by time point. Here, we analyzed the number of stems of the individual plants within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Number of stems	Model	Analysis of variance	Post hoc test
June 01, 2023	glmer(Stems_01.06.2021 ~ C * CR + (1 B/P) + (1 D), family = poisson, control = glmerControl(optimizer = "Nelder_Mead"))	Anova()	emmeans(model, list(pairwise ~ C), adjust = "tukey")
June 22, 2021	glmer(Stems_22.06.2021 ~ C * CR + (1 B/P) + (1 D), family = poisson, control = glmerControl(optimizer = "Nelder_Mead"))	Anova()	emmeans(model, list(pairwise ~ C), adjust = "tukey")
October 28, 2021	glmer(Stems_28.10.2021 ~ C * CR + (1 B/P) + (1 D), family = poisson)	Anova()	-
July 06, 2022	glmer(Stems_06.07.2022 ~ C * CR + (1 B/P) + (1 D), family = poisson)	Anova()	-

Plant height: We analyzed six measurements of the height per plant separately by time point. Here, we analyzed the number of stems of plants' height (cm) within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block

(B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Height (cm)	Model	Analysis of variance	Post hoc test
June 01, 2023	<code>lmer(Height_01.06.2021 ~ C x CR + (1 B/P) + (1 D))</code>	Anova()	-
June 22, 2021	<code>lmer(Height_22.06.2021 ~ C x CR + (1 B/P) + (1 D))</code>	Anova()	-
October 28, 2021	<code>lmer(Height_28.10.2021 ~ C x CR + (1 B/P) + (1 D))</code>	Anova()	<code>emmeans(model, list(pairwise ~ Chemotype), adjust = "tukey")</code>
May 14, 2022	<code>lmer(Height_14.05.2022 ~ C x CR + (1 B/P) + (1 D))</code>	Anova()	-
July 06, 2022	<code>lmer(Height_06.07.2022 ~ C x CR + (1 B/P) + (1 D))</code>	Anova()	-
October 05, 2022	<code>lmer(Height_05.10.2022 ~ C x CR + (1 B/P) + (1 D))</code>	Anova()	-

Above-ground dry weight: There was one measurement of the above-ground dry weight per plant on October 28, 2021. Here, we analyzed plants' weight (g) within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P), and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Above-ground dry weight (g)	Model	Analysis of variance	Post hoc test
October 28, 2021	<code>lmer(sqrt(Dry_biomass_28.10.2021) ~ C * CR + (1 B/P) + (1 D))</code>	Anova()	-

Above-ground fresh weight: There was one measurement of the above-ground fresh weight per plant on October 05, 2022. Here, we analyzed plants' weight (g) within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P), and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Above-ground fresh weight (g)	Model	Analysis of variance	Post hoc test

October 05, 2022	<code>lmer(sqrt(Fresh_biomass_05.10.2022) ~ C * CR + (1 B/P) + (1 D))</code>	Anova()	-
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Reproductive traits

Cumulative number of flower heads: From June 01 to October 28, 2021, mature flower heads were counted and collected from individual plants. Here, we analyzed the total number of flower heads produced by each plant within the stands differing in chemotype richness during that period. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Cumulative number of flower heads	Model	Analysis of variance	Post hoc test
From June 01, 2021, to October 28, 2021	<code>glmer(Flowerheads ~ C * CR + (1 B/P) + (1 D), family = poisson)</code>	Anova()	<code>emmeans(model1, list(pairwise ~ C), adjust = "tukey")</code>

Flowering index: There was one measurement of the flowering index per plant on July 06, 2022. Here, we analyzed the flowering index of plants within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Cumulative number of flower heads	Model	Analysis of variance	Post hoc test
July 06, 2022	<code>lmer(Floweringindex_06.07.2022 ~ C * CR + (1 B/P) + (1 D))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ C), adjust = "tukey")</code>

1.3.2.2. Effects of daughter, plot-level chemotype richness, and the interaction between daughter and plot-level chemotype richness on plant-level traits

We second analyzed the effect of daughter identity (D), plot-level chemotype richness (CR), and their interaction (D x CR) on four plant traits of individual plants within the plots: Number of stems, height (cm), and above-ground dry weight (g) on October 28, 2021, and cumulative number of

flower heads produced in 2021. We carried out a separate analysis per chemotype to test for differences between daughters within a chemotype, and another analysis to directly compare daughters by using all 18 levels of daughter identity (D). We included Plot nested in Block (B/P) as a random factor. Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plant trait	Model	Analysis of variance	Post hoc test
Number of stems: October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-high (D: 11, 14, 17)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-low (D: 101, 103, 104)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Chrys-acet (D: 94, 95, 100)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-high (D: 21, 23, 30)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	-
Mixed-low (D: 64, 67, 68)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Daughter ID (D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 2e5)), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Height (cm): October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-high (D: 11, 14, 17)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-low (D: 101, 103, 104)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Chrys-acet (D: 94, 95, 100)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-high (D: 21, 23, 30)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	-
Mixed-low (D: 64, 67, 68)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Daughter ID	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")

(D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)			
Above-ground dry biomass (g): October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))	Anova()	-
Bthu-high (D: 11, 14, 17)	lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-low (D: 101, 103, 104)	lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Chrys-acet (D: 94, 95, 100)	lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-high (D: 21, 23, 30)	lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-low (D: 64, 67, 68)	lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Daughter ID (D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)	lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Cumulative number of flower heads: From June 01, 2021, to October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	-
Bthu-high (D: 11, 14, 17)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-low (D: 101, 103, 104)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Chrys-acet (D: 94, 95, 100)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	-
Mixed-high (D: 21, 23, 30)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-low (D: 64, 67, 68)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Daughter ID (D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")

Plot-level traits

1.3.2.3. Effects of chemotype presence, plot-level chemotype richness, and the interaction between chemotype presence and plot-level chemotype richness on plot-level traits

We first averaged each plant trait at the plot level to test the effects of chemotype and chemotype richness on plot-level plant traits (Community-Weighted Means -CWM-). To test the effect of the presence/absence of a chemotype on plot-level trait values, we carried out a separate analysis per chemotype. This was done by running a linear model with Block (B), chemotype presence (CP- indicating whether a specific chemotype is present in the plot), plot-level chemotype richness (CR), and their interaction (CP x CR) as fixed effects, separately for each chemotype.

Growth traits

Number of stems: We analyzed four measurements of the number of stems per plot separately by time point. Here, we analyzed the average number of stems of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level number of stems	Model	Analysis of variance
June 01, 2021		
Athu-Bthu (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
June 22, 2021		
Athu-Bthu (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()

Bthu-high (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
October 28, 2022		
Athu-Bthu (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
July 06, 2022		
Athu-Bthu (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()

Plant height: We analyzed six measurements of the height (cm) per plot separately by time point. Here, we analyzed the average height of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their

interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level height (cm)	Model	Analysis of variance
June 01, 2021		
Athu-Bthu (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
June 22, 2021		
Athu-Bthu (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
October 28, 2022		
Athu-Bthu (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Mixed-high	lm(Height_28.10.2021 ~ B + CR * CP)	anova()

(CP: 1/0)		
Mixed-low (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
May 14, 2022		
Athu-Bthu (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
July 06, 2022		
Athu-Bthu (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
October 05, 2022		
Athu-Bthu (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()

Mixed-low (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
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Above-ground dry weight: We analyzed one measurement of the above-ground dry weight (g) at plot-level. Here, we analyzed the average weight of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level above-ground dry weight (g)	Model	Analysis of variance
October 28, 2021		
Athu-Bthu (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()

Above-ground fresh weight: We analyzed one measurement of the above-ground fresh weight (g) at plot-level. Here, we analyzed the average weight of plants within the stands differing in chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level above-ground fresh weight (g)	Model	Analysis of variance
October 05, 2022		
Athu-Bthu (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()

Chrys-acet (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()

Reproductive traits

Cumulative number of flower heads: From June 01 to October 28, 2021, mature flower heads were counted and collected from individual plants. Here, we analyzed the average cumulative number of flower heads of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level cumulative number of flower heads	Model	Analysis of variance
June 01 - October 28, 2021		
Athu-Bthu (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()

Flowering index: There was one measurement of the flowering index per plant on July 06, 2022. Here, the average flowering index of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level flowering index	Model	Analysis of variance
July 06, 2022		
Athu-Bthu (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()

1.3.3. Models of effects on overyielding indexes

For each analysis, we give the model run in R.

1.3.3.1. Effects of plot-level chemotype richness on the overyielding indexes

We analyzed the effect of plot-level chemotype richness (CR) on the overyielding indexes of four plant traits calculated at plot-level. Random effect included was Block (B).

Overyielding index	Model	Analysis of variance
Above-ground dry biomass (g): October 28, 2021	lmer(Dry_biomass_28.10.2021 ~ CR + (1 B))	Anova()
Above-ground fresh biomass (g): October 05, 2022	lmer(Fresh_biomass_05.10.2022 ~ CR + (1 B))	Anova()
Cumulative number of flower heads: From June 01, 2021, to October 28, 2021	lmer(Flowerheads ~ CR + (1 B))	Anova()
Flowering index: July 06, 2022	lmer(Floweringindex_06.07.2022 ~ CR + (1 B))	Anova()

1.3.4. Models of chemodiversity

For each analysis, we give the model run in R.

1.3.4.1. Effects of plot-level chemotype richness on the plot-level theoretical leaf chemodiversity metrics

Theoretical plot-level leaf terpenoid diversity metrics were calculated by summing up the absolute leaf terpenoid concentrations ($\text{nmol} \times \text{g}^{-1}$) of each chemotype/daughter present in each plot, based on the chemical analysis of leaves from greenhouse plants in 2020 (Neuhaus-Harr *et al.*, 2023). We analyzed the effect of plot-level chemotype richness (CR) on each of the diversity metrics (terpenoid concentration, richness, Shannon diversity and evenness) using a linear model.

Diversity metric	Model	Analysis of variance
Squared plot-level theoretical total terpenoid concentration ($\text{nmol} \times \text{g}^{-1}$)	$\text{lm}((\text{Concentration})^2 \sim \text{CR})$	Anova()
Plot-level theoretical terpenoid richness	$\text{lm}(\text{Richness} \sim \text{CR})$	Anova()
Plot-level theoretical terpenoid Shannon diversity	$\text{lm}(\text{Shannon} \sim \text{CR})$	Anova()
Plot-level theoretical terpenoid evenness	$\text{lm}(\text{Evenness} \sim \text{CR})$	Anova()

1.3.4.2. Effects of plot-level chemotype richness on the plot-level realized volatile chemodiversity metrics

Realized plot-level volatile chemodiversity was based on terpenoids collected in the headspace ($\text{ng} \times \text{h}^{-1}$) in May 2022. We analyzed the effect of plot-level chemotype richness (CR) on each of the diversity metrics (terpenoid concentration, richness, Shannon diversity, and evenness) using a linear mixed model that included Block (B) and Day of headspace VOC collection (D) as random factors.

Diversity metric	Model	Analysis of variance
Squared root of plot-level realized total volatile terpenoid emission ($\text{ng} \times \text{h}^{-1}$)	$\text{lmer}(\text{sqrt}(\text{Concentration}) \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()
Squared plot-level realized volatile terpenoid richness	$\text{lmer}((\text{Richness})^2 \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()
Plot-level realized volatile terpenoid Shannon diversity	$\text{lmer}(\text{Shannon} \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()
Plot-level theoretical terpenoid evenness	$\text{lmer}(\text{Evenness} \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()

Intraspecific chemical variation of *Tanacetum vulgare* affects plant growth and reproductive traits in field plant communities

Supplementary Information 1 (S1): Supplementary Methods

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1.1. Detailed description of methods

1.1.1. Chemotypic characterization of *T. vulgare* lines and biological replicates

We used six *T. vulgare* chemotypes that were also used in Neuhaus-Harr *et al.* (2023). Based on an unsupervised hierarchical k-means clustering calculated on a dissimilarity matrix of the terpenoid profile obtained from hexane extraction of leaves of 27 *T. vulgare* plants found in Jena, Germany (50.93°N, 11.58°E), we randomly chose two plants from each of 6 of the resulting 7 clusters (hereafter 'mother' plant) and mass-sown their seeds. We selected ten healthy seedlings from each mother plant (120 plants, hereafter 'daughter' plant) and chemotyped those plants. Based on another unsupervised hierarchical clustering calculated on the terpenoid profile from hexane extraction of those 120 daughter plants in 2021, we obtained 6 clusters. We chose three daughter plants from the same mother for each cluster, resulting in 6 chemotypes and 18 daughter plants. It is essential to note that, despite being daughters of the same mother plant, the chemotypes among offspring are not guaranteed to be identical, as elucidated in Neuhaus-Harr *et al.* (2024). In this related work, a hierarchical clustering analysis involving 120 daughters from twelve mothers, which encompassed the six maternal chemotypes utilized in both studies, demonstrated that daughters from the same mother may exhibit distinct chemotypic clustering patterns.

1.1.2. Propagation of plant material for the field experiment

Stem parts from the 18 selected daughters were trimmed and used to produce 27-40 cuttings per daughter. Individual cuttings were cut 1-2 cm below and 4-5 cm above a leaf node. The leaf size was reduced by 60% to reduce evapotranspiration and improve the survival rate by shortening and trimming the leaflet. Stem cuttings were placed into seedling trays with soaked potting substrate and protected with a clear plastic propagation cover. After three weeks and root and shoot formation, the cover was gradually opened to allow the cuttings to acclimate. As the cuttings grew, they were transplanted into 10 cm pots and later into 17 cm pots before transplanting in the field site in May 2021. Potted plants were automatically watered from the bottom and fertilized as needed with Universol Blue fertilizer ® (18%N - 11%P - 18%K; ICL Deutschland, Nordhorn, Germany). During propagation and growth, plants were not treated with chemical insecticides or fungicides, but we applied biological control when needed. At the end of the growing period, there were multiple cloned plants from each of the 18 daughters. Cloned plants from each of the three daughters of each chemotype were used in the experimental design.

1.1.3. Plant morphological trait measurements

We measured six morphological plant traits for individual plants, including four growth traits (the number of stems per plant, the height of the highest stem, and above-ground fresh and dry weight) and two reproductive traits (the cumulative number of flower heads and the flowering index).

Three times in 2021 (June 01, June 22, and October 28), we counted the number of stems larger than 5 centimeters and measured plant height as the distance between the ground and the longest stem without stretching out leaves.

As a measure of reproductive success, we counted and cut off all ripe flower heads weekly during the 2021 season (from June 01 to October 28). Flower heads were cut off to avoid re-seeding plots with new plants. We thus refer to the total number of flower heads collected as the cumulative number of flower heads. At the end of the season (October 28, 2021), we obtained the above-ground dry weight of each plant; plants were cut off 5 cm above the ground, placed in single paper bags, and dried for 72 hours at 60°C in a drying room (Thermo-Scientific) of the University of Jena facilities.

In 2022, we counted the number of stems once (July 06) and measured plant height three times (May 14, July 06, and October 05). The phenological state of each stem of each plant was determined once (on July 06) using numerical categories: [1] No inflorescence; [2] Inflorescence visible but closed; [3] Open inflorescence; [4] Beginning seed set (unripe); [5] Ripe seeds; [6] Mature seeds turning brown (Fig. S1-1). To analyze phenology at the plant level, we calculated a flowering index for each plant by dividing the sum of all stem-level phenological stages by the number of stems (between 1 = all stems without inflorescence and 6 = all stems with mature seeds). We averaged plant-level flower indices per plot to obtain a measurement at the plot level.

At the end of the second season, all plants were again cut off 5 cm above ground but immediately weighted in the field to obtain fresh weight (October 05, 2022). From this, we calculated both plant-level and plot-level weights.

1.1.4. Headspace VOC collection

Headspace volatile organic compound (VOC) emissions were collected at the plot level (including all six individual plants) between May 12 and 14, 2022, using a closed-push-pull system for 2 hours (Fig. 1f-g). Weeds were removed by hand from the plots ten days before the measurements

to reduce the collection of volatiles from plants different from tansy. In addition, one extra new plot was prepared by thoroughly cleaning out the plant material ten days before and used as a volatile background profile (red plot in Fig. 1d).

A squared bag made from Polyethylene terephthalate PET (110 cm x 110 cm x 40 cm) foil was installed for VOC collections, covering the whole plot. Air entered the system after passing through an activated charcoal filter at a flow rate of 1.5 L/min and was pumped out through a trap at 1 L/min. The trap contained 25 mg of Poropak-Q absorbent (Volatile Collection Trap (VCT) LLC, USA) (Fig. 1f). VOCs were collected over a period of three days with three rounds of ten plots per day (two entire blocks + two background plots = 30 plots per day). Plots were assigned beforehand to ensure each plot-level chemotype richness level were included in each round.

After VOC collection, the traps were eluted with 200 μ l dichloromethane containing nonyl-acetate as an internal standard (Sigma-Aldrich, 10 ng $\times$ μ l⁻¹). VOCs were analyzed using a Hewlett-Packard model 6890 gas chromatograph coupled to a Hewlett-Packard model 5973 mass spectrometer (GC-MS). The GC was operated with helium as carrier gas at 1 ml/min, split-less injection (injection temperature: 220 °C, injection volume: 1 μ l), a DB-5MS column (30 m $\times$ 0.25 mm, 0.25 μ m film, J & W Scientific, Folsom, CA, USA), and a temperature program from 40 °C (2 min hold) to 350 °C (2 min hold) with a first gradient of 7 °C min⁻¹ to 155 °C, and a second gradient of 60 °C min⁻¹ to 300 °C. The GC was coupled to a single quadrupole mass spectrometer (Hewlett-Packard model 5973) operated in electron impact ionization mode. The transfer line temperature was 270 °C, the ionization potential was 70 eV, and a scan range of m/z 40–350 was employed.

VOCs were identified by comparing retention times and mass spectra with commercial standards (when available) and by comparison to the mass spectral libraries Wiley 275 (Wiley and National Institute of Standards) and NIST05a (National Institute of Standards and Technology, Gaithersburg, MD). We verified the VOC identity by calculating Kovats retention indices. The qualitative and quantitative analysis of the volatile data is beyond the scope of this study; here, we report only on volatile terpenoid diversity metrics at the plot level.

1.2. Design of the field experiment

1.2.1. Leaf terpenoid composition of chemotypes

Table S1-1: Leaf terpenoid composition (nmol/g) of chemotypes of *T. vulgare* plants. The table is partitioned into three sections showing different terpenoids in alphabetic order. Each section lists the chemotypes tested (6), the three daughter plants chosen for each chemotype (18), and the concentration of each terpenoid found in each daughter after hexane extraction of leaf material. Chemotypes are named after their dominant compounds, and numbers identify daughters. Plant chemotyping and chemotype selection are described in more detail in Neuhaus-Harr *et al.* (2023).

Chemotype	Daughter	1-terpin-4-nyl acetate	α -chrysanthenyl acetate	α -farnesene	α -pinene	α -terpinene	α -thujene	α -thujone	artemisia- β -acetate	artemisia alcohol	artemisia ketone	β -carvyl acetate	β -caryophyllene	β -ocimene	β -pinene	β -thujone	borneol	camphene	camphor
Athu-Bthu	55	0.01	0.00	0.00	0.17	0.01	0.00	27.66	0.05	0.00	0.00	0.00	0.00	0.05	0.85	28.25	0.00	0.00	0.01
Athu-Bthu	56	0.01	0.07	0.00	0.34	0.00	0.00	24.05	0.13	0.52	0.00	0.00	0.00	0.01	0.11	24.67	0.30	0.00	0.01
Athu-Bthu	57	0.02	0.12	0.00	0.34	0.00	0.00	22.70	0.32	0.62	0.60	0.00	0.00	0.02	0.10	23.10	0.26	0.00	0.01
Bthu-high	11	0.02	0.08	0.70	0.29	0.00	0.00	0.20	0.64	0.69	0.00	0.06	0.00	0.05	3.28	39.76	0.43	0.00	0.01
Bthu-high	14	0.01	0.16	0.00	0.37	0.00	0.00	0.19	0.00	0.00	0.05	0.00	0.00	0.00	0.24	40.37	0.54	0.00	0.01
Bthu-high	17	0.02	0.00	0.00	0.33	0.01	0.11	0.20	0.00	0.94	0.00	0.20	0.00	0.04	0.45	42.55	0.00	0.00	0.01
Bthu-low	101	0.02	0.00	0.00	0.20	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	29.33	0.00	0.02	0.01
Bthu-low	103	0.02	0.10	0.00	0.22	0.01	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.03	5.59	23.29	0.41	0.01	0.01
Bthu-low	104	0.01	0.12	0.00	0.18	0.01	0.11	0.18	0.00	0.00	0.05	0.00	0.00	0.02	4.66	32.59	0.41	0.01	0.01
Chrys-acet	94	0.01	0.05	0.00	2.09	0.00	0.00	0.00	0.03	0.00	0.25	0.00	0.00	0.02	0.07	0.00	0.18	0.42	0.02
Chrys-acet	95	0.01	0.02	0.00	2.51	0.00	0.07	0.00	0.03	0.00	0.29	0.00	0.00	0.07	0.49	0.00	0.31	0.40	0.79
Chrys-acet	100	0.01	0.04	0.00	2.86	0.01	0.05	0.00	0.08	0.00	0.15	0.00	0.00	0.02	0.12	0.00	0.00	0.51	0.02
Mixed-high	21	0.03	0.00	0.00	2.87	0.01	0.33	0.00	0.00	0.00	0.00	0.11	0.00	0.18	0.83	0.00	7.59	2.32	0.01
Mixed-high	23	0.01	0.00	0.00	2.30	0.01	0.16	0.00	0.20	0.78	0.00	0.00	0.00	0.08	0.73	0.00	7.63	1.80	0.01
Mixed-high	30	0.02	0.00	0.00	3.58	0.00	0.36	0.00	0.00	0.66	0.00	0.14	0.00	0.03	1.00	0.00	7.96	2.91	0.01
Mixed-low	64	0.03	0.12	0.00	6.30	0.01	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.02	2.63	0.00	0.37	0.06	0.02
Mixed-low	67	2.80	0.00	0.00	5.35	0.01	0.07	0.00	0.09	0.00	0.00	0.00	0.75	1.55	1.04	0.00	3.63	1.50	0.05
Mixed-low	68	0.02	0.00	0.00	4.96	0.00	0.16	0.00	0.00	0.00	0.72	0.00	0.09	0.01	3.25	0.00	0.00	0.01	0.01

Table S1-1 (continued): This section shows the results for the second part of Table S1-1, partitioned by terpenoid.

Chemotype	Daughter	chrysanthenyl acetate	cis-chrysanthenol	cis-miroxide	cis-sabinene hydrate	cis-verbanol acetate	eucalyptol	eugenol	γ-terpinene	limonene	methyloisoborneol	mustakone	myrcene	p-cymene	pinocarvone	sabinene	santolina triene	trans-chrysanthenol	trans-sabinene hydrate
Athu-Bthu	55	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.10	0.51	1.09	0.85	0.01	0.00	0.10
Athu-Bthu	56	0.00	0.00	0.01	0.00	0.00	0.01	0.02	0.06	0.00	0.00	0.00	0.00	0.32	0.01	0.51	0.00	0.09	0.00
Athu-Bthu	57	0.00	0.02	0.01	0.07	0.00	0.02	0.01	0.03	0.00	0.05	0.00	0.00	0.24	0.46	0.42	0.01	0.00	0.00
Bthu-high	11	0.00	0.01	0.01	0.08	0.00	0.02	0.00	0.01	0.09	0.00	0.00	0.00	0.33	0.06	3.22	0.00	0.00	0.00
Bthu-high	14	0.00	0.00	0.02	0.07	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.06	0.21	0.06	1.60	0.00	0.03	0.00
Bthu-high	17	0.00	0.01	0.05	0.07	0.00	0.02	0.04	0.01	0.00	0.00	0.00	0.00	0.43	0.00	6.52	0.00	0.00	0.00
Bthu-low	101	0.00	0.01	0.02	0.10	0.00	0.12	0.03	0.02	0.00	0.00	0.00	0.06	0.43	0.03	0.04	0.01	0.00	0.00
Bthu-low	103	0.00	0.07	0.01	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.66	0.01	5.59	0.01	0.00	0.00
Bthu-low	104	0.00	0.00	0.01	0.06	0.00	0.24	0.03	0.01	0.00	0.02	0.00	0.10	0.45	0.76	4.68	0.01	0.05	0.12
Chrys-acet	94	48.13	2.32	0.02	0.08	0.00	0.78	0.05	0.85	0.00	0.58	0.00	0.02	0.84	0.01	0.73	0.01	0.00	0.10
Chrys-acet	95	45.84	1.68	0.01	0.04	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.30	0.01	0.49	0.01	0.02	0.07
Chrys-acet	100	46.13	1.95	0.01	0.08	0.00	0.00	0.02	0.70	0.00	0.00	0.00	0.02	0.75	0.00	0.80	0.00	0.00	0.04
Mixed-high	21	0.00	0.00	0.03	16.90	0.00	0.00	0.00	0.18	0.00	7.64	0.00	0.00	0.09	0.01	5.70	0.00	0.00	0.00
Mixed-high	23	0.00	0.08	0.02	17.07	0.00	0.00	0.00	0.11	0.00	7.84	3.19	0.03	0.00	0.07	3.95	0.00	0.00	1.29
Mixed-high	30	0.00	0.01	0.01	16.57	0.00	0.04	0.01	0.45	0.00	8.03	0.00	0.03	0.00	0.00	6.41	0.00	0.00	0.10
Mixed-low	64	0.00	0.43	0.02	0.03	0.00	0.00	0.03	1.13	0.00	0.00	0.00	0.00	1.18	0.01	11.62	0.01	0.06	0.03
Mixed-low	67	0.15	0.03	0.02	0.07	2.56	0.04	0.16	2.33	0.00	1.07	0.00	0.03	0.00	0.01	6.45	0.00	0.00	0.18
Mixed-low	68	0.00	0.01	0.02	0.42	0.00	0.03	0.00	0.51	0.00	0.00	0.00	0.11	0.04	0.01	13.04	0.01	0.00	0.26

Table S1-1 (continued): This section shows the results for the third and final part of Table S1-1, partitioned by terpenoid.

Chemotype	Daughter	trans-sabinyl acetate	Unknown terpenoid	Unknown sesquiterpene 1	Unknown sesquiterpene 2	Unknown sesquiterpene 3	Unknown sesquiterpene 4	Unknown sesquiterpene 5	yomogi alcohol
Athu-Bthu	55	0.00	0.01	0.00	0.00	0.07	0.00	0.00	0.03
Athu-Bthu	56	0.00	0.02	0.09	0.06	0.09	0.00	0.01	0.08
Athu-Bthu	57	0.00	0.01	0.00	0.13	0.22	0.00	0.00	0.00
Bthu-high	11	0.00	0.02	0.00	0.00	0.00	2.26	0.00	0.06
Bthu-high	14	0.00	0.01	0.00	0.16	0.15	0.00	0.00	0.09
Bthu-high	17	0.01	0.01	0.03	0.00	0.00	0.00	0.00	0.08
Bthu-low	101	0.00	0.01	0.09	0.05	0.17	0.00	0.00	0.16
Bthu-low	103	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.13
Bthu-low	104	0.00	0.01	0.00	0.00	0.10	0.00	0.00	0.08
Chrys-acet	94	0.00	0.81	0.02	0.00	0.00	0.00	0.13	0.05
Chrys-acet	95	0.00	0.79	0.12	0.05	0.06	0.00	0.00	0.00
Chrys-acet	100	0.00	1.07	0.00	0.01	0.09	0.00	0.00	0.09
Mixed-high	21	0.01	6.53	0.05	0.00	0.00	0.00	0.00	0.06
Mixed-high	23	0.00	6.92	0.00	0.06	0.25	0.00	0.44	0.06
Mixed-high	30	0.00	9.19	0.00	0.00	0.00	0.00	0.00	0.08
Mixed-low	64	0.00	0.02	0.06	0.09	0.19	0.00	0.00	0.10
Mixed-low	67	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.09
Mixed-low	68	0.00	0.02	0.03	0.00	0.18	0.00	0.00	0.00

1.2.2. Assignment of plants to plots

Table S1-2: Assignment of plants to plots. The table is partitioned into 11 sections, showing the plant identity in order. The field experiment contained 84 plots: 12, 30, 30, and 12 replicate plots for plot-level chemotype richness levels 1, 2, 3, and 6, respectively. Plots were distributed equally in six randomized blocks. Each block consisted of 14 plots: two plots of chemotype richness level 1, five plots of chemotype richness level 2, five plots of chemotype richness level 3, and two plots with chemotype richness level 6. Each plot consisted of 6 plants, which position within the plot was randomly assigned (Plot position), and which chemotype and daughter identities are listed here.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
1	1	1	1	3	Athu-Bthu	57
1	1	2	2	3	Chrys-acet	100
1	1	3	3	3	Chrys-acet	94
1	1	4	4	3	Athu-Bthu	55
1	1	5	5	3	Bthu-low	103
1	1	6	6	3	Bthu-low	101
1	2	7	1	2	Mixed-low	68
1	2	8	2	2	Mixed-low	67
1	2	9	3	2	Athu-Bthu	55
1	2	10	4	2	Athu-Bthu	57
1	2	11	5	2	Athu-Bthu	56
1	2	12	6	2	Mixed-low	64
1	3	13	1	3	Mixed-high	30
1	3	14	2	3	Mixed-high	21
1	3	15	3	3	Chrys-acet	94
1	3	16	4	3	Chrys-acet	100
1	3	17	5	3	Bthu-low	101
1	3	18	6	3	Bthu-low	104
1	4	19	1	2	Athu-Bthu	56
1	4	20	2	2	Athu-Bthu	57
1	4	21	3	2	Bthu-low	101
1	4	22	4	2	Bthu-low	104
1	4	23	5	2	Athu-Bthu	55
1	4	24	6	2	Bthu-low	103
1	5	25	1	3	Chrys-acet	95
1	5	26	2	3	Bthu-high	14
1	5	27	3	3	Bthu-high	11
1	5	28	4	3	Mixed-high	21
1	5	29	5	3	Chrys-acet	94
1	5	30	6	3	Mixed-high	30
1	6	31	1	6	Mixed-low	68
1	6	32	2	6	Bthu-low	104
1	6	33	3	6	Bthu-high	11
1	6	34	4	6	Mixed-high	30
1	6	35	5	6	Chrys-acet	100
1	6	36	6	6	Athu-Bthu	55

Table S1-2 (continued): This section shows the results for the second part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
1	7	37	1	6	Athu-Bthu	55
1	7	38	2	6	Bthu-low	101
1	7	39	3	6	Bthu-high	17
1	7	40	4	6	Mixed-low	64
1	7	41	5	6	Mixed-high	21
1	7	42	6	6	Chrys-acet	94
1	8	43	1	2	Chrys-acet	94
1	8	44	2	2	Bthu-low	101
1	8	45	3	2	Chrys-acet	100
1	8	46	4	2	Chrys-acet	95
1	8	47	5	2	Bthu-low	103
1	8	48	6	2	Bthu-low	104
1	9	49	1	1	Mixed-high	21
1	9	50	2	1	Mixed-high	30
1	9	51	3	1	Mixed-high	21
1	9	52	4	1	Mixed-high	30
1	9	53	5	1	Mixed-high	23
1	9	54	6	1	Mixed-high	23
1	10	55	1	1	Bthu-high	11
1	10	56	2	1	Bthu-high	17
1	10	57	3	1	Bthu-high	14
1	10	58	4	1	Bthu-high	14
1	10	59	5	1	Bthu-high	11
1	10	60	6	1	Bthu-high	17
1	11	61	1	2	Bthu-high	17
1	11	62	2	2	Bthu-high	11
1	11	63	3	2	Chrys-acet	94
1	11	64	4	2	Chrys-acet	95
1	11	65	5	2	Chrys-acet	100
1	11	66	6	2	Bthu-high	14
1	12	67	1	2	Bthu-low	103
1	12	68	2	2	Bthu-low	101
1	12	69	3	2	Mixed-high	23
1	12	70	4	2	Bthu-low	104
1	12	71	5	2	Mixed-high	21
1	12	72	6	2	Mixed-high	30
1	13	73	1	3	Bthu-low	104
1	13	74	2	3	Mixed-low	68
1	13	75	3	3	Mixed-low	64
1	13	76	4	3	Bthu-low	101
1	13	77	5	3	Athu-Bthu	56
1	13	78	6	3	Athu-Bthu	57
1	14	79	1	3	Athu-Bthu	55
1	14	80	2	3	Mixed-low	64
1	14	81	3	3	Bthu-high	11
1	14	82	4	3	Athu-Bthu	56
1	14	83	5	3	Mixed-low	68
1	14	84	6	3	Bthu-high	17

Table S1-2 (continued): This section shows the results for the third part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
2	15	85	1	2	Bthu-low	101
2	15	86	2	2	Mixed-low	64
2	15	87	3	2	Mixed-low	67
2	15	88	4	2	Mixed-low	68
2	15	89	5	2	Bthu-low	104
2	15	90	6	2	Bthu-low	103
2	16	91	1	6	Athu-Bthu	57
2	16	92	2	6	Chrys-acet	95
2	16	93	3	6	Bthu-low	103
2	16	94	4	6	Bthu-high	14
2	16	95	5	6	Mixed-low	67
2	16	96	6	6	Mixed-high	23
2	17	97	1	2	Mixed-high	21
2	17	98	2	2	Bthu-high	14
2	17	99	3	2	Mixed-high	23
2	17	100	4	2	Mixed-high	30
2	17	101	5	2	Bthu-high	17
2	17	102	6	2	Bthu-high	11
2	18	103	1	3	Bthu-high	17
2	18	104	2	3	Mixed-high	23
2	18	105	3	3	Athu-Bthu	57
2	18	106	4	3	Bthu-high	14
2	18	107	5	3	Mixed-high	30
2	18	108	6	3	Athu-Bthu	55
2	19	109	1	2	Mixed-low	68
2	19	110	2	2	Mixed-low	64
2	19	111	3	2	Chrys-acet	95
2	19	112	4	2	Mixed-low	67
2	19	113	5	2	Chrys-acet	100
2	19	114	6	2	Chrys-acet	94
2	20	115	1	2	Bthu-high	17
2	20	116	2	2	Athu-Bthu	56
2	20	117	3	2	Bthu-high	14
2	20	118	4	2	Athu-Bthu	57
2	20	119	5	2	Bthu-high	11
2	20	120	6	2	Athu-Bthu	55
2	21	121	1	3	Mixed-high	23
2	21	122	2	3	Mixed-high	30
2	21	123	3	3	Athu-Bthu	55
2	21	124	4	3	Chrys-acet	95
2	21	125	5	3	Athu-Bthu	57
2	21	126	6	3	Chrys-acet	100
2	22	127	1	6	Athu-Bthu	56
2	22	128	2	6	Mixed-high	23
2	22	129	3	6	Bthu-high	14
2	22	130	4	6	Bthu-low	104
2	22	131	5	6	Mixed-low	64
2	22	132	6	6	Chrys-acet	95

Table S1-2 (continued): This section shows the results for the fourth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
2	23	133	1	3	Bthu-high	14
2	23	134	2	3	Mixed-low	67
2	23	135	3	3	Bthu-high	11
2	23	136	4	3	Mixed-low	68
2	23	137	5	3	Bthu-low	104
2	23	138	6	3	Bthu-low	103
2	24	139	1	1	Bthu-low	104
2	24	140	2	1	Bthu-low	104
2	24	141	3	1	Bthu-low	101
2	24	142	4	1	Bthu-low	101
2	24	143	5	1	Bthu-low	103
2	24	144	6	1	Bthu-low	103
2	25	145	1	1	Mixed-low	67
2	25	146	2	1	Mixed-low	64
2	25	147	3	1	Mixed-low	68
2	25	148	4	1	Mixed-low	67
2	25	149	5	1	Mixed-low	68
2	25	150	6	1	Mixed-low	64
2	26	151	1	3	Bthu-high	14
2	26	152	2	3	Bthu-high	17
2	26	153	3	3	Mixed-low	67
2	26	154	4	3	Chrys-acet	95
2	26	155	5	3	Mixed-low	64
2	26	156	6	3	Chrys-acet	100
2	27	157	1	3	Bthu-high	14
2	27	158	2	3	Bthu-high	17
2	27	159	3	3	Bthu-low	104
2	27	160	4	3	Mixed-high	23
2	27	161	5	3	Mixed-high	30
2	27	162	6	3	Bthu-low	103
2	28	163	1	2	Mixed-high	23
2	28	164	2	2	Chrys-acet	95
2	28	165	3	2	Chrys-acet	94
2	28	166	4	2	Chrys-acet	100
2	28	167	5	2	Mixed-high	21
2	28	168	6	2	Mixed-high	30
3	29	169	1	2	Bthu-low	104
3	29	170	2	2	Bthu-high	14
3	29	171	3	2	Bthu-low	103
3	29	172	4	2	Bthu-high	17
3	29	173	5	2	Bthu-low	101
3	29	174	6	2	Bthu-high	11
3	30	175	1	3	Mixed-high	23
3	30	176	2	3	Mixed-high	21
3	30	177	3	3	Bthu-high	11
3	30	178	4	3	Bthu-low	101
3	30	179	5	3	Bthu-high	17
3	30	180	6	3	Bthu-low	103

Table S1-2 (continued): This section shows the results for the fifth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
3	31	181	1	2	Mixed-low	68
3	31	182	2	2	Mixed-high	21
3	31	183	3	2	Mixed-high	30
3	31	184	4	2	Mixed-low	67
3	31	185	5	2	Mixed-high	23
3	31	186	6	2	Mixed-low	64
3	32	187	1	6	Bthu-low	103
3	32	188	2	6	Mixed-low	68
3	32	189	3	6	Chrys-acet	94
3	32	190	4	6	Mixed-high	23
3	32	191	5	6	Athu-Bthu	56
3	32	192	6	6	Bthu-high	11
3	33	193	1	2	Athu-Bthu	56
3	33	194	2	2	Athu-Bthu	55
3	33	195	3	2	Chrys-acet	100
3	33	196	4	2	Chrys-acet	95
3	33	197	5	2	Chrys-acet	94
3	33	198	6	2	Athu-Bthu	57
3	34	199	1	1	Athu-Bthu	56
3	34	200	2	1	Athu-Bthu	55
3	34	201	3	1	Athu-Bthu	57
3	34	202	4	1	Athu-Bthu	56
3	34	203	5	1	Athu-Bthu	57
3	34	204	6	1	Athu-Bthu	55
3	35	205	1	1	Chrys-acet	94
3	35	206	2	1	Chrys-acet	100
3	35	207	3	1	Chrys-acet	100
3	35	208	4	1	Chrys-acet	95
3	35	209	5	1	Chrys-acet	95
3	35	210	6	1	Chrys-acet	94
3	36	211	1	3	Chrys-acet	100
3	36	212	2	3	Mixed-high	21
3	36	213	3	3	Bthu-high	11
3	36	214	4	3	Bthu-high	14
3	36	215	5	3	Chrys-acet	94
3	36	216	6	3	Mixed-high	23
3	37	217	1	3	Athu-Bthu	56
3	37	218	2	3	Mixed-low	67
3	37	219	3	3	Chrys-acet	94
3	37	220	4	3	Athu-Bthu	57
3	37	221	5	3	Chrys-acet	100
3	37	222	6	3	Mixed-low	68
3	38	223	1	2	Mixed-high	30
3	38	224	2	2	Mixed-high	21
3	38	225	3	2	Athu-Bthu	56
3	38	226	4	2	Mixed-high	23
3	38	227	5	2	Athu-Bthu	57
3	38	228	6	2	Athu-Bthu	55

Table S1-2 (continued): This section shows the results for the sixth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
3	39	229	1	3	Mixed-low	67
3	39	230	2	3	Mixed-low	64
3	39	231	3	3	Mixed-high	21
3	39	232	4	3	Bthu-high	17
3	39	233	5	3	Bthu-high	11
3	39	234	6	3	Mixed-high	30
3	40	235	1	3	Mixed-low	68
3	40	236	2	3	Mixed-high	21
3	40	237	3	3	Athu-Bthu	57
3	40	238	4	3	Athu-Bthu	56
3	40	239	5	3	Mixed-high	23
3	40	240	6	3	Mixed-low	64
3	41	241	1	2	Bthu-high	11
3	41	242	2	2	Bthu-high	14
3	41	243	3	2	Mixed-low	67
3	41	244	4	2	Mixed-low	64
3	41	245	5	2	Mixed-low	68
3	41	246	6	2	Bthu-high	17
3	42	247	1	6	Chrys-acet	100
3	42	248	2	6	Bthu-low	103
3	42	249	3	6	Mixed-low	64
3	42	250	4	6	Mixed-high	21
3	42	251	5	6	Bthu-high	11
3	42	252	6	6	Athu-Bthu	55
4	43	253	1	1	Chrys-acet	100
4	43	254	2	1	Chrys-acet	95
4	43	255	3	1	Chrys-acet	95
4	43	256	4	1	Chrys-acet	94
4	43	257	5	1	Chrys-acet	94
4	43	258	6	1	Chrys-acet	100
4	44	259	1	1	Athu-Bthu	57
4	44	260	2	1	Athu-Bthu	55
4	44	261	3	1	Athu-Bthu	56
4	44	262	4	1	Athu-Bthu	55
4	44	263	5	1	Athu-Bthu	56
4	44	264	6	1	Athu-Bthu	57
4	45	265	1	2	Athu-Bthu	55
4	45	266	2	2	Athu-Bthu	57
4	45	267	3	2	Athu-Bthu	56
4	45	268	4	2	Chrys-acet	94
4	45	269	5	2	Chrys-acet	100
4	45	270	6	2	Chrys-acet	95
4	46	271	1	2	Bthu-high	17
4	46	272	2	2	Bthu-high	14
4	46	273	3	2	Mixed-low	64
4	46	274	4	2	Mixed-low	68
4	46	275	5	2	Bthu-high	11
4	46	276	6	2	Mixed-low	67

Table S1-2 (continued): This section shows the results for the seventh part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
4	47	277	1	6	Athu-Bthu	57
4	47	278	2	6	Mixed-low	67
4	47	279	3	6	Mixed-high	21
4	47	280	4	6	Bthu-low	104
4	47	281	5	6	Chrys-acet	100
4	47	282	6	6	Bthu-high	14
4	48	283	1	3	Bthu-low	101
4	48	284	2	3	Bthu-high	11
4	48	285	3	3	Mixed-high	21
4	48	286	4	3	Bthu-low	103
4	48	287	5	3	Bthu-high	17
4	48	288	6	3	Mixed-high	23
4	49	289	1	3	Mixed-low	67
4	49	290	2	3	Mixed-high	21
4	49	291	3	3	Mixed-high	30
4	49	292	4	3	Bthu-high	11
4	49	293	5	3	Mixed-low	68
4	49	294	6	3	Bthu-high	17
4	50	295	1	6	Mixed-high	23
4	50	296	2	6	Bthu-high	14
4	50	297	3	6	Bthu-low	101
4	50	298	4	6	Mixed-low	67
4	50	299	5	6	Athu-Bthu	56
4	50	300	6	6	Chrys-acet	94
4	51	301	1	3	Bthu-high	14
4	51	302	2	3	Bthu-high	11
4	51	303	3	3	Chrys-acet	95
4	51	304	4	3	Chrys-acet	100
4	51	305	5	3	Mixed-high	21
4	51	306	6	3	Mixed-high	23
4	52	307	1	3	Athu-Bthu	56
4	52	308	2	3	Chrys-acet	100
4	52	309	3	3	Athu-Bthu	55
4	52	310	4	3	Mixed-low	64
4	52	311	5	3	Mixed-low	67
4	52	312	6	3	Chrys-acet	95
4	53	313	1	2	Mixed-low	68
4	53	314	2	2	Mixed-high	23
4	53	315	3	2	Mixed-low	64
4	53	316	4	2	Mixed-high	21
4	53	317	5	2	Mixed-low	67
4	53	318	6	2	Mixed-high	30
4	54	319	1	2	Bthu-high	11
4	54	320	2	2	Bthu-high	14
4	54	321	3	2	Bthu-low	104
4	54	322	4	2	Bthu-high	17
4	54	323	5	2	Bthu-low	101
4	54	324	6	2	Bthu-low	103

Table S1-2 (continued): This section shows the results for the eighth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
4	55	325	1	2	Athu-Bthu	56
4	55	326	2	2	Athu-Bthu	57
4	55	327	3	2	Mixed-high	30
4	55	328	4	2	Athu-Bthu	55
4	55	329	5	2	Mixed-high	21
4	55	330	6	2	Mixed-high	23
4	56	331	1	3	Mixed-low	68
4	56	332	2	3	Athu-Bthu	56
4	56	333	3	3	Mixed-low	67
4	56	334	4	3	Athu-Bthu	55
4	56	335	5	3	Mixed-high	23
4	56	336	6	3	Mixed-high	21
5	57	337	1	1	Mixed-low	67
5	57	338	2	1	Mixed-low	64
5	57	339	3	1	Mixed-low	68
5	57	340	4	1	Mixed-low	64
5	57	341	5	1	Mixed-low	68
5	57	342	6	1	Mixed-low	67
5	58	343	1	3	Bthu-high	17
5	58	344	2	3	Mixed-low	64
5	58	345	3	3	Bthu-high	14
5	58	346	4	3	Chrys-acet	94
5	58	347	5	3	Mixed-low	68
5	58	348	6	3	Chrys-acet	95
5	59	349	1	6	Athu-Bthu	57
5	59	350	2	6	Mixed-low	67
5	59	351	3	6	Bthu-high	17
5	59	352	4	6	Bthu-low	103
5	59	353	5	6	Chrys-acet	95
5	59	354	6	6	Mixed-high	21
5	60	355	1	3	Bthu-high	14
5	60	356	2	3	Bthu-low	103
5	60	357	3	3	Bthu-low	104
5	60	358	4	3	Mixed-high	23
5	60	359	5	3	Bthu-high	17
5	60	360	6	3	Mixed-high	30
5	61	361	1	3	Mixed-high	23
5	61	362	2	3	Mixed-high	30
5	61	363	3	3	Athu-Bthu	57
5	61	364	4	3	Athu-Bthu	56
5	61	365	5	3	Bthu-high	17
5	61	366	6	3	Bthu-high	14
5	62	367	1	2	Mixed-high	21
5	62	368	2	2	Chrys-acet	95
5	62	369	3	2	Chrys-acet	100
5	62	370	4	2	Mixed-high	30
5	62	371	5	2	Chrys-acet	94
5	62	372	6	2	Mixed-high	23

Table S1-2 (continued): This section shows the results for the ninth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
5	63	373	1	1	Bthu-low	101
5	63	374	2	1	Bthu-low	104
5	63	375	3	1	Bthu-low	103
5	63	376	4	1	Bthu-low	104
5	63	377	5	1	Bthu-low	101
5	63	378	6	1	Bthu-low	103
5	64	379	1	3	Mixed-high	30
5	64	380	2	3	Athu-Bthu	57
5	64	381	3	3	Mixed-high	23
5	64	382	4	3	Athu-Bthu	56
5	64	383	5	3	Chrys-acet	94
5	64	384	6	3	Chrys-acet	95
5	65	385	1	6	Bthu-high	17
5	65	386	2	6	Mixed-high	30
5	65	387	3	6	Mixed-low	68
5	65	388	4	6	Athu-Bthu	56
5	65	389	5	6	Chrys-acet	95
5	65	390	6	6	Bthu-low	103
5	66	391	1	3	Bthu-high	11
5	66	392	2	3	Bthu-low	103
5	66	393	3	3	Mixed-low	64
5	66	394	4	3	Bthu-low	104
5	66	395	5	3	Bthu-high	14
5	66	396	6	3	Mixed-low	68
5	67	397	1	2	Mixed-high	30
5	67	398	2	2	Mixed-high	23
5	67	399	3	2	Bthu-high	11
5	67	400	4	2	Bthu-high	14
5	67	401	5	2	Bthu-high	17
5	67	402	6	2	Mixed-high	21
5	68	403	1	2	Mixed-low	67
5	68	404	2	2	Mixed-low	68
5	68	405	3	2	Chrys-acet	94
5	68	406	4	2	Chrys-acet	100
5	68	407	5	2	Chrys-acet	95
5	68	408	6	2	Mixed-low	64
5	69	409	1	2	Athu-Bthu	56
5	69	410	2	2	Bthu-high	11
5	69	411	3	2	Bthu-high	17
5	69	412	4	2	Bthu-high	14
5	69	413	5	2	Athu-Bthu	55
5	69	414	6	2	Athu-Bthu	57
5	70	415	1	2	Mixed-low	68
5	70	416	2	2	Mixed-low	64
5	70	417	3	2	Mixed-low	67
5	70	418	4	2	Bthu-low	104
5	70	419	5	2	Bthu-low	103
5	70	420	6	2	Bthu-low	101

Table S1-2 (continued): This section shows the results for the tenth part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
6	71	421	1	2	Bthu-low	101
6	71	422	2	2	Athu-Bthu	57
6	71	423	3	2	Athu-Bthu	56
6	71	424	4	2	Bthu-low	103
6	71	425	5	2	Athu-Bthu	55
6	71	426	6	2	Bthu-low	104
6	72	427	1	1	Bthu-high	14
6	72	428	2	1	Bthu-high	17
6	72	429	3	1	Bthu-high	11
6	72	430	4	1	Bthu-high	11
6	72	431	5	1	Bthu-high	17
6	72	432	6	1	Bthu-high	14
6	73	433	1	2	Chrys-acet	94
6	73	434	2	2	Bthu-low	103
6	73	435	3	2	Chrys-acet	95
6	73	436	4	2	Bthu-low	104
6	73	437	5	2	Chrys-acet	100
6	73	438	6	2	Bthu-low	101
6	74	439	1	6	Athu-Bthu	55
6	74	440	2	6	Mixed-low	68
6	74	441	3	6	Bthu-low	101
6	74	442	4	6	Bthu-high	11
6	74	443	5	6	Mixed-high	30
6	74	444	6	6	Chrys-acet	94
6	75	445	1	2	Mixed-high	30
6	75	446	2	2	Bthu-low	104
6	75	447	3	2	Mixed-high	21
6	75	448	4	2	Bthu-low	103
6	75	449	5	2	Mixed-high	23
6	75	450	6	2	Bthu-low	101
6	76	451	1	3	Bthu-low	101
6	76	452	2	3	Chrys-acet	100
6	76	453	3	3	Mixed-high	30
6	76	454	4	3	Bthu-low	104
6	76	455	5	3	Mixed-high	21
6	76	456	6	3	Chrys-acet	95
6	77	457	1	3	Athu-Bthu	55
6	77	458	2	3	Bthu-low	104
6	77	459	3	3	Mixed-low	64
6	77	460	4	3	Athu-Bthu	57
6	77	461	5	3	Bthu-low	101
6	77	462	6	3	Mixed-low	67
6	78	463	1	2	Athu-Bthu	56
6	78	464	2	2	Athu-Bthu	55
6	78	465	3	2	Mixed-low	67
6	78	466	4	2	Mixed-low	64
6	78	467	5	2	Athu-Bthu	57
6	78	468	6	2	Mixed-low	68

Table S1-2 (continued): This section shows the results for the eleventh part of Table S1-2.

Block	Plot	Plant	Plot position	Plot-level chemotype richness	Chemotype	Daughter
6	79	469	1	3	Bthu-high	14
6	79	470	2	3	Mixed-high	30
6	79	471	3	3	Mixed-high	21
6	79	472	4	3	Chrys-acet	100
6	79	473	5	3	Bthu-high	11
6	79	474	6	3	Chrys-acet	94
6	80	475	1	6	Bthu-low	103
6	80	476	2	6	Mixed-low	64
6	80	477	3	6	Chrys-acet	100
6	80	478	4	6	Mixed-high	30
6	80	479	5	6	Athu-Bthu	57
6	80	480	6	6	Bthu-high	17
6	81	481	1	3	Athu-Bthu	55
6	81	482	2	3	Chrys-acet	95
6	81	483	3	3	Bthu-low	101
6	81	484	4	3	Bthu-low	103
6	81	485	5	3	Chrys-acet	94
6	81	486	6	3	Athu-Bthu	56
6	82	487	1	1	Mixed-high	23
6	82	488	2	1	Mixed-high	21
6	82	489	3	1	Mixed-high	30
6	82	490	4	1	Mixed-high	23
6	82	491	5	1	Mixed-high	30
6	82	492	6	1	Mixed-high	21
6	83	493	1	3	Mixed-low	67
6	83	494	2	3	Athu-Bthu	57
6	83	495	3	3	Mixed-low	68
6	83	496	4	3	Bthu-high	17
6	83	497	5	3	Athu-Bthu	55
6	83	498	6	3	Bthu-high	11
6	84	499	1	2	Chrys-acet	94
6	84	500	2	2	Chrys-acet	100
6	84	501	3	2	Bthu-high	14
6	84	502	4	2	Chrys-acet	95
6	84	503	5	2	Bthu-high	11
6	84	504	6	2	Bthu-high	17

1.2.3. Stem phenology

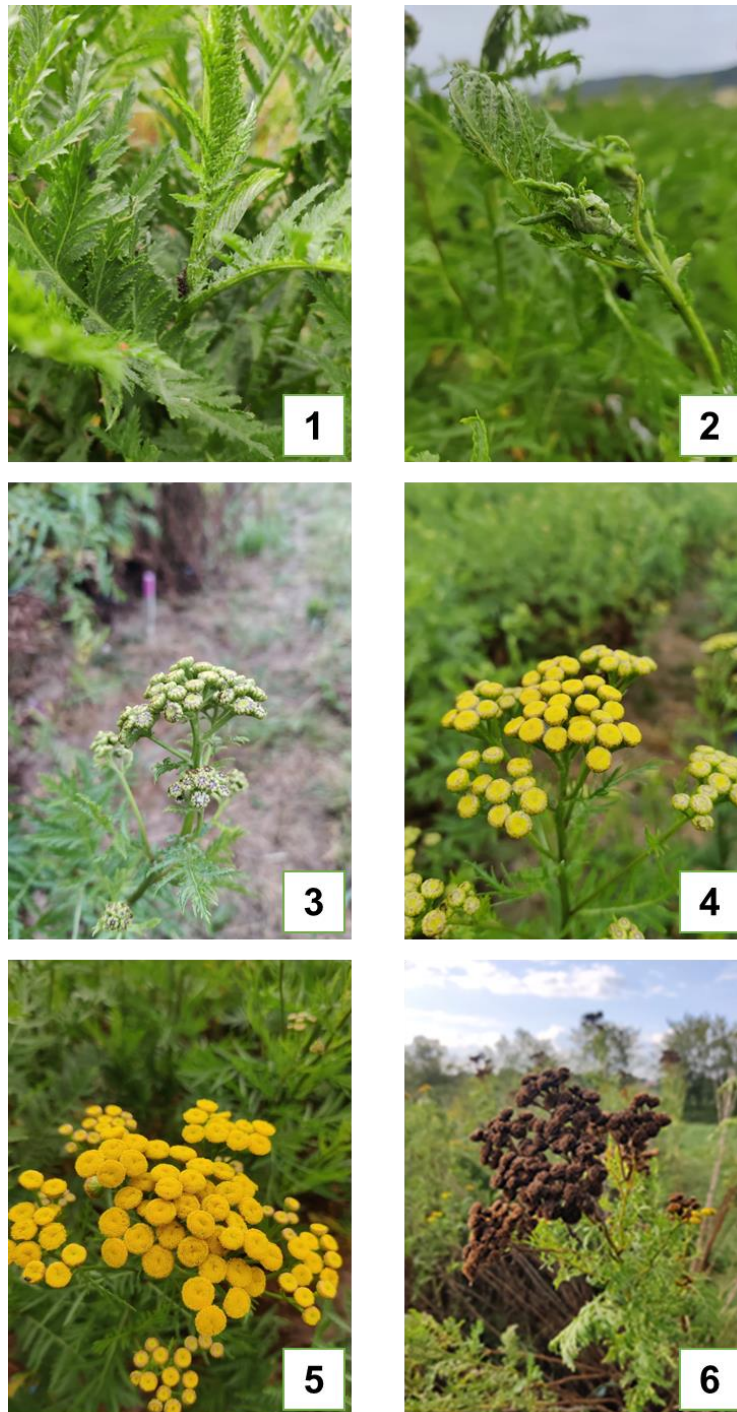


Figure S1-1: Stem phenology (*left-to-right then top-to-bottom*): [1] No inflorescence; [2] Inflorescence visible but closed; [3] Open inflorescence; [4] Beginning seed set (unripe); [5] Ripe seeds; [6] Mature seeds turning brown.

1.3. Details of the statistical analyses

1.3.1. Variables used in the analyses

Variable name	Description	Variable type	Factor levels
B	Experimental block	Factor	1 to 6
P	Experimental plot	Factor	1 to 84
CR	Plot-level chemotype richness	Integer	1, 2, 3, 6
C	Chemotype identity	Factor	Athu-Bthu, Bthu-high, Bthu-low, Chrys-acet, Mixed-high, Mixed-low
D	Daughter identity	Factor	Daughter ID of a particular chemotype
D: Athu-Bthu	Daughter identity	Factor	55, 56, 57
D: Bthu-high	Daughter identity	Factor	11, 14, 17
D: Bthu-low	Daughter identity	Factor	101, 103, 104
D: Chrys-acet	Daughter identity	Factor	94, 95, 100
D: Mixed-high	Daughter identity	Factor	21, 23, 30
D: Mixed-low	Daughter identity	Factor	64, 67, 68
CP	Chemotype presence	Factor, binary	Presence/absence (1/0) of a particular chemotype
CP: Athu-Bthu	Particular chemotype	Factor, binary	Athu-Bthu presence/absence (1/0) at plot level
CP: Bthu-high	Particular chemotype	Factor, binary	Bthu-high presence/absence (1/0) at plot level
CP: Bthu-low	Particular chemotype	Factor, binary	Bthu-low presence/absence (1/0) at plot level
CP: Chrys-acet	Particular chemotype	Factor, binary	Chrys-acet presence/absence (1/0) at plot level
CP: Mixed-high	Particular chemotype	Factor, binary	Mixed-high presence/absence (1/0) at plot level
CP: Mixed-low	Particular chemotype	Factor, binary	Mixed-low presence/absence (1/0) at plot level
Day	Day of headspace VOC collection	Factor	1 to 3

1.3.2. Models of effects on plant traits

For each analysis, we give the model run in R.

Plant-level traits

1.3.2.1. Effects of chemotype, plot-level chemotype richness, and the interaction between chemotype and plot-level chemotype richness on plant-level traits

We first analyzed the effect of chemotype identity and plot-level chemotype richness on the performance of individual plants within the plots.

Growth traits

Number of stems: We analyzed four measurements of the number of stems per plant separately by time point. Here, we analyzed the number of stems of the individual plants within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Number of stems	Model	Analysis of variance	Post hoc test
June 01, 2023	glmer(Stems_01.06.2021 ~ C * CR + (1 B/P) + (1 D), family = poisson, control = glmerControl(optimizer = "Nelder_Mead"))	Anova()	emmeans(model, list(pairwise ~ C), adjust = "tukey")
June 22, 2021	glmer(Stems_22.06.2021 ~ C * CR + (1 B/P) + (1 D), family = poisson, control = glmerControl(optimizer = "Nelder_Mead"))	Anova()	emmeans(model, list(pairwise ~ C), adjust = "tukey")
October 28, 2021	glmer(Stems_28.10.2021 ~ C * CR + (1 B/P) + (1 D), family = poisson)	Anova()	-
July 06, 2022	glmer(Stems_06.07.2022 ~ C * CR + (1 B/P) + (1 D), family = poisson)	Anova()	-

Plant height: We analyzed six measurements of the height per plant separately by time point. Here, we analyzed the number of stems of plants' height (cm) within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Height (cm)	Model	Analysis of variance	Post hoc test
June 01, 2023	<code>lmer(Height_01.06.2021 ~ C x CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	-
June 22, 2021	<code>lmer(Height_22.06.2021 ~ C x CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	-
October 28, 2021	<code>lmer(Height_28.10.2021 ~ C x CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	<code>emmeans(model, list(pairwise ~ Chemotype), adjust = "tukey")</code>
May 14, 2022	<code>lmer(Height_14.05.2022 ~ C x CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	-
July 06, 2022	<code>lmer(Height_06.07.2022 ~ C x CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	-
October 05, 2022	<code>lmer(Height_05.10.2022 ~ C x CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	-

Above-ground dry weight: There was one measurement of the above-ground dry weight per plant on October 28, 2021. Here, we analyzed plants' weight (g) within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P), and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Above-ground dry weight (g)	Model	Analysis of variance	Post hoc test
October 28, 2021	<code>lmer(sqrt(Dry_biomass_28.10.2021) ~ C * CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	-

Above-ground fresh weight: There was one measurement of the above-ground fresh weight per plant on October 05, 2022. Here, we analyzed plants' weight (g) within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P), and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Above-ground fresh weight (g)	Model	Analysis of variance	Post hoc test
October 05, 2022	<code>lmer(sqrt(Fresh_biomass_05.10.2022) ~ C * CR + (1 B/P) + (1 D))</code>	<code>Anova()</code>	-

Reproductive traits

Cumulative number of flower heads: From June 01 to October 28, 2021, mature flower heads were counted and collected from individual plants. Here, we analyzed the total number of flower heads produced by each plant within the stands differing in chemotype richness during that period. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Cumulative number of flower heads	Model	Analysis of variance	Post hoc test
From June 01, 2021, to October 28, 2021	glmer(Flowerheads ~ C * CR + (1 B/P) + (1 D), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ C), adjust = "tukey")

Flowering index: There was one measurement of the flowering index per plant on July 06, 2022. Here, we analyzed the flowering index of plants within the stands differing in chemotype richness. We evaluated the effects of chemotype identity (C), plot-level chemotype richness (CR), and their interaction (C x CR). Random effects included were Plot nested in Block (B/P) and Daughter (D). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Cumulative number of flower heads	Model	Analysis of variance	Post hoc test
July 06, 2022	lmer(Floweringindex_06.07.2022 ~ C * CR + (1 B/P) + (1 D))	Anova()	emmeans(model1, list(pairwise ~ C), adjust = "tukey")

1.3.2.2. Effects of daughter, plot-level chemotype richness, and the interaction between daughter and plot-level chemotype richness on plant-level traits

We second analyzed the effect of daughter identity (D), plot-level chemotype richness (CR), and their interaction (D x CR) on four plant traits of individual plants within the plots: Number of stems, height (cm), and above-ground dry weight (g) on October 28, 2021, and cumulative number of flower heads produced in 2021. We carried out a separate analysis per chemotype to test for differences between daughters within a chemotype, and another analysis to directly compare daughters by using all 18 levels of daughter identity (D). We included Plot nested in Block (B/P) as a random factor. Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plant trait	Model	Analysis of variance	Post hoc test
Number of stems: October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-high (D: 11, 14, 17)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-low (D: 101, 103, 104)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Chrys-acet (D: 94, 95, 100)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-high (D: 21, 23, 30)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	-
Mixed-low (D: 64, 67, 68)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Daughter ID (D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)	glmer(Stems_28.10.2021 ~ D * CR + (1 B/P), control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 2e5)), family = poisson)	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Height (cm): October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-high (D: 11, 14, 17)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Bthu-low (D: 101, 103, 104)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Chrys-acet (D: 94, 95, 100)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-high (D: 21, 23, 30)	lmer(Height_28.10.2021 ~ D * CR + (1 B/P))	Anova()	-

Mixed-low (D: 64, 67, 68)	<code>lmer(Height_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Daughter ID (D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)	<code>lmer(Height_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Above-ground dry biomass (g): October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	<code>lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	-
Bthu-high (D: 11, 14, 17)	<code>lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Bthu-low (D: 101, 103, 104)	<code>lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Chrys-acet (D: 94, 95, 100)	<code>lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Mixed-high (D: 21, 23, 30)	<code>lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Mixed-low (D: 64, 67, 68)	<code>lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Daughter ID (D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)	<code>lmer(sqrt(Dry_biomass_28.10.2021 ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Cumulative number of flower heads: From June 01, 2021, to October 28, 2021			
Athu-Bthu (D: 55, 56, 57)	<code>lmer(Flowerheads ~ D * CR + (1 B/P))</code>	Anova()	-
Bthu-high (D: 11, 14, 17)	<code>lmer(Flowerheads ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Bthu-low (D: 101, 103, 104)	<code>lmer(Flowerheads ~ D * CR + (1 B/P))</code>	Anova()	<code>emmeans(model1, list(pairwise ~ D), adjust = "tukey")</code>
Chrys-acet (D: 94, 95, 100)	<code>lmer(Flowerheads ~ D * CR + (1 B/P))</code>	Anova()	-

Mixed-high (D: 21, 23, 30)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Mixed-low (D: 64, 67, 68)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")
Daughter ID (D: 11, 14, 17, 21, 23, 30, 55, 56, 57, 64, 67, 68, 94, 95, 100, 101, 103, 104)	lmer(Flowerheads ~ D * CR + (1 B/P))	Anova()	emmeans(model1, list(pairwise ~ D), adjust = "tukey")

Plot-level traits

1.3.2.3. Effects of chemotype presence, plot-level chemotype richness, and the interaction between chemotype presence and plot-level chemotype richness on plot-level traits

We first averaged each plant trait at the plot level to test the effects of chemotype and chemotype richness on plot-level plant traits (Community-Weighted Means -CWM-). To test the effect of the presence/absence of a chemotype on plot-level trait values, we carried out a separate analysis per chemotype. This was done by running a linear model with Block (B), chemotype presence (CP- indicating whether a specific chemotype is present in the plot), plot-level chemotype richness (CR), and their interaction (CP x CR) as fixed effects, separately for each chemotype.

Growth traits

Number of stems: We analyzed four measurements of the number of stems per plot separately by time point. Here, we analyzed the average number of stems of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level number of stems	Model	Analysis of variance
June 01, 2021		
Athu-Bthu (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Bthu-high	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()

(CP: 1/0)		
Bthu-low (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_01.06.2021 ~ B + CR * CP)	anova()
June 22, 2021		
Athu-Bthu (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_22.06.2021 ~ B + CR * CP)	anova()
October 28, 2022		
Athu-Bthu (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_28.10.2021 ~ B + CR * CP)	anova()
July 06, 2022		
Athu-Bthu (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()

Chrys-acet (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Stems_06.07.2022 ~ B + CR * CP)	anova()

Plant height: We analyzed six measurements of the height (cm) per plot separately by time point. Here, we analyzed the average height of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level height (cm)	Model	Analysis of variance
June 01, 2021		
Athu-Bthu (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_01.06.2021 ~ B + CR * CP)	anova()
June 22, 2021		
Athu-Bthu (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_22.06.2021 ~ B + CR * CP)	anova()
October 28, 2022		

Athu-Bthu (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_28.10.2021 ~ B + CR * CP)	anova()
May 14, 2022		
Athu-Bthu (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_14.05.2022 ~ B + CR * CP)	anova()
July 06, 2022		
Athu-Bthu (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_06.07.2022 ~ B + CR * CP)	anova()
October 05, 2022		
Athu-Bthu (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Bthu-high	lm(Height_05.10.2022 ~ B + CR * CP)	anova()

(CP: 1/0)		
Bthu-low (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Height_05.10.2022 ~ B + CR * CP)	anova()

Above-ground dry weight: We analyzed one measurement of the above-ground dry weight (g) at plot-level. Here, we analyzed the average weight of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level above-ground dry weight (g)	Model	Analysis of variance
October 28, 2021		
Athu-Bthu (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(log(Dry_biomass_28.10.2021 ~ B + CR * CP)	anova()

Above-ground fresh weight: We analyzed one measurement of the above-ground fresh weight (g) at plot-level. Here, we analyzed the average weight of plants within the stands differing in chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level above-ground fresh weight (g)	Model	Analysis of variance
October 05, 2022		
Athu-Bthu	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()

(CP: 1/0)		
Bthu-high (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(log(Fresh_biomass_05.10.2022 ~ B + CR * CP)	anova()

Reproductive traits

Cumulative number of flower heads: From June 01 to October 28, 2021, mature flower heads were counted and collected from individual plants. Here, we analyzed the average cumulative number of flower heads of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness (CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level cumulative number of flower heads	Model	Analysis of variance
June 01 - October 28, 2021		
Athu-Bthu (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(log(Flowerheads ~ B + CR * CP)	anova()

Flowering index: There was one measurement of the flowering index per plant on July 06, 2022. Here, the average flowering index of plots of different chemotype richness. We evaluated the effects of block (B), chemotype presence (CP), plot-level chemotype richness

(CR), and their interaction (CP x CR). Post hoc tests were only calculated if differences within a factor in the analysis of variance were significant.

Plot-level flowering index	Model	Analysis of variance
July 06, 2022		
Athu-Bthu (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Bthu-high (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Bthu-low (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Chrys-acet (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Mixed-high (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()
Mixed-low (CP: 1/0)	lm(Floweringindex_06.07.2022 ~ B + CR * CP)	anova()

1.3.3. Models of effects on overyielding indexes

For each analysis, we give the model run in R.

1.3.3.1. Effects of plot-level chemotype richness on the overyielding indexes

We analyzed the effect of plot-level chemotype richness (CR) on the overyielding indexes of four plant traits calculated at plot-level. Random effect included was Block (B).

Overyielding index	Model	Analysis of variance
Above-ground dry biomass (g): October 28, 2021	lmer(Dry_biomass_28.10.2021 ~ CR + (1 B))	Anova()
Above-ground fresh biomass (g): October 05, 2022	lmer(Fresh_biomass_05.10.2022 ~ CR + (1 B))	Anova()
Cumulative number of flower heads: From June 01, 2021, to October 28, 2021	lmer(Flowerheads ~ CR + (1 B))	Anova()
Flowering index: July 06, 2022	lmer(Floweringindex_06.07.2022 ~ CR + (1 B))	Anova()

1.3.4. Models of chemodiversity

For each analysis, we give the model run in R.

1.3.4.1. Effects of plot-level chemotype richness on the plot-level theoretical leaf chemodiversity metrics

Theoretical plot-level leaf terpenoid diversity metrics were calculated by summing up the absolute leaf terpenoid concentrations ($\text{nmol} \times \text{g}^{-1}$) of each chemotype/daughter present in each plot, based on the chemical analysis of leaves from greenhouse plants in 2020 (Neuhaus-Harr *et al.*, 2023). We analyzed the effect of plot-level chemotype richness (CR) on each of the diversity metrics (terpenoid concentration, richness, Shannon diversity and evenness) using a linear model.

Diversity metric	Model	Analysis of variance
Squared plot-level theoretical total terpenoid concentration ($\text{nmol} \times \text{g}^{-1}$)	$\text{lm}((\text{Concentration})^2 \sim \text{CR})$	Anova()
Plot-level theoretical terpenoid richness	$\text{lm}(\text{Richness} \sim \text{CR})$	Anova()
Plot-level theoretical terpenoid Shannon diversity	$\text{lm}(\text{Shannon} \sim \text{CR})$	Anova()
Plot-level theoretical terpenoid evenness	$\text{lm}(\text{Evenness} \sim \text{CR})$	Anova()

1.3.4.2. Effects of plot-level chemotype richness on the plot-level realized volatile chemodiversity metrics

Realized plot-level volatile chemodiversity was based on terpenoids collected in the headspace ($\text{ng} \times \text{h}^{-1}$) in May 2022. We analyzed the effect of plot-level chemotype richness (CR) on each of the diversity metrics (terpenoid concentration, richness, Shannon diversity, and evenness) using a linear mixed model that included Block (B) and Day of headspace VOC collection (D) as random factors.

Diversity metric	Model	Analysis of variance
Squared root of plot-level realized total volatile terpenoid emission ($\text{ng} \times \text{h}^{-1}$)	$\text{lmer}(\text{sqrt}(\text{Concentration}) \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()
Squared plot-level realized volatile terpenoid richness	$\text{lmer}((\text{Richness})^2 \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()
Plot-level realized volatile terpenoid Shannon diversity	$\text{lmer}(\text{Shannon} \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()
Plot-level theoretical terpenoid evenness	$\text{lmer}(\text{Evenness} \sim \text{CR} + (1 \text{B}) + (1 \text{Day}))$	Anova()

Appendix B. Publication and Licensing Rights

B-I. Confirmation – Dissertation Figures

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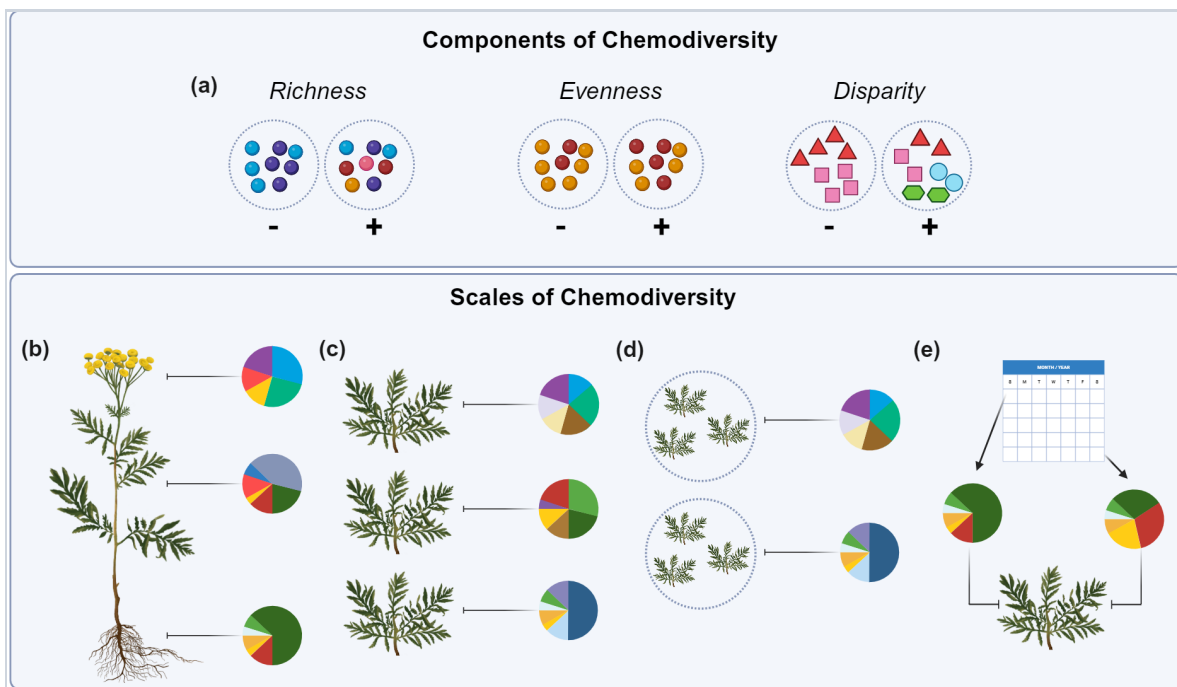
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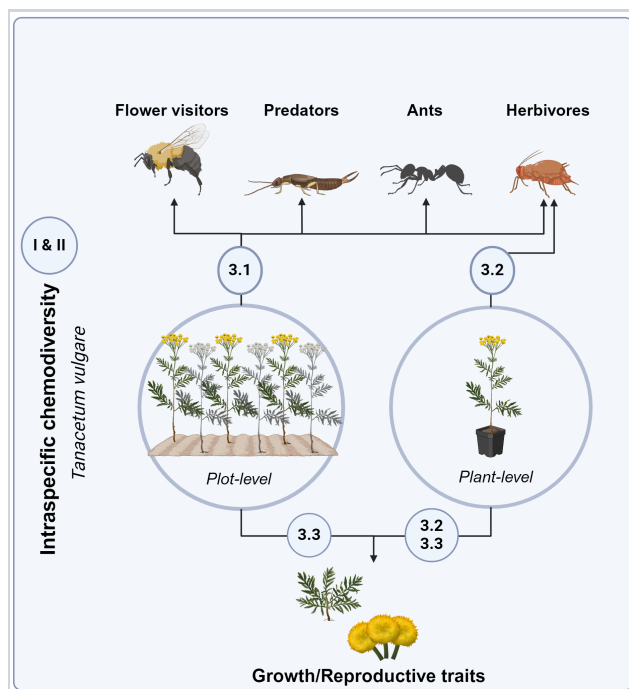
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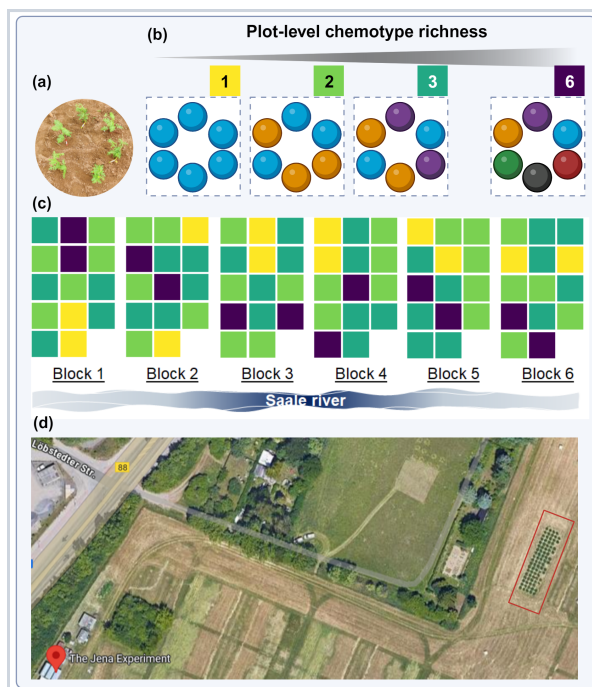
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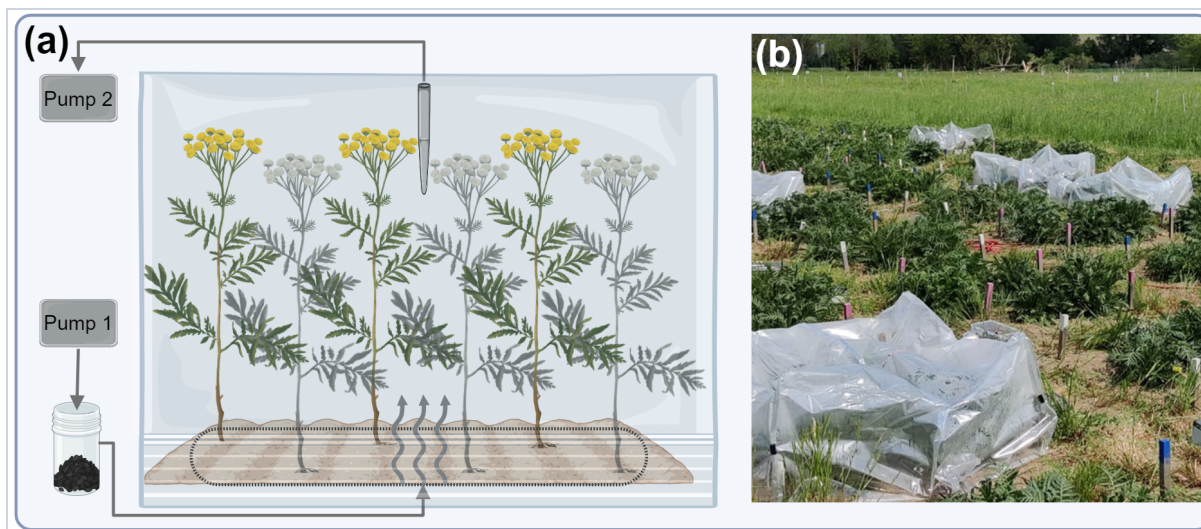
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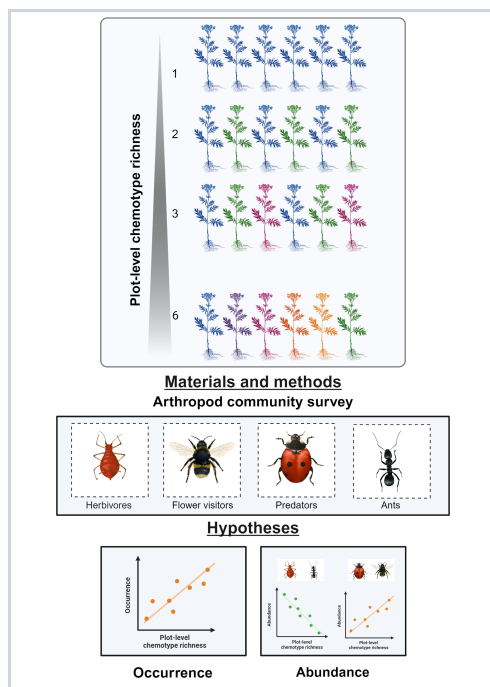
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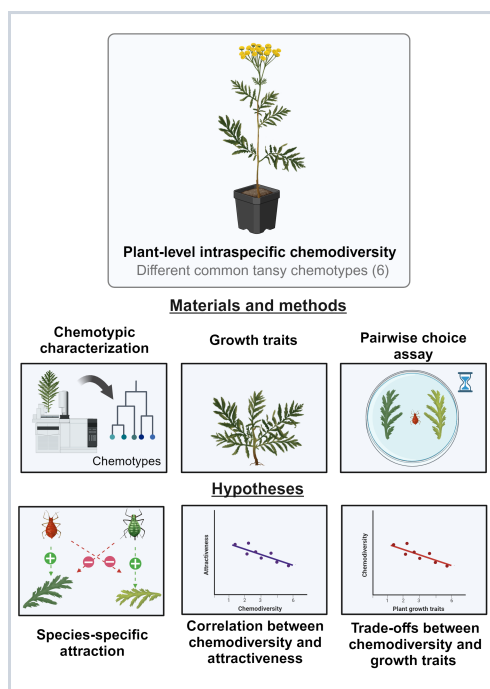
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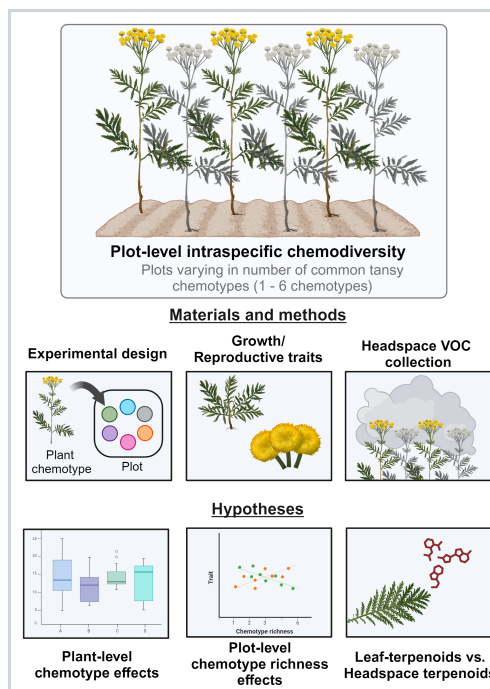
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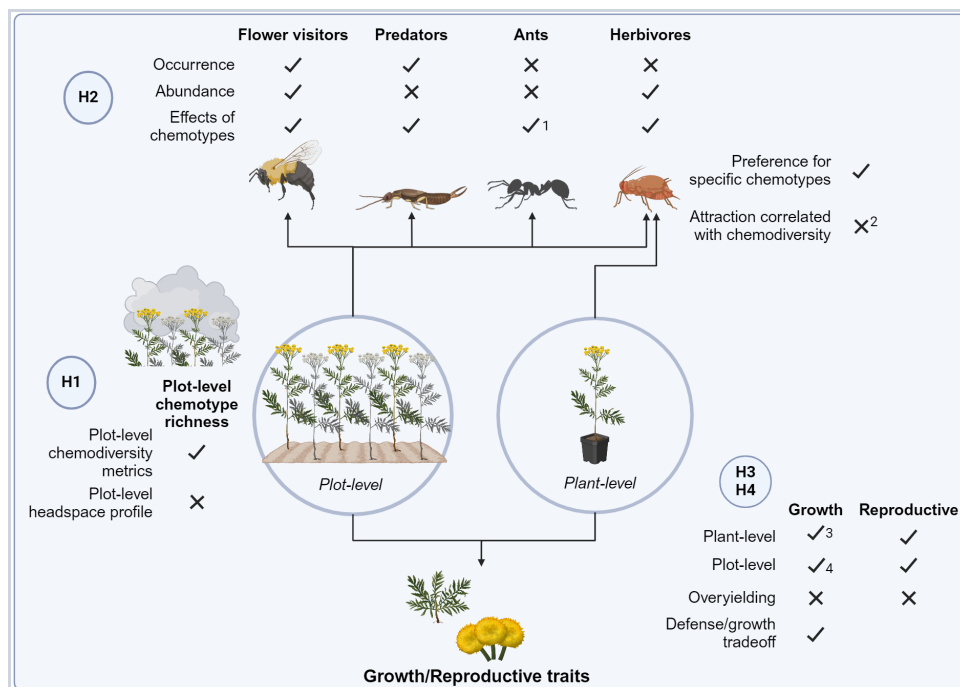
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B-II. Confirmation – Published research articles



Chemodiversity affects preference for *Tanacetum vulgare* chemotypes in two aphid species

Author: Robin Heinen, Wolfgang W. Weisser, Caroline Müller, et al

Publication: Oikos

Publisher: John Wiley and Sons

Date: Jan 3, 2024

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Licensed Content Publication Plant Biology

Licensed Content Title Intraspecific chemical variation of *Tanacetum vulgare* affects plant growth and reproductive traits in field plant communities

Licensed Content Author L. Ojeda-Prieto, P. Medina-van Berkum, S. B. Unsicker, et al

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