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Seed–substrate combinations: The establishment of species-rich meadows as Green Infrastructure

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Content

Abstract

Grasslands are biodiversity hotspots and provide multiple ecosystem services. However, they are globally endangered ecosystems due to widespread land-use change. When designing Green Infrastructure, as for example river dikes, ecosystem services can be combined with biodiversity. For this aim, establishment of species-rich grasslands requires a suitable combination of seed mixtures and substrates. This thesis investigates promising seed–substrate combinations within the context of landscape effects, temporal contingency, and environmental fluctuations. The questions of this thesis are: (i) What is the potential of Green Infrastructure to foster ecosystem services and biodiversity? (ii) Do trait-based seed mixtures improve restoration outcomes? (iii) What are the main drivers of restoration outcomes? (iv) How high is the temporal turnover of restored sites?

As backbone of this dissertation, three greenhouse experiments and one field experiment on a dike were conducted with different seed–substrate combinations. Moreover, dike grasslands were monitored over five years along the River Danube, SE Germany. We analyzed soil samples and surveyed vegetation to calculate, for example target species richness and beta diversity. Furthermore, the studied plots were compared with reference sites of hay meadows and calcareous grasslands.

Important ecosystem services of dikes were identified like dike security, conservation, recreation, and biomass production. Trait-based seed mixtures had limited success. However, hay meadow mixtures performed better in the north exposition than calcareous grassland mixtures. Different seed mix types for dike grasslands developed towards their reference regardless of substrate type, indicating a desired priority effect by seeding. Year effects by weather during establishment, like droughts, had a lasting negative effect on vegetation development. The main drivers influencing the spatial variation of established dike grassland were the topographical factor exposition, but also landscape factors like distance to the nearest biotope. Less important were substrate depth or seed density. Finally, I identified significant year-to-year turnover in restored dike grasslands challenging the evaluation of restoration outcomes.

Restoration practice should vary its approaches within one area to avoid biotic homogenization. Therefore, restoration should vary seed mixtures, substrates, and management within a given framework. This approach implies that instead of a specific restoration target, a target area or set of target states of the vegetation should be defined.

Kurzfassung

Wiesen und Magerrasen sind ein Hotspot der biologischen Vielfalt und erbringen zahlreiche Ökosystemleistungen. Sie sind jedoch aufgrund weit verbreiteter Landnutzungsänderungen weltweit gefährdete Ökosysteme. Bei der Gestaltung von Grüner Infrastruktur, wie zum Beispiel bei Flussdeichen und Deponien, können Ökosystemleistungen mit Biodiversität kombiniert werden. Die Etablierung von artenreichem Grünland erfordert dazu eine geeignete Kombination von Saatgutmischungen und Substraten. In dieser Arbeit werden vielversprechende Saatgut-Substrat-Kombinationen im Kontext von Landschaftseffekten, zeitlicher Kontingenz und Umweltschwankungen untersucht. Die Fragen dieser Arbeit lauten: (i) Welches Potenzial hat die Grüne Infrastruktur zur Förderung von Ökosystemleistungen und Biodiversität? (ii) Verbessern *trait*-basierte Saatgutmischungen die Ergebnisse der Wiederherstellung? (iii) Was sind die Hauptfaktoren für die Ergebnisse der Renaturierung? (iv) Wie hoch ist die zeitliche Fluktuation der renaturierten Flächen?

Im Rahmen dieser Dissertation wurden drei Gewächshausversuche und ein Freilandversuch auf einem Deich mit verschiedenen Saatgut-Substrat-Kombinationen durchgeführt. Darüber hinaus wurden Deichgrünlandflächen entlang der Donau in Süddeutschland über fünf Jahre hinweg beobachtet. Wir analysierten Bodenproben und untersuchten die Vegetation, um zum Beispiel den Zielartenreichtum und die Beta-Diversität zu berechnen. Darüber hinaus wurden die untersuchten Parzellen mit Referenzflächen aus Mähwiesen und Trockenrasen verglichen.

Es wurden wichtige Ökosystemleistungen von Deichen wie Deichsicherheit, Naturschutz, Erholung und Biomasseproduktion ermittelt. Saatgutmischungen auf der Grundlage von Merkmalen hatten nur begrenzten Erfolg. Allerdings schnitten Mähwiesenmischungen in der Nordexposition besser ab als Trockenrasenmischungen. Unterschiedliche Saatgutmischungen für Deichgrünland und Deponien entwickelten sich unabhängig vom Substrattyp in Richtung ihrer Referenz, was auf eine gewünschte vorrangige Wirkung der Ansaat hinweist. Witterungseinflüsse während der Etablierung, wie zum Beispiel Dürreperioden, wirkten sich nachhaltig negativ auf die Vegetationsentwicklung aus. Die wichtigsten Einflussfaktoren für die räumliche Variation des etablierten Deichgrünlands waren der topografische Faktor Exposition, aber auch Landschaftsfaktoren wie die Entfernung zum nächstgelegenen Biotop. Weniger wichtig waren die Substrattiefe oder die Samendichte. Schließlich stellte ich fest, dass sich die wiederhergestellten Deichwiesen von Jahr zu Jahr stark verändern, was die Bewertung der Ergebnisse der Renaturierung erschwert.

Kurzfassung

Die Renaturierungspraxis sollte ihre Ansätze innerhalb eines Gebiets variieren, um eine biotische Homogenisierung zu vermeiden. Daher sollten bei der Wiederherstellung innerhalb eines bestimmten Rahmens unterschiedliche Saatgutmischungen, Substrate und Bewirtschaftungsmaßnahmen eingesetzt werden. Dieser Ansatz impliziert, dass anstelle eines spezifischen Wiederherstellungsziels ein Zielgebiet oder eine Reihe von Zielzuständen der Vegetation definiert werden müssten.

1 General introduction

1.1 The challenge of predictive restoration

Over two-thirds of the global ecosystems have been converted or severely degraded (Millennium Ecosystem Assessment [MEA], 2005)[1]. The United Nations decade on ecosystem restoration began in 2021 because ecological restoration is believed to be an essential tool for sustainable development (United Nations [UN], 2019). Ecological restoration should help to conserve biodiversity (Ruiz-Jaen & Aide, 2005), provide ecosystem services (Montoya, Rogers, & Memmott, 2012), and to adapt to climate change (Harris, Hobbs, Higgs, & Aronson, 2006). Restoration is part of the UN Sustainable Development Goals 14 and 15 (UN, 2015) and of the Convention on Biological Diversity (Conference of the Parties [COP], 2014). Recently, the EU parliament voted for the **Nature Restoration Law**, which would be the first continent-wide, comprehensive restoration law (European Parliament [EP], 2023). The relevance of restoration in policies is a huge responsibility for a young, applied science and restoration efforts still need to be more effective. There is a widespread 'recovery debt' due to slow and incomplete restoration (Moreno-Mateos et al., 2017), as a global meta-analysis showed: degraded sites had 51% of the biodiversity of reference sites and restored sites only increased this value to 86% (Rey-Benayas, Newton, Diaz, & Bullock, 2009), and this problem remained a decade later (Jones et al., 2018).

The ultimate aim of restoration ecology is to provide knowledge for **predictive restoration** at landscape scale (Brudvig, 2011). However, there needs to be more reliable predictability in restoration outcomes, resulting in effective restoration and, thus, higher restoration success (Suding, 2011). So far, the same restoration measure applied in different locations and years results in contrasting outcomes (Stuble, Fick, & Young, 2017). Furthermore, restoration trajectories can be different (linear, asymptotic, stochastic) and do not necessarily have to maintain or even reach the reference state (Figure 1; Bullock, Aronson, Newton, Pywell, & Rey-Benayas, 2011). Thus, there exists no perfect 'cookbook' for ecological restoration, which is why it is critical to account for uncertainty and to inform practitioners about this limitation and the effectiveness of restoration measures to maintain the credibility of the field, and to stimulate new research (Hilderbrand, Watts, & Randle, 2005; Mouquet et al., 2015; Suding, 2011). The Society of Ecological Restoration introduced principles for restoration, called 'The Standards', to establish criteria for effective restoration (Gann et al., 2019). The Standards require the comparison of restoration sites with reference models by six key ecosystem attributes like

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[1] American English and citation style of Journal of Applied Ecology

abiotic conditions and species composition (Principle 3) in respect of targets, goals, objectives which are measured by indicators (Principle 5) to seek for the highest level of recovery (Principle 6) on a landscape scale (Principle 7; Gann et al., 2019).[2]
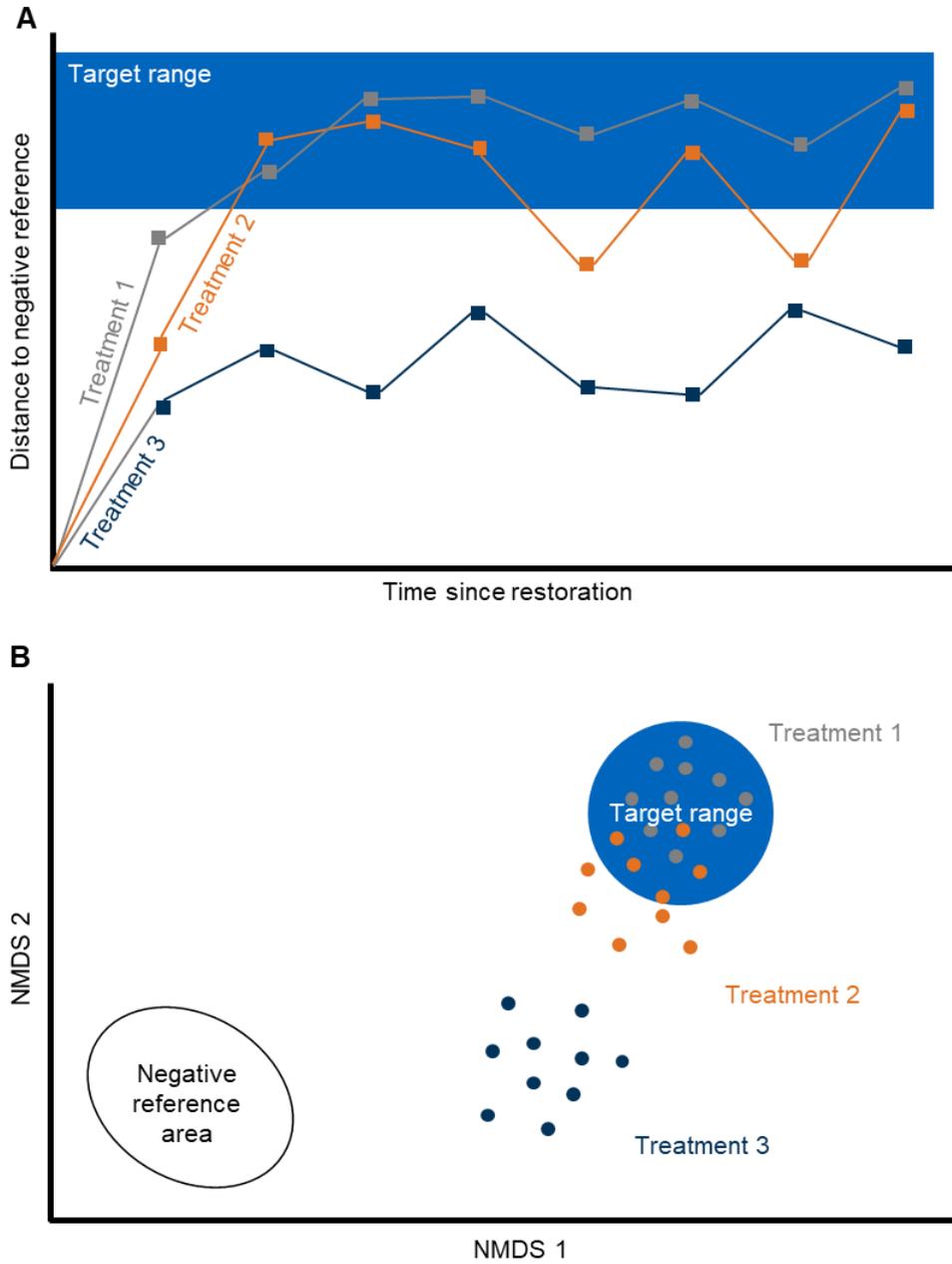
Figure 1. Temporal turnover **(A)** and spatial variation **(B)** of restoration outcomes. Comparison with a target species composition is vital to evaluate restoration outcomes and to mark a range of target compositions (blue area). Experiments and vegetation surveys that identify the differences between Treatment 1 and 3 advance the knowledge. However, restoration outcomes may vary in space and time between target and non-target conditions (Treatment 2), at least partly due to uncontrolled variation among sites or years.

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[2] Gann et al. ((2019)) highlight not only technical criteria but also engage participation of stakeholders and the implementation of socio-cultural needs (Principles 1 and 2).

Restoration must be able to adapt the measures, in a general way, to local site conditions. This sounds contradictory but is possible when adaptation is guided by **general ecological principles** (Perring et al., 2015). A crucial question is whether restoration can control the driving factors or can only fine-tune communities mainly shaped by uncontrollable factors (Grman, Bassett, & Brudvig, 2013). Principally, three outcomes are possible: (i) variability is controlled, leading to perfect recipes for restoration; (ii) variability is uncontrolled, and restoration must learn from further projects; or (iii) the restoration outcomes are sufficiently controlled so that uncontrolled variability remains in a desired range and is beneficial for biodiversity. The latter is "the key […] to develop approaches that result in the widest possible variety of outcomes within the range of desired conditions" (Brudvig et al., 2017).

Wilsey (2021) suggests that **grasslands** are an ideal **model ecosystem** to move forward the abilities of ecological restoration. For this purpose, experiments are needed to analyze deterministic drivers and their relative importance (Brudvig et al., 2017; Keddy & Laughlin, 2022; Suding, 2011) like they exist for biodiversity–ecosystem functioning research with the Jena experiment (Weisser et al., 2017), the European Agrodiversity Experiment (Kirwan et al., 2014), or the European BIODEPTH project (Minns et al., 2001), but also global long-term restoration experiments which were established especially in forests (Gellie et al., 2018). One of the oldest single-site restoration experiments is in the Konza Prairie in the USA (Collins, Knapp, Riggs, Blair, & Steinauer, 1998; Hartnett & Ratajczak, 2020). Though, Kaulfuß, Rosbakh, and Reisch (2022) emphasize that surveys of real-world restoration projects which are less standardized are also necessary. The reduced standardization could be due to participated stakeholders with different restoration goals, and practical and financial restrictions. In conclusion, long-term experiments and surveys are important to advance predictive restoration, and restoration is necessary to conserve already threatened grassland biodiversity.

1.2 Threatened grasslands and their potential for Green Infrastructure

Semi-natural temperate grasslands cover more than 25% of the land surface of the earth (Török & Dengler, 2018), provide several ecosystem services such as carbon sequestration (Bengtsson et al., 2019), are among the most species-rich ecosystems, and have a high conservation value (Dengler, Janišová, Török, & Wellstein, 2014; Wilson, Peet, Dengler, & Pärtel, 2012). **Grasslands** are undergoing widespread **degradation**, destruction, and fragmentation (Bardgett et al., 2021). More than 50% of grasslands have been destroyed in Europe, North or South America in the past decades (Buisson, Archibald, Fidelis, & Suding,

2022; Habel et al., 2013), making grassland habitats the second most threatened after peatlands in Europe (Janssen et al., 2016). The intensification of land use in some areas and the abandonment of others lead to a biotic homogenization of grassland communities (Felipe-Lucia et al., 2020; Gossner et al., 2016). However, grasslands are not mentioned or emphasized in the Aichi Biodiversity Targets (COP, 2014), the IPBES global report (Brondízio, Settele, Díaz, & Ngo, 2019), nor the European Biodiversity Strategy (European Commission [EC], 2020). Furthermore, global restoration projects aim to afforest grasslands (Veldman et al., 2015). Nevertheless, many grassland types are part of the European Habitat Directive, which protects and supports threatened habitats (FFH Directive, 2018).

Restoration of semi-natural grasslands can counteract ongoing degradation (Bardgett et al., 2021). However, there is a further opportunity to restore grasslands as part of the Green Infrastructure in urban and agricultural landscapes. This raises the possibility of integrating biodiversity and infrastructure maintenance, which is referred to as **'renewal ecology'** or 'ecological engineering' (Bowman et al., 2017; Stokes et al., 2014). These concepts can be encompassed by ecological restoration, if they are, for example oriented on native ecosystems (Principle 3, Gann et al., 2019), and seek for highest level of recovery (Principle 6) or, in this case, highest level of development. Within the concept of the Green Infrastructure, grasslands are part of a policy, the **European Green Infrastructure Strategy**, where Green Infrastructure is defined as 'a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services' which should support the European Biodiversity Strategy (EC, 2013).

Green Infrastructure consists, for example of dikes, landfills, parks, road verges and green roofs and is usually based on substrates created for the needs of a specific infrastructure or, in particular, on Technosols[3] (Arenas, Escudero, Mola, & Casado, 2017; Bátori et al., 2020; L. K. Fischer, Lippe, Rillig, & Kowarik, 2013; Molineux, Gange, Connop, & Newport, 2015; Nagase & Dunnett, 2010). However, the application of the concept of Green Infrastructure can easily neglect biodiversity (Garmendia, Apostolopoulou, Adams, & Bormpoudakis, 2016; Suding et al., 2015). Indeed, functionality of Green Infrastructure as corridor and habitat for grassland specialists is restricted (Hooftman et al., 2021; Koeser, Gilman, Paz, & Harchick, 2014). Functional Green Infrastructure should increase ecological integrity of habitats and can be established by specific combinations of seed mixtures and substrates.

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[3] > 20 vol% artifacts in the first 100 cm; World Reference Base for Soil Resources (WRB) (2014)

1.3   Theory for seed–substrate combinations

Restoration should move beyond case studies that identify and control individual drivers of restoration success (Perring et al., 2015). Already Bradshaw (1987) claimed that restoration is an 'acid test' for ecology, meaning that restoration projects should be implemented experimentally to test ecological theories in the real world. This link between theory and practice is still incomplete, which is why it is frequently addressed (Brudvig, 2017; Cadotte, Barlow, Nuñez, Pettorelli, & Stephens, 2017; Mouquet et al., 2015; Perring et al., 2015; Török & Helm, 2017; Wainwright et al., 2018). **Theory-driven experiments** in collaboration with restoration practitioners enable both explanatory and anticipatory predictions (Mouquet et al., 2015). Explanatory predictions increase ecological understanding and allow evidence-based evaluation of restoration approaches (Cooke et al., 2018). The resulting ecological knowledge is the basis for anticipatory predictions, which are needed in a changing world (Mouquet et al., 2015).

1.3.1   Assembly theory

The theory of community ecology is useful for grassland restoration because it describes the assembly, coexistence and function of plant communities, and such communities often serve as restoration goals (Wainwright et al., 2018). **Community assembly** refers to the process by which species from a regional pool colonize a local site, survive, and interact with each other, resulting in a site-specific community (HilleRisLambers, Adler, Harriet Milligan, Levine, & Mayfield, 2012). Whereas, **coexistence** refers to the long-term maintenance of diversity in the same area by species with similar ecological requirements (Chesson, 2000). Processes which add species to a species pool are historical dispersal and speciation, and then the community is shaped by ecological drift, habitat filtering, biotic interactions, as well as ongoing dispersal (Götzenberger et al., 2012; Vellend, 2010). Understanding these fundamental processes is necessary to improve restoration outcomes (Figure 2).

The basic theories of community ecology are **deterministic assembly** which includes niche theory (Chesson, 2000; Clements, 1916; Hutchinson, 1957; MacArthur & Wilson, 1967) and the **neutral theory** (Gleason, 1926; Hubbell, 2001). Both ecological theories can be linked to 'cultural theories' (Box 1; Kirchhoff, 2014). The neutral theory states that speciation, demographic stochasticity (ecological drift), and dispersal are the main factors in community assembly, but not habitat filtering or competition (Hubbell, 2001; Vellend, 2010). For restoration this would mean that seeding is a useful restoration approach but modifying the environment not. Deterministic assembly describes mechanisms that lead to a particular community, such as habitat filtering and biotic interactions (Götzenberger et al., 2012). Habitat filtering excludes

species that cannot grow under certain site conditions (Cornwell, Schwilk, & Ackerly, 2006), and biotic interactions create the realized niches because they can lead to competitive exclusion[4] (Kraft, Godoy, & Levine, 2015). Deterministic assembly allows restoration ecologists to identify drivers of effective restoration.

Coexistence is possible through **stabilizing and equalizing mechanisms** (Chesson, 2000). Equalizing mechanisms reduce fitness differences but always lead to competitive exclusion (HilleRisLambers et al., 2012). Therefore, coexistence requires stabilizing niche differences which means resource partitioning but also fluctuation-dependent mechanisms such as the storage effects or relative non-linearity of competition (Chesson, 2000). This means for restoration that spatial heterogeneity of restoration sites would improve biodiversity as well as temporal variability of environmental factors like the management. The storage effect is like temporal resource partitioning, which means that the same resources are used but at different times. In addition, bad times lead to a reduction in abundance but are overcome by, for example, dormancy (Chesson, 2000). Relative non-linearity of competition means that two species differ in their response to a resource and that this resource fluctuates, allowing coexistence to continue (Chesson, 2000).

Box 1: Niche and neutral theories as cultural theories

The two main concepts of community assembly niche and neutral theory (Hubbell, 2001; MacArthur & Levins, 1967) are underpinned by different concepts of history (Kirchhoff, 2014, 2015):

Niche theory expects trade-offs between species leading to coexistence through resource partitioning and the storage effect, which leads to the assumption that similar species cannot coexist ('limiting similarity'). Competitive exclusion and niche compression lead to a community under certain environmental conditions. That is, colonization is expected to end when all niches are occupied. Neutral theory expects that coexisting species do not compete at all and that biotic interactions are always outcompeted by stochastic events (environmental fluctuations, dispersal).

According to Kirchhoff (2014), the niche theory is structurally similar to the *concept of linear-directional history* in the sense of steady (economic) progress through the division of labor (= niches) (Smith, 1776). The neutral theory is based on an *occasional history concept*, which does not expect an ascending development but rather a random sequence of changes that are caused by discontinuous, unpredictable stochastic events (Foucault, 1966).

Niche and neutral theories can be integrated by hierarchically ordering the mechanisms described (Götzenberger et al., 2012). The neutral theory can explain processes operating at

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[4] Biotic interactions include not only competition (−/−), amensalism like shading (0/−), predation and parasitism (+/−) but also facilitation such as mutualism (+/+) or commensalism like a safe site (+/0).

global and regional scales, such as (i) speciation and historical dispersal and (ii) contemporary dispersal and ecological drift, respectively, whereas deterministic coexistence explains processes operating at small scales, such as (iii) habitat filtering that defines the local species pool, and (iv) biotic interactions occurring at even smaller scales (Bello et al., 2013). Furthermore, these theories are integrated into the concept of metacommunities.

1.3.2   The metacommunity concept and restoration

A metacommunity is "a set of local communities that are linked by dispersal of multiple potentially interacting species" (Leibold et al., 2004). On the one hand, the concept expects deterministic assembly by habitat filtering and biotic interactions. On the other hand, the **metacommunity concept** incorporates dispersal by expecting patch dynamics through competition–colonization trade-offs and sink habitats through mass effects (Leibold et al., 2004). The patch-dynamic concept expects stochastic local extinctions by ecological drift, and then the free niche can be filled first by a good disperser and later by a bad disperser but a good competitor (Leibold et al., 2004). Mass effects occur when species disperse from source habitats where they are superior to sink habitats where they cannot reproduce sufficiently locally (Leibold et al., 2004). The metacommunity concept does not include speciation, which is, however, included in the species pool concept, that is needed later to evaluate restoration outcomes. Furthermore, historical contingencies are important for community assembly because the order and timing of past events have a lasting legacy effect on community assembly (Fukami, 2015). Such contingencies can be due to disturbances, environmental fluctuations, land-use legacies, or the arrival of species, called priority effects, and lead to alternative stable or alternative transient states (Fukami, 2015). Transient states imply a different trajectory to the same final stable state.

The metacommunity concept and the recognition of historical contingencies are useful for restoration ecology because they improve the understanding of biodiversity patterns and the biodiversity–ecosystem function relationships (Chase, Jeliazkov, Ladouceur, & Viana, 2020). More specifically, this theoretical background has two practical implications. First, restoration can actively modify ecological factors that are understood and controllable; for example, restoration can influence habitat filtering and biotic interactions and can account for land-use legacies by manipulating the local soil conditions and by the initial management (Figure 2; Halassy et al., 2016; Török, Helm, Kiehl, Buisson, & Valkó, 2018). Furthermore, dispersal limitation and priority effects can be modified by using seed mixtures and the preparation of corridors (Figure 2; Halassy et al., 2016; Török et al., 2018). Seed mixtures can also be specified for certain site conditions to seed–substrate combinations to increase restoration effectiveness (Laughlin, 2014a). Second, restoration projects can benefit from spatial

heterogeneity of the landscape and the specific restoration site, temporal fluctuations of weather and management, or demographic stochasticity because these processes prevent competitive exclusion and thus increase biodiversity (Figure 2). However, this variability challenges the predictability of community development which is a major aim of restoration ecology as already stated (cf. Figure 1).
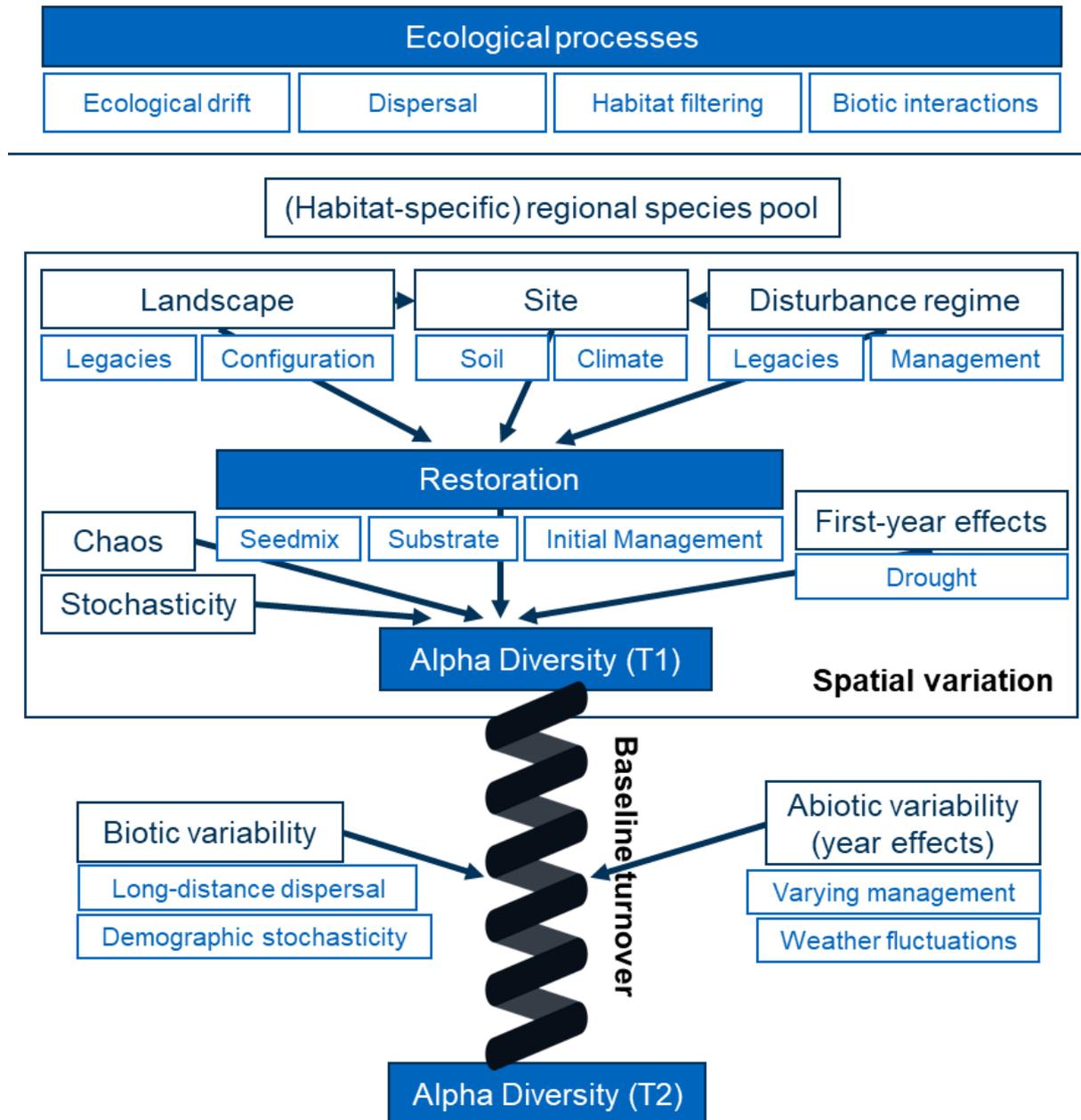
Figure 2. Restoration is dependent on landscape, site and disturbance factors, and first-year effects after restoration. All these factors act within the regional species pool, and they are underpinned by four main ecological processes. Furthermore, baseline turnover modifies the local diversity from year to year. This core concept of the doctoral thesis is based on Bello, Lavorel, Gerhold, Reier, and Pärtel (2010), Brudvig (2011), and Brudvig et al. (2017). Feather image by good1 via Pixabay.

1.4 Factors influencing seed–substrate combinations

1.4.1 Non-fluctuation deterministic factors

For predictive restoration ecology, it is essential to know the **key drivers** of community assembly and which of them can be influenced during restoration (Grman et al., 2013; Keddy & Laughlin, 2022). (i) All possible restoration outcomes are located within the framework of the **regional species pool** (Figure 2; Brudvig, 2011), which is the result of contemporary dispersal and biogeographic history consisting of past dispersal and speciation (Zobel, 2016). The regional species pool sets the frame for possible restoration outcomes, but seed dispersal to restoration areas is commonly limited (Myers & Harms, 2009). The species pool can be influenced by restoration through the selection of habitat-specific species for seed mixtures (Laughlin, 2014a). (ii) **Local site conditions** include edaphic and climatic conditions, with soil type often modified by restoration approaches (Brudvig, 2011) through topsoil removal, carbon amendment, or substrate mixing (Chenot-Lescure, Jaunatre, Buisson, Ramone, & Dutoit, 2022; Halassy et al., 2016; Török, Vida, Deák, Lengyel, & Tóthmérész, 2011) (Figure 2).

The identification of appropriate seed–substrate combinations is a major task of restoration ecology. However, seed–substrate combinations are exposed to further factors: (iii) **landscape configuration** particularly influences dispersal and thus colonization probability (Fahrig, 2017) through patch size (MacArthur & Wilson, 1967; but see Fahrig, 2017), habitat connectivity (Damschen et al., 2019; Hanski, 1998), or edge effects (Tscharntke et al., 2012) (Figure 2). Landscape factors are rarely explored in restoration ecology (Brudvig, 2011), and it is difficult to manipulate the mass effect of propagule pressure from the surroundings of undesired species. (iv) The **disturbance regime**, such as fire, grazing, or mowing, modifies biotic interactions and can be altered by changing management after restoration (Buisson et al., 2022; Halassy et al., 2016). (v) **Past events** can have long-term effects on species composition (Figure 2; Fukami, 2015). These could be desired effects of restoration measures that set the intended trajectory (Wilsey, 2021), but typically undesired legacies are meant by land-use history prior to restoration (Grman et al., 2013; Kettle, Rich, Kindscher, Pittman, & Fu, 2000) or by year effects during the establishment phase after restoration (Werner, Stuble, Groves, & Young, 2020). Former landscape configurations (Conradi, Temperton, & Kollmann, 2017), the soil seed bank (Bakker, Poschlod, Strykstra, Bekker, & Thompson, 1996), or residual phosphorus in agricultural soils can cause these legacy effects on biodiversity (Ceulemans et al., 2014). **Year effects** are, for example, the result of weather fluctuations and phenomena such as frost and drought (Figure 2; Werner et al., 2020).

1.4.2 Environmental fluctuations and chaos

There is still much unexplained variation in restoration outcomes (Grman et al., 2013). One reason is unmeasured deterministic factors (= noise), but also baseline turnover (Figure 2). **Baseline turnover** includes fluctuations in species composition due to deterministic fluctuations in filters (e.g., weather fluctuations) and neutral processes such as long-distance dispersal events or demographic stochasticity (Magurran, Dornelas, Moyes, & Henderson, 2019; Warren et al., 2015). Moreover, varying management regimes also cause small changes, for example, due to practical or economic reasons, and can lead to temporal variability (Kun et al., 2019; Vadász, Máté, Kun, & Vadász-Besnyői, 2016). Besides, Participation is Principle 1 of The Standards (Gann et al., 2019), why induced variability by management practice should be taken into account in restoration ecology. Many of the mentioned temporal fluctuations are chaotic, meaning they are deterministic but highly dependent on initial conditions, limiting the long-term predictability of restoration outcomes (Landres, Morgan, & Swanson, 1999; Rogers, Johnson, & Munch, 2022).

Baseline turnover and dynamic equilibria should be investigated and incorporated into the definition of **restoration goals** to avoid simplistic equilibrium expectations (Rogers et al., 2022; Warren et al., 2015). Furthermore, restoration ecologists should avoid the one-size-fits-all solutions commonly sought by engineers (Hiers, Jackson, Hobbs, Bernhardt, & Valentine, 2016). This is to avoid biotic homogenization (Holl, Luong, & Brancalion, 2022) and to spread the risk of environmental hazards during establishment (Fivash et al., 2022). Besides, temporal variability increases species richness, which in turn leads to greater stability of ecosystem functioning (Box 2; Craven et al., 2018; Isbell et al., 2015; Tredennick, Adler, & Adler, 2017). Nevertheless, there is not only baseline turnover but also directional trends driven by global change and evolution which challenges restoration and its desired predictability (Leibold, Govaert, Loeuille, Meester, & Urban, 2022; Magurran et al., 2019).

Box 2: Temporal insurance hypothesis

The temporal insurance hypothesis (Yachi & Loreau, 1999) or the portfolio effect (Tilman, 1999) explain the diversity–stability relationship through species asynchrony. Asynchrony creates stability of ecosystem states and processes by compensatory dynamics: (i) endogenous compensatory cycles due to relative non-linearity of competition and (ii) exogenously driven compensatory fluctuations through the temporal storage effect against environmental fluctuations (Chesson, 2000; Gonzalez & Loreau, 2009; Tredennick et al., 2017).

1.5 Trait-based seed mixtures for restoration

A promising tool for combining ecological knowledge with practical restoration goals is the use of **functional traits** to develop seed–substrate combinations (Lavorel & Garnier, 2002; Wainwright et al., 2018). Functional traits are morphological, physiological, or phenological plant characteristics that are measurable in individuals and indirectly affect fitness through their effects on growth, reproduction, and survival (Violle et al., 2007). Traits can be divided into response and effect traits (Lavorel & Garnier, 2002). Response traits are those traits that are influenced by the environment and are the vehicle for environmental sorting; effect traits are those traits that affect ecosystem functioning (Violle et al., 2007). Functional traits are a quantification of the niche theory, which expects trade-offs between species in a multidimensional space. There is strong evidence for a leaf economic spectrum, ranging from fast to slow resource acquisition strategies (Wright et al., 2004). The spectrum spans from a fast return of invested energy, through high photosynthetic rates, low dry mass investment, and short leaf lifespans, to a slow return of invested energy (Wright et al., 2004). This spectrum is represented not only at the level of individuals but also at the level of species (Díaz et al., 2016) and communities (Bruelheide et al., 2018). The leaf economic spectrum is frequently represented by the specific leaf area (Wright et al., 2004).

Westoby, Falster, Moles, Vesk, and Wright (2002) highlighted other trade-offs, such as the seed size–seed output trade-off, which leads from many small seeds that have a higher chance of occupying an empty patch to few large seeds that withstand harsh environmental conditions. In addition, plant height is an indicator of the trade-off competitive ability for light vs. shade tolerance, or rapid early height within the frame of succession and disturbance frequency (Falster & Westoby, 2003). Therefore, Westoby (1998) proposed a **leaf–height–seed scheme** which updates Grime's (1977) triangle of species strategies and which should move Grime's strategy scheme from a site-specific, species-based one to a general trait-based scheme (Westoby, 1998). Meanwhile, additional traits have been proposed to capture relevant variation in plant strategies (Laughlin, 2014b): flowering traits (E-Vojtkó, Bello, Durka, Kühn, & Götzenberger, 2020), root traits (Bardgett, Mommer, & Vries, 2014), clonal traits (E.-Vojtkó et al., 2017), wood density (Westoby & Wright, 2006), and regeneration traits (Larson & Funk, 2016b). Root traits are particularly important for estimating the erosion resistance of slopes which are a common feature of Green Infrastructure (Vannoppen, Poesen, Peeters, Baets, & Vandevoorde, 2016).

The aim of understanding the functional traits of plant communities is to identify general patterns and their underlying mechanisms that allow predictions to be made (McGill, Enquist,

Weiher, & Westoby, 2006). The resulting comprehension allows restoration ecologists to test modifications to seed mixtures and substrates to successfully establish the intended vegetation and ecosystem functions (Carlucci, Brancalion, Rodrigues, Loyola, & Cianciaruso, 2020). For example, functional plant traits can be used to design seed mixtures that might prevent plant invasions (Funk, Cleland, Suding, & Zavaleta, 2008). The plant traits of individuals can be transferred to the community level via community-weighted means (CWM; Lavorel et al., 2008) or functional diversity (Mason, Mouillot, Lee, & Wilson, 2005) by using the large databases of species traits (Guerrero-Ramírez et al., 2020; Kattge et al., 2020; Klimešová, Danihelka, Chrtek, Bello, & Herben, 2017). The CWM approach incorporates the mass ratio hypothesis, which states that more abundant species are more relevant to ecosystem functioning (Grime, 1998).

Autochthonous seed mixtures are commonly used for grassland restoration (Kiehl, Kirmer, Donath, Rasran, & Hölzel, 2010; Török et al., 2010). However, the seed mixtures are based on expert knowledge rather than on a universal, quantitative measure such as functional traits (Clark et al., 2012; Merchant, Henn, Silva, van Cleemput, & Suding, 2022). Laughlin (2014a; Laughlin et al., 2018) developed a **trait-based model** called **Traitspace**, which is based on a hierarchical Bayesian framework and incorporates intraspecific trait variability. This model calculates the abundance values of species to achieve desired CWMs of certain functional plant traits while diversifying other functional plant traits at the same time (Laughlin et al., 2018), which enables the application of the response and effect framework of Suding et al. (2008).

An aim of restoration is to develop seed–substrate combinations by modifying a response trait to adapt a seed mixture to the site. Simultaneously one can diversify an effect trait, such as flowering date, to improve flower availability for pollinators. The advantage of **trait-based seed mixtures** is that they are based on general principles and, therefore, adaptable to different sites, different regional species pools, or novel conditions, which can increase restoration success by reducing the effects of habitat filtering or competitive exclusion (Balazs et al., 2020; Bernard-Verdier et al., 2012; Pywell et al., 2003). Such seed mixtures are less dependent on expert knowledge, although experts are still needed to define the species pool and relevant traits and trait values (Keddy & Laughlin, 2022; Laughlin, 2014a). The selection of appropriate traits and trait values remains a key challenge in using functional traits (Funk et al., 2017).

1.6   Evaluating seed–substrate combinations

The Standards require ecological integrity for ecological restorations which encompasses six **key ecosystem attributes**: absence of threats, physical conditions, species composition, structural diversity, ecosystem function and external exchanges (Gann et al., 2019). In this thesis, I focus on the effect of different substrates (physical conditions) and seed mixtures on the plant biodiversity (species composition) and integrate the landscape context (external exchanges). Structural diversity and ecosystem functions are only touched by this thesis. Biodiversity is the common goal of restoration (Ruiz-Jaen & Aide, 2005), but there are 15 different aspects depending on the scale and index (McGill, Dornelas, Gotelli, & Magurran, 2015). In this thesis, I focus on the local and on the metacommunity scale for the investigation of seed–substrate combinations, but not on the biogeographic or global scale. However, I use all indices, i.e., biomass, alpha diversity, spatial beta diversity, and temporal beta diversity. Alpha diversity (= species richness) at the local scale is a common measure of biodiversity but does not detect shifts in species composition (Blowes et al., 2019; Dornelas et al., 2014; Hillebrand et al., 2018; Larsen, Chase, Durance, & Ormerod, 2018). Shifts in **species composition** can be identified using beta diversity, which measure differences from site to site ('spatial variation') or of one single site over time ('temporal turnover') (Anderson et al., 2011; R. H. Whittaker, 1960). Spatial variation can be decomposed into two additive parts, 'replacement' and 'nestedness', where replacement accounts for the substitution of species by others and nestedness refers to the difference in species richness between communities (Baselga, 2010, 2012). Both components indicate different ecological processes: replacement is driven by balanced environmental sorting, dispersal or historical contingencies and nestedness by selective unbalanced habitat filtering or lower habitat heterogeneity (R. J. Whittaker & Fernández-Palacios, 2007).

Species composition varies in space but also in time (F. M. Fischer, Chytrý, Těšitel, Danihelka, & Chytrý, 2020), challenging the traditional expectation of a static climax endpoint (Hilderbrand et al., 2005; Magurran et al., 2019). Temporal beta diversity can be calculated (Legendre, 2019), allowing further investigation of its patterns and underlying processes (Hillebrand et al., 2018; Magurran et al., 2019; Török & Helm, 2017). Ideally, space and time should be integrated into a single approach, but the methods are still in their infancy (Tatsumi, Iritani, & Cadotte, 2021).

Beta diversity is a promising metric for the study of biodiversity-ecosystem function relationships, but also for guiding restoration (Mori, Isbell, & Seidl, 2018; Socolar, Gilroy, Kunin, & Edwards, 2016). High spatial variation can be beneficial for ecosystem functioning (Wang et

al., 2021). However, Socolar et al. (2016) emphasized that neither nested structured areas nor a shift from habitat specialists to generalists is desired in conservation. High beta diversity, in general, is insufficient for conservation, who is interested in species identity (Jax & Heink, 2015). This means that replacement is not, per se, positive if there is a balanced turnover from specialists to generalists, why reference communities are required for an evaluation of restoration outcomes (Larsen et al., 2018).

The species pool concept can be used for the goal of typical biodiversity by defining a **habitat-specific species pool** (sensu Zobel, 2016). This includes a separation of species richness into characteristic species and derived species richness (Helm, Zobel, Moles, Szava-Kovats, & Pärtel, 2015), and this distinction can be based on expert knowledge (e.g., Ellenberg, Weber, Düll, Wirth, & Werner, 2001) or on classification by big data (Chytrý et al., 2020). Classically, the reference for restoration should be indigenous historical ecosystems, which are now challenged by directional climate change and the reduced relevance of equilibrium concepts (Jackson & Hobbs, 2009; Perring et al., 2015). History should be a puzzle piece to guide restoration, not a template (Higgs et al., 2014). A reference can be established by expanding data sources through the use of data from local to regional scales and from the past, the present, and future projections (Shackelford, Dudney, Stueber, Temperton, & Suding, 2021). For example, global databases of vegetation surveys can be used to collect references at larger scales (Dengler et al., 2011; Sabatini et al., 2021).

1.7 Open questions and aim of the studies

Trait-based models and spatial and temporal beta diversity are of increasing interest in ecology (Magurran et al., 2019; Mori et al., 2018; Zakharova, Meyer, & Seifan, 2019). In particular, the application in restoration ecology should be further developed (cf. Socolar et al., 2016; Wainwright et al., 2018). This thesis tackles different **current topics of ecological restoration**: (i) predictable restoration while allowing for uncertain and dynamic outcomes, (ii) the influence of environmental heterogeneity. Furthermore, the studies touch (iii) the potential of Green Infrastructure for biodiversity, (iv) the effect of landscape on restoration outcomes, and (v) connectivity in agricultural landscapes (Ockendon et al., 2018). The aim is to use dike grasslands as a study ecosystem to develop seed–substrate combinations for restoration, considering environmental (spatial) variation and (temporal) fluctuations.

The **study system** for the following questions are **river dikes**. In Germany, there are approximately 8,000 km of river dikes that have been or will be upgraded or relocated to

mitigate increased flood risks due to climate change (Tourment et al., 2018; e.g., in Bavaria, Bayerisches Staatsministerium für Umwelt und Verbraucherschutz [StMUV], 2014). Dikes can promote habitats for many plant and animal species that are missing in the surrounding agricultural landscape (Almásy, Essl, Berger, & Schulze, 2021; Bátori et al., 2016; Torma & Császár, 2013). However, it is important to keep in mind that dikes are responsible for the loss of large areas of valuable floodplains (Box 3). The establishment of species-rich dike grasslands can be quite successful (Husicka, 2003; Liebrand & Sykora, 1996), but there is still a restoration debt compared to semi-natural grasslands (Bátori et al., 2020), which needs to be further closed. Therefore, I addressed the following questions:

1. Dikes are engineered landscape features that prevent flooding in agricultural areas and protect settlements in floodplains but what **ecosystem services** exactly do they provide, and what are the (potential) **relationships with biodiversity**? (Publication: Teixeira, Bauer, Moosner, & Kollmann, 2023)

2. A trait-based model to design seed mixtures has been developed, but scarcely tested in experiments (Laughlin, 2014a; Laughlin et al., 2018). If the model has been tested, it has only been in a greenhouse and not for different environmental conditions such as nutrient supply or moisture experiments (Möhrle, Reyes-Aldana, Kollmann, & Teixeira, 2021; Yannelli, Karrer, Hall, Kollmann, & Heger, 2018). In this thesis, **seed–substrate combinations** are tested in greenhouse experiments with different environmental conditions and in a field experiment over four years with functionally different seed mixtures on different substrates. Such combinations should increase predictable restoration outcomes. (Publications: Bauer, Huber, & Kollmann, 2023d; Bauer, Krause, Heizinger, & Kollmann, 2022b)

3. Restoration is influenced by local site conditions, but also by hard-to-control landscape effects and historical contingencies. Studies with vegetation plots distributed on a landscape scale are required to identify such additional drivers of restoration outcomes (Suding, 2011). Uncontrolled **spatial variation** of restoration outcomes can be beneficial if there is a balanced replacement of target species, and most studies of spatial variation are based on one year of surveys. Therefore, the plots were distributed across the study region, surveyed four times and several drivers were analyzed separately for replacement and nestedness (Publication: Bauer, Huber, & Kollmann, 2023a).

4. Dispersal, demographic stochasticity, environmental fluctuations, and slight variations in management for economic and practical reasons (e.g., mowing dates) lead to

continuous **temporal turnover** in species composition, also referred to as 'baseline change' (Magurran et al., 2019). To my knowledge, this has not been quantified for restoration, although it would be important to identify realistic restoration goals and to avoid the still dominant image of a static climax vegetation (Rohwer & Marris, 2016; Shackelford et al., 2021). Brudvig et al. (2017) accounted for variability in restoration outcomes but did not include temporal turnover as a cause of variability in species composition. Therefore, the year-to-year turnover of monitored plots was measured (Publication: Bauer et al., 2023a).

2 Objectives and outline

The objective of this cumulative thesis is to improve seeding as a restoration approach by testing trait-based seed mixtures specified for different soil conditions while improving the understanding of its limitations at the landscape scale. Therefore, I worked at different scales (greenhouse, field, landscape) and varied the degree of control (experiment, monitoring of real-world restorations) (Figure 3). For both experiments, I manipulated the seed mixtures and the substrates. For the field studies, I could use dikes as a study system along the Danube River in Bavaria, SE Germany. There, I could do vegetation monitoring and use data from four years. The greenhouse experiment ran only over three months, and the field survey monitored less standardized real-world restorations. Therefore, these two study parts mark the ends of the trade-off between mechanistic understanding and the description of real (complex) patterns (Figure 3).

I hypothesized that well-specified trait-based seed mixtures would lead to a more successful vegetation development (higher biomass, higher persistence of seeded species) than trait-based seed mixtures designed for opposing environmental conditions. I further assumed that perfect seed–substrate combinations are limited in real-world restorations by uncontrolled spatial factors, environmental fluctuations and management variability.
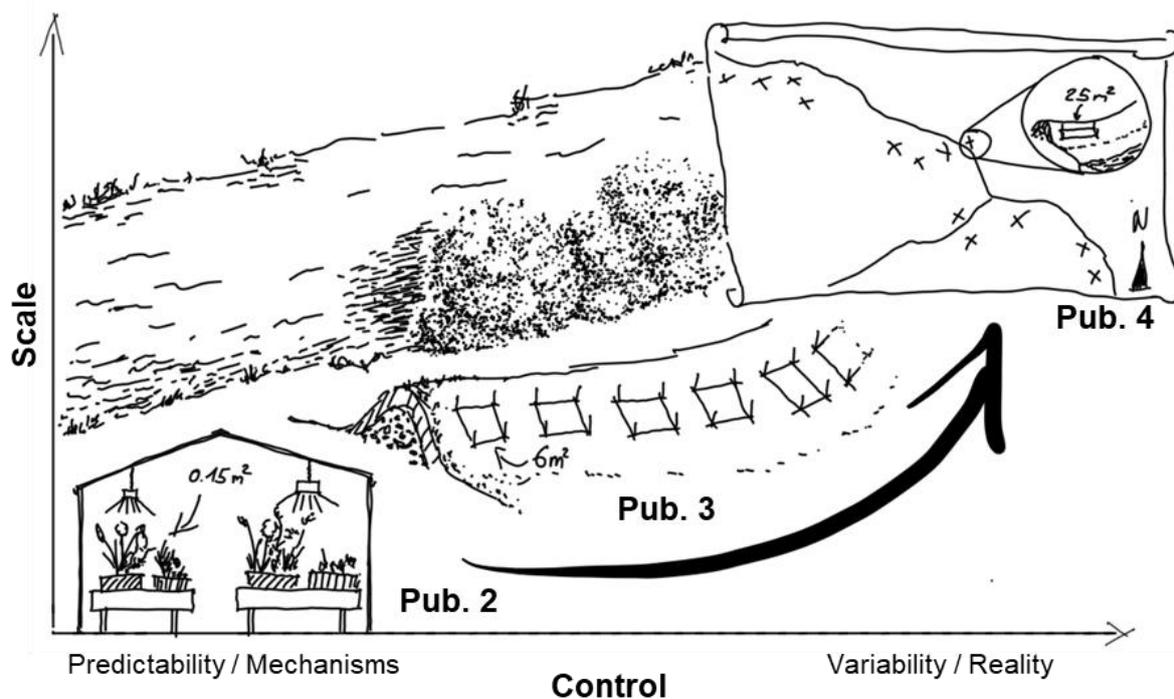
Figure 3. The publications span over three scales and several levels of control. From greenhouse experiments (Pub. 2, Bauer, Krause, et al., 2022b), over a field experiment (Pub. 3, Bauer et al., 2023d) to a field survey in the study region (Pub. 4, Bauer et al., 2023a).

Teixeira et al. (2023) argued that river dike grasslands can reconcile biodiversity and multiple ecosystem services.

Bauer, Krause, et al. (2022b) used greenhouse experiments to measure the establishment of specific trait-based seed mixtures. The different mixtures were sown on different soil types and were treated with different water regimes, and biomass was used as a fitness indicator.

Bauer et al. (2023d) tested the application of different seed–substrate combinations on both sides of a dike in a field experiment under more realistic conditions and over four years. The seed mixtures were based on the species pools of lowland hay meadows and calcareous grasslands.

Bauer et al. (2023a) surveyed over five years the development of dike grasslands after restoration measures which were carried out 4–17 years ago. This study puts seed–substrate combinations in the context of landscape effects and environmental fluctuations that are part of real-world restorations. For this study, spatial and temporal beta diversity was calculated from vegetation surveys conducted from 2017–2021 and was related to different drivers.

3 Study region and methods

3.1 Study region and experimental sites

Field observations were conducted along the Danube River in SE Germany (WGS84 (lat, lon): 48.82903, 12.94671; 302–318 m a.s.l.; Figure 4). The river reach of interest was between Straubing and Vilshofen, had a length of 63 km, and is located in the ecoregion 686 'Western European broadleaf forests' (Dinerstein et al., 2017), the region D65 'Lower Bavarian uplands and Isar-Inn gravel plains' (Ssymank, 1994; Naturraum-Haupteinheit: 'Unterbayerisches Hügelland und Isar-Inn-Schotterplatten') and in the sub-region 064 'Dungau' (Meynen et al., 1953–1962; Naturraum-Einheit). The dikes are in the floodplain of the Danube River, which separates the Bavarian Forest from the lowlands called Gäuboden with its intensive agriculture on loess soils. The climate is temperate and suboceanic (III.3, Troll/Pfaffen) with a mean annual temperature of 8.4 °C and precipitation of 984 mm (1981–2010, Deutscher Wetterdienst [DWD], 2021). The dikes are surrounded by farmland, with a dominance of grassland in the small active floodplain and agriculture in the fossil floodplain. In the region of the Isar estuary, alluvial forests are sometimes adjacent. The dikes are mown once or twice a year and grazed if the shepherd has sufficient capacity. The desired vegetation types for the dike grasslands are lowland hay meadows (Arrhenatherion elatioris, CM01A, code of the European Vegetation Survey, Mucina et al., 2016), and calcareous grasslands (Cirsio-Brachypodion pinnate, DA01B); both are endangered to critically endangered in Germany (Finck, Heinze, Raths, Riecken, & Ssymank, 2017).

The area along the Danube River is one of the oldest settlement areas in Germany (Jankuhn, 1969), and river regulation started in 1836 accompanied by the melioration of the floodplain, and full dikes replaced the small summer dikes since 1936 (Blum, 2011). The recent river development is driven by the project 'Lebensader Donau' and includes the widening of the waterway and the improvement of flood protection (www.lebensader-donau.de) (Box 3). For this project, new dikes have been built, and old ones will be upgraded to meet the latest flood standards (i.e., HQ_{100}) as part of the flood protection concept of Bavaria (StMUV, 2014). The aim of the 'Bayerische Kompensationsverordnung' (BayKompV) is to promote the combination of land use and nature conservation (Bayerisches Landesamt für Umwelt [LfU], 2014a), which means for the dikes that species-rich meadows should be established (ArGe Baader + Bosch, 2015; LfU, 2014b; Kleber-Lerchbaumer, Berger, & Veit, 2017), which are protected by the Habitats Directive 92/43/EEC via § 30 BNatSchG and Art. 23 BayNatSchG (BayNatSchG, 2011; BNatSchG, 2009; FFH Directive, 2018).
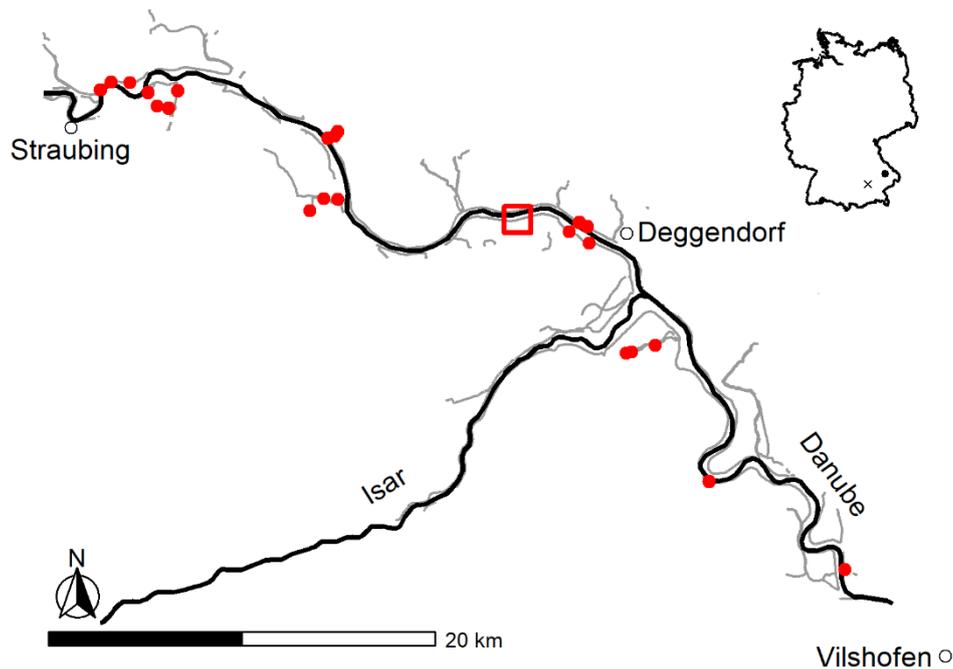
Figure 4. Restored dikes along the Danube River from Straubing to Vilshofen were surveyed (red dots and black dot on the Germany map). The field experiment was conducted on an old dike near Deggendorf (red square), and the greenhouse experiments were carried out in Dürnast near Freising (cross in the map of Germany). The black lines are the rivers Danube and Isar, and the gray lines are the dikes of the big rivers and their tributaries.

Box 3: Dikes reduce floodplains

Dikes have much potential for biodiversity and ecosystem services, but they are also responsible for the reduction of active floodplains. Floodplains are biodiversity hotspots, and they are among the most threatened ecosystems (Tockner & Stanford, 2002). In Europe and North America, up to 90% of floodplains are degraded (Tockner & Stanford, 2002). In Germany, only about one third of the morphological floodplain can be inundated, and within this active floodplain, floods are rare because small floods are kept within the deepened river course (Bundesumweltministerium [BMU] & Bundesamt für Naturschutz [BfN], 2021). As a result, only 3% of the morphological floodplain has changed very little or little (BMU & BfN, 2021). Dikes cut off the floodplains from floods, which are critical to this ecosystem because they cause disturbance, provide nutrients, transport seeds, and cause groundwater fluctuations (Junk, Byley, & Sparks, 1989). The European Union aims to restore 25.000 km of rivers until 2030 mainly by removing barriers for longitudinal connectivity but also by integrating more fossil floodplains into the river system (EC, 2020, 2022). Germany aims to increase the active floodplain by 10% compared to 1980 but achieved only 1.5% by 2020 (BMU & BfN, 2021). The development of species-rich grasslands on dikes should be targeted at relocated dikes to improve biodiversity while providing more space for floodplain meadows and forests.

For the monitoring, established dike grasslands from Straubing to Vilshofen were surveyed (Figure 4). The dikes were greened between 2002 and 2013, resulting in a plot age of 4–19 years, as the plots were surveyed in 2017–2019 and 2021. Not only dikes of the Danube and the Isar estuary were selected, but also dikes of tributaries of the Danube. The plots and the region can be viewed on the interactive map:

https://markusbauer.shinyapps.io/shiny_app_map_danube

The dike experiment was conducted near Deggendorf, Germany, and was set up in 2018 and surveyed until 2021 (WGS84 (lat, lon): 48.82903, 12.94671; 313 m above sea level; Figure 4). The dike was built in 1931 and renovated in 1980. For the greenhouse experiments, the Greenhouse Laboratory Center Dürnast of the Technical University of Munich was used (WGS 84 (lat, lon): 48.40526, 11.68909; 481 m above sea level; Figure 4). Three experiments were conducted: two in 2019 and one in 2020.

3.2 Seed mixtures

3.2.1 Target vegetation and seed source

The target vegetation for the field experiment consisted of two target vegetation types: hay meadows and calcareous grasslands (Table 1); specifically, medium nutrient-rich, mesic mown meadow of the lowland of the Arrhenatherion elatioris alliance and calcareous semi-dry grasslands of the Cirsio-Brachypodion pinnate alliance (Mucina et al., 2016). Autochthonous seeds were provided by Krimmer[5] from the region UG16, which is mandatory in Germany since 2020 (§ 40, BNatSchG, 2009), to provide genetic variability for the conditions of this defined region with similar environmental conditions and biogeographical history (Bucharova et al., 2019; Prasse, Kunzmann, & Schröder, 2010).

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Table 1. Target vegetation of this thesis. Abbreviations of habitat types and their endangerment 1–2 = endangered to critically endangered.

	Reference	Hay meadow	Calcareous grassland
European Vegetation Survey	Mucina et al.	CM01A	DA01B
EUNIS habitat code	Chytrý et al.	R22	R1A
FFH habitat type	LfU & LWF	6510	6210
BayKompV	LfU	G214-GU651E/L	G312-GT6210
Red List Europe	Janssen et al.	Vulnerable	Vulnerable
Red List Germany	Finck et al.	1–2	1–2

LfU, 2014a; LfU & Bayerische Landesanstalt für Wald und Forstwirtschaft [LWF], 2022; Chytrý et al., 2020; Finck et al., 2017; Janssen et al., 2016; Mucina et al., 2016.

3.2.2 Bauer et al. (2023d): Field experiment

Habitat-specific species pools were defined for both target types (Appendix of Bauer et al., 2023d; Helm et al., 2015). First, all target species were collected from the literature:

- Character species (Oberdorfer, 1993a, 1993b)
- Typical species of the EU habitat types 6510 and 6210 (LfU & LWF, 2022)
- Typical species of the German habitat types GT and GU (LfU, 2018)
- Species of the Bavarian guideline: tables 30, 34, 35, 36 (LfU, 2022)
- Mapped species on surrounding dikes by ArGe Danubia and ArGe DonauPlan (2012)

Second, species were excluded that were not mapped in the surrounding area (ArGe Danubia & ArGe DonauPlan, 2012), were undesirable, or were unavailable from the seed producer. The species pool contained 58 species for the hay meadows and 55 for the calcareous grasslands. From these species pools, each plot randomly received 20 species, including seven grasses, nine herbs, three legumes, and one hemiparasite (Table 2). The grass ratio was constrained to 60 wt% and the legume ratio to 5 wt% (Table 3). The different species pools resulted in higher community weighted means (CWM) of specific leaf area (SLA) and lower values of seed mass values (Table 3). The recommended seeding density of 4 g m^{-2} (Kirmer, 2019) was tested against a high seeding density of 8 g m^{-2}.

3.2.3 Bauer, Krause, et al. (2022b): Greenhouse experiments

Only the hay meadow was the target community for the greenhouse experiment. From the total species pool, I excluded species whose seeds were unavailable from the seed producer as

well as deep-rooting species with a rooting depth >1 m (Kutschera & Lichtenegger, 1982, 1992; Landolt & Bäumler, 2010) to account for limited substrate depth and the sealing layer of landfills which were the initial application case. In total, 41 species remained in the pool, and each plot randomly received 20 species, including five grasses, twelve herbs and three legumes (Table 2).

I designed three seed mix types: 'vigorous', 'intermediate' and 'robust'. The robust seed mixture had the lowest SLA, the lowest grass ratio, the highest seed mass, and the highest legume ratio (Table 3). The mean Ellenberg R-value was constrained to seven for all seed mixtures. The values for SLA, seed mass and grass ratio were derived from the communities described in Oberdorfer (1993b) and from regional seed mixtures from the company Krimmer (Appendix of Bauer, Krause, et al., 2022b). The target values for each seed mixture were achieved for each plot by adjusting the weight of the seeds of each species. To calculate the correct values, the function 'selectSpecies' of the package 'Select' was used (Laughlin et al., 2018). The designed seed mixtures were compared with a non-regional standard mixture (*Regel-Saatgut-Mischung* RSM 7.1.2 'landscape lawn with forbs'; DIN 18917, 2018). The grass ratio and the seeding density of the standard mix were higher than those of all designed mixtures (Table 3). R-indicator values were taken from Ellenberg et al. (2001), trait values were obtained from the TRY database (Kattge et al., 2020), and nomenclature follows World Flora Online (2021).

Table 2. The composition of the functional groups for the seed mixtures of the field experiment and of the greenhouse experiments

| Functional plant type | Field experiment | | | | | | Greenhouse experiments | | |
| | Calcareous grassland | | | Hay meadow | | | | | |
	Pool [#]	Seed mix [#]	Seeding density per species [wt%]	Pool [#]	Seed mix [#]	Seeding density per species [wt%]	Pool [#]	Seed mix [#]	Seeding density per species [wt%]
(Tall) grasses	5	3	8.6	6	3	8.6	12	5	individual
Small grasses	8	4	8.6	3	1	8.6	–	–	–
Additional small grasses	–	–	–	5	3	8.6	–	–	–
Herbs	22	6	3.3	25	6	3.3	25	12	Individual
Additional herbs	14	3	3.3	9	3	3.3	–	–	–
Legumes	7	3	1.7	5	3	1.7	4	3	Individual
Hemiparasites	2	1	5	2	1	5	–	–	–

Table 3. Community-weighted means (CWM) of functional traits of seed mixtures and further restrictions. All seed mixtures contained 20 species except the 'standard' mixture with 17 species. SLA = specific leaf area.

Seed mixture	SLA [mm^2 mg^{-1}]	Seed mass [mg]	Grass ratio [wt%]	Legume ratio [wt%]	Forb ratio [wt%]	Ellenberg R	Rooting depth [cm]	Seeding density [g m^{-2}]
Field experiment								
Calcareous grassland	19.9 ± 0.9	0.95 ± 0.19	60.0	5.0	35.0	–	–	4 vs. 8
Hay meadow	23.8 ± 0.7	0.79 ± 0.15	60.0	5.0	35.0	–	–	4 vs. 8
Greenhouse experiments								
Robust	20.0	1.25	30.0	15.0	55.0	7.0	0–100	4
Intermediate	21.5	1.00	45.0	10.0	45.0	7.0	0–100	4
Vigorous	23.0	0.75	60.0	5.0	35.0	7.0	0–100	4
Standard	19.0	0.74	98.3	0.3	1.4	4.9	0– >200	20

3.3   Study design and data sampling

3.3.1   Bauer, Krause, et al. (2022b): Greenhouse experiments

Three experiments were conducted in a greenhouse: two in 2019 for 14 weeks in a semi-open greenhouse and one in 2020 for 13 weeks in a closed greenhouse (Figure 5A, B). The seed–substrate combinations were tested in plastic trays (50 cm × 30 cm × 6 cm) with holes in the bottom, placed on tables. During the experiment, unsown species were removed. Ultimately, the aboveground biomass was cut at ground level and weighed the dried material. The biomass served as an indicator of fitness (Younginger, Sirová, Cruzan, & Ballhorn, 2017). All bricks were provided and crushed to 4–16 mm by Leipfinger-Bader[6], and mixed with loamy soil from Wurzer Umwelt[7].

Experiment 1 tested different seed mixtures (standard, robust, intermediate, vigorous), brick ratios (5 and 30%), pre-treatments of bricks with phosphoric acid (yes, no) and moisture regimes (dry, medium dry, medium moist, moist). The bricks were clean production waste from the factory without mortar or plaster. The experiment was fully factorial and had a randomized complete block design with a split plot (Figure 5A, Figure 7C). For the moisture treatment, a split plot was used since each table was watered by one pump. Eight tables were used, resulting in two true replicates for the four moisture levels. At the plot level (= trays), the tables served as blocks for the remaining treatments, which were therefore replicated eight times. In total, Experiment 1 had 128 trays, which were re-randomized within a table after seven weeks.

Experiment 2 had the same design as experiment 1 (Figure 5A), but different treatments were studied: at the block level (= tables), there was still the moisture treatment, but at the plot level (= tray), only two seed mixtures (sandy, loamy) were studied, but with two brick types (clean production waste, demolition bricks with plaster and mortar), and two brick ratios (5 and 30%). All bricks were pre-treated with phosphoric acid. The eight replicates at the plot level resulted in 64 trays.

For experiment 3, 72 trays were used, distributed over two tables (Figure 5B, Figure 7D). The experimental design was fully factorial and completely randomized with three replicates. All trays were re-randomized thrice in 13 weeks to avoid an effect by the two tables for the three replicates. Four treatments were studied: soil texture (sandy, medium, loamy), brick ratio (5 and 30%), compaction (low, high), and pelletized activated carbon (0 and 1 t ha^{-1}). All bricks

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[7] Wurzer Umwelt GmbH, Am Kompostwerk 1, 85462 Eitting, GER; +49 8122 991 90, info@wurzer-umwelt.de

were demolition bricks which were treated with phosphoric acid. All trays were watered every 5–8 days to avoid water stress.
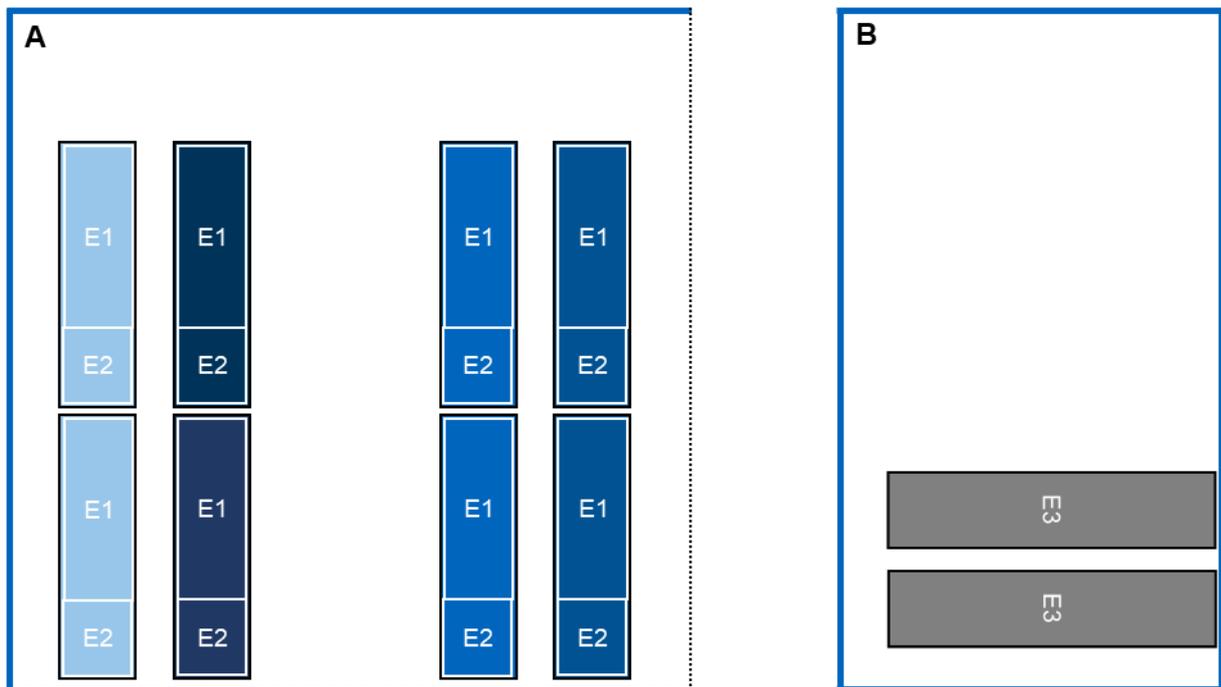
Figure 5. The experimental setup for the greenhouse experiments in **(A)** a semi-open greenhouse (Experiments 1 and 2) and **(B)** a closed greenhouse (Experiment 3). The semi-open greenhouse has a glassy roof, two glass walls (blue line) and two sides with only a mesh (dotted line). Experiments 1 and 2 were conducted simultaneously with four different water treatments from very dry to very wet (blue tones).

3.3.2   Bauer et al. (2023d): Field experiment

For this experiment, 288 plots were established in April 2018 and surveyed 2018–2021 on the north and south side of a dike (Figure 6, Figure 7E, F, G). A randomized complete block design with split plots was used for the experiment, which was placed on a 1.5 km stretch of dike. Plots were established halfway up the dike, had 6 m² (2 m × 3 m), were arranged in six blocks, and within each block, the plots were 1 m apart from each other. Five treatments were studied: exposition (north, south), substrate depth (15 and 30 cm), sand ratio (0, 25 and 50 vol%), seed mixture (hay meadow, calcareous grassland), seed density (4 and 8 mg m⁻²) The experiment was full factorial, resulting in 48 plots per block. The vegetation was surveyed in June and July using the Braun-Blanquet approach (Braun-Blanquet, 1928/1964) and the Londo scale (Londo, 1976).
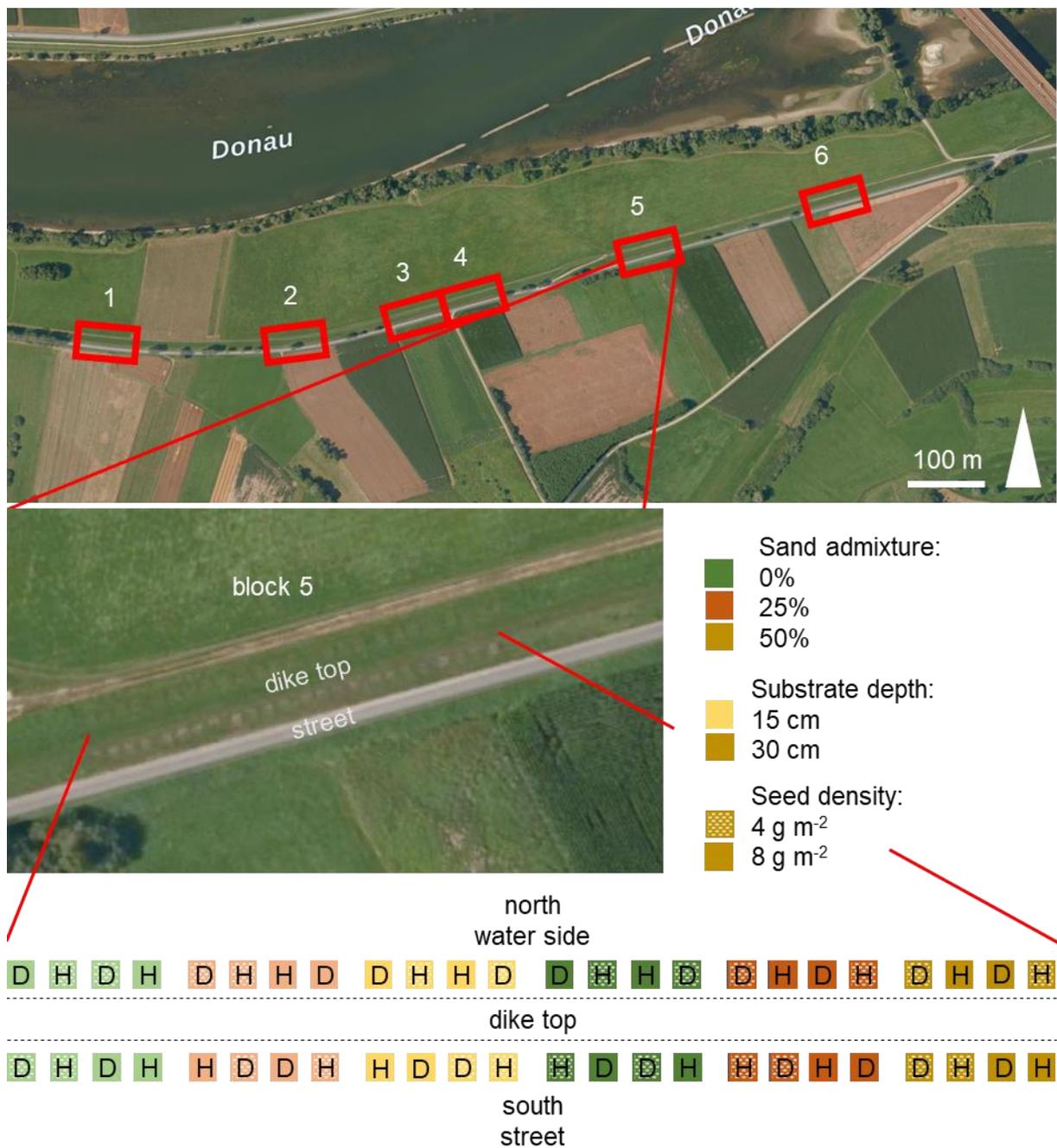
Figure 6. The experimental design of the field experiment near Deggendorf with six blocks containing 48 plots each (total 288 plots). Four treatments were applied: sand admixture to the agricultural soil, depth of mixed substrate, seed density and type of seed mix: D = dry, calcareous grassland, H = hay meadow. The orthophoto is from the BayernAtlas (Bayerische Vermessungsverwaltung, 2023).

3.3.3   Bauer et al. (2023a): Surveys

From the initial 70 plots, in 2021, I selected plots that had already been surveyed three times (2017–2019) and were north or south-exposed, resulting in 41 plots (Figure 4, Figure 7A, B). The study design was completely random, since north- and south-exposed plots were not always paired. Vegetation was surveyed in June or July with plots of 25 m² (12.5 m × 2.0 m) and placed at half height of the slopes. Surveys were conducted using the Braun-Blanquet approach (Braun-Blanquet, 1928/1964) with the Pfadenhauer scale (Pfadenhauer, Poschlod, & Buchwald, 1986). In each plot, soil samples were collected in August and September 2017, and the following soil parameters were measured: pH; topsoil depth; clay, silt, and sand ratio; calcium carbonate, humus, C:N ratio, nitrogen, nitrogen concentration, phosphorus, potassium and magnesium. The soil parameters were scaled and entered into a Principal Component Analysis (PCA) to reduce complexity.

3.4   Statistical analyses

The analyses are described in detail in the corresponding papers, and the code and model evaluations are stored on Zenodo (Bauer, Huber, & Kollmann, 2023b, 2023c; Bauer, Krause, Heizinger, & Kollmann, 2022a; Bauer, Teixeira, Moosner, & Kollmann, 2022). I have refrained from using P values whenever possible for following reasons. P values have long been criticized for their susceptibility to misinterpretation (Cohen, 1994). The criterion that $P < 0.05$ is significant favors P hacking (Simmons, Nelson, & Simonsohn, 2011; Veresoglou, 2015) and causes the 'file drawer problem' for non-significant results (Csada, James, & Espie, 1996). Both phenomena increase the false positive rates, which can be further increased through implausible hypotheses (Nuzzo, 2014), leading to the statement that "most published research findings are false" (Ioannidis, 2005). Furthermore, the P values are fickle even when a standard power of 0.8 is used, leading to irreproducible results (Halsey, Curran-Everett, Vowler, & Drummond, 2015). Recommendations for the future treatment of statistics suggest omitting the term 'statistical significant' (Wasserstein, Schirm, & Lazar, 2019) or at least replacing it with 'statistically clear' (Dushoff, Kain, & Bolker, 2019). Moreover, unlike P values, uncertainty and effect sizes should be evaluated separately (Halsey, 2019). Focusing on effect sizes requires sound prior knowledge of which effect size is meaningful in a given ecological context (Halsey, 2019). Attention to uncertainty leads to better experiments with larger sample sizes, better measures or more sensitive designs (Wasserstein et al., 2019). Bayesian statistics can help focus on meaningful effect sizes and uncertainty, which is why I used it to analyze the field experiment (Applestein, Caughlin, & Germino, 2022; Halsey, 2019; Wasserstein et al., 2019).

Besides, avoiding *P* values, I provide FAIR data of my studies (Box 4). FAIR data is important so that restoration ecologists and practitioners can learn from other restoration projects (Cadotte et al., 2017; Mouquet et al., 2015). Good data management, including good metadata, allows meta-analyses to overcome the spatial and temporal limitations of individual studies (Michener, 2006).

Box 4: FAIR data management

The FAIR data principles lead to an accumulation of data (Mouquet et al., 2015) and are necessary to improve reproducibility in science (Munafò et al., 2017). Wilkinson et al. (2016) defined the FAIR criteria: data must be findable (F), which means that the data have a persistent identifier such as a DOI. The data must be accessible (A), which means that the data can be retrieved using the DOI. Interoperable (I) means that the metadata is written in a formal language that is widely used in the field, and the raw data is ready for use by software, e.g., stored as CSV files. The data should be reusable (R), which means that there is rich metadata not only for the whole project but also for each data file and that the data have a user license such as 'CC BY 4.0'. In addition to FAIR data, a clean R code and standard storage is a key element for reproducible science (Figueiredo, Scherer, & Cabral, 2022; Filazzola & Lortie, 2022). The storage of FAIR data and code improves the transparency and reproducibility of scientific studies and increases reusability to improve data-intensive science (Powers & Hampton, 2019; Wilkinson et al., 2016).

All data and code is published and stored in Zenodo (European Organization for Nuclear Research & OpenAIRE, 2013) via the connection to GitHub (https://github.com/markus1bauer) under the CC-BY-4.0 license (https://creativecommons.org/licenses/by/4.0/). Finally, the data should be stored on PANGAEA (Felden et al., 2023) that it is findable and standardized for biodiversity meta-analyses.

Figure 7. Bauer et al. (2023a): **(A)** Established dike grassland along the river Danube **(B)** was surveyed with 2.0 × 12.5 m² plots. Bauer, Krause, et al. (2022b): **(C)** Experiment 1 and 2 in a semi-open greenhouse and **(D)** Experiment 3 in a closed greenhouse. Bauer et al. (2023d): **(E)** One block of the field experiment at river Danube with **(F)** 288 plots in total with a **(G)** size of 2.0 × 3.0 m² each. © Markus Bauer (7)

4 Summary of publications

4.1 Teixeira et al. (2023): Dike grasslands, biodiversity and ecosystem services

Teixeira, LH*, **Bauer M***, Moosner M, Kollmann J (2023). River dike grasslands can reconcile biodiversity and different ecosystem services to provide multifunctionality. – *Basic and Applied Ecology* 66, 22–30. https://doi.org/10.1016/j.baae.2022.12.001

* Both authors contributed equally to the manuscript

4.1.1 Author contributions

LHT, **MB**, JK developed the concept of the opinion. **MB** did the analysis for Fig. 1, MM for Fig. 2. JK drafted section 1, **MB** section 2, LHT section 3, 4 and Fig. 3, 4. All co-authors revised critically all parts.

4.1.2 Graphical abstract
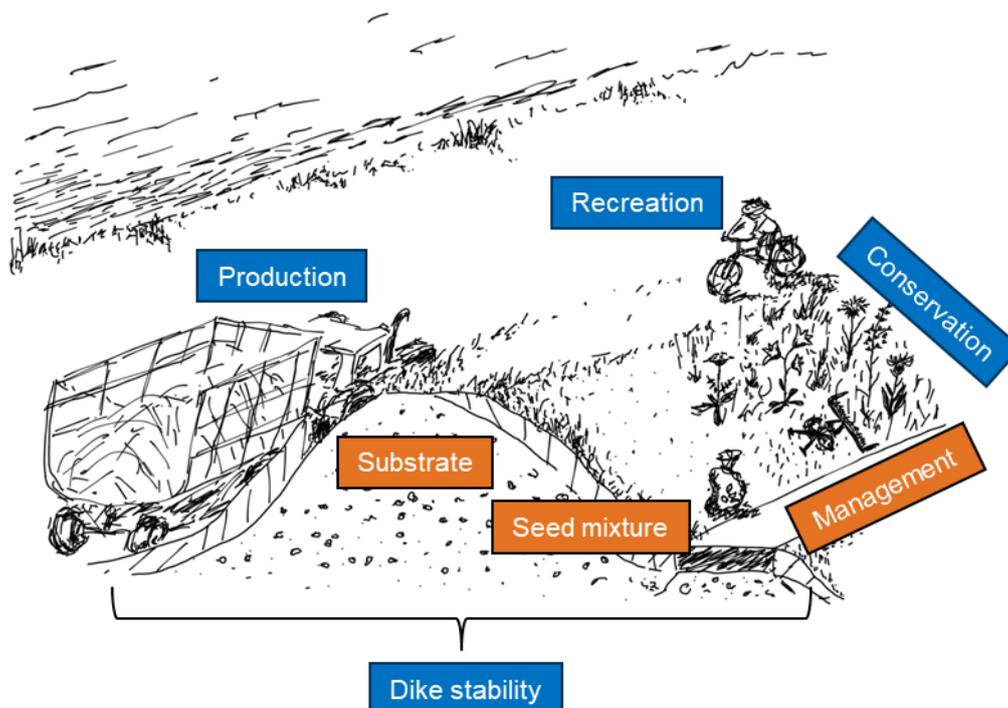
4.1.3 Abstract

River dikes are built to gain and save space for agriculture and settlements. As a side effect, the dike roads have become important regional bicycle paths, rare species could establish in dike grasslands, and mown biomass can be used. We argue that species-rich dike grasslands are part of the Green Infrastructure and can reconcile the different ecosystem services (ESS) such as erosion control for dike stability, conservation of typical and rare grassland species, recreational opportunities and high-quality biomass for fodder and energy production. We can show from the literature that a positive relationship could be expected with all four ESS. The multiple ESS can be modified by appropriate substrates, seed mixtures, and the mowing regimes. Mixing substrates and using trait-based seed mixtures are promising restoration approaches that need to be further tested. Dike grasslands provide opportunities to experimentally test different combinations of restoration approaches, substrates, and management regimes to improve biodiversity and multiple ESS. These experiments should be linked to theory, which would mean that with an experiment could systematically test different possible solutions for dikes, concurrently theory would be tested with this experimental data, and the results would guide projects in other urban areas. Overall, river dikes have the potential to serve as a green infrastructure for biodiversity and concurrently as the original "grey infrastructure". Experimental results can guide ecological restoration in other urban areas and such experiments should be set up in cooperation with nature conservation and water authorities as well as with dike construction companies.

4.2 Bauer, Krause, et al. (2022b): Testing seed mixtures with greenhouse experiments

Bauer M, Krause M, Heizinger V, Kollmann J (2022) Using crushed waste bricks for urban greening with contrasting grassland mixtures: No negative effects of brick-augmented substrates varying in soil type, moisture and acid pre-treatment. – *Urban Ecosystems* 25, 1369–1378. https://doi.org/10.1007/s11252-022-01230-x

4.2.1 Author contributions

MB and JK designed the study. All authors designed the substrates and **MB** and JK the regional seed mixtures. **MB** set up the experiment, conducted data sampling, performed the statistical analyses, and wrote the manuscript. VH pre-treated demolition bricks and MK developed and conducted the acid treatments. **MB** wrote the manuscript, and JK, MK and VH substantially contributed to the revisions.

4.2.2 Graphical abstract
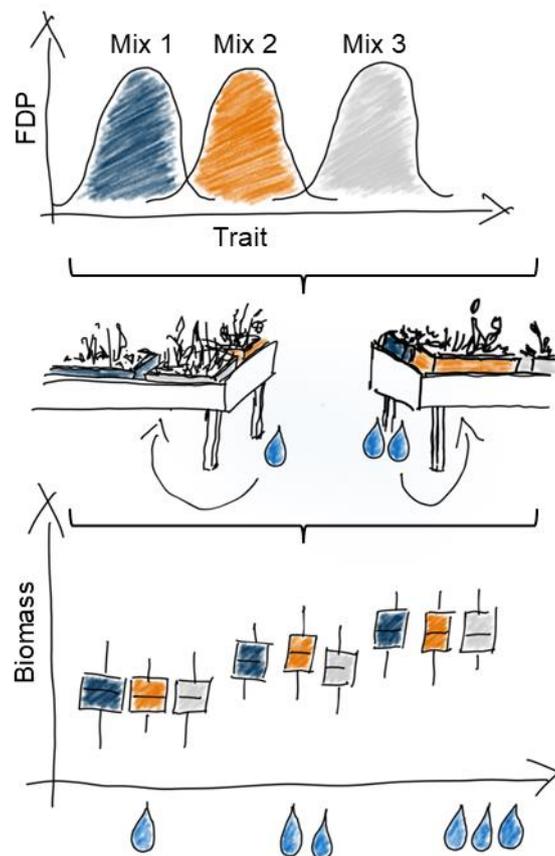
4.2.3 Abstract

Trait-based seed mixtures could be a universal restoration approach which is adaptable to specific site conditions of river dikes based on general ecological principles. However, evidence for the success of trait-based seed mixtures for Green Infrastructure is scarce. Therefore, three greenhouse experiments were conducted to study the establishment phase and to exclude confounding factors of landscape or historical effects. The aim was to test whether contrasting seed mixtures respond in opposite ways to different soil and moisture conditions. We tested four seed mixtures under different soil types, brick additions and watering regimes. We developed three contrasting seed mixtures of 20 species each and compared them to a standard grass-dominated seed mix. The robust seed mixture, constrained for dry and nutrient-poor conditions, had a low mean specific leaf area, high seed mass, low grass ratio, and high legume ratio. The vigorous mix had opposite values and the intermediate mix was in between. Abundance values were calculated using the new function of Laughlin et al. (2018). After three months, biomass was harvested and measured as a fitness indicator. The three designed seed mixtures did not differ from each other regardless of the moisture regime. A useful result for the application of regional seed mixtures was that under dry conditions the designed seed mixtures produced a similar amount of biomass compared to the standard grass mixture. This suggests that regional, species-rich seed mixtures can substitute standard mixtures on river dikes while still providing a sufficient biomass for erosion protection. The addition of bricks had little effect on biomass production, which may make them suitable for use as substrates without compromising vegetation fitness in Green Infrastructure especially in urban areas.

4.3 Bauer et al. (2023d): Testing seed mixtures on a field experiment

Bauer M, Huber JK, & Kollmann J (2023b) Fit by design: Developing seed–substrate combinations to adapt dike grasslands to microclimatic variation. – *Journal of Applied Ecology* 60, 2413–2424. https://doi.org/10.1111/1365-2664.14497

4.3.1 Author contributions

JKH and JK designed the experiment. JH did the surveys in the years 2018–2020, and **MB** in 2019 and 2021. **MB** did the analyses and wrote the manuscript. JK and JKH critically revised the manuscript.

4.3.2 Graphical abstract
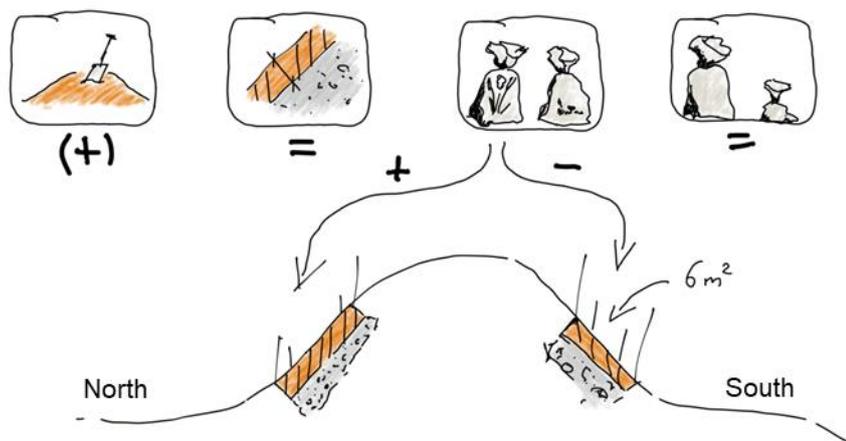
4.3.3 Abstract

Using seeds for grassland restoration is common in restoration and is encouraged in Germany since 2020 by the law on the use of autochthonous seeds for greening. However, combining seed mixtures with substrates offers the opportunity to increase the effectiveness of seeding of Green Infrastructure like on river dikes. We tested different seed–substrate combinations to identify a combination which improves dike security as well as biodiversity. Modification of substrates should reduce habitat filtering and modifying seed mixtures should reduce competitive exclusion. An experiment with 48 treatment combinations was set up, replicated six times in SE Germany on a river dike and was monitored 2018–2021. We tested three sand

admixtures (0, 25, 50%), two substrate depths (15 vs. 30 cm), two seed mixtures (hay meadow, calcareous grassland) and two seed densities (4 vs. 8 g m^{-2}). To evaluate the effects of the treatments, the persistence of sown species and the Favorable Conservation Status (FCS) of target species were measured. In addition, the plots were contrasted with the seed mixture and real reference sites in the surroundings. These data were used to calculate recovery completeness. After four years, there was only a small effect of sand admixture and no effect of substrate depth, seed mixture or seed density on persistence and the FCS. Consistently, the south-facing plots performed worse than the north-facing ones. This might be due to a severe drought during the establishment phase that created a negative legacy effect on the south-exposed plots. Vegetation developed in the desired direction, but at a reduced rate after the first year, and a recovery debt remained after four years. An exception was the mesic-meadow mixtures in south exposure, which did not develop towards their reference sites. In north exposition, mesic meadows developed closer to their reference communities than did the dry-grassland mixtures. In conclusion, site-adapted seed mixture can improve restoration success on river dikes, but further management is needed to close the recovery debt.

4.4 Bauer et al. (2023a): Monitoring of restored dike vegetation

Bauer M, Huber JK, Kollmann J (2023a) Beta diversity of restored dike grasslands is strongly influenced by uncontrolled spatio-temporal variability. – *EcoEvoRxiv*. https://doi.org/10.32942/X2959J

4.4.1 Author contributions

JKH and JK designed the study. JKH conducted the surveys in the years 2017–2019 and **MB** in 2021. JH collected the soil samples. **MB** did the analyses and wrote the manuscript. JK and JKH critically reviewed the manuscript.

4.4.2 Graphical abstract
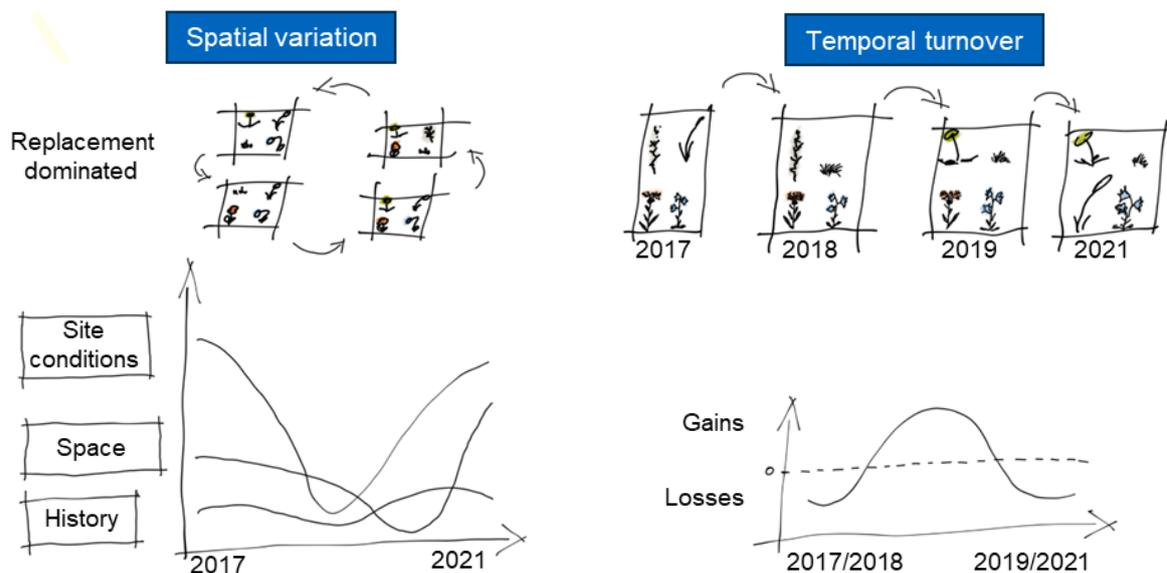
4.4.3 Abstract

Each ecological restoration, like the application of trait-based seed mixtures, is embedded in a landscape and influenced during establishment by several hard-to-control factors such as the land-use history, landscape context, interannual weather fluctuations, or management variations. The objective of this study was to set local restorations on river dikes in context to historical, spatial, and temporal drivers by quantifying the influence of the different factors on

the dike grasslands along the Danube River. For this reason, we monitored 41 plots at 12 sites over five years (2017–2021). The plots were restored 4–19 years ago and were distributed along 63 river km. We quantified spatial variation and separated it into the two additive components replacement and nestedness. 37–51% of the plots reached the status of a targeted habitat type per year and 0–15% failed and were classified as ruderal vegetation. Spatial variation was constant at 32–34% and was largely dominated by the replacement component (27–29%). Replacement was mainly driven by local factors like exposition, but also by the spatial location of the plots. The year-to-year temporal turnover was 37 ± 11%, and gains and losses changed in dominance from year to year but were balanced over time. The high replacement component and the balanced but high temporal turnover highlight the spatio-temporal fluctuation of species composition. For restoration, this means that the effect of substrate manipulation is constrained by many further factors influencing the vegetation. At the same time, the results may change the perspective on variability, as biodiversity is promoted by high replacement rates and balanced turnover according to enhanced species coexistence. This would suggest that introducing varying site conditions and seed mixtures to create Green Infrastructure, rather than applying one 'ideal' seed–substrate combination, would enhance biodiversity.

5 General discussion

Restoration ecology investigates the effects of deterministic and stochastic factors on plant communities in order to move restoration practice towards more predictive approaches like the establishment of a Green Infrastructure. Thus, the aim of this study was to understand the establishment of species-rich dike grasslands based on specific seed–substrate combinations. For this reason, I conducted a series of greenhouse and a field experiments. Many filters are fluctuating, as well as population characteristics, which hampers the understanding of deterministic factors. These fluctuations are the reason why the established vegetation was monitored on old dikes over four years.

5.1 Seed–substrate combinations

5.1.1 Substrates

The main reason why restoration ecologists are concerned about substrates is the reduction of nutrients in the soil. High productivity of a site (Freitag et al., 2021), and especially high amounts of nitrogen (Isbell et al., 2013) or phosphorus in the soil (Ceulemans et al., 2014), are important factors limiting biodiversity in European grasslands. During the restoration of former arable fields, high nutrient amounts should be reduced by burying the topsoil through deep cultivation (Pywell et al., 2002), carbon amendment (Kardol et al., 2008) or removing the topsoil layer (Hölzel & Otte, 2003; Kiehl & Pfadenhauer, 2007; Tallowin & Smith, 2001; Verhagen, Klooker, Bakker, & Diggelen, 2001). The creation of novel substrates is more rarely investigated, for example by mixing topsoil with other materials like sand, gravel or brick rubble (Bauer et al., 2023d; Bauer, Krause, et al., 2022b; Chenot-Lescure et al., 2022). Irrespective of the kind of treatment, all lead to significant reductions in nitrogen and phosphorus, and are beneficial for species diversity in calcareous and mesic grasslands (Kardol et al., 2008; Pywell et al., 2002). Though, deep cultivation or carbon amendment have no lasting effect on soil fertility (Kardol et al., 2008; Pywell et al., 2002). The tested substrates (Bauer et al., 2023d; Bauer, Krause, et al., 2022b) were calcareous but within the recommended range for pH (recommended: 5.0–7.5, Husicka, 2003; or 6.0–6.4 mesotrophic grasslands and 6.8–7.9 calcareous grasslands, Walker et al., 2004) and at least the substrates of the field experiment were within the recommended range for P (4–11 mg l^{-1}, Walker et al., 2004) and clay ratio (17–25%, Husicka, 2003).
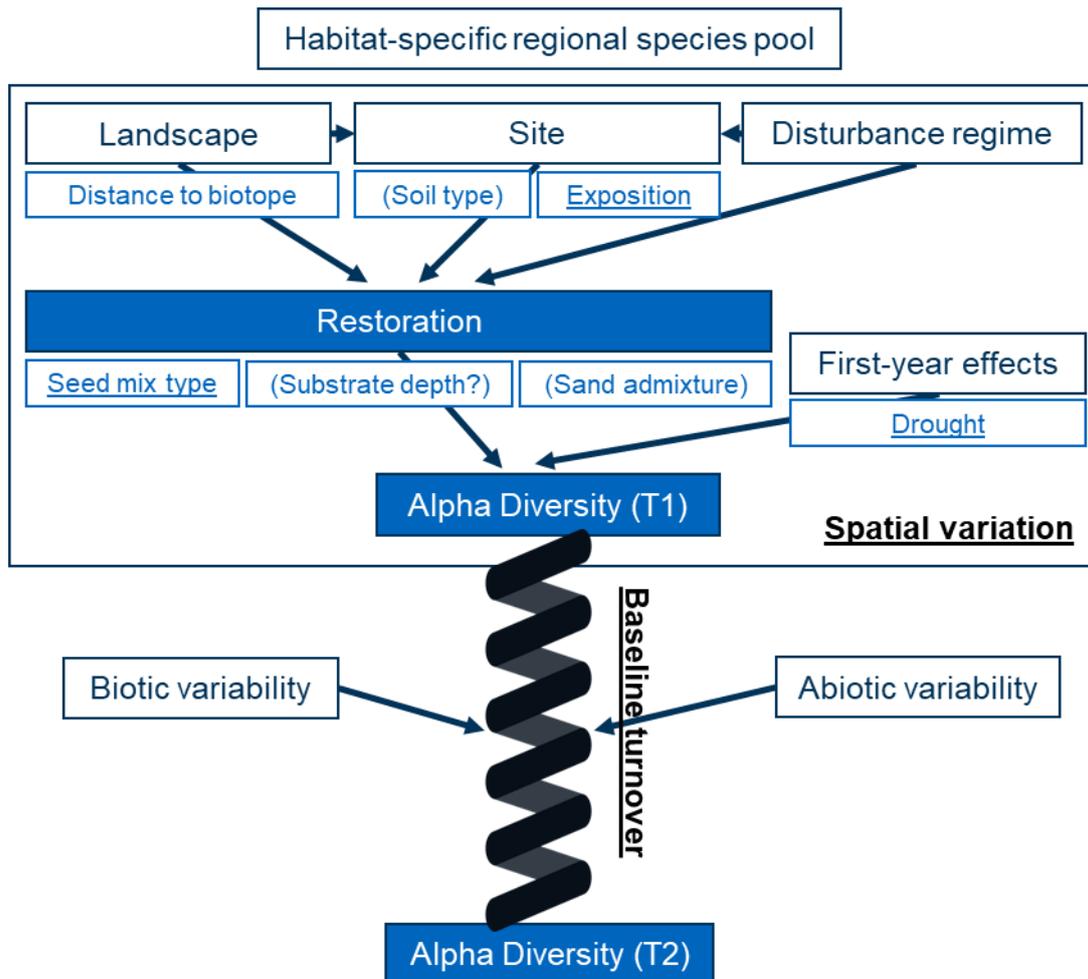
Figure 8. Factors driving establishment of species-rich dike grasslands at rivers. The type of seed mixture was important (regional vs. commercial; hay meadow vs. calcareous grassland), while the trait-based configuration of seed mixtures had limited effects. Furthermore, exposition influenced species composition, and northern exposition was beneficial for hay meadows, while drought had a negative legacy effect on south-exposed plots. There were mixed results for substrate depth and minor effects of soil fertility. Spatial variation was constant over time, but the significant factors varied from year to year. Nevertheless, exposition and, in part, distance to the nearest grassland were significant drivers of spatial variation. Temporal turnover was significant but balanced over the years. Copyright of black feather icon: 'good1' via Pixabay.

Beyond the modification of substrates to reduce nutrient amounts, using waste materials can combine environmental protection with conservation. The so-called Constructed Technosols consist of organic and mineral waste and are designed for specific ecosystem services in Green Infrastructure in urban contexts (Deeb et al., 2020; Séré et al., 2008). Different waste materials were already successfully tested by soil scientists, like crushed bricks or sewage sludge (Molineux et al., 2015; Rokia et al., 2014). Experiments on Constructed Technosols used mostly trees (Bretzel et al., 2020; Cannavo, Guénon, Galopin, & Vidal-Beaudet, 2018), or seed mixtures for calcareous grasslands on green roofs (Graceson, Monaghan, Hall, &

Hare, 2014; Molineux et al., 2015; Schröder & Kiehl, 2021), but rarely with the target of species-rich meadows as I did (Bauer, Krause, et al., 2022b). In contrast to the other studies on green roofs, I compared not different waste components but the effect of an increased brick ratio in the substrate. The results show no negative effect of brick addition on the development of grasslands during early successional stages. However, there was neither a beneficial effect by the water storage capacity of bricks (Bauer, Krause, et al., 2022b). This suggests scaling up the investigation of brick-based substrates within a field experiment.

Substrate depth, meant as rooting depth, can affect the species composition of grasslands in prairies (Dornbush & Wilsey, 2010) although not in all cases (Baer, Blair, Collins, & Knapp, 2004). Substrate depth, which determines the rooting volume, does not influence the species composition of dike grasslands (Husicka, 2003). The field experiment confirmed this finding (Bauer et al., 2023d), but it was in contrast to the survey on old dike grasslands where soil depth influenced the spatial variation in species composition (Bauer et al., 2023a) (Figure 8). My results suggest that substrate depth is less relevant during early-successional stages, which may be a 'neutral phase' of community assembly (sensu Fisher & Mehta, 2014). In late-successional stages ('niche phase'), substrate depth causes different species compositions but not a species richness gradient (= nestedness) (Bauer et al., 2023a). This means that competitive exclusion or habitat filtering, and the development of new niches are balanced in the investigated range of soil depth (8–32 cm).

Many studies found that seed addition is or seems to be more important than soil fertility for the development of species-rich grasslands (Halassy, Botta-Dukát, Csecserits, Szitár, & Török, 2019; Kardol et al., 2008; Kiehl, Thormann, & Pfadenhauer, 2006; Pywell et al., 2002) as long as no species becomes dominant under nutrient-rich conditions (Baer et al., 2004; Tallowin & Smith, 2001). For this reason, substrate modification alone is insufficient, and specific seed–substrate combinations are required.

5.1.2   Comparing seed mixtures

Usually, potential seed limitation is investigated by testing the effect of seeding (Freitag et al., 2021; Halassy et al., 2019; Kaulfuß et al., 2022; Orrock et al., 2023) or by investigating different seed transfer techniques like direct seeding, hay transfer, threshing, or their combinations (Engst et al., 2016; L. K. Fischer, Lippe, Rillig, & Kowarik, 2013; Hedberg & Kotowski, 2010). Overall, there is clear evidence that seed transfer is crucial to overcome dispersal limitations in fragmented landscapes (Kiehl et al., 2010). The next step is to test different seed mixtures (Bauer et al., 2023d; Bauer, Krause, et al., 2022b), in order to adapt the vegetation to specific site conditions which do not have a natural reference like in urban contexts, to adapt to future conditions, or to achieve certain ecosystem services (Laughlin, Strahan, Huffman, & Sánchez

Meador, 2017). In the context of alternative stable states, different seed mixtures can determine the restoration outcome based on priority effects for the same site conditions (Fukami, 2015; Standish et al., 2014; Suding & Hobbs, 2009), which increases the possibilities for restoration practitioners to influence restoration outcome by seed mixtures. For restoration, priority effects were already demonstrated in forbs sown one year earlier than grasses (Young, Stuble, Balachowski, & Werner, 2017).

5.1.3   Habitat-specific species pool

The first step to develop adapted seed mixtures is identifying a habitat-specific species pool representing the typical species of a certain habitat type within a specific region (Zobel, 2016). At this point, conservation can intervene by choosing typical and desired species (Figure 9), while excluding undesired species. These decisions are partly non-scientific but societal (Jax & Heink, 2015) and should be made before including species in mathematical models. In my habitat-specific species pool, I included characteristic plants of Arrhenatherion and Cirsio-Brachypodion, but also transition species between calcareous grasslands or meadows and ruderal vegetation like *Centaurea stoebe*, *Echium vulgare* and *Verbascum lychnitis* (Müller, Ritz, Welk, & Wesche, 2021). These species established well and partly became dominant, which changed the vegetation to a more ruderal composition. Especially *C. stoebe* and *E. vulgare* were present in more plots than were seeded at the beginning, indicating that both species were not dispersal limited (Bauer et al., 2023d). The advantage of these species for dike greening is the coverage of the dike despite a drought, though the disadvantage is the suppression of other species by their large rosettes. The rosettes are especially problematic for species diversity when these species become dominant within a plot.

5.1.4   Trait-based seed mixtures

Functional traits are expected to represent general associations between communities and the environment independent of species identities (Lavorel & Garnier, 2002). For restoration, the predictive ability of traits would enable modifying community-weighted means of specific traits to adapt seed mixtures to (future) site conditions (Funk et al., 2008; Laughlin, 2014a; Merchant et al., 2022). The trait-based model of Laughlin (2014a) was applied in grassland experiments of our research group (Bauer et al., 2023d; Bauer, Krause, et al., 2022b; Möhrle et al., 2021; Yannelli et al., 2018). However, these results show that the trait-based framework must be more specific and predictable to be applicable in restoration practice (Merchant et al., 2022).

Figure 9. *Campanula patula* is a key species in the habitat-specific species pool of temperate hay meadows. © Markus Bauer.

One problem might be translating the model into practice because species abundance is typically captured by estimating the cover. However, seed mixtures can only be modified by seed number or weight, which need not be correlated with cover. Orrock et al. (2023) identified in a prairie experiment only minor predictive ability of traits for restoration outcomes and concluded that traits are useful on the global scale but less on the local scale of restorations. Indeed, environment-trait relationships for communities are often targeted on a global level (McGill et al., 2006; Suding et al., 2008; Westoby & Wright, 2006), although traits are intended to be applicable at the local scale (Lavorel & Garnier, 2002). Even on the global scale, the relationship between traits and macro-filters is weak (Bruelheide et al., 2018). Therefore, Bruelheide et al. (2018) suggest that micro-filters must be responsible for the weak correlation, which was not proven by an urban field study (L. K. Fischer, Lippe, & Kowarik, 2013) and neither by my results of the greenhouse experiment testing for different levels of water availability (Bauer, Krause, et al., 2022b) and neither by the field experiment investigating the effect of soil fertility (Bauer et al., 2023d).

Several studies investigated trait–environment relationships. Zirbel and Brudvig (2020) counted seedlings of prairie restorations and found interactions of specific leaf area (SLA) with

light availability, and root mass fraction with soil moisture. For example, seedling establishment was positively correlated with light availability at high SLA, and negatively with low SLA. This contrasted my expected simple positive correlation between SLA and soil productivity which I derived from local and global field surveys (Bernard-Verdier et al., 2012; Ordoñez et al., 2009). Freitag et al. (2021) also found interactions like a better establishment of low SLA species, especially under low productive conditions and of species with higher seed mass under high productive conditions. In the context of ex-arable fields, it is worth noting that Ordoñez et al. (2009) found no correlation between SLA and soil P.

There are different potential explanations for the weak trait–environment relationships. First, common traits like SLA are soft traits that are not perfectly functional and, therefore, might be too imprecise to predict trait–environment relationships (Shipley et al., 2016). Additionally, plant traits were taken from adult plants, but during establishment from seeds, species might have different trait values or even different traits might be important (Larson & Funk, 2016a). Other important traits might be traits of roots, especially fine roots, or clonal traits might cover an important dimension of trait-environment relationships (E.-Vojtkó et al., 2017; Freschet et al., 2017; Klimešová, Martínková, & Ottaviani, 2018) and are also of interest as effect traits for reducing soil erosion, for example on dikes (Freschet & Roumet, 2017; Ola, Dodd, & Quinton, 2015). Second, the measure of critical environmental gradients like soil nutrients and water availability are not standardized like the measuring of plant traits guided by standard protocols (cf. Pérez-Harguindeguy et al., 2013), which increases the methodological noise in the environmental data (Shipley et al., 2016). Third, intraspecific trait variability and species interactions could also modify trait-environment relationships on the community level (Funk et al., 2017). The plasticity of traits is integrated into the model of Laughlin (2014a), but the model expects the same variability for every species. Including different values of potential plasticity could improve the model as well as the inclusion of germination rates of seeds that are used for a project.

There are significant problems to proof assembly theory in empirical studies (Götzenberger et al., 2012) which hampers the application of this theory for practical purposes (Merchant et al., 2022). Nevertheless, restoration experiments can target both aims, improve empiricism and test application at the same time (Figure 10; Mouquet et al., 2015). For example, disturbance or post-restoration management is a main factor on the local scale, which is not included in the concept of seed–substrate combinations (Grime, 2006; Halassy et al., 2016; Tölgyesi et al., 2022). For example, herbivory or mowing can change the dominance structure and thus increase biodiversity (Halassy et al., 2016; Koerner et al., 2018).

Figure 10. Restoration project combined with experiments can help to predictively establish vegetation containing typical calcareous grassland species like *Centaurea scabiosa*. © Markus Bauer.

5.2 Hard-to-control factors cause spatial variation

5.2.1 Small-scale topography

Exposition could be identified as one of the most important factors influencing dike vegetation (Figure 8, Bauer et al., 2023a, 2023d). Restoration practice has to handle topography not only in dike projects. Topography significantly modifies general climate conditions on a site. For example, steep south expositions are up to 7 °C warmer than steep north expositions (Suggitt et al., 2011). This results in different hydrological differences and, finally, different species compositions (Moeslund et al., 2013). In combination with climate warming, this can hamper specialist species in south-exposed slopes (Mazalla, Diekmann, & Duprè, 2022).

5.2.2 Unexplained spatial variation

Local restorations can influence the dispersal, abiotic and biotic filters, for example, by seeding, fertilizing, and mowing (Halassy et al., 2016). However, only a minor part of total spatial variation in species composition after grassland restorations can be explained (e.g., 32–34% Bauer et al., 2023a; ca. 25% Grman et al., 2013). In comparison, in old-growth calcareous grasslands, Conradi et al. (2017) could explain 81–84% of the spatial variation in species

composition. The reasons must be unmeasured deterministic factors, chaotic factors, or purely stochastic changes.[8] Chaos is created by sensitivity to initial conditions, which leads to strong diverging trajectories in the long term, although all trajectories will remain within a particular set of states ('attractor'; Hastings, Hom, Ellner, Turchin, & Godfray, 1993). Chaos challenges the equilibrium concept by highlighting short-term predictability and by limiting the ability of long-term predictability and the influence of management and abiotic filters on restoration outcomes (Munch et al., 2022). Chaos is prevalent in ecosystems (Rogers et al., 2022), especially in multi-species communities and heterogeneous landscapes (Munch et al., 2022). Therefore, ecologists should keep the chaos in mind and should not dismiss all unexplained variation as noise (Munch et al., 2022). Noise is created by unmeasured factors and stochasticity, which is purely random. Stochasticity is often associated with (long-distance) dispersal events (Hubbell, 2001; Nathan, 2006), which are likely to be more important in low fertility landscapes (Conradi et al., 2017).[9]

5.2.3 Historical contingencies

Unmeasured deterministic factors can cause unexplained spatial variation like abiotic historical contingencies. Historical contingencies can result from former land use, year effects, but also restoration technique. Historical contingencies from former land use, like residues from fertilizer as phosphorus in ex-arable soil, can be excluded from our study since P was implemented in the model (Bauer et al., 2023a), and it was rather scarce for agricultural soils in our field experiment (Bauer et al., 2023d). Moreover, no flood reached the experimental plots during the study period.

Year effects are filters that work during the planting year, vary from year to year and have a lasting effect on restoration trajectories (Werner et al., 2020). Year effects during the establishment phase by precipitation, temperature extremes (drought, frost), or herbivores influence the assembly trajectory and, ultimately, the restoration outcome (Stuble et al., 2017; Werner et al., 2020). The mechanism behind year effects could be that seedlings get lost by drying out or being devoured by herbivores, or some species are favored by the year effects, and these species preempt the niche for other species in the seed mixture (Fukami, 2015). Experiments proof that the weather during the establishment phase is a crucial year effect (Atkinson, Groves, Towers, Catano, & Brudvig, 2023; Eckhoff, Scott, Manning, & Baer, 2023; Groves, Bauer, & Brudvig, 2020) and was considered in our study because I included site age,

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[8] Munch, Rogers, Johnson, Bhat, and Tsai (2022) emphasize that chaotic factors are not stochastic but deterministic (only) in the short term.

[9] Munch et al. (2022) contradict this view of dispersal as a driver of stochasticity and argue that different dispersal rates of competing species can also cause chaotic dynamics.

locality, and weather conditions during establishment in the model (Bauer et al., 2023a). This means that only small-scale weather differences, not measured by the meteorological service or short weather extremes (frost, drought), could have caused unexplained spatial variation in our study (Bauer et al., 2023a). There was a severe drought in 2018 (Hari, Rakovec, Markonis, Hanel, & Kumar, 2020), which may have had a pronounced effect on the south exposition in our field experiment (Suggitt et al., 2011), where vegetation establishment was worse than on the north exposition (Bauer et al., 2023d).

Furthermore, it was not possible to control for restoration technique, initial management and long-term management because I conducted a survey, not a fully controlled experiment (Bauer et al., 2023a). The restoration technique of seed transfer alters the sequence of species arrival and thus biotic historical contingency through priority effects (Fukami, 2015). If the technique, which changed indeed at the restoration sites at the Danube dikes, if it changed within the twelve localities, then this could be an important factor for unexplained variation in my model (see the section on seed–substrate combinations). Moreover, within one restoration approach like hay transfer variability can be induced by different source habitats or seed maturity due to the timing of mowing or weather conditions (Bischoff, Hoboy, Winter, & Warthemann, 2018). This means that year effects not only influence the establishment of vegetation but also the seed quality.

In addition, Grman and Brudvig (2014) could show that the richness of seed mixtures of the restoration has a positive effect on beta diversity and found only little evidence that habitat filtering is the reason. For example, an efficient seed transfer by hay with perfect timing resulting in a collection of many viable seeds could increase not only species richness but also differences in species composition independent of substrate differences. This means that species-rich seed mixtures can improve biodiversity independent of site conditions. However, this independence also means a reduction of predictability of the restoration outcome with increasing species number in the seed mixture (Grman & Brudvig, 2014).

5.2.4   Non-captured management details and landscape effects

On the study dikes, long-term management was applied with an extensive mowing regime and grazing with sheep (Bauer et al., 2023a). Management can vary in mowing frequency, timing of mowing, machines, or grazing intensity. Practitioners may vary management slightly even within a locality because of practical and economic reasons, and these differences have a significant impact on species diversity (Kun et al., 2019). Therefore, I included locality in my models.

Landscape effects are another factor influencing local plant diversity (Tscharntke et al., 2012), and it is related to the species pool concept (Pärtel, Szava-Kovats, & Zobel, 2011; Zobel, 2016). On the one hand, the size of the regional species pool that consists of the grassland species in the surroundings has a positive effect on alpha diversity in grasslands (Conradi & Kollmann, 2016; Janišová, Michalcová, Bacaro, & Ghisla, 2014), and on the other hand, the habitat connectivity improves dispersal which increases plant diversity (Damschen et al., 2019).[10] I included metrics of landscape structure, such as distance to the closest grassland (and grassland area) in the surroundings and this had in more than one of four observed years a significant effect on the spatial variation of dike communities (Figure 8, Bauer et al., 2023a). Especially old-growth grasslands nearby can increase specialist richness and explain spatial variation (Bagaria, Rodà, & Pino, 2019; Bischoff, Warthemann, & Klotz, 2009; Conradi & Kollmann, 2016) as well as distance to former, no longer existing grasslands (Conradi et al., 2017). Not only the distance to grasslands but also the compositional or configurational heterogeneity of grassland types may explain some variability (cf. Fahrig, 2017). Though, environmental filters vary not only in space but also in time and cause fluctuations in species compositions.

5.3 Environmental fluctuations and ecological drift

5.3.1 Variability by temporal turnover

Temporal turnover is the variability of species composition over time (Anderson et al., 2011), and it acts on three different scales: (i) the seasonal turnover within one year, (ii) the non-directional year-to-year fluctuations, and (iii) the decadal turnover, which includes directional changes for example due to global change (Hédl & Chudomelová, 2020). Information on the extent of non-directional year-to-year turnover can raise awareness of the nature conservation of fluctuations within the vegetation. These fluctuations have to be taken into account during the evaluation of restoration outcomes or conservation areas. The field survey revealed a temporal turnover of 37 ± 11% (mean ± SD; Bauer et al., 2023a; Figure 8), which was higher than in calcareous grasslands of about 20% (Looy, Lejeune, & Verbeke, 2016). Other studies have already monitored grasslands over long time spans but rarely quantified it in a way that is comparable between studies (e.g., F. M. Fischer et al., 2020; Mathar, Kleinebecker, & Hölzel, 2015) or the studies were not extensively replicated (cf. Looy et al., 2016). The measurement

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[10] This is especially the case in a fragmented modern landscape with a low habitat density; Leibold et al. (2004) explain that a too high connectivity, especially for generalists, can cause homogenization and a decrease of beta diversity.

of temporal turnover is always accompanied by observer-driven pseudoturnover but can be drastically decreased by species aggregating, as I did in our study (Bauer et al., 2023a; Boch et al., 2022). For instance, Boch et al. (2022) could decrease pseudoturnover from 29% to 17% by aggregating. In addition, relocation and seasonality bias influence temporal turnover (Kapfer et al., 2017). Relocation was a minor problem due to using a modern GPS device and the location in the middle of a dike slope. Further improvement would be to orient the start of the vegetation surveys at the phenological season.

Non-directional annual turnover is also called 'baseline change' or 'baseline turnover' and is necessary to estimate the amount of directional turnover, for example, by global change (Magurran et al., 2019). Baseline turnover is caused, for instance, by environmental fluctuations, which result in deterministic turnover or by ecological drift, which causes stochastic turnover (Chase et al., 2020).

5.3.2 Ecological drift and environmental variability

Ecological drift is mainly investigated by population ecology because it is influenced by birth, death, local extinction, and colonization rates (Chase et al., 2020). In particular, small and isolated populations with weak abiotic and biotic filters are prone to demographic stochasticity, and can increase unexplained variability in restoration outcomes (Vellend, 2010). Colonization of restoration sites can be modified by changes in the surrounding landscape which causes 'colonization credit' or 'extinction debt', for example, by changing habitat area, differentiation or configuration (Jackson & Sax, 2010; Török & Helm, 2017).

Environmental variability cause every year turnover in species composition (Werner et al., 2020). Such year-to-year dynamics can be driven by weather fluctuations of the current or previous season (F. M. Fischer et al., 2020). However, management can vary slightly not only from site to site but also from year to year due to practical or economic reasons (Allan et al., 2014; Kun et al., 2019). Furthermore, biotic factors like rodents, pests or parasites can vary annually (Werner et al., 2020). The intensity of temporal turnover is high, especially on nutrient-rich soils immediately after a disturbance event in forest understorey vegetation (Kaarlejärvi, Salemaa, Tonteri, Merilä, & Laine, 2021; Maliniemi, Happonen, & Virtanen, 2019; but see Hodapp et al., 2018). The size of the regional species pool also affects temporal turnover and increases the turnover intensity (Hodapp et al., 2018). Despite these results, much more knowledge is necessary about the size and drivers of year-to-year turnover of species composition.

5.4 Implications for restoration ecology

5.4.1 Seed–substrate combinations

In restoration ecology, it is known that overcoming the dispersal filter by seed transfer is necessary in fragmented landscapes with a low habitat density or in urban areas (Török et al., 2018). Moreover, reducing soil nutrients is necessary to weak environmental filtering before seeding (Freitag et al., 2021; Marrs, 1993). Evidence-based restoration can be developed by quantifying the effect sizes of restoration approaches and comparing them with each other to discover the decisive factors for restorations. The most important factor for restoration success is seed transfer (e.g., Grman et al., 2013; Halassy et al., 2016; Kardol et al., 2008; Kiehl et al., 2006; Pywell et al., 2002). Nutrient reduction had a minor effect on restoration success in our experiment (Bauer et al., 2023d), and only a replacement effect for specialist species in the older dike grasslands (Bauer et al., 2023a). I conclude that it is important to identify a range of acceptable nutrient loads for species-rich grasslands as it was done for nitrogen depositions (Bobbink et al., 2010). This would avoid extensive restoration approaches which remove soil biota (Kardol et al., 2008), such as topsoil removal or sand addition, which are also expensive.

Seeding needs further development by modifying seed mixtures for specific site conditions to improve establishment success. Laughlin (2014a) provided a function to create trait-based seed mixtures, but it has not been successfully applied for seed mixtures in greenhouse experiments, yet (Bauer, Krause, et al., 2022b; Möhrle et al., 2021; Yannelli et al., 2018). My results suggest, on the one hand, a strong priority effect by seed mixtures which means that the applied seed mix type developed the respective vegetation type independent of the site characteristics (Bauer et al., 2023d). On the other hand, the differences in functional trait values between the seed mix types seemed not to affect the established vegetation. After three years, both types had similar trait values for SLA, canopy height, and seed mass (Beck, 2022). Furthermore, the substrate had only a minor effect on the trait values of the established vegetation (Beck, 2022). The community-weighted mean of canopy height was mainly reduced by sand addition (Beck, 2022).

Further research is needed on priority effects of seeding and on trait-based seed mixtures to make this approach applicable. Creating differences by seed mixtures in dependence on site conditions is necessary to develop seed–substrate combinations. One problem is that seed mixtures can only be modified by seed weight in a mixture. However, research on trait-environment relationships is based on abundance values, which may prohibit the successful application of Laughlin's (2014a) function for grassland restoration. Perhaps more fundamental knowledge about functional traits, especially the link to intrinsic growth rates, is necessary

before being applicable in restoration practice (Laughlin, Gremer, Adler, Mitchell, & Moore, 2020). Furthermore, research on seed–substrate combinations does not investigate different (early) management approaches, which may miss important interactions being necessary for a successful application (Brudvig et al., 2017; Halassy et al., 2016; Tölgyesi et al., 2022).

5.4.2 Baseline turnover

There is strong criticism on evaluating biodiversity by species loss via richness (e.g., Larsen et al., 2018) which masks significant temporal turnover in species composition (Hillebrand et al., 2018). The focus of analyzing temporal turnover is mainly on the directional turnover induced by global change (Magurran et al., 2019). However, for monitoring restoration projects, it is essential to know the size of the expectable baseline turnover of certain ecosystems. A temporal turnover of 37 ± 11% (mean ± SD) was identified, which is far higher than the directional turnover (Bauer et al., 2023a). Considering annual turnover should lead to a more cautious interpretation of monitoring results. Annual turnover is a confounding factor for comparing just two points in time within a restoration or a comparison between a reference and the restoration outcomes (cf. Hédl & Chudomelová, 2020). Beyond this, baseline turnover highlights the need to define a target range or a set of target states incorporating temporal variability rather than a specific target (point) (cf. Shackelford et al., 2021). This approach would reduce the pronunciation of steady climax states and considers non-directional temporal dynamics. These temporal fluctuations of species abundances create temporal niches which enable co-existence and improve biodiversity (Adler, HilleRisLambers, Kyriakidis, Guan, & Levine, 2006; Chesson, 2000). Time and space are never isolated, which in this case, means that temporal niches still require a larger species pool to compensate for local extinctions (Tredennick et al., 2017). Future research would be able to use an applicable method to analyze simultaneously spatial variation and temporal turnover (cf. Tatsumi et al., 2021). Restoration ecology can visualize target ranges, using reference databases (e.g., sPlotOpen, Sabatini et al., 2021; European Vegetation Archive (EVA), Chytrý et al., 2016; ReSurveyGermany, Jandt et al., 2022). Additionally, restoration ecology can provide new data by conducting annual resurveys and/or many different surveys within a region over many years. EUNIS already take variability into account in their classification algorithms (Chytrý et al., 2020).

Besides providing reference states, restoration ecology should investigate the drivers of temporal turnover to understand the underlying processes (Magurran et al., 2019). Only a few studies investigated drivers, but these were not based on an annual basis and were not conducted in grasslands but in understorey vegetation (e.g., Kaarlejärvi et al., 2021; Maliniemi et al., 2019). In contrast to these forest vegetation studies, there was no clear indication that

soil fertility is a main driver of, in my case, year-to-year turnover (unpublished analysis; Bauer, Huber, & Kollmann, 2022).

5.5 Implications for establishment and management of Green Infrastructure

5.5.1 Seed–substrate combinations

Our results suggest defining the habitat-specific species pool more restrictive by excluding species related to ruderal vegetation, like *Centaurea stoebe*, *Echium vulgare*, and *Verbascum lychnitis* (Figure 11, Figure 12). These species can dominate after dry years, leading to a more ruderal trajectory. All in all, specified (trait-based) seed–substrate combinations are not yet applicable and need further research (Bauer et al., 2023d; Bauer, Krause, et al., 2022b). Though, there is evidence to recommend seeding mesic lowland hay meadows in north expositions and semi-dry calcareous grasslands in southern exposures, which would be even more pronounced under future conditions with climate change (Mazalla et al., 2022). Furthermore, there was no evidence that increasing seeding density from 4 to 8 g m^{-2} improves vegetation establishment (Bauer et al., 2023d; Kaulfuß et al., 2022).

Figure 11. A plot of the dike experiment dominated by *Echium vulgare* and *Verbascum lychnitis*. Both species should not be included in a seed mixture for dikes. © Markus Bauer

5.5.2 Substrate

In Bavaria, it is recommended to use a maximum of 5 cm topsoil to establish species-rich dike grassland (LfU, 2014b). This recommendation has no reference but dates back most likely to the recommendations from dike greenings at River Lech (Bayerisches Landesamt für Wasserwirtschaft, 1984; Jürging & Gröbmaier, 1984). However, this recommendation does not refer to a study nor an experiment. Husicka (2003) criticized this recommendation because he found species-rich dike grasslands on the river Rhine independent of the substrate depth of 5–30 cm. Similarly, my results show no difference between 15 and 30 cm for different species diversity measures (Bauer et al., 2023d) and suggest that substrate depth causes species replacements but not a richness gradient (Bauer et al., 2023a). In prairies, no differences were found when 20 or 25 cm rooting depth was compared with 42 cm or unrestricted rooting depth (Baer et al., 2004; Dornbush & Wilsey, 2010). Therefore, my data does not support the recommendation of only a 5 cm topsoil layer to establish species-rich dike grasslands (Figure 12).

New but crushed bricks are commonly used for green roofs. However, using demolition bricks for brick-based restoration substrate in urban contexts might be a promising way to reduce the dumping of bricks in landfills (Bauer, Krause, et al., 2022b; Roth-Kleyer, 2018). Thus, bricks should be tested on a larger scale before being applicated in practice (Figure 12). Especially the acceptable variability of brick characteristics must be evaluated. These characteristics depend, for example, on the source clay, manufacturing, brick age, or adhesions of mortar and plaster. Guidelines in Germany for the evaluation are, for example, the DüMV (2012) and the FLL for green roofs (Forschungsgesellschaft Landschaftsentwicklung Landschaftsbau [FLL], 2018).

Seed-substrate combination
- Exclude *Centaurea stoebe*, *Echium vulgare* and *Verbascum lychnitis* from the habitat-specific species pool
- Seed lowland hay meadows in north exposition of dikes
- Increasing seeding density from 4 to 8 g m^{-2} is not necessary

Substrate
- Substrate depths between 5–30 cm are acceptable for dike greening
- Crushed bricks are a promising substrate component to avoid dumping of waste bricks and save topsoil

Drought during establishment phase
- Reseeding might be necessary, after severe drought during the establishment phase

Improving beta diversity by restoration
- Active diversification of seed mixes, substrates and management within a restoration project, but also within certain boundaries such as habiatat-specific species pool, no more than 30 cm of topsoil, and first cut not in May.

Figure 12. Implications of this thesis for restoration practice

5.5.3 Drought during the establishment phase

Harmful site conditions during establishment, like drought, can have negative effects on the establishment success (Groves & Brudvig, 2019; Larson, Ebinger, & Suding, 2021; but see

Eckhoff et al., 2023) and can lead to a more ruderal trajectory at least four years after seeding (Figure 8, Bauer et al., 2023d). For this reason, I would suggest reseeding sites in the following year if seedlings were heavily damaged by unfavorable conditions (Figure 12). It could be possible that this effect will disappear after many years, though there is no trend in this direction within the first four years (Bauer et al., 2023d).

5.5.4   Diversification of seed mixtures, substrates, and management

Restoration ecology faces two contrasting problems: on the one hand, restoration outcomes are largely not explainable by models, which means that they are unpredictable (Brudvig et al., 2017). On the other hand, restorations are not complex enough, leading to biotic homogenization, such as a lower gamma diversity than in reference landscapes (Fivash et al., 2022; Holl et al., 2022). Restoration should be predictable, but at the same time, approaches should "result in the widest possible variety of outcomes within the range of desired conditions" to improve biodiversity (Brudvig et al., 2017). The dike survey shows that differences in dike communities are mainly driven by replacement and not by richness gradients (Bauer et al., 2023a). Our field experiment indicates similar differences to the reference states regardless of seed mix type, substrate depth or sand admixture (Bauer et al., 2023d). The strong replacement component and the variation in restoration outcomes with similar distance to reference mean indicate that there is a turnover that fosters biodiversity. Biodiversity can be further increased by inducing variability using different seed mixtures within a restoration project.

I would suggest actively diversifying the approaches and using different substrate depths, soil fertilities, and seed mix types within one restoration to increase the beta diversity of the whole project (Figure 12). Staggering plantings over time and space is also suggested by Eckhoff et al. (2023) to enhance heterogeneity in restored areas. Moreover, diversifying the approaches can ensure restoration success by avoiding complete failure due to unfavorable events (Fivash et al., 2022). This risk management strategy is called 'diversified bet-hedging' and maximizes yields when uncertainty about the future is high (Walters, Ramiah, & Moosa, 2016). In addition, the management has a diversifying potential, which means spatio-temporal complex management can increase alpha, beta and gamma diversity (Kun et al., 2019; Vadász et al., 2016). In contrast, restoration ecology should still search for general principles by experiments.

All in all, diversification of restoration approaches and management would be beneficial for biodiversity if not too nutrient-rich soils are used, unsuitable species are seeded, or the management becomes too extensive or too intensive, leading to the decline of specialist species (cf. Bagaria et al., 2019; Diekmann et al., 2019). This is why target ranges instead of certain target states should be defined by visualizing several reference communities monitored

over several years and sites and stored in databases. This would set a range for the spatial and temporal variability of target communities under varying site conditions.

6 Conclusion

My motivation for this thesis was to contribute to the improvement of land use that reconciles biodiversity with other ecosystem services. The concept of 'renewal ecology' combines Grey Infrastructure with Green Infrastructure (Bowman et al., 2017). Dikes are suitable landscape features for this approach because they are common infrastructure objects and can support species-rich grasslands with a low-intensity management. Many dikes harbor threatened grassland types and are valuable for conservation both in terms of habitat area and connectivity. However, this will only be the case if dikes do not further reduce the available active floodplain.

With the experiments, seed–substrate combinations were tested to investigate their potential to reach specific restoration goals guided by theoretical knowledge. Such a predictive restoration is essential to fulfill the high expectation for biodiversity protection placed in restorations. I modified species pools for the seed mixtures and used trait-based methods. The results show that hay meadows were more suitable in north exposition, brick-based substrates were not adverse for grassland establishment, and regional seed mixtures performed similarly to commercial standard seed mixtures. However, there was only restricted success with specified seed–substrate combinations and trait-based methods. Therefore, more research is necessary to reach predictive restoration and make the theoretical knowledge about traits applicable to restoration practice. Traits are the 'holy grail' (Lavorel & Garnier, 2002) and need still further understanding (Laughlin et al., 2020).

The field experiment and the surveys on older dikes highlight different aspects apart from the dispersal, abiotic and biotic filters. Priority effects through seeding and year effects through drought can modify the trajectories of vegetation development. Furthermore, the results showed the importance of uncontrolled landscape factors affecting the spatial variation of restoration outcomes. Furthermore, I found a strong replacement component within spatial variation and balanced temporal turnover, which emphasizes the importance of variability in vegetation by stochasticity, year effects or varying management. This underlines the warning of Rogers et al. (2022) to be cautious with steady-state approaches in conservation and restoration.

Restoration ecology has two aims to develop predictive restoration techniques by understanding and modifying ecological mechanisms and to foster biodiversity. These aims can be contradicting if one strives for a one-fits-all solution. Restoration ecology should establish experiments to reduce complexity and increase understanding of mechanisms

However, restoration practice for Green Infrastructure should increase complexity in restoration approaches and management (within certain borders) to increase small-scale heterogeneity and avoid biotic homogenization by restoration. One can control if the variability of restoration outcomes is within certain borders; a large set of reference plots should be used for comparison. The restoration ecological experiments should be set up in cooperation stakeholders to improve the exchange between science, practice and local communities (Figure 13; Principle 1 and 2 of The Standards, Gann et al., 2019) and create experiments with clear goals and theoretical and practical relevance (Principle 5). This is the base to upscale restoration (Principle 7) and increase the aimed recovery (Principle 6).

Figure 13. Our experiment on the dike of River Danube near Deggendorf in Germany. The experiment was set up in cooperation with the water and conservation authorities as well as the dike builder. © Markus Bauer

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List of publications

Publications in journals

Preprints

Bauer M, Huber JK, Kollmann J (2023) Beta diversity of restored dike grasslands is strongly influenced by uncontrolled spatio-temporal variability. – *EcoEvoRxiv*. https://doi.org/10.32942/X2959J

Peer-review paper

Overview on Google Scholar

Bauer M, Huber JK, Kollmann J (2023) Fit by design: Developing seed–substrate combinations to adapt dike grasslands to microclimatic variation. – *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.14497

Bauer M, Krause M, Heizinger V and Kollmann J (2023) Ecological application of waste bricks: Brick-augmented substrates have no adverse effects on urban trees. – *Trees* 37, 875–889. https://doi.org/10.1007/s00468-023-02391-8

Teixeira L*, **Bauer M***, Moosner M, Kollmann J (2023) River dike grasslands can reconcile biodiversity and different ecosystem services to provide multifunctionality. – *Basic and Applied Ecology* 66, 22–30. https://doi.org/10.1016/j.baae.2022.12.001

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Habel JC, Teucher M, Ulrich W, **Bauer M**, Rödder D (2016) Drones for butterfly conservation: Larval habitat assessment with an unmanned aerial vehicle. – *Landscape Ecology* 31, 2385–2395. https://doi.org/10.1007/s10980-016-0409-3

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Other publications

Bauer M, Huber JK, Kollmann J (2023) Fluktuierende Vegetationsbestände. Eine Herausforderung für naturschutzfachiche Bewertung. – *nodium* 15, 106–107. ISBN 978-3-948278-37-3

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Bauer M, Kiefer J, Albrecht H (2020) Vegetationsveränderungen auf Dauerbeobachtungsflächen im Naturschutzgebiet Garchinger Heide über 35 Jahre. – *Berichte der Bayerischen Botanischen Gesellschaft* 90, 43–66. ISSN 0373-7640

Presentations

Oral presentations

Bauer M, Huber JK, Kollmann J (2022) Restoration of dike grasslands. Testing substrate-seed mix combinations. – *Ecological Society of Germany, Austria and Switzerland* (**GfÖ**) and Société Française d'Écologie et d'Évolution (sfe²) and European Ecological Federation (eef), 51st Annual Meeting, Metz, France.

Bauer M, Huber JK, Kollmann J (2022) Does biodiversity on river dike grasslands profit from spatio-temporal variability? – *International Association of Vegetation Science* (**IAVS**), 64th Annual Symposium, Madrid, Spain.

Bauer M, Krause M, Heizinger V, Kollmann J (2021) Testing designed grassland mixtures on brick-based substrates to increase ecosystem services of restored land. – *Society for Ecological Restoration* (**SER**), 9th World Conference, Virtual, United States.

Bauer M, Kollmann J (2019) Developing novel restoration substrates – Re-use of waste bricks for land-fill coverage and urban tree planting. – *Ecological Society of Germany, Austria and Switzerland* (**GfÖ**), 49th Annual Meeting, Münster, Germany.

Poster presentations

Bauer M, Kollmann J (2023) Fit by design: Seed–substrate combinations for adapted restorations. A new experiment with river dike grasslands. – *Ecological Society of Germany, Austria and Switzerland* (**GfÖ**), 52nd Annual Meeting, Leipzig, Germany.

Bauer M, Huber JK, Kollmann J (2021) Spatio-temporal variability of dike grassland due to soil and microclimate. – *Specialist Group Plant Population Biology* (**PopBio**), 33rd annual meeting, virtual, Czech Republic.

Bauer M, Albrecht H (2019) Long-term monitoring in a 100-year-old calcareous grassland reserve in Germany. Vegetation change despite being well preserved. – *International Association of Vegetation Science* (**IAVS**), 62nd Annual Symposium, Bremen, Germany.

Data and code publication

GitHub (github.com/markus1bauer)

Bauer M, Huber JK, Kollmann J (2022) Data and code for Bauer et al. (2023) J Appl Ecol (v1.1.0) [Data set]. – Zenodo. https://doi.org/10.5281/zenodo.7713396

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Bauer M, Albrecht H (2022) Vegetation surveys from the calcareous grassland of the nature reserve Garchinger Heide. – *PANGAEA*. https://doi.org/10.1594/PANGAEA.940643

Bauer M, Dorbath K, Kollmann J (2022) Data and code for Bauer et al. (2018) Tuexenia (v1.1.0) [Data set]. – *Zenodo*. https://doi.org/10.5281/zenodo.6125176

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Curriculum Vitae

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ORCID | Google Scholar | GitHub | Stackoverflow | Linkedin | Mastodon

Professional experience

Since 06/2022   **Freelancer** for vegetation mapping, 'Landschaftsökologie Bauer', Freising

Since 01/2019   **Research assistant**, Chair of Restoration Ecology, TUM
Projects (e.g.): Testing brick-added substrates for restorations; Monitoring concept and first survey for the conservation area Garchinger Heide

Professional preparation

06/2021–08/2023   **PhD**, Chair of Restoration Ecology, TUM
PhD thesis: The establishment of species-rich meadows as Green Infrastructure.
Supervisor: Prof. Dr. Johannes Kollmann

10/2016–12/2018   **M.Sc.**, Environmental Planning and Ecological Engineering, TUM
Master's thesis: Monitoring of the Garchinger Heide. Vegetation ecological studies of a reference ecosystem under changed environmental conditions over 34 years.
Supervisor: PD Dr. Harald Albrecht

10/2012–10/2016   **B.Sc.**, Landscape architecture and landscape planning, TUM
Bachelor's thesis: Zweites Monitoring von Rohbodenstandorten des Inns nach Renaturierungsmaßnahmen.
Supervisor: Prof. Dr. Johannes Kollmann

09/2011–08/2012   **Apprenticeship** to landscape gardener at MGM-Landschaftsbau, Hebertshausen

4/2011   **Abitur** at Gymnasium Markt Indersdorf, Germany

Internships

2013–2018
(5 days–2 months)

Landscape planning office ('peb', Dachau), **Lower conservation authority** (Munich); **Student assistant** (TUM); 'Bergwaldprojekte' like peatland rewetting

Stays abroad

10/2014–02/2015
(4 months)

Internship: Botanical Garden, León, Nicaragua

07/2014
(1 month)

Long excursions: Vegetation ecology, Kyrgyzstan and Kazakhstan
Guide: Professor Jörg Pfadenhauer (Chair of Restoration Ecology, TUM)

03–04/2014
(2 months)

Field research: Rooiklip Research Camp of TUM, Namibia
Field experiments about seed predation with *Crotalaria podocarpa* DC.

2013–2018
(each 3–10 days)

Short excursions: Lake Neusiedel, Sardegna, Tagliamento, Alps, Luxembourg, Lake Garda, Coast of Baltic Sea, Coblenz (Hunsrueck)

Specific skills and engagement

Languages	English (fluently), Spanish (basic), French (very basic)
Computer	Frequentist and Bayesian statistics and data managenent with R (very good) Shiny with R (advanced) GIS with R and QGIS (good) MS Access (advanced)
Teaching experience	Experimental restoration ecology (2019, 2020, 2023), Master's project (2020), Botanical and ecological excursions (2019, 2022)
Supervised theses	Two Bachelor's theses of (2022, 2023)
Professional society memberships	International Association of Vegetation Science (IAVS), Brussels Ecological Society of Germany, Austria, Switzerland (GfÖ), Berlin Floristisch-soziologische Arbeitsgemeinschaft (FlorSoz), Göttingen Bayerische Botanische Gesellschaft (BBG), Gröbenzell Alumni-Club Landschaft TUM (ACL), Freising
Reviewer	Applied Vegetation Science (1 manuscript), Flora (2), Journal of Vegetation Science (2), Perspectives in Plant Ecology, Evolution and Systematics (1), Restoration Ecology (3), see ORCiD
Awards	Award of the major of Freising (2020) for the best master's thesis of the department landscape architecture and landscape planning in the year 2018/19 Scholarship of the German Federal Foundation for the Environment (DBU) (2021–2023)