Technische Universität München
TUM School of Life Sciences

Managing a native invader in wet grasslands: Effects on target species, community composition and grassland multifunctionality

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Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades einer

Doktorin der Naturwissenschaften (Dr. rer. nat.)

genehmigten Dissertation.

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Die Dissertation wurde am 22.12.2022 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 08.03.2023 angenommen.

Plants stand still and wait to be counted.

John L. Harper (1977)

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SUMMARY

Temperate semi-natural grasslands belong to the most altered ecosystems worldwide. Although mainly created by historical land use, they are nowadays threatened by intensification as well as abandonment. While their species richness makes them valuable for nature conservation, characteristic plant diversity of the remaining sites is still declining. Moreover, changes in grassland management lead to alterations in community structure and can facilitate invasion by both non-native and native invaders. These species can have detrimental effects not only on diversity and community composition but also on ecosystem services such as forage quantity or quality. Conventional control methods are often time-consuming, costly or go along with undesirable side effects. In addition, especially management of native invaders may conflict with conservation objectives due to possible trade-offs between control measures and conservation of plant diversity.

The aim of this thesis was therefore to assess the possibilities and consequences of ecological management of a native invader. The theoretical background of the approach was based on the modification of ecological filters to increase competition for key resources. The management options developed were intended to reduce the abundance of the native invader *Jacobaea aquatica* (marsh ragwort) without negatively affecting plant diversity and multifunctionality of the grasslands. Within the pre-alpine region of Allgäu in Southern Germany, wet grassland sites of different productivity and land use intensity were selected representing a gradient of site conditions within the ecological amplitude of the study species. Treatments consisting of different mowing intensities were used to increase competition for light and thus decrease plant fitness and abundance of the invader. Abundance of *J. aquatica*, changes in community composition and effects on grassland multifunctionality were monitored to assess suppression success and possible negative biodiversity effects of the designed measures.

Publication 1 analysed the effects of shading on vegetative and generative growth of *J. aquatica.* To disentangle effects of light reduction from those of other site conditions, a controlled greenhouse experiment was implemented. The results indicate that shading negatively influenced plant survival and generative growth. A comparison to the field data (in which shading was determined by measuring the amount of light reaching plant rosette level under different management regimes) showed that effects were not as pronounced at the grassland sites. Nevertheless, abundance of *J. aquatica* declined. The study demonstrates that depending on site productivity, management intensity can regulate competition for light and suppress the native invader.

Publication 2 focused on the effects of temporary abandonment and decreased mowing intensity on the abundance of *J. aquatica* as well as on functional diversity and species richness of grassland communities. Comparison of the data from the start and end of the four-year field experiment confirmed a negative influence of reduced mowing intensity on the abundance of *J. aquatica.* This effect was independent of the productivity level of the site. Reduced management intensity led to a decline in the abundance of dicotyledons and occasional species losses at very low intensities. Changes in community composition were confirmed by the analysis of functional diversity indices, which revealed an overall tendency of decreased functional dispersion and increased functional redundancy. Nevertheless, changes in community composition and species richness were less pronounced and inconsistent among productivity levels and management intensities. Still, moderately intensive control measures are preferable to avoid plant diversity losses.

Publication 3 investigated the synergies and trade-offs between the control of *J. aquatica* and the maintenance of ecosystem multifunctionality in wet grasslands. Multifunctionality of the grasslands was given by the simultaneous assessment of eleven indicators of ecosystem services associated with grassland productivity and conservation. The ability of the grasslands to fulfil various ecosystem functions and simultaneously provide multiple goods and services declined with decreasing management intensity but only at low to intermediate levels of functioning. Nevertheless, several indicators of ecosystem services were significantly affected by changes of management intensity. This was shown when assessing different classes of management intensity. More intense management promoted ecosystem service indicators related to productivity but led to a simultaneous increase in the abundance of *J. aquatica.* These findings indicate that moderate suppression is the most effective way to reconcile the control of the studied native invader and the maintenance of grassland multifunctionality.

The general discussion of the thesis integrates the different aspects investigated in the three publications. Each aspect is reviewed in terms of its implications for native invader management. Furthermore, the aspects are evaluated together and management recommendations to control *J. aquatica* are given based on the findings. The transferability of the results to the control of other native invasive species is evaluated, and advice is given which aspects should be considered when management concepts based on the modification of environmental filters are developed.

ZUSAMMENFASSUNG

Halbnatürliches Grünland der gemäßigten Breiten gehört zu den am stärksten veränderten Ökosystemen weltweit. Obwohl hauptsächlich durch historische Landnutzung entstanden, ist es heute durch Intensivierung oder Nutzungsaufgabe bedroht. Ihr Artenreichtum macht die verbliebenen Flächen naturschutzfachlich wertvoll. Jedoch nimmt auch auf diesen Flächen die charakteristische Pflanzenvielfalt weiter ab. Darüber hinaus führen Änderungen in der Grünlandbewirtschaftung zu strukturellen Veränderungen der Pflanzengesellschaften, was die Invasion sowohl gebietsfremder als auch einheimischer Arten begünstigen kann. Die Ausbreitung dieser Arten kann sich nicht nur nachteilig auf die Vielfalt und Zusammensetzung der Grünlandgesellschaften auswirken, sondern auch auf die Bereitstellung bestimmter Ökosystem-Dienstleistungen wie Futtermenge und -qualität. Herkömmliche Bekämpfungsmethoden sind oft zeitaufwändig, kostspielig oder haben unerwünschte Nebeneffekte. Darüber hinaus kann insbesondere die Bekämpfung von sich ausbreitenden einheimischen Arten (‚*native invaders*‘) mit Erhaltungszielen kollidieren, da möglicherweise Kompromisse zwischen Bekämpfungsmaßnahmen und dem Erhalt der Pflanzenvielfalt eingegangen werden müssen.

Das Ziel der vorliegenden Arbeit war es daher, die Möglichkeiten und Folgen eines ökologischen Managements eines solchen *native invaders* zu untersuchen. Die Herangehensweise basiert auf der Theorie, dass durch Modifizierung ökologischer Filter die Konkurrenz um wichtige Ressourcen erhöht werden kann. Die entwickelten Managementoptionen zielten darauf ab, die Häufigkeit der einheimischen invasiven Art *Jacobaea aquatica* (Wasser-Greiskraut) zu reduzieren, ohne die Pflanzenvielfalt und Multifunktionalität des Grünlands negativ zu beeinflussen. In der voralpinen Region des Allgäus in Süddeutschland wurden dazu Feuchtgrünlandstandorte mit unterschiedlicher Produktivität und Nutzungsintensität ausgewählt, die einen Gradienten der Standortbedingungen innerhalb der ökologischen Amplitude der untersuchten Art darstellen. Die einzelnen Behandlungen bestanden aus unterschiedlichen Mahdintensitäten, die die Konkurrenz um Licht erhöhen und damit die Fitness der Pflanzen und die Abundanz des Eindringlings verringern sollten. Die Häufigkeit von *J. aquatica*, die Veränderungen in der Zusammensetzung der Pflanzengemeinschaft und die Auswirkungen auf die Multifunktionalität des Grünlands wurden beobachtet, um den Erfolg sowie mögliche negative Effekte der geplanten Maßnahmen auf die Biodiversität zu bewerten.

Veröffentlichung 1 untersuchte die Auswirkungen von Beschattung auf das vegetative und generative Wachstum von *J. aquatica*. Um die Folgen des reduzierten Lichteinfalls von denen anderer Standortbedingungen zu trennen, wurde ein kontrolliertes Gewächshaus-Experiment durchgeführt. Es stellte sich heraus, dass die Beschattung das Überleben und generative Wachstum der Pflanzen negativ

beeinflusst. Ein Vergleich mit den Felddaten (bei denen die Beschattung durch Messung der Lichtmenge bestimmt wurde, die die Pflanzenrosetten bei verschiedenen Bewirtschaftungsformen erreichte) zeigte, dass die Auswirkungen an den Grünlandstandorten weniger ausgeprägt waren. Dennoch verringerte sich die Häufigkeit von *J. aquatica*. Die Ergebnisse deuten darauf hin, dass die Intensität der Bewirtschaftung je nach Produktivität des Standorts die Konkurrenz um Licht regulieren und den *native invader* unterdrücken kann.

Veröffentlichung 2 befasste sich mit den Auswirkungen vorübergehender Nutzungsaufgabe und verringerter Mahdintensität auf die Abundanz von *J. aquatica* sowie auf die funktionelle Diversität und den Artenreichtum der Grünlandflächen. Die Analyse der Daten von Beginn und Ende des vierjährigen Feldversuchs bestätigte den negativen Einfluss der verringerten Mahdintensität auf die Häufigkeit von *J. aquatica*. Dieser Effekt war unabhängig vom Produktivitätsniveau des Standortes. Eine verringerte Bewirtschaftungsintensität führte zu einem Rückgang der Häufigkeit von Dikotyledonen und gelegentlichen Artenverlusten bei sehr geringen Bewirtschaftungsintensitäten. Die Veränderungen in der Zusammensetzung der Pflanzengemeinschaften wurden durch die Analyse der Indizes für funktionelle Diversität bestätigt, die eine allgemeine Tendenz zur Abnahme der funktionellen Streuung und zur Zunahme der funktionellen Redundanz ergab. Jedoch waren die Veränderungen in der Zusammensetzung der Pflanzengemeinschaft und im Artenreichtum geringer und je nach Produktivitätsniveau und Bewirtschaftungsintensität unterschiedlich ausgeprägt. Trotz allem sind bei der Bekämpfung mäßig intensive Maßnahmen vorzuziehen, um Verluste der Pflanzenvielfalt zu vermeiden.

Veröffentlichung 3 untersuchte das Zusammenwirken und Zielkonflikte zwischen der Bekämpfung von *J. aquatica* und der Aufrechterhaltung der Multifunktionalität des Ökosystems Feuchtgrünland. Die Multifunktionalität des Grünlands wurde durch die kombinierte Bewertung von elf Indikatoren für Ökosystem-Dienstleistungen ermittelt, die mit der Produktivität und dem Schutz von Grünland in Verbindung gebracht werden. Die Fähigkeit von Grünland verschiedene Ökosystemfunktionen zu erfüllen und gleichzeitig mehrere Güter und Dienstleistungen bereitzustellen, verringerte sich unter abnehmender Bewirtschaftungsintensität. Dies gilt jedoch nur im Hinblick auf niedrige bis mittlere Funktionsniveaus. Dennoch wurden mehrere Indikatoren für Ökosystem-Dienstleistungen durch Änderungen der Bewirtschaftungsintensität erheblich beeinflusst. Das zeigte sich am deutlichsten bei der Bewertung verschiedener Bewirtschaftungsklassen. Eine intensivere Bewirtschaftung förderte beispielsweise Indikatoren für Ökosystem-Dienstleistungen im Zusammenhang mit der Produktivität, führte aber gleichzeitig zu einer Zunahme der Häufigkeit von *J. aquatica*. Diese Ergebnisse deuten darauf hin, dass ein moderates Unterdrückungsmanagement der effektivste Weg sein kann, um die

Kontrolle des untersuchten *native invaders* und die Erhaltung der Multifunktionalität des Grünlands in Einklang zu bringen.

In der übergreifenden Diskussion der Arbeit werden die verschiedenen Aspekte, die in den drei Veröffentlichungen untersucht wurden, zusammengefasst und miteinander verknüpft. Jeder Aspekt wird im Hinblick auf seine Auswirkungen auf die Bekämpfung von *native invaders* überprüft. Darüber hinaus werden die einzelnen Komponenten gemeinsam bewertet und auf der Grundlage der Ergebnisse Empfehlungen für die Bekämpfung von *J. aquatica* gegeben. Die Übertragbarkeit der Ergebnisse auf die Bekämpfung anderer *native invaders* wird erörtert und es werden Empfehlungen gegeben, welche Aspekte bei der Entwicklung von Bewirtschaftungskonzepten, die auf der Veränderung von Umweltfiltern basieren, zu berücksichtigen sind.

INTRODUCTION

Temperate grasslands

Ranging from the 'prairies' in North America over the 'pampas' (South America) and 'velds' (Southern Africa) to the Eurasian 'steppe' regions (Faber-Langendoen et al., 2020), temperate grasslands represent one of the largest biomes in the world. While they make up 7–10% of the Earth's total terrestrial surface (White et al., 2000), temperate grasslands cover around 22% of the area in the Eurasian region, known as the Palaearctic biogeographical realm (Török & Dengler, 2018). Natural grasslands in this region, such as alpine grasslands or steppes, were shaped by climatic conditions and grazing of wild herbivores, whereas the so-called semi-natural grasslands of Central Europe developed under long-term human activity (Hejcman et al., 2013). Although mainly created by historical land use, today temperate semi-natural grasslands are among the most altered and endangered ecosystems (Henwood, 2010). While abandonment as well as land use intensification are considered to be the most important threats, habitat losses often result from conversion to arable land, forests or built-up areas (Török et al., 2020). In fact, an analysis of the status of grasslands in the year 2000 found that around 41% of temperate grasslands around the world have been converted to agricultural use, while another 13.5% were lost to urban areas and afforestation (White et al., 2000). Moreover, more recent studies report on area losses of 25% for natural grasslands and 40% for semi-natural grasslands in the Palaearctic realm, with even higher losses in some of the areas, e.g. in Eastern Europe 92% of natural grasslands have vanished, while in Northern Europe 75% of semi-natural grasslands are lost (Dengler et al., 2020).

As highly resilient systems, temperate semi-natural grasslands provide a variety of ecological goods and services for humankind; thus, they significantly contribute to important ecosystem functions and services such as production of fodder and raw materials, pollination or invasion resistance (Török et al., 2018). Only few of the provided services have been given market values, such as the quantity and quality of the provisioned forage for animals or the animal products themselves (e.g. meat, milk, wool or leather; Fig. 1; Sala & Paruelo, 1997). Others, such as conservation of biodiversity, climate regulation, protection against natural hazards or cultural values have received little recognition, despite their increasing importance (Sala & Paruelo, 1997). Moreover, grassland functions contribute to various biological, physical and chemical processes, as reflected in their role in nutrient cycling, habitat provision, water regulation, carbon storage, or pest control (Fig. 1; Lamarque et al., 2011). The ability to provide this multitude of functions and resulting services – the so-called 'ecosystem multifunctionality' – depends to a large extent on the biodiversity of the respective grassland. In addition to its intrinsic value, biodiversity can have positive effects on production stability, product quality or resilience to disturbances (van der Plas, 2019).

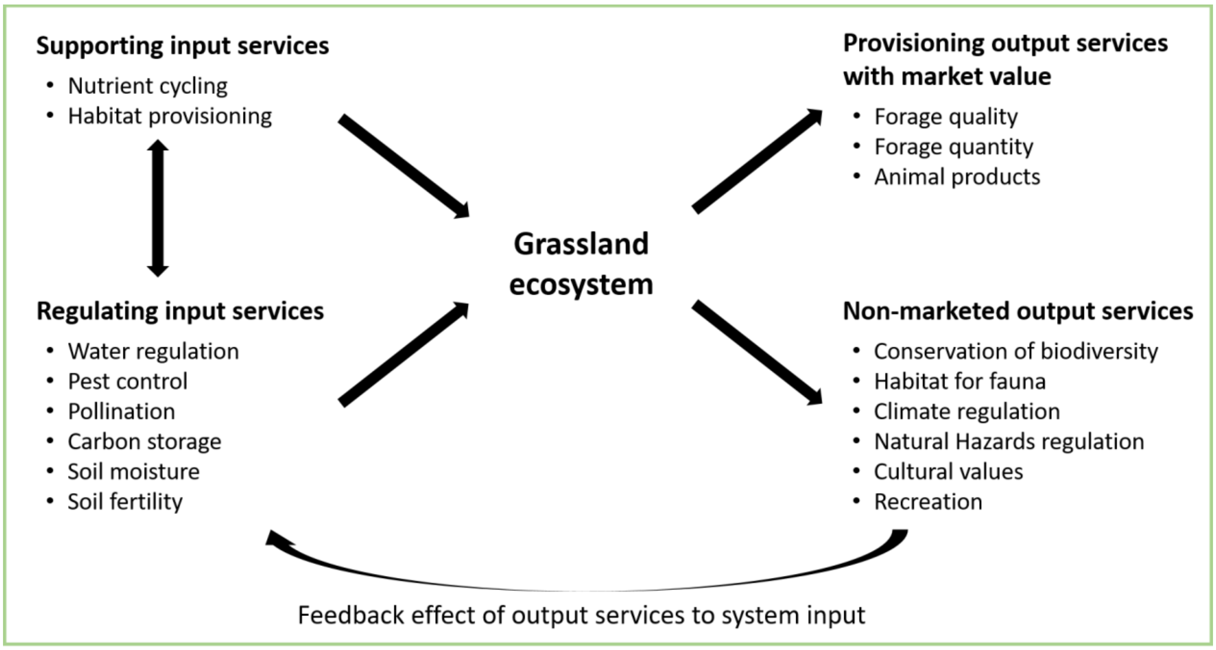

Fig. 1: Ecosystem services of temperate grasslands.
A variety of supporting and regulating 'input services' provide the basis for the requested directly or indirectly valued 'output services'. Directions and interaction of the relations are simplified. Figure adapted from Lamarque et al. (2011) and Zhang et al. (2007).

Moreover, synergies and trade-offs between biodiversity and individual ecosystem functions and services vary with land-use type and management intensity, further influencing the ability of the grassland to provide multiple services (Lamarque et al., 2011; Neyret et al., 2021). An example is the sole focus on maximized fodder production in high-intensive production grasslands, which comes at the expense of various regulating or cultural services such as groundwater protection, soil nutrient retention or aesthetics (Raudsepp-Hearne et al., 2010; Austrheim et al., 2016). Despite the strong dependence of grassland farming on the functionality of these systems, degradation of grasslands is still progressing, threatening grassland biodiversity, the provision of diversity-dependent services and reducing the multifunctionality of grasslands (Schils et al., 2022).

In Europe, the diversity of semi-natural grasslands strongly contributes to the historical cultural landscape. According to the European Nature Information System (EUNIS) the occurring semi-natural and natural grassland habitat types can be classified into seven categories: dry , mesic , seasonally wet and wet , alpine and subalpine grasslands, woodland fringes and clearings and tall forb stands, inland salt steppes and sparsely wooded grasslands (European Environment Agency, 2012). These categories reflect local differences in physical environment but also differences in traditional and modern management (Hopkins & Holz, 2006). European grasslands provide distinct habitats for a large number of plant and animal species and are considered to be local biodiversity hotspots (Habel et al., 2013). Reports range from 41 vascular plant species in non-fertilized wet grassland sites (Oelmann et al., 2009) up to 98 vascular plant species per 10 m^2 in dry meadows in Transylvania (Dengler et al., 2014). In fact, 18% of European endemic vascular plants are bound to grassland habitats (Habel et al., 2013). Dry grasslands harbour many rare and endangered species, many of which are also endemic. Mesic and wet grasslands are habitats of various taxa that are sensitive to changes in management regime, e.g. Liliaceae, Orchidaceae, Cyperaceae and Juncaceae (Török et al., 2018). Nevertheless, many of these ecologically valuable systems have been affected by declines in area and detrimental management effects at the remaining sites (Hopkins & Wilkins, 2006).

Grassland management

While grasslands were often utilized as part of complex agricultural systems in the past, management intensity had mostly been low, focusing on extensive grazing and mowing (Gilhaus et al., 2017). Grassland production largely depended on the natural fertility of the sites, as traditional management was characterised by a low nutrient input and no artificial improvement of soil fertility (Isselstein et al., 2005). This 'low-input — low-output' management (Lepš, 1999) allowed the development of a diverse vegetation including less competitive species with low to moderate nutrient demands. Only since the middle of the 20th century, management regimes shifted to more intensive pastures and meadows (Rose et al., 2012). Major changes in utilization were the use of (mineral) fertilizer and the shift from hay to silage on the more productive sites (Hopkins & Wilkins, 2006), accompanied by abandonment of low productive or less accessible sites (Critchley et al., 2003). Fertility of the soils was raised by liming and regular use of artificial fertilizers or concentrated manure based on slurry (Isselstein et al., 2005; Boch et al., 2020). In wet grasslands the implementation of drainage systems also led to intensified mowing and cattle grazing.

Nowadays, the remaining grasslands, which have not been intensified, are threatened by abandonment, habitat fragmentation or eutrophication due to atmospheric nitrogen deposition (Duprè et al., 2010; Joyce, 2014). While these land use changes are still ongoing, they already led to severe changes in composition and structure of grassland vegetation, a decrease in grassland diversity and floristic impoverishment of remaining areas (Speier, 1996; Wesche et al., 2012). Agricultural intensification is particularly associated with taxonomic and functional diversity losses and dominance of economically valuable species, i.e. competitive mowing-tolerant grasses with high fodder value (Wesche et al., 2012). These changes in sward composition can destabilize the community, leading towards a homogenization of communities and losses of specialists (Blüthgen et al., 2016; Gossner et al., 2016). Contrastingly, abandonment changes the sward structure by reducing the amount of suitable micro-habitats for the establishment of low competitive species, thus leading to a loss of specialist species as well (Rosenthal, 2010; Valkó et al., 2018).

Overall, the change in management focus in the past decades led to a decrease in grassland biodiversity and a simultaneous reduction of multifunctionality (Wesche et al., 2012; Diekmann et al., 2019; Neyret et al., 2021). Basic trade-offs occur between high intensity management focusing on production services and more extensive management aiming at biodiversity conservation (Power, 2010). While the described land use changes generally cause a reduction in biodiversity and impaired provision of multiple ecosystem services, they can also lead to invasion or expansion of alien as well as of certain native plant species, e.g. ruderal or weedy species (Prach, 2008).

Invasive species

There are several ways of defining invasive species, depending on the respective perspective (Heger et al., 2013). This research works' perspective follows an ecological point of view where the focus is set on the species' competitive advantage, which occurs after the breakdown of ecological or geographical barriers (Valéry et al., 2008). This advantage leads to a rapid spread of the species and can occur either as a result of 'a change *of* the environment […] or a change *in* the environment' (Valéry et al., 2008). Thus, both native and alien species can possess traits or characteristics of invasive species (Valéry et al., 2008). Invasive species have various impacts on resident plants' populations and communities, ecosystem services as well as regional economies (Vilà et al., 2011). They can reduce abundance of other species, decrease the plant diversity of the invaded site and alter community productivity (Vilà et al., 2011). Invasive plants can also directly affect fitness and growth of other species, contributing in the worst case to the threat of those species (Carey et al., 2012). Moreover, invasive species might also be poisonous, thus reducing forage quality and usability of the grassland site.

While the overall proportion and impact of invasive alien plant species in European grasslands is generally lower than in other habitat types (Chytrý et al., 2008), some invasive alien species can still lead to major changes. Examples are *Solidago gigantea*, *Solidago canadensis* and *Reynoutria* species (e.g. *R. japonica, R. x bohemia*)[1] which form dominant stands and drastically reduce plant species richness or even negatively influence the occurrence of invertebrates (Hejda et al., 2009). Similar consequences arise from the expansion of native species, such as *Brachypodium pinnatum, Pteridium aquilinum, Calamagrostis epigejos* or *Jacobaea spp.* which can heavily spread and become dominant in different grassland communities (Schuhmacher & Dengler, 2013; Suttner et al., 2016; Redhead et al., 2019; Schlegel & Riesen, 2021). As these species share aspects of invasion by alien species, i.e. sudden and rapid population growth and range expansion, they can be termed as 'native invaders' (sensu Carey et al., 2012).

Several attempts have been made to define the 'ideal invader' or to predict traits common to all invasive plant species (Kolar & Lodge, 2001; Cadotte et al., 2006; van Kleunen et al., 2011). While various traits have been analysed, an extensive review of comparative and congeneric multispecies studies suggests only plant height, vegetative spatial growth, specific leaf area and time of flowering as traits widely associated with promoting invasiveness (Pyšek & Richardson, 2008). Likewise, traits related to high reproductive success, i.e. high fecundity, efficient seed dispersal, easy germination and long-term seed banks, as well as higher resource capture ability and utilization efficiency positively relate to invasion success (Pyšek & Richardson, 2008). All those attributes enable invaders to occupy

[1] Nomenclature following *World Flora Online*, no date

empty niches efficiently. More importantly, alien and native invasive species showed a high functional similarity in most investigated traits (Thompson et al., 1995; Nackley et al., 2017).

Other aspects of plant invasion to be considered are the invasibility of communities and the interaction between community and invader (Richardson & Pyšek, 2006). As mentioned above, invasion can follow a competitive advantage. This advantage can either derive directly from advantageous traits or because changes in the environment open opportunities for invasion. An increase in resource availability, often induced by disturbance or reduction of competitive pressure, presents such an opportunity (Davis et al., 2000). If the fluctuation in resource availability coincides with high propagule pressure of the invader, the invasibility of communities increases (Richardson & Pyšek, 2006). As resource availability can occur independently of species richness and community productivity, neither factor can be associated with higher invasion resistance *per se* (Davis et al., 2000). Instead, biodiversity loss, community composition and species identity occur as co-varying factors of invasion success (Naeem et al., 2000; Lepš et al., 2001). The last two factors also influence the interaction between community and invader. An example is the resistance against invasion due to high competition, which can appear either through effective niche exploitation under high plant diversity or through the occurrence of highly competitive dominant species, or species functionally similar to the invader (Emery & Gross, 2007; Frankow-Lindberg, 2012). Moreover, the influence of each aspect on plant invasion, i.e. occurrence of propagule pressure, resource availability as abiotic and invader traits or community interactions as biotic characteristics of the invaded habitat, may be mediated by changes in climate or human activities, especially increasing the risk of native species to become invaders (Catford et al., 2009; Carey et al., 2012). These invasions pose severe risks, as native invaders can have similar harmful impacts on communities and ecosystems than alien invasive species (Carey et al., 2012).

Invasion management

Management of invasive species usually covers direct control measures to reduce the abundance and prevent further spread. However, as awareness rises and research advances, management approaches increasingly integrate concepts that consider relations to ecosystem processes and landscapes, and incorporate risk assessment as well as stakeholder involvement (Dehnen-Schmutz & Novoa, 2021). Traditional management measures to combat invasive species include mechanical control, such as hand-pulling, digging, mowing or grazing, use of biological or chemical control options (i.e. release of target enemies, herbicides), or suppression through revegetation (DiTomaso, 2000; Weidlich et al., 2020). Recently developed management strategies additionally include remote sensing, modelling approaches, stakeholder engagement or citizen science to predict invasion, monitor spread or define management goals according to impact and financial resources (Dehnen-Schmutz & Novoa, 2021). These integrated approaches use a combination of several control measures to enhance their effectiveness.

Depending on the applied control measures, different aspects of plant invasion can be influenced. While biological and chemical control as well as some mechanical control measures act on the invasive plant itself, land management activities aim at affecting the invasibility of communities by influencing resource availability and propagule pressure (Brooks, 2008). The practical applicability of each measure varies depending on management aim, control resources and identity and population size of the target species. For instance, hand-pulling, which is best applied for plants vulnerable to complete removal of above-ground biomass, is most effective in loose soil or for low infestations (DiTomaso, 2000). In contrast, mowing reduces carbohydrate reserves and prevents seed production (DiTomaso, 2000), but effects might only be transient (Brooks, 2008). Transient effects can also occur when chemical control agents are applied, which often have high initial effects but also negatively impact the plant community if non-selective herbicides are used (Mason & French, 2007; Gehring et al., 2022).

Besides the individual differences, effectiveness of control measures increases when applied early during invasion. When only limited financial resources are available, measures should be spatially prioritized and eventually target factors promoting invasion (Meier et al., 2014). Yet, environmental conditions or land use regulations define which management options can be applied. As a result, invasion in nature conservation areas tend to be more difficult to combat as the integrity of natural process and ecosystem properties needs to be maintained, thus excluding control measures with potential negative effects on the ecosystem (Brooks, 2008).

Using a community assembly framework to control grassland invasion

Ecological management concepts are built upon the community assembly framework and use the theoretical background of functional and community ecology to suppress invaders and enhance community resistance (Dehnen-Schmutz & Novoa, 2021). A key aspect is the modification of ecological filters, more precisely the manipulation of dispersal, environmental or biotic factors, which can be used as mechanism to decrease resource availability and increase biotic resistance (Funk et al., 2008). Underlying principles are enhancement of density-dependent resource competition and niche pre-emption by species functionally similar to the invader (Möhrle et al., 2021). In other words, higher species diversity increases niche occupation and leads to higher competition for light and nutrients, thus increasing invasion resistance at small scales (Naeem et al., 2000; Fargione & Tilman, 2005). Moreover, if the community is functionally diverse, availability of niches suitable for invasion will decrease through resource complementarity within the community and direct suppression effects of species functionally similar to the invader, also known as 'limiting similarity' (Hooper & Dukes, 2010; Frankow-Lindberg, 2012). A synthesis of studies examining limiting similarity found supportive evidence only in studies using artificial communities (Price & Pärtel, 2013). Other studies found that co-occurring factors such as dominant species identity and traits, phylogenetic relatedness, or seed density effects were more important in explaining community resistance (Yannelli et al., 2017, 2018; Möhrle et al., 2021; Rojas-Botero et al., 2021).

Studies testing the theoretical framework often focused on designing seed mixtures for the suppression of invading species during early stages of community assembly or for restoration of a native plant cover after invader control (Byun et al., 2018; Yannelli et al., 2018; Möhrle et al., 2021). Within this context, selection of species and combination of functional aspects is important to enhance effectiveness (Byun et al., 2018). Alternatively, altering management regimes and nutrient supply directly focuses on establishing dispersal or environmental filters, e.g. enhancing competition for light through development of a closer canopy (Hautier et al., 2018). Nevertheless, practices such as adaptation of mowing intensity and cutting time, or modified fertilization strategies act on functional trait composition and species occurrence by influencing plant diversity and abundance (Oelmann et al., 2009; Humbert et al., 2012). In fact, adaptation of mowing regimes reportedly reduced abundance and fecundity of invasive species (Bassler et al., 2016; Nagy et al., 2022).

Besides the desired suppression of the invader, such management practices can negatively affect important characteristics of the local plant community such as species composition, evenness, and richness (Chapin et al., 2000). For example, delayed mowing or mulching instead of mowing may lead to a shift in the proportions of functional groups, usually with an increase in the abundance of monocotyledons (Seither & Elsässer, 2014; Bassler et al., 2016). In addition, grassland abandonment can result in competitive shifts, including local elimination of species (Joyce, 2014). Indeed, both abandonment and high fertilization can lead to a dominance of tall graminoids (Klimeš & Klimešová, 2002). Such negative impacts raise concerns about maintaining the conservation value of grasslands managed to control invasive species. Nevertheless, depending on the intensity and duration of control measures and the productivity of the managed grassland, suppression effects and their consequences for plant communities may differ (Poptcheva et al., 2009; Skurski et al., 2013). In the short term, losses in species numbers may be marginal and thus tolerable, while the suppression of invaders is already more pronounced (Seither & Elsässer, 2014; Bassler et al., 2016). As a result, ecological management concepts should be evaluated not only in terms of control success, but also in terms of their impact on plant diversity and community composition.

Study system: Wet grasslands

The research presented in this thesis was conducted in pre-alpine wet grasslands in Southern Germany. As biologically diverse ecosystems, wet grasslands play an important role for both, conservation and agriculture (Joyce et al., 2016). The interplay of temporarily high groundwater levels with occasional flooding and regular management by grazing or mowing shaped the characteristic, species-rich vegetation of these mostly semi-natural grasslands (Joyce et al., 2016). Traditionally, wet grasslands were managed at low intensities. More productive and dryer sites were usually grazed or used for hay making during summer, whereas undrained very wet sites were hand-cut and the obtained material was used for livestock bedding due to its low nutritional quality (Middleton et al., 2006). Wet grasslands are important habitats for many endangered plant and animal species adapted to the unique ecosystem characteristics (Oelmann et al., 2009). They are characterized by an abundance of graminoid species (often sedges and rushes) and vary in species diversity depending on habitat heterogeneity and plant community diversity (Edwards & Kučera, 2019). Furthermore, wet grasslands provide various ecosystem services such as carbon sequestration, water retention (including flood attenuation and groundwater recharge), erosion protection, and recreational benefits (Joyce & Wade, 1998).

Whereas most of these grasslands depend on low intensity use to persist, they are currently threatened by abandonment on the one hand, and intensification including drainage, higher mowing frequency, use of fertilizer and herbicides or destruction through ploughing on the other hand (Kołos & Banaszuk, 2021). Recent estimates suggest a decline in wet grassland of up to 80% during the 20th century (Joyce, 2014), mostly due to drainage, fertilization, and land use conversion (Prach, 2008). The remaining wet grasslands suffer from a decline in their characteristic diversity because traditional management is no longer profitable (Joyce & Wade, 1998; Čop et al., 2009). Several studies report losses of rare and endangered species, and a significant decrease in mean species richness of monitored plots (Rosenthal, 2010; Immoor et al., 2017; Diekmann et al., 2019), while abundance of common species is also declining (Krause et al., 2014). Trait-wise, species with low nutrient demands, insect-pollinated species and indicators of wet grasslands were replaced by more competitive, nitrogen-demanding species (Krause et al., 2014; Immoor et al., 2017). These changes lead to an unbalanced species composition favouring further habitat degradation and facilitating plant invasions.

Although grasslands generally contain low amounts of neophytes in their species composition, wet grasslands are among the most-invaded grassland types (Chytrý et al., 2008; Axmanová et al., 2021). Examples of frequent neophyte species in wet grasslands are *Solidago gigantea, Epilobium ciliatum* and *Impatiens glandulifera* (Axmanová et al., 2021). Moreover, invasion by tall competitive natives such as *Phragmites australis* or *Filipendula ulmaria* is reported as a consequence of land use abandonment (Rosenthal, 2010; Berg et al., 2012). Meanwhile, the expansion of species detrimental to grassland use leads to higher risk of abandonment and further changes in resident plant communities due to altered competition (Nackley et al., 2017). Examples are poisonous species such as *Colchicum autumnale* or *Senecio* and *Jacobaea* species, which reduce the economic value of affected grasslands (Winter et al., 2014; Suttner et al., 2016). Large abundances often result in either land use intensification or abandonment and thus further deterioration of the grassland state (Winter et al., 2014).

Challenge of managing invasive native species

Current research mostly focuses on invasion potential, invasion pathways, and management of alien species, while tackling native invasions will gain importance due to ongoing anthropogenic disturbances (Nackley et al., 2017). Thus, insights into the causes and details of change are needed to develop appropriate management concepts (Bielfelt & Litt, 2016). However, management of native invaders often faces additional challenges as species impacts are often not well documented or established control systems are missing. Moreover, definition of objectives can be challenging as conflicting interests emerge more often (Carey et al., 2012; Muñoz-Vallés & Cambrollé, 2015). For example, depending on the public interest on the target species, social perception can influence or question management objectives and decrease support of control measures (Carey et al., 2012). In addition, the perception of a native species being invasive depends on the location (Carey et al., 2012), which increases the difficulties for research and management. Understanding the mechanisms leading to a native species becoming invasive is crucial to develop appropriate management strategies. As these species have their role within their ecosystems, management goals must differ from strategies targeting alien invasive species where the goal is complete elimination (Bielfelt & Litt, 2016).

Consequently, the aim is to reduce the abundance of the native invader and minimize negative impacts on other native plants and the resident community (Bielfelt & Litt, 2016). Management approaches based on ecological knowledge can reduce negative impacts and provide suitable methods of invader control (Booth et al., 2003). For instance, if the physiological response of the invader to changes in various resources is known, management approaches can be developed that translate these responses into control strategies based on community assembly theory (Pearson et al., 2018). According to this theory species composition and abundance are determined by a series of filters acting on the species traits (Pearson et al., 2018). Phytosociological surveys can be used to measure reduction success and to examine possible additional changes in the plant community of the managed sites. Furthermore, data analysing potential impacts on ecosystem processes and functions should also be included in the assessment of measures (Edwards & Kučera, 2019). This can help to develop the best possible management options and rule out negative trade-offs.

OBJECTIVES OF THE PhD THESIS

The aim of this thesis is to explore the scientific background for sustainable management of native invasive plants. Based on the theoretical foundation of the community assembly framework, modification of ecological filters should be used to enhance competition for key resources, thus reducing the abundance of native invasive plant species without negatively affecting plant diversity and multifunctionality of the respective grasslands.

The native invasive *Jacobaea aquatica* was used as a study species. This light-demanding species naturally occurs in wet grasslands of Central Europe. In recent decades, regional abundances of *J. aquatica* have increased considerably, leading to serious problems in grassland use. The goal of this study was to evaluate different control strategies to reduce *J. aquatica* abundance in terms of their effectiveness and impact on the conservation value of the resident communities. Within the pre-alpine region of Allgäu in Southern Germany, wet grassland sites of different productivity and usage were selected representing a gradient of site conditions within the ecological amplitude of the study species. Based on the idea of influencing environmental as well as biotic filters to reduce invader establishment and performance, different treatments aiming at high competition for light and creation of dense swards were established.

By monitoring not only the abundance of the study species but also investigating changes in community composition and grassland multifunctionality, the thesis aims at new insights into the possibilities and consequences of measures designed to control *J. aquatica*. More specifically, the objectives are to:

1) Quantify the effects of shading on *J. aquatica* performance and assess whether competition for light is an effective control option in the field;
2) Estimate possible trade-offs between the control of *J. aquatica* and species richness and functional composition of the plant community; and
3) Predict the influence of control measures on the provision of different ecosystem services and ecosystem multifunctionality.

The results contribute to identify sustainable control options for the studied species and to develop a management guide for practitioners. More importantly, the research conducted can provide a framework to develop scientifically sound management recommendations for other native invasive species as well.

OUTLINE OF THE PhD THESIS

Starting with an introductory and methodology section, the cumulative PhD thesis includes a summary of each publication (Publication 1–3) constituting this thesis and is completed by a discussion and conclusion section covering and combining the different aspects of the topic. The three publications assess distinct aspects of the described objectives covering a gradient between controllability and complexity. While **Publication 1** focuses on the effects of the developed management methods on the target species, **Publication 2** investigates the induced changes in community composition, and **Publication 3** evaluates the consequences on grassland multifunctionality (Fig. 2).

More specifically, **Publication 1** (Krieger, Ditton, Albrecht, Linderl, et al., 2022) studies the effects of enhanced shading and other site conditions on *J. aquatica*. It assesses the consequences of reducing light quantity on the survival, growth and generative reproduction of *J. aquatica* plants under controlled greenhouse conditions and compares them to monitored changes in the field. **Publication 2** (Krieger, Ditton, Albrecht, Baaij, et al., 2022) reports on the changes in abundance of *J. aquatica*, dicotyledons and monocotyledons under different management treatments. Moreover, changes in functional diversity indices and species richness are discussed. In **Publication 3** (Krieger et al., 2023), indicators of ecosystem services associated with productivity and conservation were correlated to different management intensities. The thresholds of service supply of each indicator at different management intensities were analysed together with the comparison of overall grassland multifunctionality at different threshold levels and management intensities.

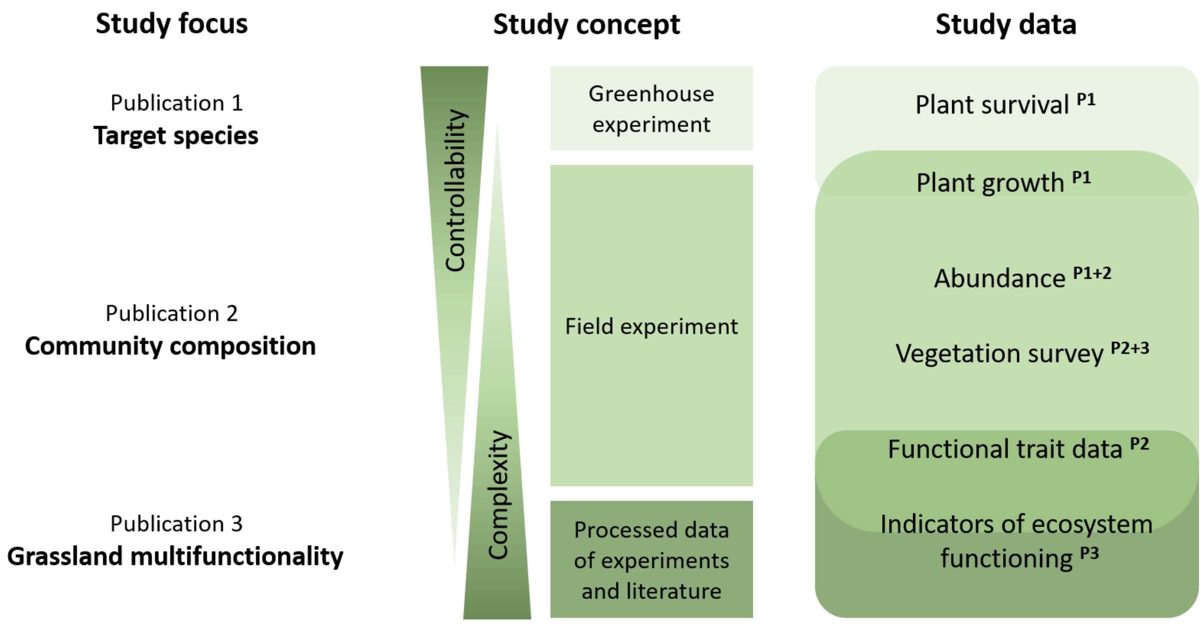

Fig. 2: Graphical overview of the PhD thesis presenting the different study foci, the underlying concepts and experiments, and the datasets used in the respective publications**.**

MATERIAL AND METHODS

Study species

Jacobaea aquatica (Hill) G. Gaertn., B. Mey. & Scherb.[2] (syn. *Senecio aquaticus*, marsh ragwort) is a biennial to short-lived perennial hemicryptophyte occurring in wet grasslands (Wagenitz, 1987). The member of the Asteraceae family can grow up to 60 cm, its basal leaves are oval with broad to lanceolate end sections (Lauber et al., 2018). *J. aquatica* usually germinates in spring or autumn, hibernates as a rosette and in its second year produces shoots with several yellow flower heads (see Fig. 3 +Fig. 4 for a detailed overview of the life cycle). The main flowering period is from late June to late August and cut plants are able to quickly regenerate lateral shoots which produce new flower heads (Bassler et al., 2017). Each flower head produces several hundred seeds which are wind-dispersed mainly over short distances and which can form highly persistent soil seed banks. Seeds are also able to germinate quickly and numerously under favourable conditions (Suter & Lüscher, 2008, 2012). Similar to other ragwort species, all parts of *J. aquatica* contain different toxic compounds. Most problematic are pyrrolizidine alkaloids, such as the name-giving senecionine or jacobine, as they accumulate in the liver, and carry-over into milk is possible (Gottschalk et al., 2018). Moreover, these toxins are persistent in hay and silage (Chizzola et al., 2018).

J. aquatica is native to Central Europe, and widely distributed in Germany. While its distribution in Northern Germany is declining, leading to it being classified at the early warning stage of the Red List in Germany (Romahn et al., 2021), the species has recently become more abundant in the pre-alpine regions of Southern Germany, Austria, and Switzerland where it locally forms dominant stands (Suter & Lüscher, 2011; Suttner et al., 2016; Fig. 5). These local hotspots cause essential problems to farmers managing affected grasslands as the contaminated material poses the risk of poisoning to livestock and humans.

Preferring moist to wet, nutrient-poor site conditions (Leuschner & Ellenberg, 2017), the light-demanding, early-successional species is favoured by frequent disturbances and low to moderate nitrogen fertilization (Forbes, 1976; Suter & Lüscher, 2008). Furthermore, changes in grassland composition following drainage or rewetting could help creating new ecological niches supporting further expansion. Where large abundances of *J. aquatica* are present, sites are prone to abandonment because population control is difficult, and the economic value of the sites is reduced. Although productivity is not the primary focus of the grasslands studied in this thesis, the problem remains as these species-rich sites rely on continuous management to persist. Recommended applications to

[2] accepted name according to *World Flora Online*, no date

control ragwort include hand-pulling and mechanical or chemical control, which are either very time-consuming or cannot be performed on nature conservation grasslands. Based on a community assembly framework, the present study tested different management strategies to reduce the abundance of *J. aquatica* such as temporary abandonment, decreased mowing intensity or mowing during peak flowering.

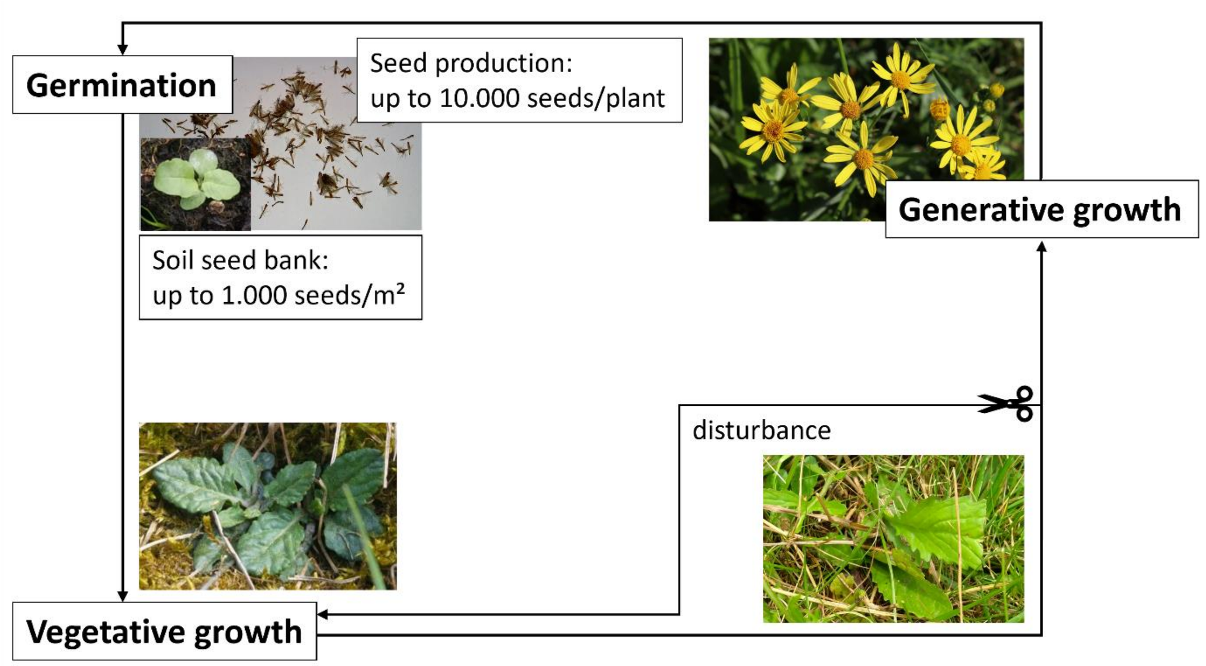

Fig. 3: Life cycle of *Jacobaea aquatica*. The species germinates quickly under favourable conditions and usually hibernates as a rosette. Several flower heads are built in the second year, producing several hundred seeds. Though the species is mainly biennial, it can become perennial under disturbance.

Fig. 4: Habitus of *Jacobaea aquatica.* From upper left to lower right: Emerging seedlings at open soil following management with heavy machines; *J. aquatica* rosette growing at a wet grassland site; the yellow flower heads are easily spotted during July and August; the species can already flower at low heights, given that enough light is available.

Fig. 5: Overview of an experimental grassland site near Stötten am Auerberg. The picture depicts the situation at the start of the project in which the site was heavily infested with *J. aquatica,* which dominated the vegetation.

Study area and experimental sites

Data for this thesis were sampled from 2018 to 2021 in 13 pre-alpine wet grasslands across the Allgäu region, Southern Germany. The study area spread over a range of around 76 km from East to West and 27 km from North to South. Altitude of the sites ranged from 576 to 843 m a.s.l. with mean annual temperatures of 8.1–10.0 °C and annual precipitations of 948–1469 mm during the study years (DWD - Deutscher Wetterdienst, no date; Table 1). All studied grasslands lie in historic fen areas which had been drained for a long time to enable peat extraction and grassland usage, and old ditches still exist although no longer maintained. Nevertheless, the studied grasslands were characterized by high soil organic matter and wet conditions, and sites were typically managed in compliance with nature conservation regulations or as ecological compensation sites. Based on the estimated annual yield as indication for productivity and the preceding mowing frequency, sites were split into seven 'low productive sites' with agricultural usage and conservation schemes (around 60–80 dt ha^{-1} yr^{-1} dry matter yield) and six 'very low productive nature conservation sites' (≤40 dt ha^{-1} yr^{-1} dry matter yield; Fig. 6; Table 1).

The field data of the first two publications were extended to include sampling of seven additional agricultural grassland sites monitored from 2017 to 2020 in the same region as part of the associated project 'Effective management of marsh ragwort in production grasslands', a cooperation between the Technical University of Munich (TUM) and the Bavarian State Research Institute for Agriculture (LfL) (Gehring et al., 2021). With mowing up to four times a year, the sites of this second experiment were classified as 'moderately productive' (Fig. 6; Table 1). As these sites spread more than 50 km from North to South, and include altitudes between 625 and 1060 m a.s.l., they distinctly broaden the extend of the study area. Moreover, their higher productivity (≥80 dt ha^{-1} yr^{-1} yield) makes it possible to draw conclusions which apply to the entire range of extensively used pre-alpine wet grasslands in Germany.

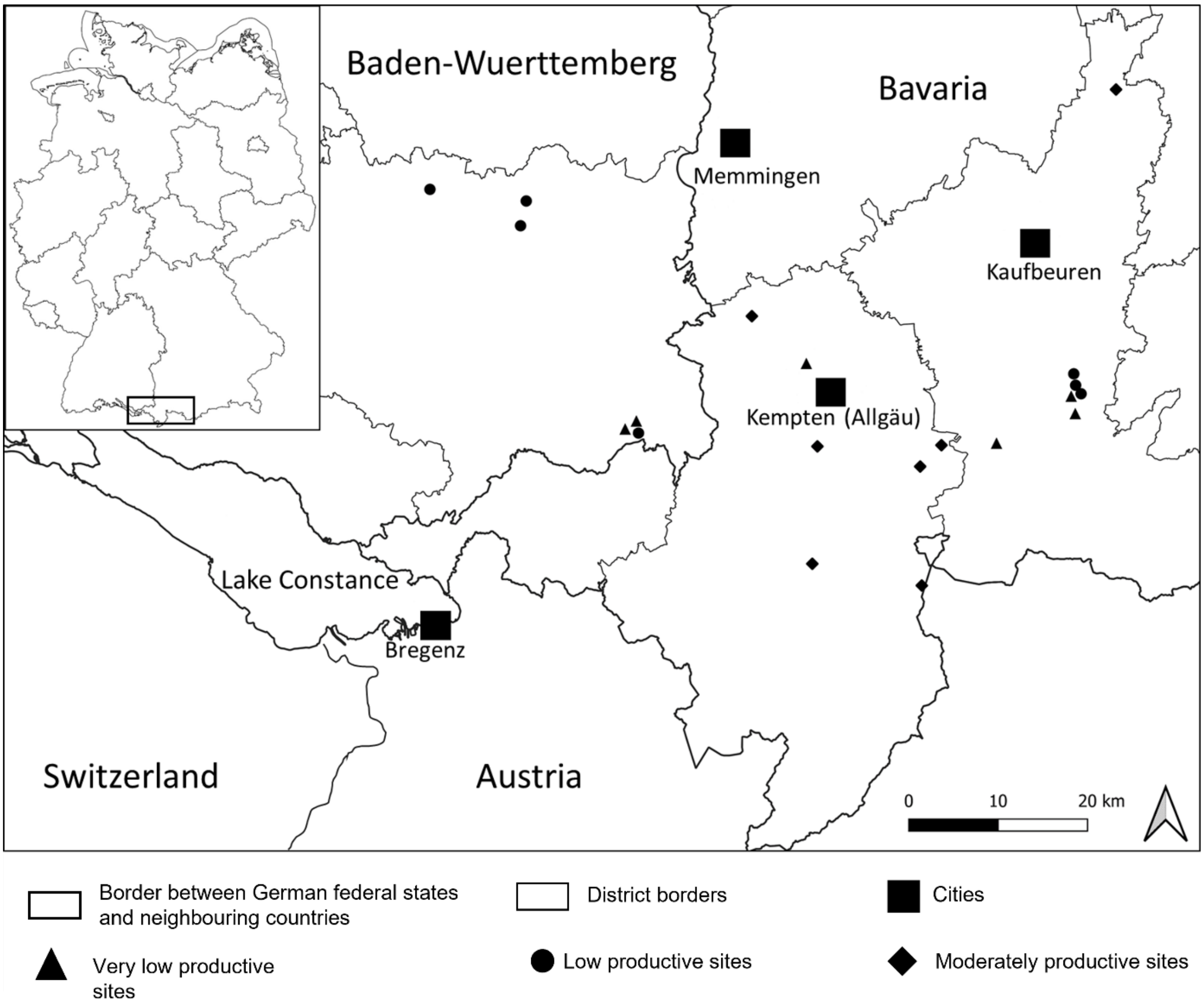

Fig. 6: Map of the study area showing the location of the experimental sites in the pre-alpine region of Southern Germany. Depending on their estimated productivity and preceding land use, sites were categorized as very low (triangles), low (circles) and moderately productive wet grasslands (diamond).

With average species numbers of 18 (low productive sites) to 20 (very low as well as moderately productive sites) per 22 m^2, the studied grasslands represent the lower range of values reported for wet species-rich grasslands in Europe by Oelmann et al. (2009) (18–41 species) and Venterink et al. (2001) (17–27 species). Species numbers are comparable to those of re-visitation studies in Northern to Central Germany (12–24 species; Diekmann et al. (2019)). The most common species were *Anthoxanthum odoratum*, *Holcus lanatus*, *Plantago lanceolata*, *Ranunculus acris*, *Trifolium pratense* and *Trifolium repens* (nomenclature following *World Flora Online*, no date). Typical wetland species such as *Caltha palustris*, *Carex nigra*, *Equisetum palustre*, *Juncus effusus*, *Myosotis scorpioides*, *Rhinanthus minor* or *Silene flos-cuculi* were less abundant, but still occurred at more than one fourth of the sites. At the start of the projects, high abundances of *J. aquatica* occurred on all sites (3 ± 1 to 40 ± 13 plants m^{-2}).

Table 1: Characteristics of the studied wet grasslands sites in the two experiments on control of the native invader *Jacobaea aquatica*. Provided are coordinates, altitude, mean annual temperature and precipitation of the study years (2018–2021 and 2017–2020) as well as soil type and percentage of soil organic matter [SOM] (MlSOM, mineral soil with 4–15% SOM; MhSOM, mineral soil with 15–30% SOM; peat, organic soil with >30% SOM; soil analyses done by AGROlab). Regionally common land use and estimated yield were used for categorizing the sites according to productivity. Table adapted from Krieger, Ditton, Albrecht, Baaij, et al., 2022; Krieger, Ditton, Albrecht, Linderl, et al., 2022.

	Site name	Coordinates	Altitude (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Soil type	Organic matter (%)	Management
Very low productive conservation sites	Heggen	47.70504 10.67289	730	8.9	984	MhSOM	22.1	Mowing 1–2 times a year, earliest cutting date July; < 4 t/ha dry matter harvest
	Holzleuten	47.67687 10.55461	843	8.1	1469	MhSOM	24.9	
	Isny 1	47.69696 10.01412	681	8.4	1112	peat	39.3	
	Isny 2	47.69477 10.02185	684	8.4	1112	MhSOM	30.0	
	Kempten	47.76065 10.27327	708	8.9	1194	peat	54.4	
	Stötten 1	47.725318 10.680817	729	8.9	984	peat	32.5	
Low productive agricultural sites	Isny 3	47.693094 10.021367	684	8.4	1112	MhSOM	27.7	Mowing twice a year, earliest cutting date mid-June; 5-8 t/ha dry matter harvest
	Riedschmiede	47.903249 9.849024	649	8.4	1112	MlSOM	11.9	
	Schlupfen	47.94084 9.7139	576	10.0	948	peat	43.4	
	Stötten 2	47.733443 10.674346	726	8.9	984	peat	36.1	
	Stötten 3	47.73478 10.67444	728	8.9	984	peat	39.2	
	Stötten 4	47.72495 10.68217	733	8.9	984	MhSOM	28.6	
	Ziegolz	47.92812 9.85793	650	8.4	1112	MhSOM	16.5	

	Site name	Coordinates	Altitude (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Soil type	Organic matter (%)	Management
Moderately productive agricultural sites	Altusried	47.809133 10.193072	701	8.6	1083	MhSOM	27.7	Mowing 3–4 times a year; > 8 t/ha dry matter harvest
	Buchloe	48.030340 10.74456	625	9.7	833	MhSOM	20.1	
	Oberschwarzenberg	47.675968 10.472537	879	8.3	1525	MhSOM	17.7	
	Rettenberg	47.558868 10.277223	728	8.3	1525	MhSOM	22.8	
	Unterjoch	47.535049 10.439386	1060	7.8	1713	MhSOM	17.1	
	Waltenhofen	47.6769783 10.2877216	714	8.3	1525	MhSOM	23.9	
	Wasenmühle	47.654866 10.440297	887	8.3	1525	MhSOM	16.6	

Study design and data sampling

Field experiment

Experimental set-ups of the first experiment included one plot per applicable treatment combination at each site (3.7 m × 6.0 m). The size of 22 m² per plot corresponds to the recommended area for vegetation sampling in grasslands (Dierßen, 1990). Treatment plots were arranged in one row and within each plot, three randomly chosen 1-m² subplots were marked with magnets buried in the soil (Fig. 7–9; Fig. 11). Reference plots representing the development under current farming conditions were marked close to the experimental set-up at each site.

In 2018, different praxis-oriented combinations of mowing and fertilization were developed in cooperation with local experts (Table 2). Treatments were designed to create high competition for light and to prevent gaps in the sward, application depended on the land use classification. At the very low productive sites, management was based on a short-term cessation of mowing and a reduced mowing frequency. At the low productive sites, control measures included delay of the first cut as well as mowing during the main flowering period. Management was mainly reduced during the first years of the experiment (2018 and 2019) and adjusted over time to a subsequent land use to evaluate the sustainability of the initial suppression effect. Regionally common management following the preceding mowing frequencies at each productivity level was used as reference.

A management intensity index was created to categorize the 14 treatments (Table 2). The intensity index was obtained by weighing and summing up all mowing events. Depending on the date of mowing, each event was assigned a certain weight with mowing earlier in the year ranked higher as it affects plant development more than late-seasonal mowing (Krieger, Ditton, Albrecht, Baaij, et al., 2022). While the index covers a wide range of intensities, from 5 (fallow 3 yr.) to 48 (3-times cut), it also confirms the generally low management intensity derived from the low productivity of the studied grasslands (Krieger et al., 2023).

During the four study years 2018–2021, vegetation surveys were conducted in the beginning of June, before the first cut. In each plot, cover of aboveground vascular vegetation, mosses, litter and soil were estimated. In addition, relative cover of each occurring species was recorded (percent of total cover). The chosen method allows detecting small changes in species occurrence and improves comparability between sites (Peratoner & Pötsch, 2015). To be able to track the development of *J. aquatica* population over the years, abundance of vegetative and generative *J. aquatica* plants per subplot was counted in beginning of June, August, and October. At these occasions, also plant fitness of vegetative and generative plants was recorded. In each subplot, three vegetative and three generative plants (three each for generative with buds and generative with flower heads) were randomly chosen and rosette diameter, plant height and total number of flower heads and seed heads were recorded. Before the respective plots were mown, biomass of 1 m² per plot was cut manually at a height of 8 cm. Samples were separated into *J. aquatica* biomass and biomass of the remaining vegetation and were weighted before and after drying at 100 °C for 24 h to calculate yield (kg m^{-2}).

A similar experimental set-up was used in the second experiment established on moderately productive grassland sites. From 2017 to 2020, different combinations of mowing and fertilization were tested on their effectiveness to reduce the abundance of *J. aquatica* (Table 3; Fig. 10). Vegetation data of each plot were collected each year in May, before first mowing and data on the abundance and growth of *J. aquatica* and the available PAR (**Publication 1**) were collected shortly before the respective mowing dates in 2019 and 2020.

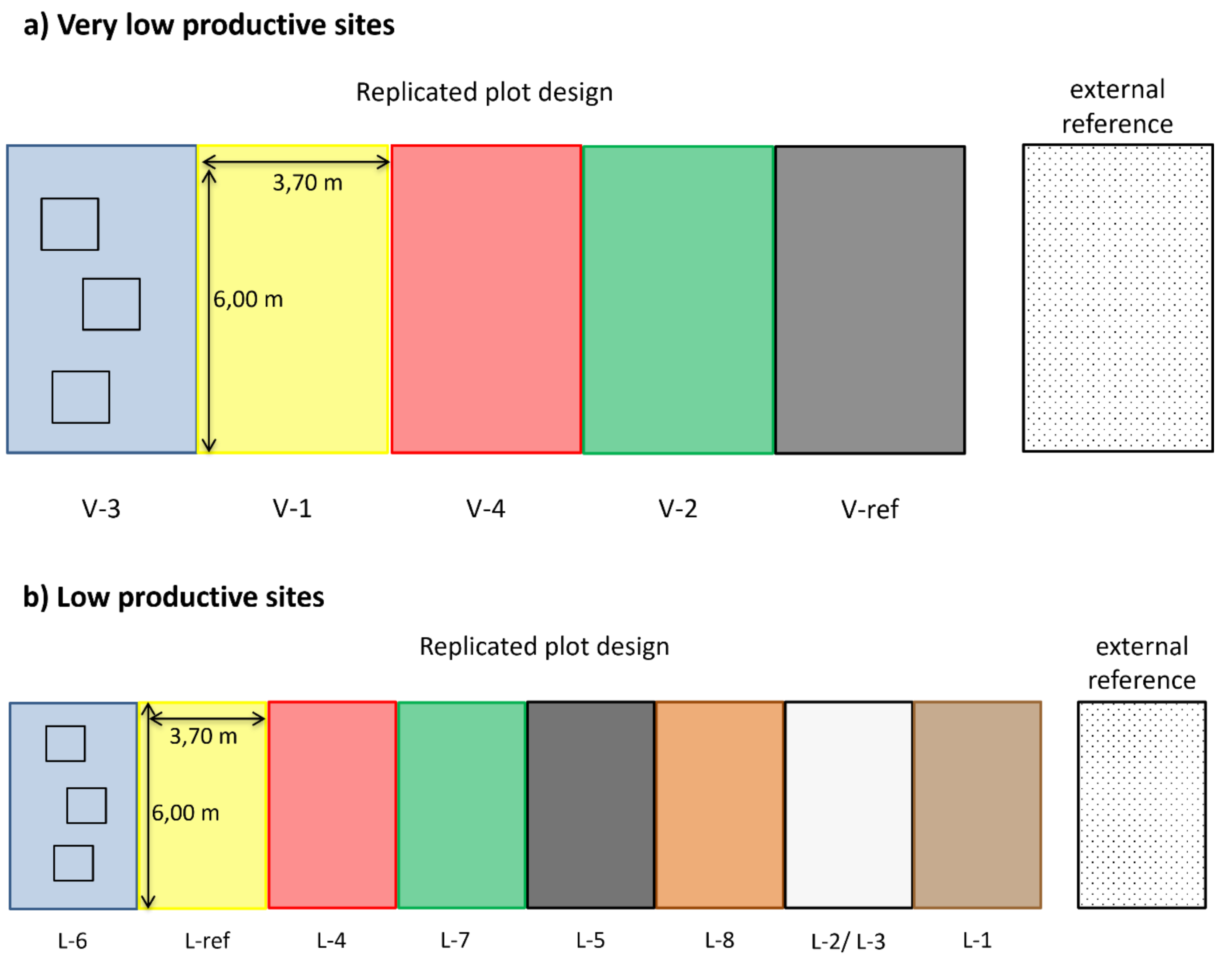

Fig. 7: Overview of the experimental set-up at very low and low productive sites.
At each site, treatments were established in a row to ensure workability. Plots were marked with wooden posts in different colours for quick differentiation.

Table 2: Overview of the experimental treatments and their management intensity within the field experiment on control of *Jacobaea aquatica* in very low and low productive wet grassland. The management intensity index was used to present the results in Publication 2 and 3. To calculate the index each cutting event was weighted according to the month it occurred (highest intensity in mid-June (6) and lowest intensity in mid-October (1)) and total number of weighted events was summed up. Table adapted from Krieger, Ditton, Albrecht, Baaij, et al. (2022); Krieger et al. (2023).

	Code	Treatment name	Treatment details	Month of cut weighted	Management intensity grade
Very low productive sites	V-1	Fallow (3 yr.)	Three yr. fallow, cut July (4th yr.)	0+0+0+5	5
	V-2	Fallow (1 yr.), late seasonal cut	One yr. fallow, cut Sept (2nd, 3rd, 4th yr.)	0+2+2+2	6
	V-3	Fallow (1 yr.), early seasonal cut	One yr. fallow, cut July (2nd + 3rd, 4th yr.)	0+5+5+5	15
	V-4	Late cut August	One late cut mid Aug, 100dt/ha manure (2 yr.), cut July + manure (3rd, 4th yr.)	3+3+5+5	16
	V-ref	Reference treatment	Two cuts July + Sept (4 yr.)	(5+2)x4	28
Low productive sites	L-1	Late cut October (3 yr.)	One late cut mid Oct (3 yr.), cut July + Sept (4th yr.)	1+1+1+5+2	10
	L-2	Fallow (2 yr.)*	Two yr. fallow, cut July + Sept (3rd, 4th yr.)	0+0+5+2+5+2	14
	L-3	Fallow (1 yr.)*	One yr. fallow, cut Sept (2nd yr.) cut July + Sept (3rd, 4th yr.)	0+2+5+2+5+2	16
	L-4	Late cut October (2 yr.)	One late cut mid Oct (2 yr.), cut July + Sept (3rd, 4th yr.)	1+1+5+2+5+2	16
	L-5	Late cut August	One late cut mid Aug (2 yr.), cut July + Sept (3rd, 4th yr.)	3+3+5+2+5+2	20
	L-6	Cut June with shift	One early cut mid-June (2 yr.), cut July + Sept (3rd, 4th yr.)	6+6+5+2+5+2	26
	L-7	Cut June	One early cut mid-June (2 yr.), cut mid-June + mid Aug (3rd, 4th yr.)	6+6+6+3+6+3	30
	L-ref	Reference treatment	Two cuts mid-June + mid Aug (4 yr.)	(6+3)x4	36
	L-8	Three-times cut	Three cuts mid-June + mid-July + Sept (4 yr.)	(6+4+2)x4	48

*Plots had to be split by sites as treatments could only be implemented on part of the sites (fallow (2 yr.): n = 4; fallow (1 yr.): n = 3).

Table 3: Overview of the experimental treatments within the field experiment on control of *Jacobaea aquatica* in moderately productive wet grassland. Treatments used in Publication 2 were assigned to a management intensity grade, further treatments used in Publication 1 were not categorized; treatment codes were adapted from the publications (table adapted from Krieger, Ditton, Albrecht, Baaij, et al. (2022); Krieger, Ditton, Albrecht, Linderl, et al. (2022)).

	Code	Treatment name	Treatment details	Treatment used in publication	Assigned management intensity grade
Moderately productive sites	M-1	Reduced cutting	Two cuts (July, Oct), 20 m³/ha slurry	P1+2	Low
	M-2	Skip of first seasonal cut	Three cuts (July, Aug, Oct), 40 m³/ha slurry	P1+2	Medium
	M-3/ M-ref	Reference treatment	Four cuts (May, July, Aug, Oct), 40 m³/ha slurry	P1+2	High
	M-4	Mulching (regular fertilization)	Two cuts (May, Aug), 40 m³/ha slurry; Two times mulching (July, Oct), 40 m³/ha slurry	P1	-
	M-5	Mulching (increased fertilization)	Two cuts (May, Aug), 40 m³/ha slurry; Two times mulching (July, Oct), 60 m³/ha slurry	P1	-

Fig. 8: Overview of the experimental site at a very low productive wet grassland south of Stötten am Auerberg, Bavaria (DE). The white sticks in the experimental plots mark the corners of the subplots.

Fig. 9: Overview of the experimental site at a low productive wet grassland south of Stötten am Auerberg, Bavaria (DE).

Fig. 10: Overview of the experimental site at a moderately productive wet grassland near Rettenberg, Bavaria (DE). The slurry tank used for the fertilization of the treatments can be seen in front of the marked treatment area.

Fig. 11: A metal frame was used for counting *Jacobaea aquatica* plants per square metre. The white sticks mark the edges of the subplot which were marked with soil magnets.

Greenhouse experiment

To assess the effects of light reduction on *J. aquatica*, a shading experiment was conducted in an unheated greenhouse at the Greenhouse Laboratory Center Dürnast (GHL), Technical University of Munich, Freising (Krieger, Ditton, Albrecht, Linderl, et al., 2022). Thirty plants with similar rosette size were collected from the experimental site in Waltenhofen in April 2018. Plants were transplanted into single pots which were randomly placed on the greenhouse tables. Customary shading nets (Fa. HaGa-Welt) were used to simulate the reduction in light quantity. Shading was simulated from end of April to mid-July. Treatments were set to 40, 60 and 85% shading following the manufacturer specifications. 100% light reduction was simulated using double layers of 85%-shading nets while control treatments were not covered (Fig. 12).

Once per month, photosynthetic active radiation (PAR) of natural lightning above and below the nets was measured to validate the given specifications. Light measurements took place between 10^{am} and 4^{pm} and times with shifting clouds or rainy days were avoided. Plant fitness was checked weekly. For this purpose, survival rates, rosette diameter, plant height and number of flower heads and seed heads per plant were collected. More detailed information of the experimental set-up can be obtained from Krieger, Ditton, Albrecht, Linderl, et al. (2022) and the respective project report (Gehring et al., 2021).

Fig. 12: Experimental set-up of the shading experiment in the Greenhouse Laboratory Center Dürnast. Customary shading nets were stretched over the pots to simulate defined light reduction. Plants were measured regularly to assess shading effects on vegetative growth and reproduction traits.

Datasets used in the publications

For **Publication 1**, available PAR was measured in the field, while surveying *J. aquatica* individuals. Data sampling took place in June and August 2019 and 2020, before mowing. These dates were chosen to account for seasonal variation and assess differences between treatments. PAR was measured three times per subplot, ensuring that data were recorded only at times without rain or shifting clouds. To assess the degree of shading, measurements were taken above the canopy and at rosette level using a Li-Cor Photometer (Li-189). Data of the environmental variables 'altitude', 'precipitation', 'temperature' and 'grassland productivity number', i.e. an indicator of the potential productivity of the respective grassland site (Deutscher Bundestag, 2007) were taken from the respective databases (*BayernAtlas-plus*, no date; DWD - Deutscher Wetterdienst, 2017) and together with the estimated disturbance frequency completed the field data used in this publication. Results were compared to the data derived from the greenhouse experiment.

In **Publication 2**, data of the vegetation surveys at the start and the end of the studies (2017 and 2020; 2018 and 2021) were used to present changes in *J. aquatica* abundance as well as changes in community composition and species richness after three years of altered management. To characterize plant community changes, abundance of monocots and dicots was determined, and functional diversity indices 'functional dispersion' and 'functional redundancy' were calculated. Functional dispersion measures trait differentiation among resident plants and gives the functional dissimilarity of a community (Laliberte & Legendre, 2010) whereas functional redundancy is a measure of functional similarity giving the possible interchangeability of species supplying similar ecosystem functions (Ricotta et al., 2016).

Publication 3 combines field data and literature to assess eleven different indicators of ecosystem services. Data of the vegetation surveys were used to extract the total number of species per plot and the number and cover of insect-pollinated plant species (Landolt et al., 2010), number of wetland specialist plants(BUND Naturschutz, no date; Prunier et al., 2019) and cover of legumes per plot for each year (2018–2021). We further calculated weighted fodder values and Ellenberg indicator values for moisture (Dierschke & Briemle, 2002; Leuschner & Ellenberg, 2017) and retrieved the total yield per plot and year to complete the dataset.

MANUSCRIPT OVERVIEW

The thesis contains three publications, for which the status of the publication process, the contribution of all authors, a graphical abstract and a brief summary are given:

PUBLICATION 1: Effects of shading and site conditions on vegetative and generative growth of a native grassland invader

Krieger, M.-T.*, Ditton, J.*, Albrecht, H., Linderl, L., Kollmann, J. & Teixeira, L.H. (2022): Effects of shading and site conditions on vegetative and generative growth of a native grassland invader. *Ecological Engineering*, 178, https://doi.org/10.1016/j.ecoleng.2022.106592 (* equal contribution)

Author contributions

HA, JK, JD, **MTK** and LL designed the research. JD, **MTK**, LL and LHT performed the experiments and monitored the field sites. LHT analysed the data with support from **MTK**. **MTK**, JK, LHT, JD and HA wrote and edited the manuscript. All authors agreed on the submitted version.

Graphical abstract

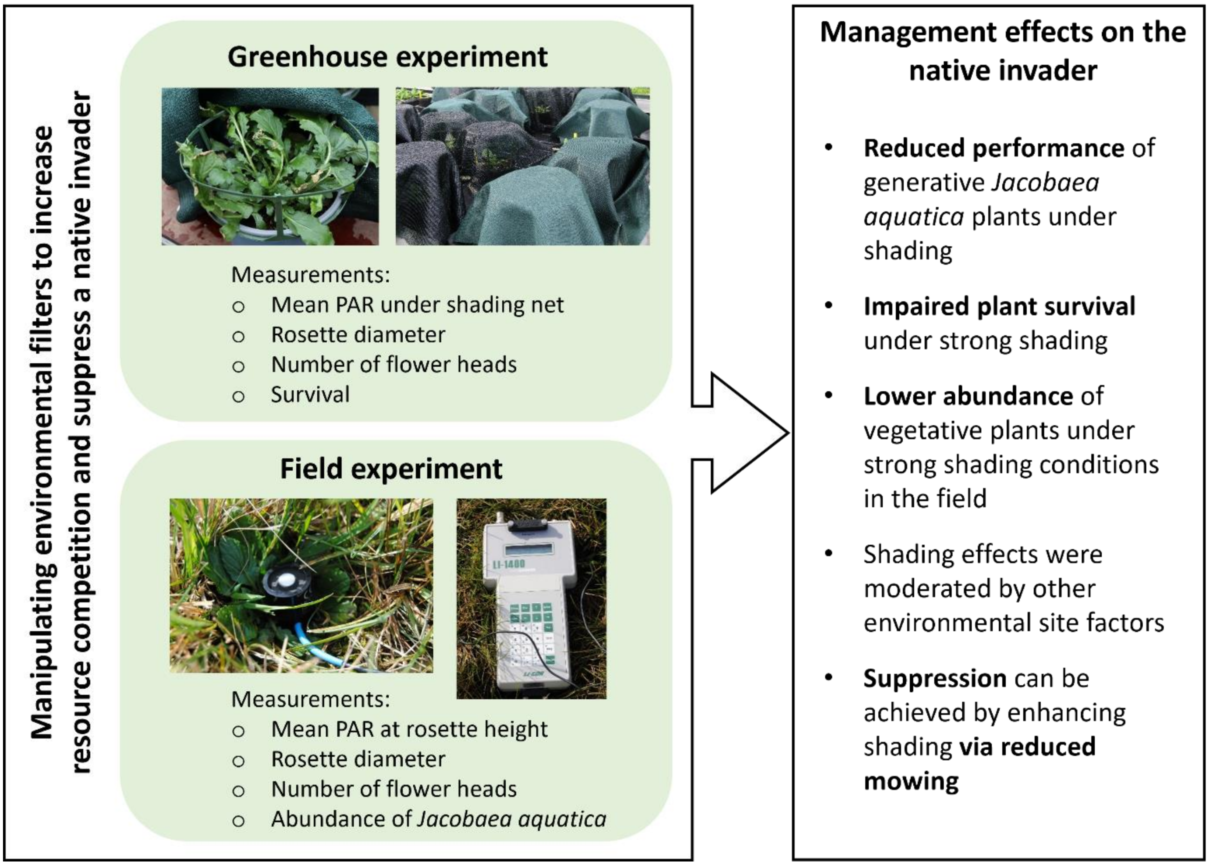

Fig. 13: Effects of shading on growth and abundance of the native invader *Jacobaea aquatica.*
The reduction in light was realized by different shading nets (greenhouse) or reduced mowing frequency (field experiment). Plant fitness and photoactive radiation (PAR) were measured and compared between experiments.

Summary

Wet grasslands suffer from both land use intensification and abandonment. These changes in the traditional low-intensity management lead to alterations in community structure which are not only expressed by species losses but also by expansion of alien and native invaders. Availability of the key resource light differs greatly depending on grassland density, and competition for it can control grassland dynamics. At plant community level, increased light availability in gaps can create microsite conditions promoting invasion while resource restriction through shading impacts plant growth and survival. Publication 1 examines if light reduction via reduced mowing is an effective method to suppress a native invader in wet grasslands of very low to moderate land use intensity. It focuses on the impacts of management intended to increase competition for light on vegetative and generative growth of *Jacobaea aquatica*, a poisonous hemicryptophyte regionally spreading in pre-alpine meadows of Central Europe.

To assess the effects of shading and other site conditions, we combined the results of a greenhouse shading experiment and data gathered from 20 field sites at which distinct gradients of grassland management and thus different shading intensities were tested (Fig. 13). Plants taken from one of the study sites were grown under different shading nets in the greenhouse simulating 40, 60, 85, or 100% shading. Under strong shading, survival of *J. aquatica* was significantly reduced. Moreover, shading negatively affected generative growth. Fewer plants developed flowers under strong shading and the number of flower heads was also significantly reduced. Plants measured in the field experiment were overall smaller and produced less flower heads, though they were not significantly affected by shading. Nevertheless, abundance of *J. aquatica* negatively correlated with light reduction in the field. Furthermore, the occurrence of *J. aquatica* was negatively associated with the calculated humidity index, grassland productivity and 'time since mowing'.

While there were clear negative effects of shading on plant survival and fitness under controlled greenhouse conditions, plant responses in the field turned out to be much more variable. Still, light availability proved to be an important factor for controlling this native invader. Negative effects of shading co-occurred with higher grassland productivity, lower precipitation, and less intense management. As stronger shading can be achieved more easily in more fertile grasslands with high production, management intensity also plays an important role in regulating light availability.

Consequently, adaptation of management to control native invaders becomes important. Reducing the mowing frequency to enhance competition and strengthening the grassland sward should be considered as an additional management tool to suppress *J. aquatica* and control its abundance in the long term. This could be achieved by postponing the first cut or short-term cessation of mowing, depending on the productivity of the respective site.

PUBLICATION 2: Controlling the abundance of a native invasive plant does not affect species richness or functional diversity of wet grasslands

Krieger, M.-T., Ditton, J., Albrecht, H., Baaij, B.M., Kollmann, J. & Teixeira, L.H. (2022): Controlling the abundance of a native invasive plant does not affect species richness or functional diversity of wet grasslands. *Applied Vegetation Science*, 25, e12676, https://doi.org/10.1111/avsc.12676

Author contributions

JK, HA, **MTK** and JD designed the research. **MTK** and JD collected the field data. **MTK**, MB and LHT worked on the plant traits data. LHT designed the statistical analyses and **MTK**, MB and LHT processed and analysed the data. **MTK**, JK, HA and LHT discussed the results. **MTK**, with contributions from JK, HA, and LHT wrote the manuscript, supported by all co-authors.

Graphical abstract

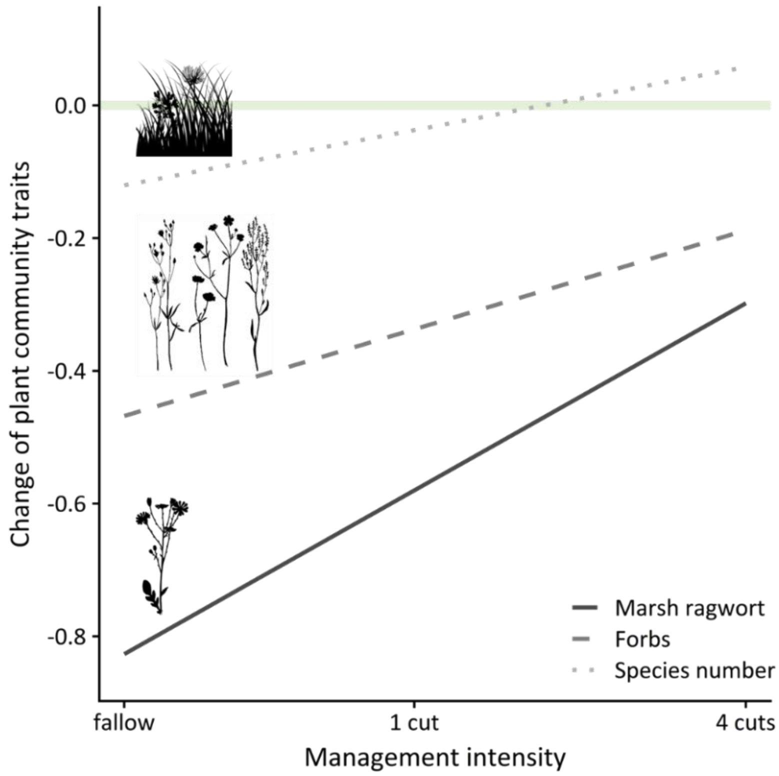

Fig. 14: Plant community changes under management strategies aiming to control *Jacobaea aquatica* in wet grasslands. Data of the different productivity levels were combined to give an overview of the occurring changes. Figure modified after Krieger, Ditton, Albrecht, Baaij, et al. (2022).

Summary

Species-rich wet grasslands are among the most threatened vegetation types in Europe. Their ranges are declining due to agricultural intensification or abandonment and remaining sites suffer from changes in their characteristic vegetation. Apart from decreases in wetland-adapted plants, those community shifts can lead to infestations with alien as well as native invaders, which further alter the resident community. Developing management strategies to control these invaders remains challenging as approaches to suppress unwanted species often conflict with preserving plant diversity of the sites. Manipulating biotic filters presents an opportunity to develop sustainable management methods balancing diverging goals.

Publication 2 evaluates the effects of temporary abandonment and decreased mowing intensity on the abundance of the native invader *Jacobaea aquatica* as well as on the functional diversity and species richness of the studied wet grasslands (Fig. 14). Experimental sites differed in productivity (very low; low; moderate) and for each productivity level, the implemented praxis-oriented management combinations were arranged as a gradient from low to high management intensity. To analyse change values subjected to differences in management intensity, we combined data on the abundance of *J. aquatica* and the co-occurring species from the start and end of the three four-year experiments with functional traits data.

Independent of the productivity level, abundance of *J. aquatica* declined with reduced management intensity. The decline in abundance was greater, the lower the management intensity was, and overall reduction was most effective at very low productive sites. Similar to the reduction of *J. aquatica*, we observed a decline in the abundance of dicots and an increase in abundance of monocots. Effects were confirmed by the analysis of functional diversity indices, which revealed an overall tendency of decreased functional dispersion (i.e. measure of functional dissimilarity) and increased functional redundancy (i.e. measure of functional similarity). Nevertheless, changes in functional composition were less pronounced and inconsistent between productivity levels and management intensities. Furthermore, overall species number changed only slightly during the experiment and observed changes of species losses under low management intensities were small.

Depending on sward density, reduced mowing frequencies proved to be an effective tool in reducing the abundance of the native invader *J. aquatica* without compromising plant diversity. Although strong reduction in management intensity most efficiently controlled the invasive species, moderate management intensities are preferable to avoid plant diversity losses. Especially at sites with high conservation value, management plans should further account for site productivity in order to develop sustainable control measures.

PUBLICATION 3: Reconciling the control of the native invasive *Jacobaea aquatica* and ecosystem multifunctionality in wet grasslands

Krieger, M.-T.*, Teixeira, L.H.*, Grant, K., Kollmann, J. & Albrecht, H. (2023): Reconciling the control of a native invasive plant and ecosystem multifunctionality in wet grasslands. *Basic and Applied Ecology*, 68, pp. 13–22. doi:10.1016/j.baae.2023.02.001. (* equal contribution)

Author contributions

HA, JK, KG and **MTK** designed the research. **MTK** with help of KG collected the field data. LHT analysed the data, and all authors discussed the results. **MTK** and LHT wrote the manuscript, supported by all co-authors.

Graphical abstract

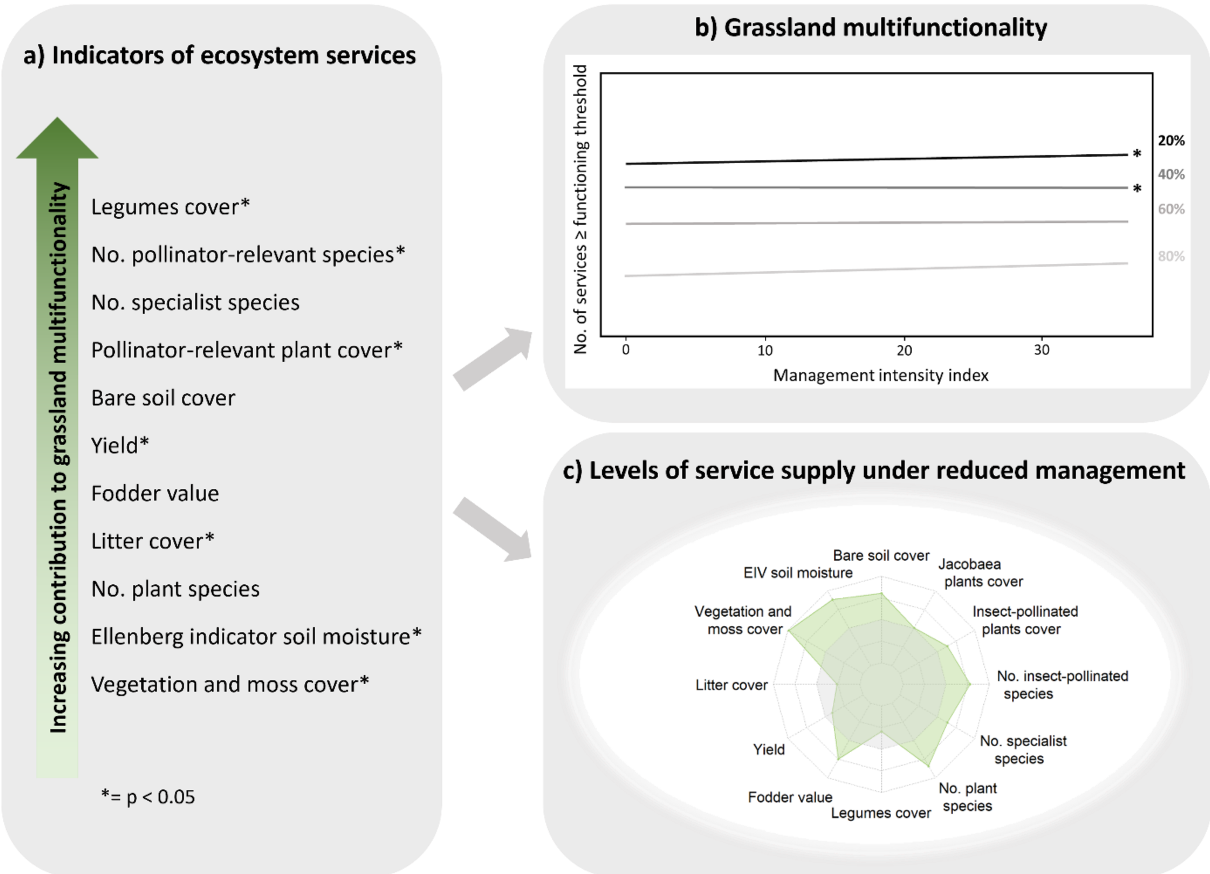

Fig. 15: Effects of controlling a native invader on grassland multifunctionality.
a) Seven out of eleven measured indicators of ecosystem service supply were significantly affected by management intensity. b) Analysing grassland multifunctionality via the threshold approach revealed positive effects of increased management but only at low to intermediate levels. c) At moderate management intensities, all but one indicator exceeded 25% of service supply.

Summary

Grasslands originally developed under human land use activities and until today, they are managed to provide various goods and services, including not only provision of food and raw materials but also regulating and maintaining services, such as environmental protection or carbon storage. Preservation of this multifunctionality is an important aspect in modern grassland management counteracting the ongoing degradation. During the last decades, intensified use of the most productive areas and abandonment of disadvantageous sites has led to losses in ecosystem service supply and biodiversity. Moreover, invasion of alien species as well as overabundance of native species can further impair the provision of ecosystem services.

Publication 3 focuses on the synergies and trade-offs of grassland management developed to control the native invader *Jacobaea aquatica* and the maintenance of ecosystem multifunctionality in wet grasslands (Fig. 15). This poisonous species is regionally spreading in pre-alpine grasslands of Central Europe reducing the economic value of the sites and ultimately leading to grassland abandonment. In this study, we tested community-based management strategies to reduce *J. aquatica* and assessed how such a regulation affected grassland multifunctionality using various indicators of ecosystem services. Aside from monitoring the abundance of *J. aquatica*, we evaluated the levels of service supply using indicators related to grassland productivity and conservation, such as forage quality and quantity or the occurrence of specialist species or insect-pollinated plants.

Out of eleven indicators, seven were significantly affected by changes of management intensity (Fig. 15a). Averaged multifunctionality decreased with decreasing management intensity, while analysis of the single threshold approach revealed that simultaneously maximizing the functioning of multiple indicators was not possible. Nevertheless, increasing management positively influenced grassland multifunctionality, but only at low to intermediate levels of functioning (thresholds ≤40%; Fig. 15b). Evaluating the performance of all indicators using different classes of management intensity revealed that more intense management promoted productivity but led to an increase in the abundance of *J. aquatica*.

Overall, most effective regulation of *J. aquatica* was achieved under the lowest management intensity, while higher management intensity positively affected multifunctionality. Following this, we conclude that a moderate suppression management can be a practical way to reconcile the control of the studied native invader and the maintenance of grassland multifunctionality (Fig. 15c).

DISCUSSION

Wet grasslands are threatened by both agricultural intensification and abandonment (Dengler et al., 2014). While their high species richness makes them valuable for nature conservation, characteristic plant diversity is still declining (Joyce, 2001). Changes in plant diversity do not only include decrease of wetland-adapted species but also invasion of ruderal, weedy or alien plants (Prach, 2008). Detrimental effects of these species, such as altered community composition or reduction of yield and forage quality, can lead to further species declines or future abandonment of affected sites (DiTomaso, 2000). Traditional control methods are often time-consuming, costly or come along with unwanted side effects. Besides, especially management of native invaders may conflict with conservation objectives due to possible trade-offs between control measures and conservation of plant diversity. Consequently, sustainable control measures must not only account for suppression success, but also for effects on community composition and grassland multifunctionality.

The objective of this thesis was to assess the possibilities and consequences of ecological management of native invaders. Development of management options was based on the use of ecological filters to enhance competition for key resources. Methods realising this approach were tested using *Jacobaea aquatica*, a native species invading pre-alpine wet grasslands. As this species is sensitive to shading, we aimed at enhancing competition for light to reduce invader establishment and performance. Using a gradient between controllability and complexity, different datasets relating to the effects on target species, community composition and grassland multifunctionality were analysed. Each publication focused on one of these aspects; the main findings are presented in Fig. 16.

In Publication 1, effects on the individual performance of the target species were analysed combining the results of a controlled greenhouse experiment and data on plants fitness and abundance in the field. Changes in the population level of the native invader and the community composition of the studied grasslands were compared in Publication 2. Further, publication 3 focused on the consequences for grassland multifunctionality and assessed the influence of different management intensities on individual indicators of ecosystem services. Each aspect is reviewed in terms of its implications for invader management. Moreover, all aspects are evaluated together to obtain a holistic overview of the effects of the implemented control measures. Finally, management recommendations for the control of the target species are given and transferability of the results to management of other native invaders is discussed.

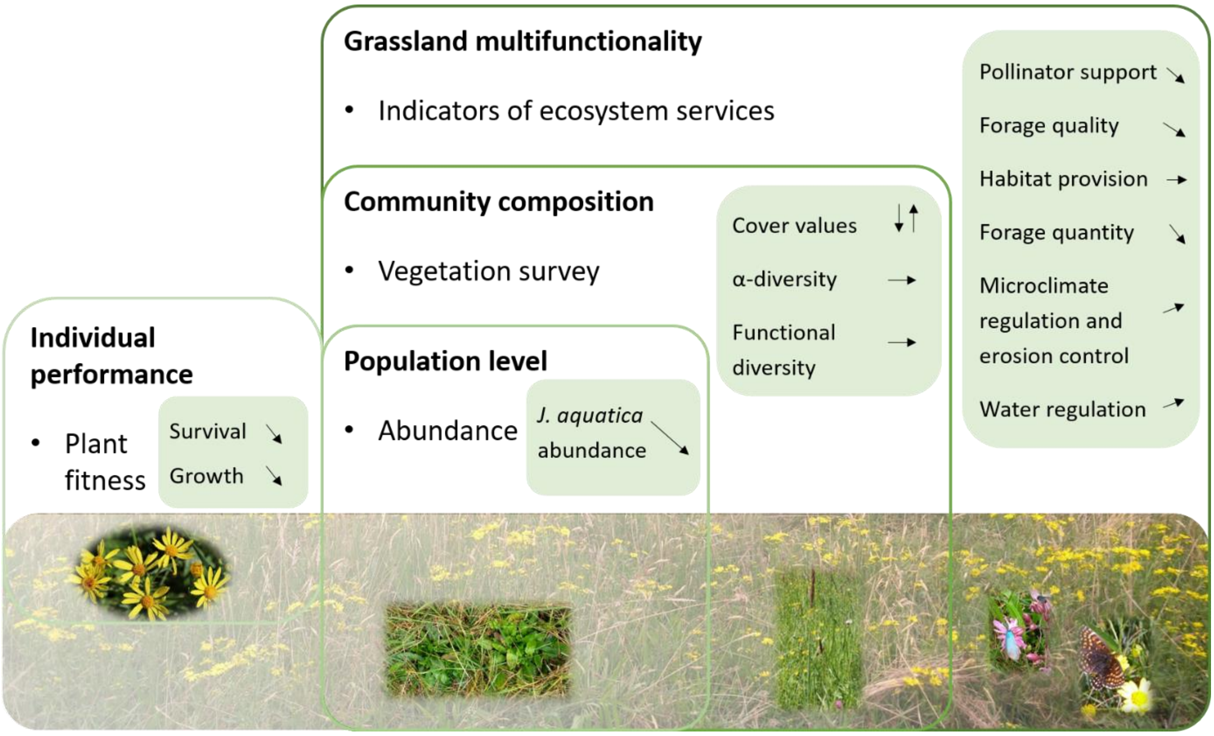

Fig. 16: Main findings of the thesis separated into the different aspects investigated in the embedded publications. Publication 1 (Krieger, Ditton, Albrecht, Linderl, et al., 2022) focused on the consequences of enhanced shading on the individual performance of *Jacobaea aquatica*, whereas Publication 2 (Krieger, Ditton, Albrecht, Baaij, et al., 2022) investigated changes on the population level and impacts on community composition. Publication 3 (Krieger et al., 2023) examined the effects on ecosystem services and their influence on grassland multifunctionality.

Manipulating ecological filters as a mechanism to control native invaders

Invasion success and invasibility of plant communities is attributed to a series of ecological filters, namely dispersal, environmental, and biotic filters (Funk et al., 2008). Each of these filters can be modified to reduce invasion probability or to actively suppress existing invaders. Native invaders do not usually have to overcome large dispersal barriers (Pearson et al., 2018). Consequently, the importance of altering environmental filters to increase abiotic constraints or changing biotic interactions to achieve competitive exclusion as control measures rises. Thus, actively limiting resources, e.g. nutrients or light, via enhanced competition presents an approach to suppress native invaders (Perry & Galatowitsch, 2006).

Altering management regimes to reduce disturbances can be a practical way to enhance crowdedness and competition for light (Boob et al., 2021). As light is supplied more or less uni-directionally, less intense management would lead to resource pre-emption by taller plant species and competitive disadvantages of shade-intolerant species (Sutherland, 2004; Craine & Dybzinski, 2013). For instance, as a rosette plant which accumulates most of its biomass close to the ground, *J. aquatica* prefers relatively open habitats and proved to be susceptible to abandonment (Rosenthal, 2010). In fact, its low tolerance to shading was proven in the greenhouse experiment of Publication 1. Shading reduced survival of *J. aquatica* individuals and negatively affected plant growth and reproduction (Krieger, Ditton, Albrecht, Linderl, et al., 2022). Similar effects have also been found in other species in which shading impaired reproduction due to a decrease in the number of flower heads (Shamsi & Whitehead, 1974; Lutman et al., 2008). Furthermore, abundance of vegetative *J. aquatica* plants decreased with reduced disturbance in the field as shown in Publications 2–3. Although effectiveness of shading (measured as reduction in available PAR) varied among grasslands and depended on productivity and other environmental factors (Krieger, Ditton, Albrecht, Linderl, et al., 2022), the demonstrated decline in plant abundance could be directly related to management intensity when considered over a longer period of time (Krieger, Ditton, Albrecht, Baaij, et al., 2022). Measured as 'time since last mowing', disturbance frequency and timing regulated competition for light, which proves that altering site management is an effective method to reduce abundance of the targeted species (Krieger, Ditton, Albrecht, Linderl, et al., 2022).

Other possibilities for enhancing resource competition and hindering seedling emergence of invaders could be the use of competitive seed mixtures (Möhrle et al., 2021) or sowing of cover crops during restoration processes (Baumann et al., 2001; Perry & Galatowitsch, 2006). Again, these methods aim at regulating sward density, and changing biotic interaction. Besides enhancing biotic filters, changes in disturbance regimes also affect nutrient availability and thus act on abiotic site conditions (Parepa et al., 2013). As eutrophication is mostly seen as driver of invasion and several studies show that increases in nutrient availability favour growth of invaders (Going et al., 2009; Perry et al., 2010), reducing anthropogenic nutrient input can be an important strategy to protect habitats from invasion (Sorrell et al., 2012). This mostly relates to limiting the availability of nitrogen or phosphorus to promote resistance and shift the competitive balance to the disadvantage of the invader (Cleland et al., 2013). Possible implementation strategies for direct nutrient reduction are nutrient sequestration in the soil or removing nutrients through harvested biomass or topsoil removal (Elgersma et al., 2017). Nutrient sequestration can be promoted via the use of carbon amendments which, for example, lower soil nitrogen availability (Cleland et al., 2013). Depletion via biomass removal depends on soil type and accumulation of biomass and might take a longer time (Tallowin & Smith, 2001). While the different nutrients interact with each other, they also influence biotic interactions through altered competition (Aerts & Berendse, 1988). In fact, abiotic characteristics determine the outcome of species interactions (Going et al., 2009). Moreover, disturbance by itself affects species interaction and can produce positive or negative legacy effects via a short-term decrease or increase in resource availability (Davis & Pelsor, 2001).

This shows that different management methods are available to modify environmental and biotic filters and that the importance of the filters can differ and also might change over time (Funk, 2021). Depending on the objective, the abiotic conditions, and possible biotic interactions that can be influenced, the appropriate method to control a native invasive species varies. Nevertheless, abiotic as well as biotic interactions together with the inherent effects of the management practices used must be taken into account when evaluating the effectiveness of the implemented approaches.

Effects on community composition and diversity

Although management measures to manipulate ecological filters aim to reduce the abundance of the targeted species, they simultaneously alter the structure of plant communities on site. These alterations must be evaluated with regard to the occurrence and extent of possible negative side effects. Especially reduction in mowing intensity or short-term cessation of mowing, but also increased fertilization can lead to changes in species composition, evenness and richness (Joyce, 2014; Immoor et al., 2017). This includes, among others, changes in proportion of functional groups, in overall trait-based functional diversity or in occurrence and abundance of individual species (Dupré & Diekmann, 2001; Wesche et al., 2012). For instance, delaying the first mowing event or mulching instead of mowing can increase the abundance of monocotyledonous species (Seither & Elsässer, 2014). Further reducing mowing frequency can decrease the abundance of small species, especially forbs, via competitive exclusion (Pavlů et al., 2011; Conradi et al., 2017). These competitive shifts occur most rapidly following cessation of mowing (Joyce, 2014). Moreover, abandonment leads to more pronounced changes than simply changing mowing frequency or timing (Poptcheva et al., 2009). Rosenthal (2010) reported a strong decrease in species diversity in the years following abandonment, starting with a decrease of typical wet meadow species. Similarly, diversity in *Molinia caerulea*-dominated wet grasslands decreased with reduced mowing (Edwards & Kučera, 2019). Both studies also reported a decrease in abundance or local extinction of *Jacobaea aquatica* (Rosenthal, 2010; Edwards & Kučera, 2019). The reported shifts in abundance were attributed to a strong light limitation which favoured the extinction of small species, particularly rosette or stoloniferous plants, while other, more shade-insensitive species were still able to coexist at lower abundances (Rosenthal, 2010; Boob et al., 2021).

In Publication 2, we report similar findings for our study sites. Reducing management intensity strongly decreased *J. aquatica* abundance (Krieger, Ditton, Albrecht, Baaij, et al., 2022). Moreover, we found that the abundance of monocots increased, while the abundance of forbs declined (Krieger, Ditton, Albrecht, Baaij, et al., 2022). The magnitude of changes differed between management measures, with treatments of lower management intensities displaying higher change values (Krieger, Ditton, Albrecht, Baaij, et al., 2022). Those findings mostly refer to changes in abundance of functional groups, whereas analysis of functional diversity indices revealed only small variation (Krieger, Ditton, Albrecht, Baaij, et al., 2022). We attributed these differences to contrasting responses of functionally dissimilar species and differences in plant adaptation or avoidance strategies (Laliberté et al., 2013; Zuo et al., 2018). Apart from changes in functional composition, species richness declined with reduced management intensity. However, these changes were small and only few species were lost (Krieger, Ditton, Albrecht, Baaij, et al., 2022). Furthermore, change values differed between productivity levels.

The relatively small changes in species diversity also became apparent in Publication 3, when number of species and number of wet grassland specialists were presented as indicators of ecosystem services. Both values only slightly changed between the assigned management intensity categories (Krieger et al., 2023). The small effect on wet grassland specialists in our study contrasts the findings of Rosenthal (2010). Yet, we only observed four years of management changes, with a maximum of three years of abandonment. This could allow for reversible effects in species occurrence, while the observed changes in number and cover of pollinator-relevant species can be attributed to the decrease in the abundance of forb species under low management intensities (Ford et al., 2012).

Our results confirm reports that an extreme reduction in mowing frequency has detrimental effects on species diversity and community composition, whereas moderately to slightly reduced management intensity has fewer negative effects (Römermann et al., 2009; van Klink et al., 2017; Tälle et al., 2018). Likewise, as mentioned above, eutrophication also shifts competition and can lead to invasion and dominance of few tall-growing, nutrient-demanding species (Klimeš & Klimešová, 2002; Immoor et al., 2017). In that case, success of control efforts depend on the efficiency of nutrient depletion, but also on other environmental variables such as changes in soil moisture or presence of soil seed banks for the re-establishment of desired species (Poptcheva et al., 2009). To sum up, various effects on community composition and species diversity can be expected from manipulating ecological filters to control native invaders. The magnitude of effect and its durability strongly depend on the selected approach, the duration of the control and additional environmental circumstances (Milberg et al., 2017). Whether the occurring side effects are tolerable depends on the previously formulated aims and must also be compared with the effectiveness of the measures against the target species.

Impact of control measures on ecosystem services and grassland multifunctionality

Another point that should be considered when evaluating measures against native invaders is, how the management affects provision of ecosystem services and grassland multifunctionality. For instance, reducing management intensity reportedly leads to changes in ecosystem services (Edwards & Kučera, 2019; Johansen et al., 2019). The direction of change differs between individual services, and trade-offs between services can compromise multifunctionality (Byrnes et al., 2014; Le Clec'h et al., 2019). On the one hand, lower management intensity reduces the number of flowering forbs, hence impairing habitat provision for pollinators (Ford et al., 2012). On the other hand, regulating services associated with nutrient cycling, water regulation or erosion control can profit from lower land use intensity (Austrheim et al., 2016). Moreover, grassland aesthetics and thus cultural ecosystem services can be negatively affected by the reduction of forbs following abandonment (Johansen et al., 2019). Likewise, high management intensities impair grassland multifunctionality as only some provisioning ecosystem services are promoted (Allan et al., 2015).

The results of publication 3 confirm that indicators related to provisioning services (e.g. indicators referring to amount and quality of yield) decreased at lower management intensities, whereas indicators of regulating services showed varying responses (Krieger et al., 2023). Furthermore, our data indicate biodiversity losses also under increased management intensity, which could again reduce provision of ecosystem services (van der Plas, 2019). As a result, intermediate management intensities might perform best in terms of providing multiple services at the same time. For instance, postponing mowing from spring to summer can have positive effects on plant species and invertebrate diversity (Humbert et al., 2012). This would improve habitat provision while still suppressing the native invader via enhanced competition.

Apart from assessing the effects of control measures on individual ecosystem services, the response of grassland multifunctionality should be evaluated. Multifunctionality of the studied grassland sites was lowest at very low management intensity, which corresponds to short-term abandonment or off-season mowing, but increased with increasing management intensity (Krieger et al., 2023). This reveals the threats of grassland abandonment on multifunctionality (Ford et al., 2012). However, intensification of land use, especially high levels of fertilization and frequent mowing, negatively influence grassland multifunctionality as well (Allan et al., 2015; Schils et al., 2022). According to Neyret et al. (2021), low-intensity land use can sustain the provision of multiple ecosystem services at moderate levels. Thus, slightly reduced management could be used to control the abundance of the native invader, while still supporting grassland multifunctionality.

Recommendations for the control of *Jacobaea aquatica*

When developing ecological management approaches, the effects on individual performance and population level of the target species as well as the impact on community composition and grassland multifunctionality must be measured. By combining and evaluating the different aspects, scientifically sound recommendations for the control of *J. aquatica* can be made. Overall, reducing the mowing frequency to enhance competition for light proved to be effective in suppressing *J. aquatica* in wet grasslands of conservation value. Under controlled conditions in the greenhouse, shading significantly influenced survival and reproduction of the target species (Krieger, Ditton, Albrecht, Linderl, et al., 2022). Although these strong effects could not be seen in the field, abundance of *J. aquatica* declined with enhanced shading. Depending on grassland productivity, short-term cessation of mowing or switching to annual mowing in fall were most effective control measures (Krieger, Ruff, Lepp, Albrecht, et al., 2022). However, changes in abundance of functional groups and in species richness were most prominent in these treatment intensities (Krieger, Ditton, Albrecht, Baaij, et al., 2022). This indicates unwanted suppression effects on phylogenetically-related species or species with similar growth forms as *J. aquatica* (Krieger, Ditton, Albrecht, Baaij, et al., 2022). Moreover, very low levels of management intensity impaired provision of productivity-related ecosystem services and thus affected multifunctionality of wet grasslands (Krieger et al., 2023).

Consequently, moderately reduced management intensities should be preferred when aiming to suppress the native invasive *J. aquatica*, especially for sites with high plant species diversity and thus conservation priority. Nevertheless, depending on the infestation of the respective site, more severe control measures might be required during an initial suppression phase (1–2 years). Those measures can still include annual off-seasonal mowing at very low and low productive sites. Subsequently, postponing the first mowing date or switching to annual mowing can support the achieved reduction on very low productive sites in the long term. On the low productive sites, alternating between an annual cut and regular mowing twice a year is recommended, depending on the development of *J. aquatica* abundance. Such management might reduce detrimental effects on plant diversity and maintain multifunctionality (Milberg et al., 2017). When resuming regular grassland use, it is essential to ensure that stands remain tall and dense and that gaps and areas with bare soil are avoided. If single individuals of *J. aquatica* remain, hand-pulling or removal of flower heads presents an effective method to prevent reproduction. At more productive sites mowing during peak flowering can also reduce seed production (Bassler et al., 2013). To prevent invasion by *J. aquatica,* enhancing sward density and avoiding to tear up soil during management is important. Thus, moderate management intensities are recommended for grasslands susceptible to invasion.

To sum up, control measures must be tailored to site productivity and severity of the infestation and should be conducted over several years. More importantly, the potential of the grassland site might define the applied control measures. At sites with high plant diversity, species conservation will guide management, whereas at other, more degraded sites, regulation of *J. aquatica* could simultaneously serve to promote some regulating or supporting ecosystem services (Ford et al., 2012). Moreover, applying different management concepts on the small scale would lead to an increased landscape diversity (Le Clec'h et al., 2019). If this spatial diversity is still managed to reduce or prevent invasion, it would increase overall multifunctionality and ecosystem service provision without contradicting the actual reason for management adaption.

Implications for native invader management

The example of *J. aquatica* shows that enhancing competition for light via reduced mowing is an effective method to suppress light-demanding species. The resulting high competition reduces plant vigour, induces stress responses and negatively impacts reproduction (Lutman et al., 2008; Casal, 2012). Alternatively, more intensive management, especially mowing during peak flowering, may reduce *J. aquatica* abundance (Forbes, 1976; Bassler et al., 2017). However, increasing the mowing frequency in our study was not successful, as the species proved to be resistant to defoliation, quickly regenerated and produced new flowers (Krieger, pers. observ.). Nevertheless, this may be quite different for other species. Depending on the species specific sensitivity to defoliation, it is possible to negatively impact resource allocation in the plant by adjusting cutting frequency and time in such a way that its vitality decreases (Bobbink & Willems, 1991; Jung et al., 2012). Cutting frequency and timing might also impact nutrient availability, and thus alter competition between the invader and the plant community (Elgersma et al., 2017). Moreover, management implementation options and control effects depend on site conditions, productivity or timing of measures (Siegrist-Maag et al., 2008). For instance, increasing management intensity might not be possible due to soil conditions, topography or conservation restrictions (Suter & Lüscher, 2008). Likewise, at sites with a high nutrient supply reduction of this nutrient supply is difficult to realize. Consequently, thorough analysis of the plant characteristics and occurring environmental factors as well as observation of management effects on individual performance and abundance of the target species is needed for success monitoring (Funk, 2021). Besides focusing on how to control the native invader, it should not be forgotten that these species are a natural part of their habitats and have their role in the ecosystem (Bielfelt & Litt, 2016). Control strategies should therefore aim at reducing the abundance rather than completely eliminating such species.

Apart from the effects on the target species, management impacts on community composition and grassland multifunctionality must be evaluated with regard to grassland conservation. Effects of control measures on community composition are preferably positive or neutral, in such a way that species diversity is maintained or even enhanced (Bobbink & Willems, 1991; Winter et al., 2014). To estimate possible side effects beforehand, a general knowledge of community responses to different management practices is needed. For instance, grazing favours the occurrence of legumes, therophytes or species with persistent seed banks (Dupré & Diekmann, 2001). In contrast, abandonment increases abundance of tall, mostly monocotyledonous species or species with vegetative regeneration (Rosenthal, 2010). Furthermore, information on the variability of ecosystem services under different management options should be acquired (Le Clec'h et al., 2019). The work of this thesis shows that even when negative effects on community composition and grassland multifunctionality occurred, their impact was lower than the effects on the native invader (Krieger, Ditton, Albrecht, Baaij, et al., 2022; Krieger et al., 2023). Even then, these effects have to be accounted for and tolerance levels might be defined when formulating management objectives. Instead of applying the same control measures at each part of the site, individual focal points could be set to allow for maintenance of especially diverse areas or conservation of abiotic resources.

To sum up, several aspects have to be accounted for to ensure sustainable management of native invaders. First, the environmental conditions and the traits of the target species determine which control measures can be implemented. Second, the aim of the management has to be formulated and a timeframe for conducting the measures has to be set. Next, possible side effects on community composition, species richness and grassland multifunctionality have to be assessed and weighed against the effectiveness of the applied management. Management application might differ depending on grassland potential. Finally, management measures must eventually comply with requirements for legally protected biotopes and directives to maintain conservation status must be observed. Therefore, a close coordination with nature conservation expertise and a regular monitoring of the area status are mandatory.

CONCLUSIONS

Invasion by alien or native species threatens usage of conservation grasslands. Traditional control methods are often not applicable; thus, approaches based on ecological knowledge need to be developed. This thesis investigated how modification of ecological filters can be used to suppress the native invasive *J. aquatica* in wet conservation grasslands and how the results can be transferred to other native invaders. The aim was to find control measures which would reduce the overabundance of the target species without negatively affecting plant diversity and grassland multifunctionality. As *J. aquatica* is sensitive to shading, treatments aimed at enhancing competition for light. The results show that *J. aquatica* abundance can be controlled via management reduction. Control success as well as negative side effects on community composition and multifunctionality differed depending on the strength of the reduction and the productivity of the respective grassland.

Reducing management intensity to enhance competition for light led to impaired plant fitness and reduced the abundance of *J. aquatica* in the field (**Publication 1**). However, the effects of other environmental factors make it difficult to achieve a consistently high degree of shading. Moreover, strong reduction also negatively affected plant species and functional diversity (**Publication 2**). Similarly, lower grassland management decreased provisioning of some ecosystem services, whereas multifunctionality was only affected at intermediate threshold levels (**Publication 3**). Responses of the native invader and effects on plant diversity and multifunctionality were consistent between productivity levels of the sites and dominated mainly by treatment effects. Overall, effects of control measures on the abundance of *J. aquatica* were higher than effects on plant species, functional diversity or ecosystem services. Control of this species must accept decreases in grassland multifunctionality and shifts in community composition. Nevertheless, these negative effects can be minimized by accounting for site productivity and intensity of the treatment. That is, intermediate management levels, i.e. delaying the first cut and reducing light availability during flowering time, are recommended which allow suppression of the native invader but have little impact on plant community and multifunctionality.

The results of this dissertation show that management concepts based on a community assembly framework can indeed be used to control grassland invasions. By analysing trait characteristics of the target species and learning about its resource requirements, environmental and biotic filters can be modified to create customized control measures. When implementing the management approach, site productivity and emerging effects on community composition, diversity and grassland multifunctionality have to be taken into account. Thus, management goals should be well defined. Moreover, regular monitoring of native invader abundance and development of the grassland site is needed to evaluate suppression success and site development. Control measures might need to be adapted over time to reduce negative impact or to counteract renewed invader increase or even secondary invasions.

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ACKNOWLEDGEMENTS

During the time of my doctoral thesis, many people accompanied and supported me, and I would like to express my gratitude to them on this occasion.

First, I would like to express my gratitude to my supervisor PD Harald Albrecht for his support, open ear and help with all the small things – whether it be joining me in the greenhouse after work to check if everything is going well or spontaneously helping in the field. Thank you for the trust you have placed in me and for the quick and professional answers to any questions. Your support was inspiring.

I would like to thank Prof. Johannes Kollmann for his guidance and efforts that supported my scientific work at the chair. Your encouragement motivated me to improve and advance this work.

Furthermore, I would like to thank my mentor Dr. Sabine Heinz for all the long talks and inspirational coffee chats which helped me clearing my mind and focussing on my work again.

A special thanks goes to my colleague Dr. Leonardo H. Teixeira, who sometimes believed more in the achieved results than I did. Thank you for your support in statistics, field work and “How to do all this stuff related to papers”. I appreciate your friendship, your positive mindset and the opportunities to talk about nerdy stuff.

Many thanks go to my co-doctoral students and scientific staff members Markus Bauer, Nadja Berger, Simon Dietzel, Julia Ditton, Jakob Huber, Dr. Marion Lang, Kathrin Möhrle, Michaela Moosner, Paula Prucker, Sandra Rojas Botero, Dr. Katharina Strobl, Dr. Alina Twerski, Miriam Wiesmeier and Romy Wöllner for sharing all the good and bad moments during our PhD times, for the occasional PhD-outings, lunch-walks and scientific exchanges. Thanks for all the shared laughter and the time spend together.

A big THANK YOU goes to Anne-Katharina Rückel who joined me as student helper almost from the first day on and until the end of the field and greenhouse work. Without her, fieldwork would not have been possible and certainly less fun! I am also thankful to Franziska Hirt who joined us in the last two years and fastened our work even more. Moreover, I am grateful to Martienke Baaij, Franz Härtl, Kathrin Möhrle and Sandra Rojas-Botero and who helped with the field work at some point in the project.

I would also like to thank my co-doctoral marsh ragwort student Julia Ditton, who shared her project experience with me and helped me getting started. It was nice to combine our work on the field sites and to draft our joined first paper together. I wish you all the best.

Another thank you goes to the remaining scientific and technical staff at the chair, especially to Elisabeth Aberl, Claudia Buchhart, Dr. Ursula Dawo, Kerstin Josten and Holger Pätsch for the scientific, organisational, technical and personal exchanges, encouragements and warm words. I am grateful to the staff at the greenhouse laboratory in Dürnast for their support of the experiments. I am also thankful to all the students, interns and pupils who at some point joined the project work.

I would like to thank the participating farmers and the project partners for the land provided and the great cooperation. Above all, the thanks go to Holger Bayer, Kerstin Grant, Alexander Martin and Andreas Stauss for their help with mowing the experimental sites. I am grateful to Gaudenzia Angerer (Enzi), Maria Wolf Andreas Schulte from the LAZBW for the possibilities to stay overnight during fieldwork, for the fantastic dinners and breakfasts and for the feeling of being well cared for.

Moreover, I gratefully acknowledge funding for my research project through the Bayerische Landesamt für Umwelt and the Landesanstalt für Umwelt Baden-Württemberg (AZ: 51-0270-37986/2018). Thanks to Anna Haußmann, Natascha Lepp, Marcel Ruff and Andreas Zehm for their support of the project, the possibility to extend the research and the pleasant exchanges.

Another thank you goes to the TUM Graduate School and the Graduate Center of Life Sciences for the doctoral support and training services and to the anonymous referees for their work on reviewing the publications. This thanks also includes my co-authors of the publications.

Thanks to all my friends for making an active life outside of doctoral studies possible. I would also like to thank JRRT and JKR for creating worlds that have made long car journeys and boring data typing so much more enjoyable and that have taught me personally important values.

Großer Dank gebührt meiner besten Freundin Julia Claussen, die immer ein offenes Ohr, einen Überraschungs-Blumenstrauß oder eine schöne Karte bereit hatte, wenn ich es gebraucht habe. Danke für deine Unterstützung.

Meiner Familie und Schwiegerfamilie danke ich für ihre Unterstützung, den Zusammenhalt und die vielen gemeinsamen Stunden. Meinem Papa danke ich für die schöne Zeit, wenn ich vom Feld aus übernachtet habe und dass er immer dafür gesorgt hat, dass ich einen fahrbaren Untersatz hatte. Tiefer Dank gebührt meiner Mama, die mich immer unterstützt und an mich geglaubt hat. Ich bewundere deine Stärke.

Mein größter Dank gebührt meinem Mann Thomas für seine Unterstützung und unglaubliche Geduld. Danke, dass du immer für mich da bist. Oder wie es David Safier in Miss Merkel (2) so schön beschrieben hat: In dir habe ich die Person gefunden, der ich vertrauen kann und die mir vertraut ist. Die Person mit der ich mich eins fühle.

APPENDIX

A2 Publication List

A2 Publication List

Peer reviewed journal publications

Krieger, M.-T., Teixeira, L.H., Grant, K., Kollmann, J. & Albrecht, H. (2023) Reconciling the control of the native invasive *Jacobaea aquatica* and ecosystem multifunctionality in wet grasslands, *Basic and Applied Ecology*, 68, pp. 13–22. doi:10.1016/j.baae.2023.02.001.

Krieger, M.-T., Ditton, J., Albrecht, H., Baaij, B.M., Kollmann, J. & Teixeira, L.H. (2022) Controlling the abundance of a native invasive plant does not affect species richness or functional diversity of wet grasslands, *Applied Vegetation Science*, 25. doi:10.1111/avsc.12676.

Krieger, M.-T., Ditton, J., Albrecht, H., Linderl, L., Kollmann, J. & Teixeira, L.H. (2022) Effects of shading and site conditions on vegetative and generative growth of a native grassland invader, *Ecological Engineering*, 178. doi:10.1016/j.ecoleng.2022.106592.

Habel, J.C., Teucher, M., Rödder, D., **Bleicher, M.-T.**, Dieckow, C., Wiese, A. & Fischer, C. (2016) Kenyan endemic bird species at home in novel ecosystem, *Ecology and Evolution*, 6. doi:10.1002/ece3.2038.

Other publications

Krieger, M.-T., Ruff, M., Lepp, N., Albrecht, H. & Kollmann, J. (2022) *Regulierung von* Senecio aquaticus *(Wasser-Kreuzkraut) in naturschutzfachlich wertvollem Grünland*. Abschlussbericht. Available at: https://mediatum.ub.tum.de/1692105

Albrecht, H. Ditton, J., Kuhn, G., Kollmann, J., **Krieger, M.-T.**, Mayer, F., Teixeira, L.H. & Gehring, K. (2022) Management von Wasser-Greiskraut (*Jacobaea aquatica*) in Wirtschaftsgrünland des ökologischen Landbaus, in *30. Deutsche Arbeitsbesprechung über Fragen der Unkrautbiologie und -bekämpfung*. Braunschweig: Julius-Kühn-Archiv, pp. 117–121.

Gehring, K. Albrecht, H., Ditton, J., Kollmann, J., **Krieger, M.-T.**, Kuhn, G., Laumer, M., Mayer, F. & Wagner, T. (2022) Management von Wasser-Greiskraut (*Jacobaea aquatica*) in der konventionellen Grünlandbewirtschaftung, in *30. Deutsche Arbeitsbesprechung über Fragen der Unkrautbiologie und -bekämpfung*. Braunschweig: Julius-Kühn-Archiv, pp. 110–116.

Kuhn, G. Mayer, F., Wagner, T., **Krieger, M.-T.**, Laumer, M., Ditton, J., Albrecht, H., Kollmann, J. & Gehring, K. (2022) Zusammenhang zwischen dem Auftreten von Wasser-Greiskraut (*Jacobaea aquatica*) und landschaftlichen sowie landwirtschaftlichen Faktoren in Bayern, in *30. Deutsche Arbeitsbesprechung über Fragen der Unkrautbiologie und -bekämpfung*. Braunschweig: Julius-Kühn-Archiv, pp. 122–127.

Krieger, M.-T., Kollmann, J. & Albrecht, H. (2020) Regulierung von Wasser-Greiskraut in naturschutz-fachlich wertvollem Grünland, *Naturschutz-Info*, 1. Available at: https://pudi.lubw.de.

Bleicher, M.-T. & Albrecht, H. (2019) „Ausdunkelung" – eine Möglichkeit, das Wasserkreuzkraut (*Senecio aquaticus*) zu reduzieren?, *ANLiegen Natur*, 41. Available at: www.anl.bayern.de/publikationen/anliegen/meldungen/wordpress/ausdunkelung_wasserkreuzkraut/.

Ditton, J. & **Bleicher, M.-T.** (2018) Regulierung unerwünschter Arten in Grünlandbeständen – Das Beispiel des Wasserkreuzkrauts im Voralpenraum. *Nachrichten der Gesellschaft für Ökologie*, 48.

Talks at international conferences

Teixeira L.H., **Krieger, M.-T.**, Grant, K., Kollmann, J. & Albrecht, H. (2022) Effects of controlling an invasive native plant on ecosystem multifunctionality of wet grasslands, *64th Annual Symposium of the International Association for Vegetation Science*, Madrid, Spain.

Teixeira L.H., Möhrle, K., **Krieger, M.-T.** & Kollmann, J. (2021) Suppressing an invasive native species in wet grasslands: effects of designed mixtures and management, *12th Conference of the Society for Ecological Restoration in Europe*, Alicante, Spain.

Bleicher, M.-T., Kollmann, J. & Albrecht, H. (2019) How can grassland management help to reduce a poisonous plant without jeopardising biodiversity?, *49th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland*, Münster, Germany.

Bleicher, M.-T., Moning, C. & Fischer, C. (2018) Movement behaviour of Northern Lapwing chicks *Vanellus vanellus* in agricultural landscapes, *48th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland*, Vienna, Austria.

Poster contributions to international conferences

Teixeira, L.H., **Krieger, M.-T.**, Albrecht, H. & Kollmann, J. (2022) Controlling an invasive native plant does not compromise species richness or functional diversity of wet grasslands, *12th International Conference on Biological Invasions (NEOBIOTA)*, Tartu, Estonia.

Krieger, M.-T., Ditton, J., Albrecht, H., Baaij, B.M., Kollmann, J. & Teixeira, L.H. (2021) Community responses to the control of the native invader *Jacobaea aquatica* in wet grassland, *Ecology Across Borders – Joint conference of the British Ecological Society and the Société Française d'Écologie et d'Évolution*, online.

Krieger, M.-T., Ditton, J., Albrecht, H., Linderl, L., Kollmann, J. & Teixeira, L.H. (2021) Suppression effects of shading and site conditions on different life stages of a native invasive plant in grasslands, *33rd Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland (GfÖ)*, online.