Priority effects in European grassland plants - The role of plant origin and phylogeny in shaping competition and plant-soil feedback

Dissertation

zur Erlangung des
Doktorgrades der Naturwissenschaften (Dr. rer. nat.)
der Naturwissenschaftlichen Fakultät I – Biowissenschaften
der Martin-Luther-Universität Halle-Wittenberg

vorgelegt von
Julia Dieskau (M.Sc.)

Verteidigt am 9.12.2025

Gutachter: Prof. Isabell Hensen, Dr. Harald Auge, Prof. Viktoria Wagner

Für Jakob

Content

Summary

Understanding the processes that govern community assembly remains a central objective in ecological research. Over the past two decades, increasing attention has been paid to the timing and order of species arrival. Priority effects, where early-arriving species influence the performance of late-arriving species, have emerged as an important driver of community composition across a wide range of taxa and ecosystems. Nevertheless, despite substantial theoretical and empirical advances in community assembly research, the mechanisms underlying priority effects in plant communities remain poorly understood.

This thesis contributes to addressing these knowledge gaps by investigating how priority effects in grassland plant communities are shaped by direct competition and plant-soil feedback. Although both mechanisms are ecologically highly relevant, empirical studies examining their interaction and explicitly linking them to priority effects remain scarce, particularly those incorporating long-term, field-based data. I further explore how these mechanisms are influenced by the origin and phylogenetic relatedness of the interacting biennial and perennial grassland species. To address these questions, both a large-scale field experiment under realistic conditions, which allowed for the investigation of general mechanisms, and controlled greenhouse experiments under standardised conditions, in which individual processes involving a greater number of species were examined in detail, were employed.

In Chapter 2, I examine how the origin of early- and late-arriving species affects competition- and soil fungi-mediated priority effects, which represent a specific subset of plant-soil feedback mechanisms, in a multi-year field experiment with six native and six exotic species. A reciprocal design including all species and treatment combinations enabled a comprehensive analysis of interactions. Herbicide and fungicide applications disentangled direct competition from soil fungal effects, revealing that both contribute to negative net priority effects in an interactive, not merely additive, manner. Early-arriving species' biomass was a key driver of competition effects. While exotic species produced more biomass when arriving early (though only in year four), their competitive impact was not stronger than that of native species. This indicates differing competitive strategies: exotics tend to dominate via rapid biomass accumulation, whereas natives were more vulnerable in early stages and inhibited by soil fungi.

These findings stress the importance of aligning restoration efforts with the life-history stages of target species.

In Chapter 3, I additionally examined how phylogenetic distance, alongside the biogeographic history (allopatric vs. sympatric) of the interacting species, mediates net priority effects. To this end, I conducted a controlled greenhouse experiment involving an expanded set of 30 species in total. I found that net priority effects were stronger among closely related species, but this pattern was evident only in the biomass production of late-arriving species, and not during their early life stages of seedling emergence and survival. This suggests the presence of ontogenetic niche shifts, whereby trait similarity becomes important only when interacting species are at the same life stage, which in the case of sequential arrival occurs only at the adult stage. Moreover, this relationship was independent of biogeographic history, indicating that origin-dependent niche divergence does not play a major role in this system.

In Chapter 4, I further investigate the role of phylogenetic and biogeographic history in priority effects, with a particular focus on plant-soil interactions. To isolate the influence of plant-soil feedback, I conducted a greenhouse experiment using the same species set and design as in Chapter 3 but removed the early-arriving species after a soil conditioning phase, prior to sowing the late-arriving species. I found that the strength of plant-soil feedback-mediated priority effects was generally inhibitory but independent of phylogenetic distance. This finding suggests that the effect of phylogenetic distance on the strength of priority effects observed in Chapter 3 is primarily driven by competitive interactions rather than plant-soil feedback. Furthermore, priority effects differed between native and exotic species, with stronger inhibition occurring in soils conditioned by native species.

This thesis contributes to a more nuanced and mechanistic understanding of priority effects in plant community assembly. I was able to disentangle the roles of direct competition and plant-soil feedback, demonstrating that both mechanisms contribute to the predominantly negative net priority effects and that their combined influence is not merely additive but involves interactive effects. Furthermore, I demonstrated how the mechanisms underlying priority effects are modulated by species' evolutionary and biogeographic histories. This contributes to a more mechanistic understanding of historical contingency in plant communities and provides valuable insights for managing invasive species and restoring ecosystems in the context of global environmental change.

Zusammenfassung

Ein zentrales Ziel ökologischer Forschung ist es, die Zusammensetzung ökologischer Gemeinschaften und ihre zugrunde liegenden Prozesse zu verstehen. In den vergangenen zwei Jahrzehnten hat in diesem Forschungsfeld insbesondere die Reihenfolge der Artenankunft zunehmend an Bedeutung gewonnen. Über eine Vielzahl von Taxa und Ökosystemen hinweg erwiesen sich in diesem Zusammenhang Prioritätseffekte, bei denen früh eintreffende Arten die Etablierung und das Wachstum später ankommender Arten beeinflussen, als ein wichtiger Prozess. Trotz bedeutender theoretischer und empirischer Fortschritte in der Gemeinschaftsökologie sind die zugrunde liegenden Mechanismen, insbesondere in Hinblick auf Pflanzengemeinschaften, bislang nur unzureichend verstanden. In Graslandgemeinschaften haben direkte Konkurrenz und Pflanze-Boden-Interaktionen eine zentrale ökologische Bedeutung. Dennoch existieren bislang nur wenige empirische Studien, welche ihr Zusammenspiel im Kontext von Prioritätseffekten untersucht, und es fehlen insbesondere langfristige Freilandversuche.

Durch die Untersuchung des Einflusses von Prioritätseffekten auf Konkurrenz und Pflanze-Boden-Interaktionen, trägt diese Arbeit zur Schließung dieser Wissenslücke bei. Darüber hinaus wird erforscht, inwiefern die geographische Herkunft und die phylogenetische Verwandtschaft der beteiligten zweijährigen und ausdauernden Graslandarten diese beiden Prozesse beeinflussen. Zur Beantwortung dieser Fragen kamen sowohl ein groß angelegtes Freilandexperiment unter realitätsnahen Bedingungen zum Einsatz, welches die Untersuchung genereller Mechanismen ermöglichte, als auch kontrollierte Gewächshausversuche unter standardisierten Bedingungen, in denen einzelne Prozesse mit einer größeren Anzahl an Arten im Detail betrachtet wurden.

In Kapitel 2 untersuche ich in einem mehrjährigen Freilandexperiment mit sechs nativen und sechs exotischen Arten, wie die geographische Herkunft früh- und spätankommender Arten die direkte Konkurrenz sowie die Interaktion mit Bodenpilzen beeinflusst. Die Bodenpilze stellen hierbei eine spezifische Teilkomponente der Pflanze-Boden-Interaktion dar. Ein reziprokes Design einschließlich aller möglichen Arten- und Behandlungskombinationen gewährleistet eine umfassende Analyse der Interaktionen. Der Einsatz von Herbiziden und Fungiziden

ermöglichte eine differenzierte Analyse von direkten Konkurrenzeffekten und über Bodenpilze vermittelten Effekten. Diese zeigt auf, dass diese Prozesse nicht nur additiv, sondern auch interaktiv sind und beide zu negativen Netto-Prioritätseffekten beitragen. Der Konkurrenzeffekt war zudem wesentlich durch die Biomasse der frühankommenden Arten bestimmt. Obwohl exotische Arten eine größere Biomasse besaßen (wenn auch nur im vierten Jahr), übten sie keinen stärkeren Konkurrenzeffekt aus. Dies deutet auf unterschiedliche Konkurrenzstrategien nativer und exotischer Arten hin. Während exotische Arten dazu tendieren durch schnelle Biomasseakkumulation Dominanz zu erlangen, erscheinen native Arten in den frühen Lebensstadien angreifbarer und zusätzlich durch Bodenpilze in ihrer Etablierung gehemmt. Dies unterstreicht die Notwendigkeit, Renaturierungsmaßnahmen an den entscheidenden Lebensphasen der Zielarten auszurichten.

In Kapitel 3 untersuche ich zusätzlich, wie die phylogenetische Distanz und die biogeographische Vergangenheit (allopatrisch vs. sympatrisch) der interagierenden Arten die Netto-Prioritätseffekte beeinflusst. Hierzu führte ich ein kontrolliertes Gewächshausexperiment mit einem erweiterten Artenspektrum von insgesamt 30 Arten durch. Es zeigte sich, dass Prioritätseffekte zwischen nahe verwandten Arten stärker ausgeprägt waren, allerdings nur in Bezug auf die Biomasseproduktion der spätankommenden Arten und nicht hinsichtlich ihrer Keimung sowie dem Überleben der Keimlinge. Dies deutet auf eine Verschiebung der Nische im Verlauf der Ontogenie hin, wodurch funktionale Ähnlichkeiten im Kontext von Prioritätseffekten erst im adulten Stadium relevant werden. Zudem war dieser Zusammenhang unabhängig von der biogeographischen Vergangenheit der Arten, was darauf hinweist, dass eine herkunftsabhängige Nischendifferenzierung in diesem System keine dominante Rolle spielt.

In Kapitel 4 widme ich mich eingehend der Bedeutung von Pflanze-Boden-Interaktionen für Prioritätseffekte und analysiere, wie diese durch die phylogenetische Distanz und die biogeographische Vergangenheit der interagierenden Arten beeinflusst wird. Dazu führte ich ein weiteres Gewächshausexperiment mit dem in Kapitel 3 verwendeten Artenspektrum und Versuchsdesign durch, bei dem jedoch die frühankommenden Arten nach einer Konditionierungsphase des Bodens vor der Einsaat der spätankommenden Arten entfernt wurden. Die Ergebnisse zeigen, dass die über Pflanze-Boden-Interaktionen vermittelten Prioritätseffekte überwiegend hemmend wirken, jedoch unabhängig von der phylogenetischen Distanz sind. Dies legt die Vermutung nahe, dass der in Kapitel 3 beobachtete Zusammenhang zwischen phylogenetischer Distanz der untersuchten Pflanzenarten und Stärke der Prioritätseffekte primär auf Konkurrenzinteraktionen zurückzuführen ist. Darüber hinaus zeigten sich Unterschiede in den Pflanze-Boden-Interaktionen zwischen nativen und exotischen Arten, wobei von nativen Arten konditionierte Böden die Etablierung nachfolgender Arten stärker beeinträchtigten.

Zusammenfassend trägt diese Arbeit zu einem differenzierteren mechanistischen Verständnis von Prioritätseffekten und ihrer Bedeutung für die Zusammensetzung von Pflanzengemeinschaften bei. Durch die Trennung der Effekte direkter Konkurrenz und Pflanze-Boden-Interaktionen zeigte sich, dass beide Mechanismen zu den vorwiegend negativen Prioritätseffekten beitragen und zudem miteinander interagieren. Darüber hinaus konnte ich aufzeigen, wie die zugrunde liegenden Prozesse durch den evolutionären und biogeographischen Hintergrund der beteiligten Arten beeinflusst werden. Dies trägt zu einem besseren Verständnis der Bedeutung von Prioritätseffekten für die Zusammensetzung von Pflanzengemeinschaften bei und liefert wertvolle Erkenntnisse für das Management invasiver Arten sowie die Renaturierung von Ökosystemen in Zeiten globaler Umweltveränderungen.

Chapter 1

General introduction

Community assembly and priority effects

Understanding how species interactions shape community assembly, the process by which species from a regional pool colonise and interact to form local communities (HilleRisLambers et al., 2012), has long been a central focus in ecology (Diamond, 1975; Gleason, 1927; Mittelbach & McGill, 2019). Disentangling the various processes that drive community assembly helps explain observed patterns of biodiversity (Mori et al., 2013; Pouteau et al., 2019; Weiher & Keddy, 1995; Xu et al., 2021), and is essential for addressing pressing challenges, including habitat restoration (Audino et al., 2017; Catano et al., 2023; Zirbel et al., 2017), biological invasions (Davis et al., 2005; Pearson et al., 2018), species conservation (Blonder et al., 2024; Godoy et al., 2024), and anticipating how ecosystems may respond to future environmental change (Götzenberger et al., 2012).

While early community assembly research predominantly emphasised functional (Tilman, 1982; Weiher & Keddy, 1995), phylogenetic (Cavender-Bares et al., 2009; Webb et al., 2002), and trait-based (Kraft et al., 2008; McGill et al., 2006; Violle et al., 2007) aspects, the timing and order of species interactions have received growing attention over the last two decades (Chase, 2003a; Debray et al., 2022; Fukami, 2015; Stroud et al., 2024). Against this background, the concept of priority effects has become increasingly established, particularly in studies conducted through the lens of community ecology. In this context, priority effects specifically refer to cases where the order of species arrival affects the composition of communities (Fukami, 2015; Stroud et al., 2024; Zou & Rudolf, 2023). In this thesis, I adopt a broad definition of priority effects as the effect of an early-arriving species on the establishment, growth, or reproduction of a late-arriving species (Alonso-Crespo et al., 2025; Grman & Suding, 2010). While this definition does not permit conclusions about whether outcomes would differ under reversed or simultaneous arrival, it nonetheless provides valuable insight into the mechanisms underlying priority effects.

Priority effects have been documented across a wide range of biological disciplines, including invasion biology (Levine et al., 2004), restoration ecology (Funk et al., 2008; Suding et al., 2004), population biology (Massot et al., 1994), community ecology (Fragata et al., 2022; Hess et al., 2019), and immunology (Gensollen et al., 2016; Shealy et al., 2021). They are also observed across various study systems, including plants (Delory et al., 2019a; Stuble & Souza, 2016; Weidlich et al., 2021), animals (Alford & Wilbur, 1985; Miller-Pierce & Preisser, 2012; Murillo-Rincón et al., 2017), and microbiota (Debray et al., 2022; Svoboda et al., 2018; Toju et al., 2018). In plants, priority effects can operate across timescales ranging from days (Alonso-Crespo et al., 2025; Gillhaussen et al., 2014; Sarneel et al., 2016; Wilsey et al., 2015) to years (Wohlwend et al., 2019; Young et al., 2017). In natural systems, such effects may arise from phenological differences in the timing of emergence (Miller, 1987) or from variation in the order and timing of species arrival. These differences are particularly evident in the introduction of exotic species into novel environments (Dickson et al., 2012; Von Holle, 2005). Several studies have investigated priority effects in the context of invasions, albeit without explicitly referring to them as such (e.g. Gioria et al., 2018; Singh et al., 2024; Torres et al., 2022; Yannelli et al., 2020). Priority effects also play a role following abiotic disturbance events such as floods, fires, storms, and earthquakes, which initiate a new round of community assembly (Fukami, 2015). In this context, their role in ecological succession has been the subject of investigation (Helsen et al., 2016; Restrepo-Carvajal et al., 2024; Valverde et al., 2021; Wilfahrt et al., 2019; H. Zhang et al., 2024a)

Mechanisms of priority effects

Building on community assembly theory, Fukami (2015) proposed a now widely accepted categorisation of priority effect mechanisms, which can be applied to a wide range of species and ecological systems. Based on the niche concept proposed by Chase and Leibold (2003), which defines a niche as comprising two components, requirements and impact, Fukami (2015) distinguishes between two mechanisms: niche preemption and niche modification. Niche preemption describes a process in which the early-arriving species occupy and deplete resources, thereby reducing their availability to late-arriving species. In consequence, niche preemption-driven priority effects are, by definition, always inhibitory. In plants, empirical studies have demonstrated that the early arrival of a species can intensify competitive interactions (Grman & Suding, 2010; van Steijn et al., 2025) and shift the competitive hierarchy relative to scenarios involving simultaneous establishment (van Steijn et al., 2025). These inhibitory effects are often driven by asymmetric competition, a key mechanism of niche preemption, in which larger individuals obtain a disproportionate share of resources relative to their size and suppress the performance of smaller individuals (Freckleton & Watkinson, 2001; Weiner, 1990). It is important to note that early- and late-arriving species often do not compete at the same developmental stage, unlike in cases of simultaneous arrival. Seedlings may exhibit distinct environmental requirements and occupy different niches from their conspecific adults, owing to ontogenetic niche shifts (Lyons & Barnes, 1998; Miriti, 2006; Müller et al., 2018; Parish & Bazzaz, 1985). Yet, despite its ecological significance, the seedling stage remains largely underrepresented in community assembly research (Larson & Funk, 2016).

In niche modification, early-arriving species alters the abiotic and biotic environment in ways that influence the development, growth, and reproduction of later-arriving species, with effects that can be either positive or negative (Fukami, 2015). Unlike niche preemption, the effects of niche modification may persist even after the early-arriving species has disappeared from the system. A prominent example of environmental modification is plant-soil feedback (hereafter referred to as PSF), a process by which a plant modifies soil conditions in ways that subsequently affect the performance of either the same individual or other individuals of the same species (referred to as intraspecific, conspecific, or direct PSFs), or a different plant species (referred to as interspecific, heterospecific, or indirect PSFs; Bever et al., 1997; van der Putten et al., 2013). Further examples of environmental modification in plants include facilitation by nurse plants, which enhance the performance of seedlings (Perea & Gil, 2014; Rolo et al., 2013; Smit et al., 2007) as well as indirect aboveground interactions mediated by a third species (Sotomayor & Lortie, 2015). In my doctoral research, I will primarily focus on the mechanisms of asymmetric competition and PSFs as key drivers of priority effects.

Plant-soil feedback as an important mechanism of priority effects in plants

For centuries, humans have recognised the importance of plant–soil interactions, particularly in agricultural and horticultural contexts (reviewed in van der Putten et al. 2013). In ecological research, a major advance was made by Bever et al. (1997), who introduced a two-phase experimental design consisting of a soil conditioning phase followed by a feedback phase. They demonstrated that PSFs can promote species coexistence when plants perform more poorly in soils they have conditioned themselves than in soils conditioned by other species. Since then, scientific interest in PSFs has increased markedly, with a substantial rise in research over the past three decades (De Long et al., 2019b; De Long et al., 2023; J. Gundale & Kardol, 2021; Nuland et al., 2016; van der Putten et al., 2013). During this time, it has become evident that plant-soil interactions can differentially influence the performance of plant species (Bever et al., 2010; Ehrenfeld et al., 2005; Kulmatiski et al., 2008) and play key roles in a range of ecological processes, including invasion (Inderjit & Cahill, 2015; Lankau, 2012; Reinhart & Callaway, 2006; Suding et al., 2013; Wolfe & Klironomos, 2005), succession (Bauer et al., 2015; Kardol et al., 2006; J. Zhang et al., 2021), ecosystem restoration (Casper et al., 2024; Eviner & Hawkes, 2008; Lance et al., 2020) and plant community responses to climate change (Fischer et al., 2014). Moreover, it is now widely recognised that most reported PSFs are negative, meaning that plants generally perform worse in soils previously conditioned by conspecifics. These negative feedbacks are considered a key mechanism promoting species coexistence by preventing competitive exclusion (Bever, 2003; Bever et al., 1997; Kulmatiski et al., 2008; Petermann et al., 2008; van der Putten et al., 2013).

In general, the net effect of PSFs can be positive, neutral, or negative, and arises from the interplay of a wide array of biotic and abiotic mechanisms. Abiotic mechanisms include, for example, shifts in soil chemistry, such as variations in pH, nutrient availability, and moisture content (Bezemer et al., 2006; Orwin et al., 2010; Waring et al., 2015) as well as the release of allelopathic compounds (Bais et al., 2003; Callaway & Ridenour, 2004; Vivanco et al., 2004) and other species-specific root exudates (Delory et al., 2021; Inderjit et al., 2011). Biotic mechanisms include the accumulation of various soil organisms, including root-feeding insects (Brown & Gange, 1990; Schädler et al., 2004), plant-parasitic nematodes (van der Putten and van der Stoel 1998), microbial communities (Berg & Smalla, 2009; Lundberg et al., 2012), and organisms within the detrital food web (Hättenschwiler et al., 2005). Furthermore, a variety of environmental factors modulate plant-soil interactions and feedback dynamics. These include nutrient availability (Cheng et al., 2024; Dostál, 2021; McCarthy-Neumann & Kobe, 2019), temperature (De Long et al., 2019c; Duell et al., 2019), soil moisture (De Long et al., 2019b; Milici et al., n.d.), light availability (McCarthy-Neumann & Kobe, 2019; Smith & Reynolds, 2015; Xi et al., 2023), and fire regimes (Hopkins & Bennet, 2024; Kardol et al., 2023; Warneke et al., 2023).

Despite the conceptual overlap between PSFs and priority effects, empirical studies that explicitly link these two processes remain surprisingly scarce (but see Grman & Suding 2010;

van de Voorde et al. 2011; Delory et al. 2021). Notably, the strength and direction of PSFs have been shown to depend on the duration of the soil conditioning phase (Kardol et al. 2013a; Lepinay et al. 2018; Liu et al. 2025). Considering their influence on a wide range of ecosystem processes, PSFs may play a key role in mediating priority effects during community assembly. While significant advances in PSF research have been made in recent years, critical knowledge gaps persist. In particular, the majority of studies have been conducted in controlled greenhouse environments and over relatively short timescales (Kardol et al. 2006; Kulmatiski et al. 2008; but see Kulmatiski et al. 2017; De Long et al. 2019a; Beckman et al. 2023), which may limit their ecological realism. Given the strong context dependency of PSFs, both environmentally and temporally, there is a pressing need for studies conducted under field-based conditions and across extended temporal frameworks to better understand their long-term ecological consequences.

Phylogenetic relationships and priority effects

Early research on plant-plant interactions focused primarily on local ecological processes, emphasising resource competition and environmental stress, while largely overlooking evolutionary relationships (Cavender-Bares et al., 2009; Grime, 2006; Tilman, 1982). The introduction of phylogenetic methods into community ecology, pioneered by Webb et al. (2002), transformed the field and revealed patterns of phylogenetic clustering and phylogenetic overdispersion. In cases of phylogenetic clustering, closely related species co-occur more frequently than expected by chance, typically as a result of environmental filtering (e.g. Cavender-Bares et al. 2006; Ndiribe et al. 2013; Stadler et al. 2017), whereas in phylogenetic overdispersion, closely related species compete strongly due to similar resource requirements, thereby reducing their likelihood of coexistence (e.g. Silva & Batalha 2009; Letcher 2010; Allan et al. 2013).

Despite the theoretical importance of phylogenetic relatedness in shaping species interactions, experimental evidence remains limited and presents inconsistent patterns. While some studies report a clear phylogenetic signal in competitive outcomes (Cadotte, 2013; Germain et al., 2016; Sheppard et al., 2018; Verdú et al., 2012; Violle et al., 2011), others fail to detect such effects (Cahill et al., 2008; Fitzpatrick et al., 2017; Fritschie et al., 2014; Godoy et al., 2014; Narwani et al., 2013). Explicit tests of the importance of phylogenetic relationships for priority effects, however, are even scarcer and likewise reveal no consistent pattern. While research on bacteria

(Tan et al., 2012), nectar yeasts (Peay et al., 2011) and freshwater green algae (Venail et al., 2014) has shown that priority effects tend to be stronger among closely related species, evidence in higher plants is less clear. For instance, Castro et al. (2014) found that colonization success of Lactuca sativa was not affected by the mean phylogenetic distance to the members of the recipient plant assemblages. Sheppard et al. (2018) reported that the establishment success of recently introduced species in temperate grasslands was positively affected by the phylogenetic relatedness to native species and previous invaders. A critical next step toward resolving these contradictory findings is to examine how phylogenetic distance shapes the underlying mechanisms of priority effects, including niche preemption and niche modification.

In ecology, it is commonly assumed that closely related species are more ecologically similar, and thus competition between them is stronger than with more distantly related species (e.g. Burns & Strauss 2011; Martin & Ghalambor 2023; Thonis & Akçakaya 2024). This assumption originates from Darwin's On the Origin of Species, in which he states that "The struggle for existence will generally be most severe between species of the same genus" (Darwin 1859). This early idea was later formalised and expanded upon in community ecology, most notably through the *limiting similarity* hypothesis (MacArthur & Levins, 1967) and the *competition-relatedness* hypothesis (Cavender-Bares et al., 2009; Webb et al., 2002). Both concepts build on the assumption that phylogenetic relatedness can serve as a proxy for ecological similarity, based on the principle of niche conservatism, the idea that closely related species are likely to retain similar traits over evolutionary time (Tan et al., 2012). This expectation is grounded in the Brownian motion model of trait evolution, which posits that random evolutionary changes accumulate over generations, leading to increasing divergence in trait values as evolutionary distance grows (Felsenstein, 1985). While these concepts are foundational in community ecology (e.g. Elton 1946; Dayan & Simberloff 2005), experimental tests remain relatively scarce (but see Cahill et al. 2008; Violle et al. 2011; Narwani et al. 2013).

In addition to direct competition, environmentally mediated effects may also be correlated with the phylogenetic relatedness of the involved species. For instance, PSFs may exhibit a phylogenetic signal, as their outcomes are shaped by ecological similarities among species in terms of soil resource requirements and acquisition strategies, life history characteristics, and interactions with herbivores, pathogens, and mutualists (Brandt et al., 2009; Burns & Strauss, 2011). However, experimental studies are very rare, and findings to date are inconsistent and highly context-dependent (Anacker et al., 2014; Fitzpatrick et al., 2017; Kempel et al., 2018;

Mehrabi & Tuck, 2015; Semchenko et al., 2014; Wandrag et al., 2020). As both the intensity of competition (van Steijn et al., 2025) and the strength and direction of PSFs (Kardol et al. 2013a) are known to depend on the timing of species interactions, the relative importance of the factors mediating competition and PSFs may also shift in the context of priority effects. However, to my knowledge, no study to date has explicitly tested the role of phylogenetic relatedness in shaping both competition and PSFs within the context of priority effects.

Influence of plant origin on plant interactions

Since the beginnings of research on invasion ecology in the mid-20th century, scientists have been investigating the differences between native and exotic plant species and their interactions with the environment (reviewed in Elton 2000; Richardson & Pyšek 2008; Lowry et al. 2013; Drake et al. 2013). Early work in the field was largely descriptive, focusing on documenting the dominance and spread of certain introduced species. Over time, however, research began to identify specific traits commonly associated with successful exotic species (reviewed in Pyšek & Richardson 2007; van Kleunen et al. 2010; Drenovsky et al. 2012). These traits include, for example, broad ecological tolerances (e.g. Higgins & Richardson 2014), effective dispersal mechanisms (e.g. Murray & Phillips 2010; Palma et al. 2021), high phenotypic plasticity (Davidson et al., 2011; Richards et al., 2006), and high relative growth rates (Dawson et al., 2011; R. Drenovsky & James, 2007; Grotkopp & Rejmanek, 2007).

In Central European grasslands, for instance, there have been frequent observations of exotic species producing greater aboveground biomass than native species (Korell et al., 2016; McLeod et al., 2016; Schmidt et al., 2020, Callaway et al., 2025). From the 1980s onwards, a more hypothesis-driven understanding emerged, aiming to explain the mechanisms of exotic species success. A central theory to emerge is the enemy release hypothesis (ERH), which proposes that introduced species experience reduced pressure from their co-evolved above- and belowground enemies (e.g., herbivores or pathogens) upon establishment in a new range. The conceptual origins of this idea date back to Elton (2000), and it was more explicitly formulated by Keane and Crawley (2002). The ERH has since been tested in numerous studies (e.g. Mitchell & Power 2003; Vilà et al. 2005; Agrawal et al. 2005; Halbritter et al. 2012; Lucero et al. 2019). Building on the ERH, the e*volution of increased competitive ability* (EICA) hypothesis (Blossey & Notzold, 1995) proposes that in the absence of natural enemies, invasive species reallocate resources from defence towards growth and reproduction. However, empirical support for this hypothesis is mixed. While some studies report findings consistent with EICA in plants (Bossdorf, 2013; Callaway et al., 2022; Uesugi & Kessler, 2013), others show limited or no support (Felker-Quinn et al., 2013; Handley et al., 2008; Najberek et al., 2020).

Furthermore, plant origin has been shown to influence PSFs. For example, it has been demonstrated that exotic species can promote native pathogen communities while escaping soil pathogens from their native range, suppress native symbiotic communities, and enhance soil communities that improve their resource acquisition (Klironomos 2002; Callaway et al. 2004; Wolfe & Klironomos 2005; Hawkes et al. 2005; Eppinga et al. 2006). In addition, biogeographic history represents an important yet relatively underexplored factor that may influence how phylogenetic distance shapes plant-plant interactions (reviewed in Cadotte et al. 2017). For instance, interspecific competition among sympatric species, those with a shared evolutionary and geographic history, can drive niche divergence, causing closely related species to differ more in ecological traits than would be expected based solely on their phylogenetic relatedness (Davies et al., 2007; Nuismer & Harmon, 2015; Schluter, 1994; Staples et al., 2016). The evolutionary consequences of long-term sympatry have been discussed at both the intraspecific level (Aarssen & Turkington, 1985; Hart et al., 2019; Sakarchi & Germain, 2023) and the interspecific level (Germain et al., 2016; Thorpe et al., 2011), highlighting how trait evolution can enhance niche differentiation and potentially reduce competitive exclusion.

Despite scientific advances, particularly over the past three decades, the role of species origin and biogeographic history in shaping competitive interactions between plant species of varying relatedness remains insufficiently understood. Yet, addressing these questions is essential for advancing our understanding of community assembly, invasion dynamics, and biodiversity maintenance, especially in the face of accelerating global environmental change.

Thesis objectives

The objective of my thesis is to advance our understanding of priority effects by investigating how plant origin and phylogenetic relationships influence the underlying mechanisms of plant-plant interactions under conditions of sequential arrival. My research focuses particularly on the mechanisms of direct plant competition and PSFs, with a special emphasis on soil fungal communities (see Figure 1.1 for a schematic representation of the priority effect mechanisms investigated in this thesis).

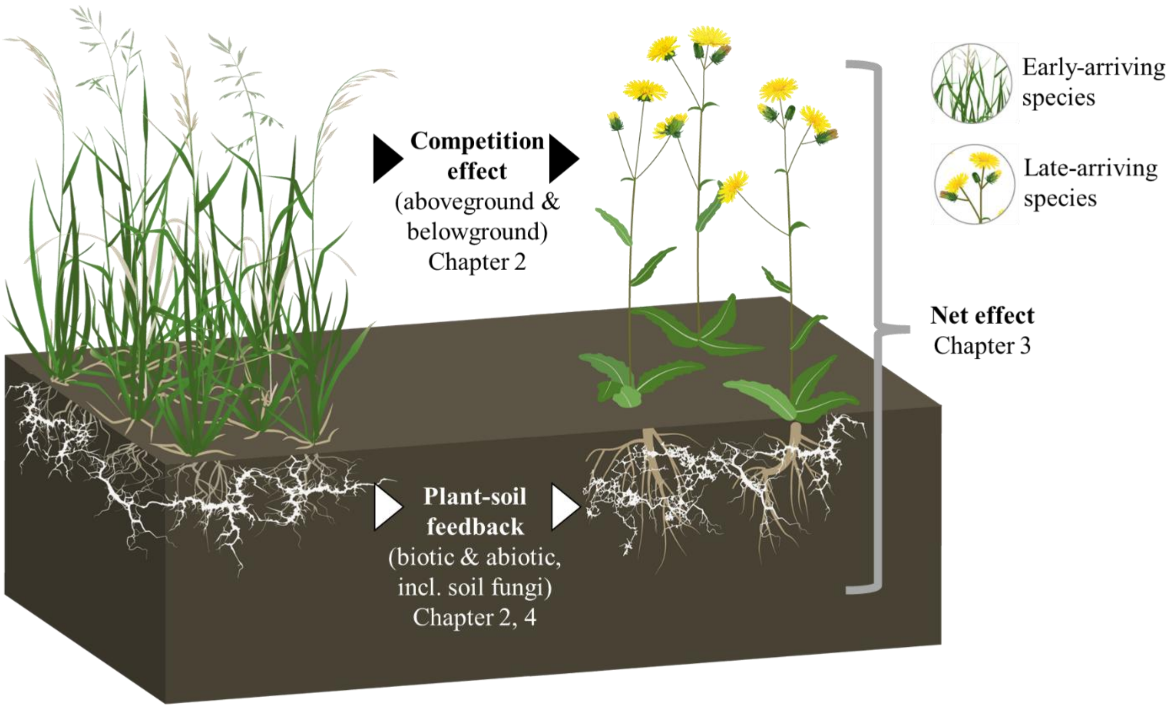


Figure 1.1: Schematic representation of the priority effect mechanism investigated in this thesis, exemplified for *Arrhenatherum elatius* as an early-arriving species and *Picris hieracioides* as a late-arriving species. Modified after Dieskau et al. (unpublished manuscript).

The three chapters that follow build sequentially upon one another, beginning with a large-scale field experiment conducted under realistic environmental and temporal conditions, and progressively delving into the details of individual mechanisms using different controlled greenhouse experiments (see Figure 1.2 for an overview of the research questions addressed).

In **Chapter 2**, I investigated how the origin of early- and late-arriving plant species shapes priority effects in a large-scale, multi-year field experiment conducted in Central Germany. Including different plant functional groups of native and exotic biennial and perennial grassland species, the experiment specifically examined competition-mediated and soil fungi-mediated priority effects, as well as their interaction. These mechanisms were tested through the selective application of herbicides and fungicides, applied individually, in combination, or not at all. This study is unique in explicitly unravelling the mechanistic drivers of priority effects under realistic environmental conditions and across ecologically relevant temporal scales.

In **Chapter 3**, I present the results of a greenhouse experiment, which involved a broader set of species than the field study. This experiment aimed to analyse the role of plant origin in shaping net priority effects. The study further examined the role of phylogenetic distance between early- and late-arriving species in influencing priority effects and explores how this relationship differs between allopatric (species with separate biogeographic histories) and sympatric (species with shared biogeographic histories) species pairs. Moreover, it assessed whether the priority effect of the early-arriving species varies across different life stages of the late-arriving species.

In **Chapter 4**, I explore the influence of phylogenetic and biogeographic history on priority effects in greater depth, with a particular focus on the role of PSF. This chapter presents the findings of a second greenhouse experiment, using the same experimental design and species pool as in Chapter 3. The key difference in this study is that the early-arriving species were removed following a soil conditioning phase, prior to the sowing of the late-arriving species, to isolate the indirect effects mediated through biotic and abiotic soil properties. In addition, a range of abiotic and biotic soil variables were analysed to gain deeper insight into the nature and strength of soil-mediated priority effects.

In **Chapter 5**, I summarise the key findings of the preceding chapters, contextualise them within the broader ecological literature, and offer perspectives for future experimental research on the mechanisms and contingencies of priority effects in plant communities.

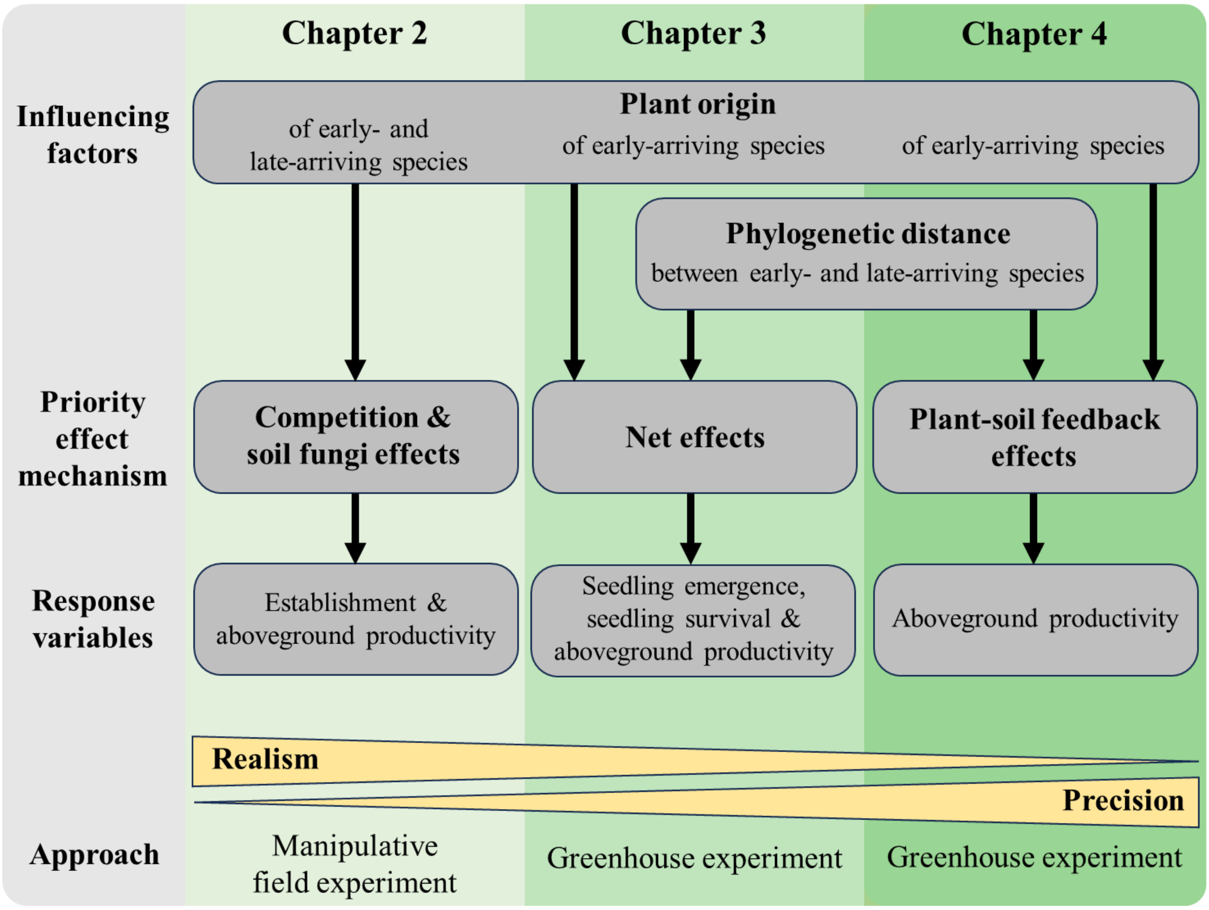


Figure 1.2: Outline of this PhD thesis. The diagram summarises which influencing factors were examined in each chapter, the corresponding priority effect mechanisms targeted, the response variables measured, and the experimental approaches used to investigate these research questions.

Chapter 2

Competition- and soil fungi-mediated priority effects differ between native and exotic European grassland plants

This chapter is submitted to *Journal of Ecology* as:

Dieskau, J., Hensen, I., Eisenhauer, N., & Auge, H. Competition- and soil fungi-mediated priority effects differ between native and exotic European grassland plants.

Abstract

1. The effect of early-arriving plant species (EAS) on the performance of later-arriving species (LAS), also known as priority effects, plays a crucial role in shaping the composition of grassland communities. Although size-asymmetric competition and soil legacies, such as accumulated soil fungi, are key drivers of these effects, their individual and interactive impacts remain underexplored, particularly with regard to the invasion success of exotic plant species.
2. To address this knowledge gap, we conducted a multi-species field experiment in Central Germany to investigate how competition and soil fungi mediate priority effects between EAS and LAS, both native and exotic. We selected 12 grassland species (six native, six exotic), which were seeded as EAS and, after two years, reintroduced as LAS. To unravel the roles of competition- and soil fungi-mediated priority effects, as well as their interaction, we applied herbicide and fungicide treatments both individually and in combination.
3. Our results showed that, where present, both competition- and soil fungi-mediated priority effects on LAS performance were consistently negative. The strength of competition effects on LAS establishment increased with aboveground biomass for both exotic and native EAS. Although exotic EAS produced more biomass than native EAS, average competition effects on LAS establishment did not differ from each other. However, when correcting for EAS biomass, native EAS exerted a stronger competition effect on LAS establishment than exotic EAS. Similarly, the establishment of native LAS was suppressed by competition, whereas exotic LAS remained largely unaffected, regardless of whether EAS biomass was included in the model. However, competition effects on per capita LAS biomass were reversed compared to effects on establishment. Soil fungi tended to inhibit native LAS establishment, and their presence reduced competition effects on LAS establishment and per capita biomass, depending on the origin of EAS and LAS.
4. *Synthesis*: Our study provides experimental evidence that both interspecific competition and soil fungi, independently and interactively, shape priority effects of plants. Moreover, the fact that native and exotic plant species respond differently to competition and soil fungi depending on their life stage has important implications for the fields of invasion and restoration ecology.

Introduction

The composition of ecological communities is often shaped by historical contingencies, as numerous studies across ecosystems have demonstrated (Chase, 2003a; Fukami et al., 2010; Toju et al., 2018). Owing to differences in dispersal strategies, environmental filtering, and small-scale disturbances during the growing season, plant species in natural communities typically arrive sequentially, with some establishing earlier than others. The effect of plant species arriving and establishing before others (hereafter referred to as early-arriving species, EAS) on the establishment, growth, and reproduction of a later-arriving species (hereafter referred to as LAS) is referred to as priority effect and can be negative, positive, or neutral (Fukami, 2015). Despite increasing evidence that priority effects play an important role in plant community assembly (Ejrnæs et al., 2006; Körner et al., 2008), the underlying mechanisms are not fully understood (Fukami, 2015). In general, EAS are commonly believed to affect LAS through a combination of size-asymmetric competition (Ejrnæs et al., 2006; Ellison & Rabinowitz, 1989; Grman & Suding, 2010), which can lead to a drastic reduction in soil nutrients and water availability (Fargione et al., 2003; Vannette & Fukami, 2014), and legacies in the soil resulting from the plant-soil feedback effects (hereafter referred to as PSF) on the soil microbial community (Grman & Suding, 2010; van de Voorde et al., 2011). The focus of this study is therefore on investigating competition- and soil fungi-mediated priority effects.

Due to initial size advantage, EAS individuals are larger and get better access to limiting resources such as light, space, water, or nutrients, for example by having their roots spread into nutrient-rich zones in the soil, forcing the LAS to occupy less favourable areas and possibly outcompeting them (e.g. Ellison and Rabinowitz, 1989; Harmon and Stamp, 2002). As a result, even EAS that are weak competitors may persist and sustain long-term dominance (Chase, 2010; Ross & Harper, 1972). Nevertheless, competition-driven priority effects (meaning the competition effect of an EAS on a LAS, hereafter referred to as competition effects) are expected to be more pronounced for competitive species that produce substantial biomass (Cleland et al., 2015; Kardol et al. 2013b). Frequent observations of exotic species in Central European grasslands producing greater aboveground biomass than native species (Korell et al., 2016; McLeod et al., 2016; Schmidt et al., 2020) suggest that, compared to native species, exotic EAS exert a stronger inhibitory competition effect on LAS, while exotic LAS tend to be less inhibited.

Conceptually in accordance with the *Janzen–Connell* hypothesis on negative density dependence of attack by natural enemies (Connell, 1971; Janzen, 1970), there is growing empirical evidence of soil community feedbacks being commonly negative in grassland plants, playing a critical role in structuring plant communities and maintaining plant diversity (Bever, 1994, 2003; Bever et al., 1997, 2015; Klironomos, 2002). The accumulation of soil fungi can play a significant role in this process (Berg & Smalla, 2009; van der Putten et al., 2013), as soil-borne fungal pathogens were shown to be a major driver of negative PSFs (Maron et al., 2011; Mills & Bever, 1998). In this context, however, the origin of plant species also appears to play a role. In line with the *enemy release* hypothesis (ERH; Keane & Crawley, 2002; Wolfe, 2002; Mitchell & Power, 2003; Brian & Catford, 2023), it has been shown that exotic plant species often benefit when introduced to regions where they encounter fewer soil-borne enemies than in their native ranges (Agrawal et al., 2005; Mitchell & Power, 2003). Moreover, an increasing body of research highlights the significant role of soil biota in facilitating the invasion success of exotic plants (Reinhart & Callaway, 2006). Based on this, we assume that the soil fungi-mediated inhibitory priority effect is less pronounced for exotic EAS and LAS compared to native species. However, as most evidence regarding PSFs is derived from short-term pot experiments (Kardol et al., 2013b), our understanding of the mechanisms through which soil fungi influence plant community structure in natural ecosystems remains limited.

Furthermore, effects of associations with microorganisms are generally studied separately from effects of competition and their relative strength and impacts on each other remain unclear (but see Bennett & Cahill, 2016; Lekberg et al., 2018). However, the effects of direct competition and soil fungi are not always purely additive but sometimes also synergistic (Lekberg et al., 2018). For example, common mycorrhizal networks can preferentially provide mineral nutrients to large host plants, potentially amplifying size-asymmetric competition (Weremijewicz et al., 2016). On the other hand, soil fungal pathogens could reduce the strength of competition effects by inhibiting the performance of the competition partner (Maron et al., 2011). Nevertheless, to our knowledge, no study has investigated this in the context of priority effects under realistic field conditions and for different combinations of native and exotic EAS and LAS.

To develop a deeper understanding of the processes underlying priority effects of native and exotic plant species under more realistic environmental conditions, we conducted a multi-species field experiment, in which LAS were introduced two years after EAS. To gain better insights into the roles of direct competition and soil fungi accumulation in this process, we applied two treatments separately and in combination: a herbicide treatment to reduce EAS biomass and thereby their direct competitive effects, and a fungicide treatment to reduce the soil fungi accumulated by EAS. We tested three hypotheses, each accompanied by a sub-hypothesis addressing the origin of EAS and LAS, respectively: H1) Competition-mediated priority effects are consistently negative and increase with the biomass of the EAS. Due to their typically greater biomass, exotic species are expected to exert stronger priority effects when arriving early and to establish more successfully when arriving late. H2) The performance of LAS is reduced by soil fungi accumulated by EAS. Due to enemy release, exotic species are expected to accumulate fewer inhibitory soil fungi when arriving early and to be less negatively affected by them when arriving late, compared to native species. H3) Soil fungi mediate competition between EAS and LAS, for instance by reducing the performance, and thereby the competitive ability, of EAS. This effect is expected to be particularly pronounced when the EAS are native.

Methods

Species selection

We conducted a multispecies field experiment involving 12 biennial and perennial target plant species commonly found in Central German grasslands. The selection included six species native to Germany and six exotic species, with each origin represented by two species from three functional groups (grasses, forbs, legumes), ensuring a diverse and balanced array of species (Table 2.1). Seed material was either collected directly from wild populations or sourced from commercial suppliers who cultivate seeds from wild progeny. Each of the 12 species was used as an early-arriving species (EAS) and as a late-arriving species (LAS) with a full combination of all possible species pairs.

Table 2.1:

List of plant species used in our experiment, including their plant functional group (PFG), family, and life span. For exotic species, the table also includes their invasion status and minimum residence time (MRT). Lifespan and minimum residence time were extracted from the Bundesamt für Naturschutz (2023) and Seebens (2020). The invasion status was assessed according to Bundesamt für Naturschutz (2023) and Nehring et al. (2013).

Species	PFG	Family	Lifespan	Invasion status	MRT (y)
Native					
Arrhenatherum elatius	grass	Poaceae	polycarpic perennial	-	-
Dactylis glomerata	grass	Poaceae	polycarpic perennial	-	-
Medicago falcata	legume	Fabaceae	polycarpic perennial	-	-
Securigera varia	legume	Fabaceae	polycarpic perennial	-	-
Daucus carota	forb	Apiaceae	biennial	-	-
Picris hieracioides	forb	Asteraceae	polycarpic perennial	-	-
Exotic					
Lolium multiflorum	grass	Poaceae	biennial	established	203
Cynodon dactylon	grass	Poaceae	polycarpic perennial	established	305
Medicago x varia	legume	Fabaceae	polycarpic perennial	established	198
Onobrychis viciifolia	legume	Fabaceae	polycarpic perennial	established	96
Echinops sphaerocephalus	forb	Asteraceae	monocarpic perennial	established	185
Pimpinella peregrina	forb	Apiaceae	polycarpic perennial	casual	17

Experimental set-up

The experiment was carried out in a former arable field located at the research station of the Helmholtz Centre for Environmental Research in Bad Lauchstädt (51.3917°N, 11.8779°E; 114 m a.s.l.; long-term average annual temperature 8.9 °C and annual precipitation 486.4 mm; for more detailed information about the climate during the experimental period see Table S 2.2 in the Supplementary information). The field, which had been abandoned since 2012, underwent preparatory measures that including ploughing to a depth of 28 cm, levelling with a wing share, and autumn application of an herbicide (Profi-MCPA, 1.5 l/ha) in 2016 to control *Cirsium arvense* and other dicotyledonous weeds. Before experimentation, we conducted a general soil characterisation by collecting 28 soil samples at depths of 0-10 cm and 10-20 cm (each sample consisting of three subsamples) from locations evenly distributed across the approximately 3300 m² experimental area. The soil exhibited relatively high nutrient levels, with a total soil carbon content of 2.004 % at 10 cm and 2.009 % at 20 cm depth, a total soil nitrogen content of 0.175% at both depths, a base saturation of 0.985 % at 10 cm and 0.983 % at 20 cm depth, a cation exchange capacity of 0.315 µmol IE/g at 10 cm and 0.320 µmol IE/g at 20 cm depth, and a pH of 6.4 at both depths (for detailed information on the soil properties we measured, see Table S 2.3 in the Supplementary information, and for characteristics of the Chernozem soil at the study site, refer to Altermann et al., 2005).

In autumn 2016, we established 288 plots measuring 2 × 2 m with 1.5 m paths between them, randomly distributed within the three replicated blocks. In this first year of the experiment, EAS were seeded in monoculture in these plots, targeting a seedling density of 1000 seedlings per m². The quantities of seeds were determined based on the germination rates obtained from a previous cold stratification experiment conducted with seeds in petri dishes for 45 days (12 h day/night, 20/10 °C; for more details, see Table S 2.1 in the Supplementary information). In cases where two seed sources were used, the seeds were mixed in a 1:1 ratio, and the average germination percentage was used to calculate the seed material. The seeds for each plot were mixed with 50 g of soybean and field bean meal to ensure a uniform seed distribution. By spring of the second experimental year, EAS seedlings were counted in two randomly selected plots per block per species (72 plots), within two randomly placed frames (0.2 × 0.5 m). Species with seedling densities below 1000 seedlings per m² were resown in June of the second experimental year, with additional seed material calculated based on average seedling emergence for each species in the field. During the EAS establishment phase, plots were carefully weeded to remove unwanted herbs and grasses, while minimising soil disturbance.

In July of the second experimental year (2017) and June of the third year (2018), we assessed the success of our EAS establishment and the impact of weeding on the proportion of our target species. To do so, we determined the aboveground biomass of EAS and the proportion of weeds. For biomass sampling, a 0.2 × 0.5 m frame was randomly placed inside each plot, and all plants inside the frame were cut 2 cm above the soil surface. The EAS and the weeds were then separated, dried at 60 °C for 72 hours, and then weighed. In the second experimental year, the proportion of biomass of our EAS relative to total biomass still varied, ranging from 48.7% (*Lolium multiflorum*) to 99.1% (*Daucus carota*). However, in the third year, the species were well established, with biomass proportions ranging from 87.0% (*Lolium multiflorum*) to 99.7% (*Echinops sphaerocephalus*; see Figures S 2.2 and S 2.3 in the Supplementary information for detailed data on EAS biomass and total biomass across years). Following each harvest and again in late summer, the plots were mown according to standard management practices for Central European grasslands (Babai et al., 2021; Tälle et al., 2018).

To examine the priority effects driven by soil fungi, we implemented a reduction in soil fungi during the EAS establishment phase in the second and third experimental years. Two different fungicides (Acrobat Plus WG, 2 kg/ha, BASF Agrar; Champion & Diamant, 1.6 l/ha, BASF Agrar) were applied to half of the plots, targeting a broad spectrum of soil fungi. These fungicides were applied alternately every three weeks during the growing seasons (April to November), resulting in four applications per year for each. The application was carried out using a watering can, with fungicide quantities per area consistent with the manual recommendations to combat leaf fungi. However, these quantities were diluted 25 times more with water to ensure adequate penetration into the ground. The remaining half of the plots received the equivalent amount of water without fungicides. To investigate the potential direct and indirect effects of fungicide application on soil characteristics, soil samples were collected in the third and fourth experimental years for the analysis of abiotic and biotic soil properties. In the third experimental year, the soil variables examined were not affected by the fungicide treatment. However, the fungicide significantly reduced the concentration of soil nitrogen and carbon in the fourth experimental year (for more details, see Table S 2.4 and the corresponding explanations in the Supplementary information).

To investigate the competition-driven priority effects, EAS were reduced in half of the plots with and without fungicide in October of the third year, before sowing LAS. The herbicide (Glyfos Supreme, Stähler Suisse SA, Zofingen) was applied using an ultra-low volume MANKAR®-Roll spraying system. The herbicide treatment significantly reduced the aboveground biomass of EAS in the following year in plots with herbicide treatment (3.25 ± 0.72 g/m², mean ± standard error) compared to untreated plots (5.35 ± 0.71 g/m²; for more details, see Table S 2.5 and the corresponding explanations in the Supplementary information). To assess the potential impact on the soil biota, soil samples were collected three weeks after treatment and analysed for microbial biomass, basal respiration, and specific respiration. However, none of the investigated variables was significantly affected by the herbicide treatment (Table S 2.7 in the Supplementary information). Furthermore, the effect on abiotic soil properties in the following year was analysed, revealing that potassium content increased significantly in plots with herbicide treatment (Table S 2.6 in the Supplementary information). To prevent possible seed removal by mice, poisoned wheat mixed with vanilla sugar was strategically placed near the identified mouse holes shortly before LAS sowing.

After a two-year establishment phase of the EAS, LAS were sown in November of the third experimental year, and each plot received either the six native or the six exotic species. For this purpose, the central 1 m² of each plot was subdivided into 25 subplots of 0.2 × 0.2 m. Each LAS was then seeded with 100 seeds per subplot across three randomly selected subplots. In July of the fourth experimental year, established adult LAS individuals were counted in each subplot and cut to a height of 2 cm. The three subplots per LAS per plot were pooled and dried at 60 °C for 48 h to determine the biomass. The EAS and the weeds were harvested following procedures in previous years. As *Cynodon dactylon* exhibited poor germination as both EAS and LAS in the field, likely due to low winter temperatures, in contrast to its performance in germination chamber experiments, we excluded this species from all analyses. Additionally, one plot was excluded due to a sowing mismatch, where *Dactylis glomerata* was mistakenly sown as the EAS instead of *Daucus carota*.

In general, the treatment combinations included the two origins of EAS (native/exotic), six EAS per origin, two origins of LAS, two fungicide treatments (with / without), and two herbicide treatments (with/without). These were replicated in a complete factorial design in three blocks, providing three replicates per treatment combination, resulting in a total of 288 experimental plots (see Figure S 2.1 in the Supplementary information for a schematic representation of the temporal sequence of the experiment).

Statistical analyses

All statistical analyses were performed with SAS (Proc GLM, SAS 9.4). First, we examined whether the biomass of native and exotic EAS differed and whether this difference varied between experimental years and depended on the fungicide treatment. A model including fungicide (with or without), EAS origin (native or exotic) and year (2nd, 3rd or 4th experimental year), along with all possible interactions, was fitted (Proc GLM with lognormal distribution). The aboveground biomass of EAS in the plots without reduction of EAS served as the response variable. To address zero values in EAS biomass, the smallest nonzero value was added to all values. Random effects included block, EAS plant functional group (PFG), EAS nested in EAS origin, interaction of fungicide × EAS nested in EAS origin, interaction of year × block, interaction of year × EAS PFG, interaction of year × EAS nested in EAS origin and interaction of year × fungicide × EAS nested in EAS origin. The year was treated as a repeated measurement, and a model with a covariance structure based on variance components rather than first-order autoregression was chosen based on lower AIC values in the model comparison. In the case of interactions, simple main effects (Woodward & Bonett, 1991) were subsequently analysed using the SLICE function to test our hypotheses as to how the role of soil fungi on the competition effect should differ between native and exotic EAS and LAS.

Second, to quantify competition-driven priority effects (CE), we compared the performance of LAS (establishment of adults, per capita biomass, and subplot biomass) in plots with (+C-F) and without (-C-F) competition from EAS, using log response ratios ($LRR_{CE|-F}$ = ln (+C-F /-C-F); Hedges et al., 1999; Figure 2.1). The application of LRRs facilitated the comparison of plant performance in various ontogenetic stages, encompassing both binary metrics such as seedling emergence and continuous variables such as biomass. The LRR calculations were conducted separately within each block. To prevent exclusion of plots with zero values from the analysis, the smallest nonzero value for the corresponding variable was added to all values. Positive LRR values indicate facilitative priority effects (better LAS performance in the respective treatment, here in plots with competition) and negative values indicate inhibitory effects (better LAS performance in control, here in plots without competition). All subplots in which a species was seeded in itself were excluded from the LRR calculation, as the analysis focused on interspecific interactions and did not aim to quantify intraspecific effects. A t-test was used to test whether the LRRs are significantly different from zero. Three models were analysed to investigate the influence of EAS origin, LAS origin and the interaction of EAS origin × LAS origin on the LRRs for the establishment, the per capita biomass, and the subplot biomass of LAS. The random effects included block, EAS PFG, LAS PFG, interaction of EAS PFG × LAS PFG, EAS nested in EAS origin, LAS nested in LAS origin and interaction of EAS × LAS nested in the interaction of EAS origin × LAS origin. Furthermore, three additional models were analysed, which also included EAS biomass in the last experimental year (centered and scaled) as an explanatory variable that included all possible interactions.

Third, priority effects derived from soil fungi were quantified using LRRs similar to the competition-driven effects ($LRR_{FE|-C}$ = ln (-C+F /-C-F); Figure 2.1). Differences between native and exotic EAS and LAS were analysed using the same model as for competition effects, excluding EAS biomass. Fourth, the influence of soil fungi on the competition effect was examined by comparing the competition effect with ($LRR_{CE|+F}$ = ln (+C+F / -C+F)) and without ($LRR_{CE|-F}$ = ln (+C+- / -C-F)) soil fungi (Figure 2.1).

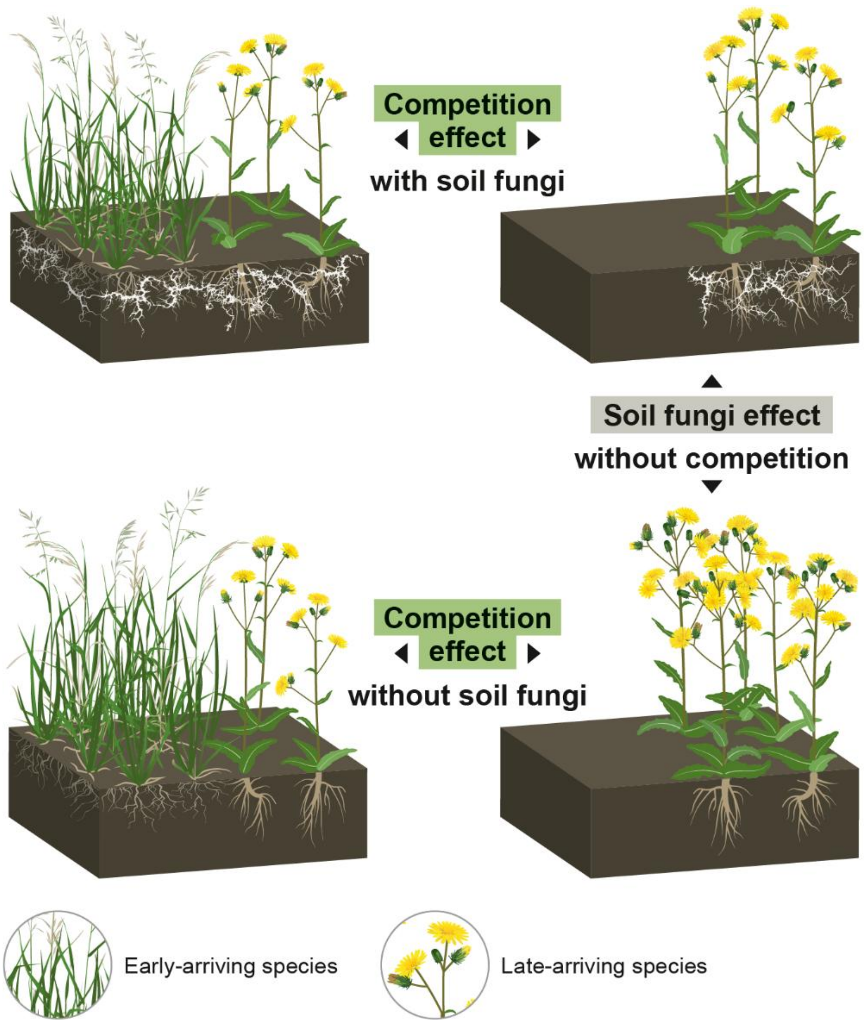


Figure 2.1: Schematic representation of the competition effect with ($LRR_{CE|+F}$ = ln(+C+F/-C+F)) and without ($LRR_{CE|-F}$ = ln(+C-F/-C-F)) soil fungi and the soil fungi effect ($LRR_{FE|-C}$ = ln(-C+F/-C-F)), exemplified for *Arrhenatherum elatius* as an early-arriving species and *Picris hieracioides* as a late-arriving species.

The same model used for the above investigated competition effect was used, with the inclusion of fungicide (with/without soil fungi) as a fixed effect in place of EAS biomass. Furthermore, the model included as additional random effects the interaction of fungicide × EAS nested within the EAS origin, the interaction of fungicide × LAS nested within LAS origin, as well as the interaction of fungicide × EAS × LAS nested within the interaction of the EAS origin × LAS origin. Furthermore, simple main effects were analysed using the SLICE function to test for differences in the competition effect between plots with and without soil fungi reduction for native and exotic EAS and LAS.

Results

Analysis of the aboveground biomass of early-arriving species (EAS) revealed a significant interaction effect of EAS origin and year (Table 2.2, Figure 2.2, see Figure S 2.2 and Figure S 2.3 for the aboveground biomass and total biomass across experimental years for each EAS).

Table 2.2: Results of the mixed-effects model analysis examining the effects of fungicide application (fungicide), early-arriving species origin (EAS origin), experimental year (year) and their interactions on the log-transformed aboveground biomass of EAS. The fungicide × EAS origin and fungicide × EAS origin interactions were further analysed by decomposing them into simple main effects of the fungicide within each origin. Degrees of freedom for the numerator (df Num) and denominator (df Den), F-statistics (F), and p-values (p) are provided. Bold values indicate significant main effects or interactions ($p < 0.05$).

Response variable: aboveground biomass of EAS

Fixed effects	df Num	df Den	F	p
fungicide	1	9	1.48	0.255
EAS origin	1	7	1.01	0.348
year	2	4	3.18	0.149
fungicide × EAS origin	1	9	2.40	0.156
fungicide × year	2	18	1.14	0.342
fungicide | 2017	1	18	0.03	0.866
fungicide | 2018	1	18	0.18	0.676
fungicide | 2019	1	18	0.356	0.076
EAS origin × year	2	14	9.57	**0.002**
EAS origin | 2017	1	14	3.00	0.105
EAS origin | 2018	1	14	1.17	0.298
EAS origin | 2019	1	14	8.99	**0.010**
year × fungicide × EAS origin	2	18	0.01	0.986

Subsequent contrast analysis revealed that native and exotic species differed marginally significantly in biomass only in the fourth experimental year (2019), where exotic EAS (551.1 ± 136.8g/m², mean ± standard error) exhibited twice the amount of biomass of native EAS (256.1 ± 131.3 g/m²). On the contrary, fungicide treatment during the establishment of EAS in the second and third experimental years did not affect the aboveground biomass of EAS, either individually or in interaction.

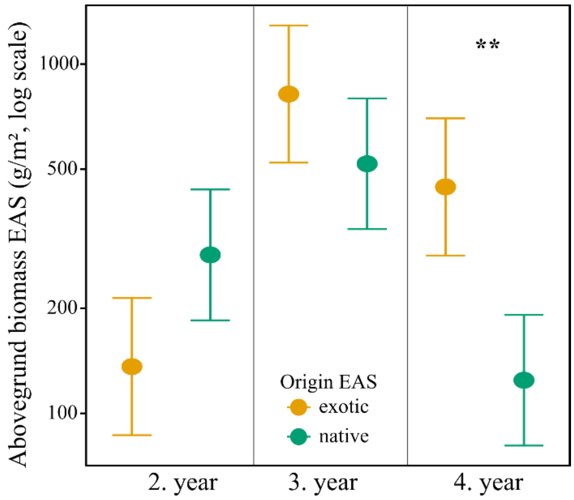


Figure 2.2: Aboveground biomass of native and exotic early-arriving species (EAS) during experimental years. The y-axis is shown on a logarithmic scale. Estimated marginal means and their standard errors are shown. The stars above the symbols indicate significant differences between native and exotic EAS within an experimental year according to the analysis of simple main effects (** $p < 0.01$).

Investigation of the competition effect (LRRCE|-F) on late-arriving species (LAS) revealed that the average effects on establishment were all negative but significantly different from zero only for native EAS (LRR = -0.851, SE = 0.273, p = 0.017) and native LAS (LRR = -0.897, SE = 0.263, p = 0.011), respectively. The strength of the competition effect on the LRR of LAS establishment was significantly influenced by the origin of LAS ($F_{1,7} = 11.03$; $p = 0.013$). While the establishment of native LAS was inhibited by the presence of EAS, the establishment of exotic LAS was not significantly affected. In the model that also included the biomass of EAS, the average effects on the establishment were also negative and, again, significantly different from zero for native EAS (LRR = –0.903, SE = 0.267, p = 0.012) and native LAS (LRR = –0.859, SE = 0.264, p = 0.014). In contrast to the model without EAS biomass, the strength of the competition effect on the LRR of LAS establishment was significantly influenced by the origin of both EAS and LAS, as well as by the biomass of EAS (Table 2.3), which was negatively correlated with the establishment of LAS (Figure 2.3). Additionally, there was a marginally significant three-way interaction between EAS origin × LAS origin × EAS biomass.

Table 2.3: Results of mixed effects model analysis showing the effects of the origin of early-arriving species (origin EAS), the origin of late-arriving species (origin LAS), the aboveground biomass of early-arriving species in the last experimental year (biomass), and their interactions on the competition effect ($LRR_{CE|-F}$ = ln(+C-F/-C-F)) on the establishment and per capita biomass of adult LAS individuals. Degrees of freedom for the numerator (df Num) and denominator (df Den), F statistics (F), and p-values (p) are provided. Bold values indicate significant main effects or interactions ($p < 0.05$).

Competition effect ($LRR_{CE|-F}$) on LAS performance

Response variable	df Num	Df Den	F	p
Establishment				
EAS origin	1	7	11.32	**0.012**
LAS origin	1	7	10.55	**0.014**
biomass	1	211	8.31	**0.004**
EAS origin × LAS origin	1	84	0.30	0.586
biomass × EAS origin	1	211	1.99	0.160
biomass × LAS origin	1	211	3.08	0.081
biomass × EAS origin × LAS origin	1	211	3.07	0.081
Per capita biomass				
EAS origin	1	7	0.00	0.972
LAS origin	1	7	9.42	**0.018**
biomass	1	28	1.08	0.307
EAS origin × LAS origin	1	33	0.00	0.991
biomass × EAS origin	1	28	0.65	0.427
biomass × LAS origin	1	28	0.04	0.846
biomass × EAS origin × LAS origin	1	28	0.19	0.670

Although the establishment of LAS was inhibited by the presence of native EAS, exotic EAS had no significant effect (Figure 2.4a). A similar pattern emerged for origin of LAS, native LAS were inhibited by the presence of EAS, while exotic LAS were not significantly affected (Figure 2.4b). On the contrary, the competition effect on the per capita biomass of LAS was only for exotic LAS significantly different from zero (LRR = -0.995, SE = 0.381, p = 0.035) and was influenced only by the origin of LAS ($F_{1,7} = 9.27$; $p = 0.019$). Although the presence of EAS did not have a significant effect on the per capita biomass of native LAS, the effect on exotic species was significantly negative and thus opposite to the effect on the establishment. This result also remained consistent when EAS biomass was included in the model (Table 2.3; Figure 2.4c). For the effects on subplot biomass, see Table S 2.8 and the corresponding explanations in the Supplementary information.

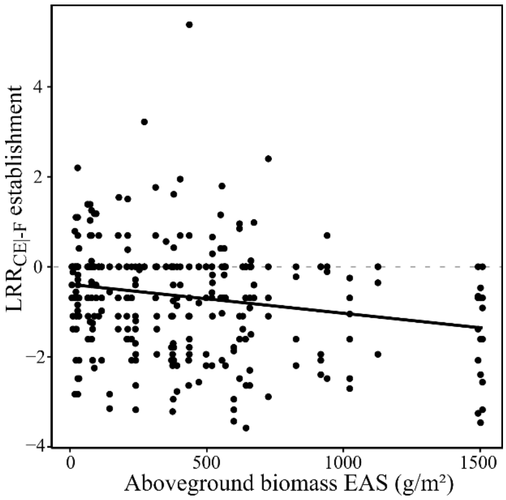


Figure 2.3: Relationship between the aboveground biomass of early-arriving species (EAS) in the final year of the experiment and the logarithmic response ratios for the competition effect ($LRR_{CE|-F} = \ln(+C\text{-}F/-C\text{-}F)$) of the establishment of late-arriving species (LAS). Negative LRR values indicate inhibitory priority effects of EAS on LAS, while positive values reflect facilitative effects.

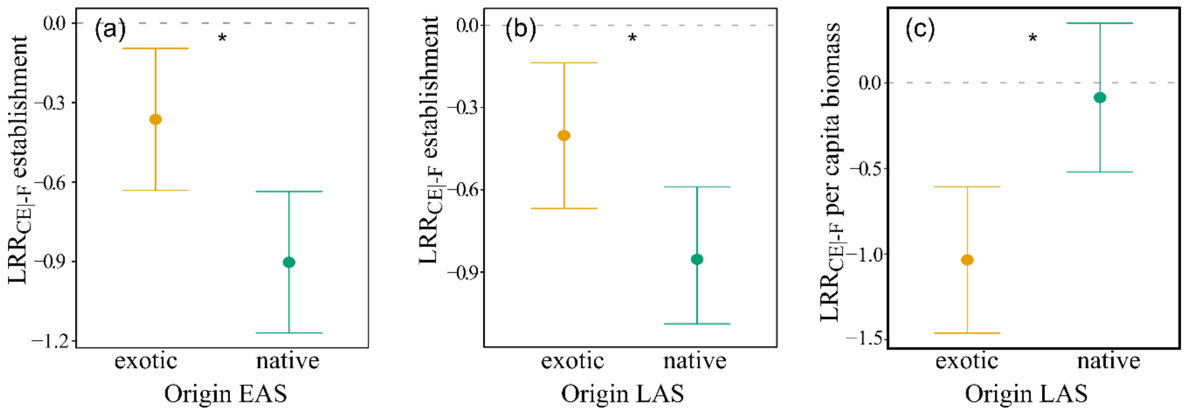


Figure 2.4: Logarithmic response ratios for the competition effect ($LRR_{CE|-F} = \ln(+C\text{-}F/-C\text{-}F)$) on (a) the establishment of late-arriving species (LAS) for exotic and native early-arriving species (EAS), (b) the establishment of late-arriving species for exotic and native LAS, and (c) the per capita aboveground biomass of exotic and native LAS. Estimated marginal means that account for EAS biomass and their standard errors are shown. Negative LRR values indicate inhibitory priority effects of EAS on LAS, while positive values reflect facilitative effects. Stars above the symbols indicate significant differences between the competition effects within native and exotic EAS and LAS, respectively, according to the analysis of the simple main effects (* $p < 0.05$).

Investigation of the soil fungi effect ($LRR_{FE|-C}$) revealed that, similar to the competition effect, the soil fungi effect was smaller than zero only for native EAS (LRR = -0.345, SE = 0.108, p = 0.015) and native LAS (LRR = -0.359, SE = 0.095, p = 0.007), respectively. However, only the difference between native and exotic LAS was marginally significant (Table 2.4), with native LAS being more strongly inhibited by the presence of soil fungi than their exotic counterparts (Figure 2.5). The soil fungi effect on per capita biomass was not significantly different from zero in any case. Furthermore, it was not influenced by the origin of either the EAS or the LAS. For the effects on subplot biomass, see Table S 2.9 and the corresponding explanations in the Supplementary information.

Table 2.4: Mixed-effects model analysis results showing the effects of the origin of early-arriving species (EAS origin), the origin of late-arriving species (LAS origin), and their interactions on the soil fungi effect ($LRR_{FE|-C}$ = ln(-C+F/-C-F)) on LAS establishment and per capita biomass of adult individuals. Degrees of freedom for the numerator (df Num) and denominator (df Den), F statistics (F), and p-values (p) are provided. Bold values indicate significant main effects or interactions ($p < 0.05$).

Soil fungi effect ($LRR_{FE|-C}$) on LAS performance

Response variable	df Num	Df Den	F	p
Establishment				
EAS origin	1	7	1.47	0.265
LAS origin	1	7	3.95	0.087
EAS origin × LAS origin	1	84	0.24	0.626
Per capita biomass				
EAS origin	1	7	0.13	0.732
LAS origin	1	7	0.42	0.539
EAS origin × LAS origin	1	49	0.04	0.848

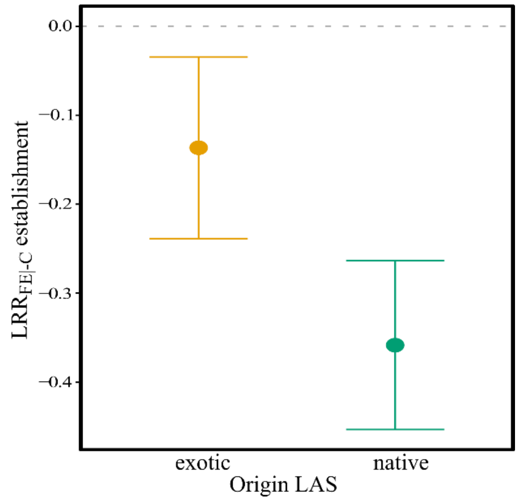


Figure 2.5: Logarithmic response ratios (LRRs) of the establishment of late-arriving species, representing the magnitude of the soil fungi effect ($LRR_{FE|-C}$ = ln(-C+F/-C-F) on native and exotic late-arriving species. Mean values and standard errors are shown. Estimated marginal means and their standard errors are shown. Negative LRR values indicate inhibitory priority effects of EAS on LAS, while positive values reflect facilitative effects. The differences presented are marginally significant ($p = 0.087$).

Comparison of the competition effect with ($LRR_{CE|+F}$ = ln(+C+F/-C+F)) and without ($LRR_{CE|-F}$ = ln(+C-F/-C-F)) soil fungi revealed that the competition effect on establishment was significantly affected by the LAS origin and fungicide treatment, and marginally significantly by the interaction between the origin of EAS and the fungicide (Table 2.5). In general, the detrimental competition effect on the establishment was stronger in plots where soil fungi were excluded (-0.66 ± 0.26) compared to plots where they were still present (-0.45 ± 0.26). Reduced soil fungi intensified the detrimental competition effect of native EAS, while the competition effect of exotic EAS was not affected by fungicide treatment (Figure 2.6a). Similarly, the competition effect on native LAS was enhanced by soil fungi reduction, while the effect on exotic LAS was not influenced by soil fungi (Figure 2.6b). The competition effect on per capita biomass was also more negative in plots where soil fungi were excluded (-0.54 ± 0.26) compared to plots where they were still present (-0.03 ± 0.26). In contrast to the effect on LAS establishment, reduced soil fungi intensified the detrimental competition effect of exotic EAS, while the competition effect of native EAS was not affected by fungicide treatment (Figure 2.6c). Similarly, the competition effect on exotic LAS was enhanced by reducing soil fungi, while the effect on native LAS was not influenced by soil fungi (Figure 2.6d).

Table 2.5: Mixed-effects model analysis results showing the effects of the early-arriving species origin (EAS origin), late-arriving species origin (LAS origin), soil fungi treatment (fungicide), and their interactions on the competition effect (LRR_{CE} = ln(+C-F/-C-F)) on LAS establishment and per capita biomass of adult individuals. The interactions of fungicide × EAS origin and fungicide × LAS origin are decomposed into the simple main effects of the fungicide on each origin. Degrees of freedom for the numerator (df Num) and denominator (df Den), F-statistics (F), and p-values (p) are provided. Bold values indicate significant main effects or interactions ($p < 0.05$).

Competition effect (LRR_{CE})

Response variable	df Num	df Den	F	p
Establishment				
EAS origin	1	7	1.34	0.285
LAS origin	1	7	16.59	**0.005**
Fungicide	1	9	7.62	**0.022**
EAS origin × LAS origin	1	84	0.00	0.967
EAS origin × fungicide	1	9	4.68	0.059
Fungicide | exotic	1	9	0.16	0.698
Fungicide | native	1	9	13.64	**0.005**
LAS origin × fungicide	1	9	0.19	0.676
Fungicide | exotic	1	9	2.44	0.153
Fungicide | native	1	9	5.74	**0.040**
EAS origin × LAS origin × fungicide	1	88	3.72	0.057
Per capita biomass				
EAS origin	1	7	0.02	0.899
LAS origin	1	7	3.52	0.103
Fungicide	1	7	5.81	**0.047**
EAS origin × LAS origin	1	22	0.75	0.395
EAS origin × fungicide	1	9	1.46	0.257
Fungicide | exotic	1	9	6.23	**0.034**
Fungicide | native	1	9	0.76	0.407
LAS origin × fungicide	1	7	3.06	0.124
Fungicide | exotic	1	7	8.98	**0.020**
Fungicide | native	1	7	0.65	0.448
EAS origin × LAS origin × fungicide	1	22	1.08	0.311

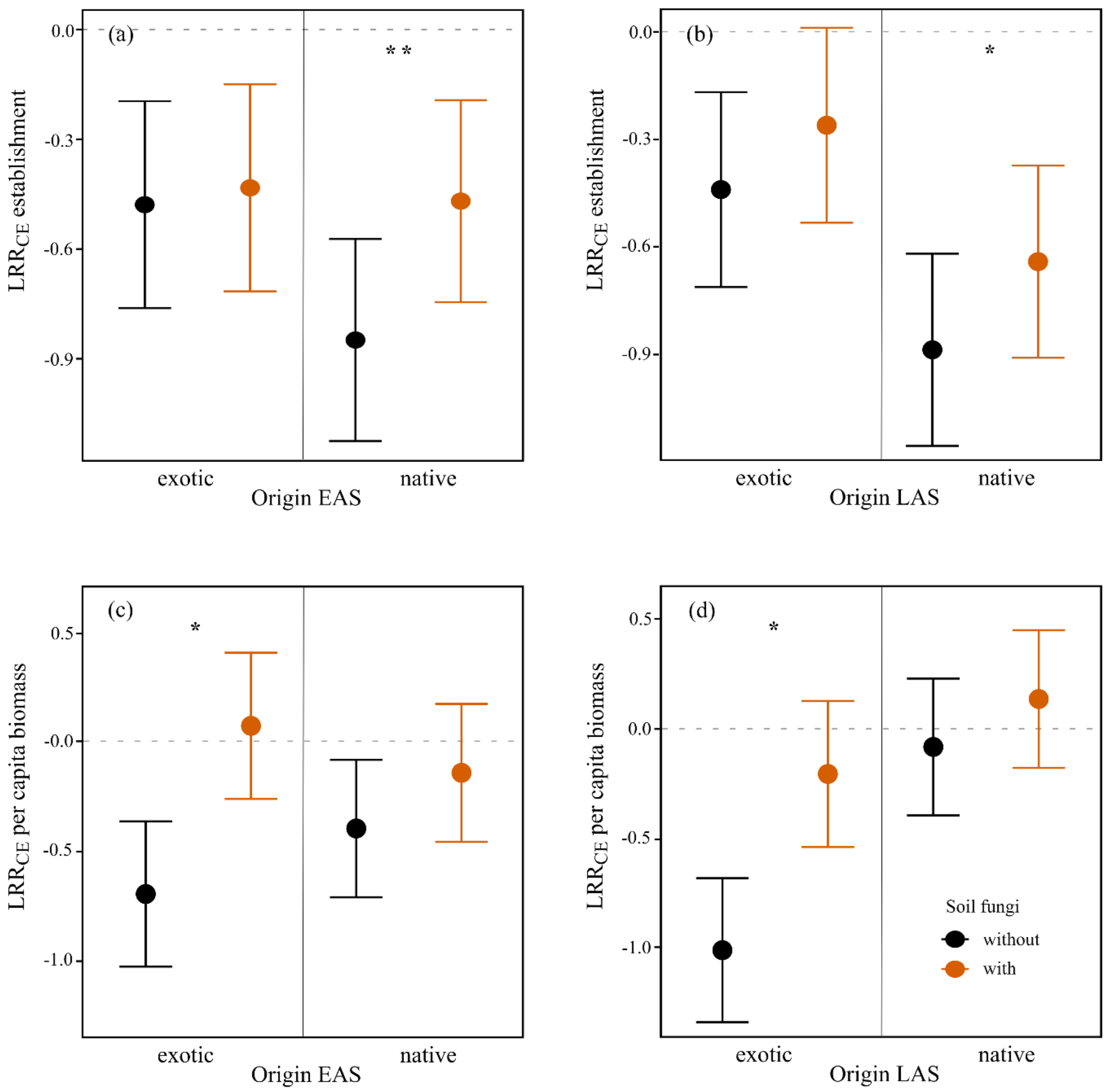


Figure 2.6: Logarithmic response ratios (LRRs) for the competition effect (LRR_{CE} = ln(+C-F/-C-F)) on (a) the establishment of late-arriving species (LAS) for exotic and native early-arriving species (EAS), (b) the establishment of exotic and native LAS, (c) the per capita biomass of LAS for exotic and native EAS, and (d) the per capita biomass of exotic and native LAS, each with and without soil fungi present. Estimated marginal means and their standard errors are shown. Negative LRR values indicate inhibitory priority effects of EAS on LAS, while positive values reflect facilitative effects. Stars above the symbols indicate significant differences between fungicide treatments within native and exotic EAS and LAS, respectively, according to the analysis of simple main effects (* $p < 0.05$; ** $p < 0.01$).

Discussion

This study investigates priority effects mediated by competition and soil fungi between native and exotic early-arriving species (EAS) and late-arriving species (LAS), while also examining potential interactions between these two factors. Consistent with our hypothesis, both competition and soil fungi exerted consistently negative effects wherever present, with the strength of these effects influenced by the origins of EAS and LAS. In addition, the competitive effect was negatively correlated with EAS biomass. Also, in line with our expectations, soil fungi predominantly inhibited native LAS, while exotic LAS remained largely unaffected. Furthermore, the presence of soil fungi reduced the strength of the competition effect. This mitigating effect was most pronounced for the establishment of LAS in native EAS and LAS, and for per capita biomass in exotic EAS and LAS.

Competition effects differ for LAS life stages and depend on EAS and LAS origin

Consistent with our expectations, the competition effect was consistently inhibitory, with LAS performing worse in plots where EAS were present than on those where EAS had been removed. Furthermore, the strength of the competition effect on the establishment of LAS was significantly negatively correlated with the aboveground biomass of EAS at the time of their interaction in the fourth year of the experiment. These results were expected, since plants with greater biomass can more effectively compete for light and other resources, thus exerting a stronger competition effect on neighbouring plants (Bonser & Reader, 1995; Michalet et al., 2023). The late arrival of LAS probably amplifies this effect, as EAS have an initial advantage, allowing them to optimise light availability and extend their roots into nutrient-rich zones before the establishment of LAS. Although glyphosate treatment can, at least temporarily, alter the activity of bacteria and fungi and lead to nutrient input from decaying plant material remaining in the soil (reviewed in Bünemann et al., 2006), we did not find any significant differences between treated and untreated plots in soil microbial biomass, basal respiration, or specific respiration three weeks after glyphosate treatment. There was only a significant increase in potassium content on the removal plots in the following year (Table S 2.6 in the Supplementary information), which may have amplified the suppressive competition effect.

Furthermore, we found differences in the productivity of native and exotic EAS, which also affected the strength of the competition effect. As expected, exotic EAS had significantly higher aboveground biomass than native EAS in the fourth year of our experiment. This is consistent with previous studies that have also found that exotic species generally exhibit higher aboveground biomass compared to native species (Wilsey et al., 2009; Wilsey & Wayne Polley, 2006). Possible explanations include, for example, higher phenotypic plasticity of exotic species compared to native ones (Richards et al., 2006), higher resource investments into competitiveness as a consequence of a release from natural enemies (*evolution of increased competitive ability*, EICA hypothesis; Blossey & Notzold, 1995) and novel weapons (*novel weapons* hypothesis; Callaway & Ridenour, 2004). Despite their higher biomass and in contrast to our expectation, exotic EAS did, on average, not exert a stronger competition effect than native EAS. However, when biomass was taken into account, only native EAS hampered the establishment of LAS, while the competition effect of exotic EAS was negligible. This indicates that other factors in addition to biomass contributed to the competition effect of native species.

These findings, along with the reduced success of native LAS establishment, suggest that native LAS face stronger biotic pressures from antagonists, limiting their establishment, whereas exotic LAS are less affected, supporting the ERH. Furthermore, native and exotic species may employ different competitive strategies. Our results show that native LAS are limited in establishment, while exotic LAS are limited in biomass, suggesting that exotics possess traits that favour late arrival and establishment, whereas natives are better competitors in established communities. This aligns with evidence that exotics often have higher relative growth rates by producing more leaf area per unit mass (James & Drenovsky, 2007; Montesinos, 2022).

Native LAS are more sensitive to the detrimental effects of soil fungi effects than exotic ones

Our results confirm our expectation that the soil fungi effect, when present, is negative, suggesting that fungal pathogens play a key role in shaping the overall impact of soil fungi in our system. In general, soil fungal communities consist of a mix of mutualistic and pathogenic fungi (Martin et al., 2000; Merges et al., 2018; Peay et al., 2013; Schroeder et al., 2019). However, when pathogenic soil fungi dominate, they generally have a negative impact on plant growth and establishment. The high diversity and abundance of pathogenic fungi are associated with suppressed plant growth, reduced seedling survival, and destabilised plant communities, particularly in grasslands and forests (Liang et al., 2021; Liu et al., 2022; Semchenko et al., 2018). Furthermore, in human-managed systems, mycorrhizal associations, which often enhance plant productivity, could also act parasitically when the net cost of the symbiosis exceeds its benefits (Johnson et al., 1997). The fact that the per capita biomass of LAS was not significantly affected by the presence of soil fungi, while their establishment was reduced, is consistent with the literature, which indicates that seedlings are generally more affected by pathogens and mycorrhizas than adult plants (Hersh et al., 2012; Kardol et al., 2013a; van Der Heijden & Horton, 2009). Given that the same pattern was observed for subplot biomass, which for both native and exotic LAS did not differ significantly from zero (Table S 2.10 in the Supplementary information), we rule out density-dependent effects as a result of increased intraspecific competition. This supports the conclusion that soil fungi primarily influence the establishment phase rather than the productivity of already established individuals. Previous studies have shown, for example, that endophytic fungi can influence plant growth in a stage-dependent manner, affecting seed germination and early seedling development in distinct ways (Geisen et al., 2021). Additionally, rhizosphere fungal dynamics have been found to vary between different stages of plant growth in sugarcane (Liu et al., 2023). However, it is also possible that pathogens have an inhibitory effect in all stages of life, but in the adult stage mutualistic relationships may play a larger role if there is a change in plant reliance on mutualists (Kardol et al., 2013a), potentially counteracting negative effects.

Given the broad-spectrum fungicides used in our study, we are confident that the abundance of soil fungi was substantially reduced. Furthermore, previous studies have shown that fungicide application typically decreases fungal abundance and diversity while increasing bacterial numbers, thus shifting the bacteria-to-fungi ratio in favour of bacteria (Pan et al., 2019; Zhang et al., 2024). Our system, a former arable field with a history of intensive land use, is likely already dominated by bacteria. On the contrary, more natural or less disturbed grassland systems, in which fungi tend to dominate, can exhibit stronger soil fungi effects than those observed here (Kandeler et al., 2019; Sünnemann et al., 2021b).

Contrary to our expectations, we found no significant differences in the soil fungi effects of native versus exotic EAS on the establishment of LAS or their per capita biomass, suggesting that both groups accumulate soil fungi to a similar extent. Therefore, it can be assumed that any potential effects driven by enemy release were not amplified by the fact that our plots were sown exclusively with either native or exotic LAS. This is in line with other studies that found that arbuscular mycorrhizal fungal communities of European semi-natural grasslands, for example, are more influenced by abiotic soil conditions than by plant species (Van Geel et al., 2018). However, there was a marginally significant effect of the origin of LAS. Although the establishment of exotic LAS was not significantly affected by the presence of soil fungi, the impact on native LAS tended to be negative, indicating coevolutionary processes leading to a higher sensitivity of native species in our system. These results support the *accumulation of local pathogens* hypothesis, which suggests that exotic species benefit from accumulating local pathogens while being less affected by them than native species (Eppinga et al., 2006). Similar effects have, for example, been documented in Californian grasslands, where viruses accumulate on exotic grasses and then spread to neighbouring native plants, reducing their performance (Malmstrom et al., 2005). Such a reduced sensitivity of exotic species to native pathogens could also have important implications for the management of invasive species. The fact that the observed differences were only marginally significant may be attributed to a reduced activity of soil organisms as a result of a severe drought during the third and fourth year of the experiment (see Table S 2.2 in the Supplementary information for details of the climatic conditions at the experimental site during the study period). Since soil organisms depend on soil moisture (Decaëns, 2010; Phillips et al., 2024), it is not surprising that both the diversity and abundance of soil fungi have been found to decline under drought conditions (Maestre et al., 2015). In addition, mutualistic arbuscular mycorrhizal fungi (AMF) can enhance plant productivity and nitrogen cycling resistance to drought stress (Jia et al., 2021). Therefore, the observed suppressive net effects might have been more pronounced in years with higher precipitation due to increased soil fungal activity and a reduced beneficial effect of mutualistic AMF. Future studies should investigate how the effect of soil fungi in the field varies under different environmental conditions and potential climate change scenarios.

Soil fungi mediate the strength of competition effects

We found that the competition effect was influenced by the presence of soil fungi. In plots treated with fungicide, the competition effect on establishment and per capita biomass were significantly stronger compared to untreated plots. Therefore, we conclude that the presence of soil fungi had a detrimental effect on the strength of the competition effect, supporting our assumption that when plant species arrive at different times, soil fungi not only directly influence the performance of the LAS but also indirectly shape competitive interactions.

A potential pathway in our study is that pathogenic soil fungi may have reduced the performance of EAS, thus weakening their competitive ability relative to LAS. By suppressing growth, soilborne pathogens can compromise a plant's ability to compete, making it more susceptible to displacement by less affected species. Such processes have, for example, been documented in coastal dune systems, where root-associated pathogens contributed to the decline of one grass species and the subsequent dominance of another (Hodge & Fitter, 2013; Maron et al., 2011; van der Putten & Peters, 1997). In addition to pathogenic soil fungi, AMF may also have influenced the observed patterns, as they form symbiotic associations with more than two-thirds of all terrestrial plant species, including the 12 species used in our experiment (Smith & Read, 2010). AMF can affect plant-plant interactions by regulating the uptake and allocation of key resources, such as carbon, nitrogen, and phosphorus, thus shaping competitive dynamics (Daisog et al., 2012; Merrild et al., 2013). Therefore, a resource shift from EAS to LAS via common mycorrhizal networks would also be conceivable. However, we consider this rather unlikely, as previous studies found that they tend to increase rather than decrease inequality between interacting individuals by preferentially supplying mineral nutrients to host individuals that are best able to provide them with fixed carbon (Facelli & Facelli, 2002; Merrild et al., 2013; Weremijewicz et al., 2016; Weremijewicz & Janos, 2013). Consequently, they would rather have intensified priority effects driven by size-asymmetric competition. However, AMF could have interacted with pathogens, influencing plant competition and coexistence by affecting plant defence mechanisms (Gille et al., 2024). In addition, it is important to note that the effects of fungi effects (Hoeksema et al., 2010; Kulmatiski et al., 2008), as well as plant competition (Rees et al., 2012), can strongly depend on resource availability. For example, on plots with soil fungi, both EAS and LAS may have been more resistant to drought stress due to their association with AMF, particularly during the exceptionally dry experimental years, compared to plots where soil fungi were excluded. This may have led to a reduction in the competition for water as a limited resource, thereby weakening the overall competition effect.

Furthermore, our results indicate that native and exotic EAS responded differently to the presence of soil fungi. The reduction of fungi affected only the establishment of LAS in the presence of native EAS, while it influenced the per capita biomass production of LAS only in the presence of exotic EAS. We conclude that native species are primarily inhibited in their establishment by pathogenic fungi, which is supported by the suppressive effect of soil fungi on native LAS found in our study. On the contrary, for exotic species, soil fungi seem to influence traits that reduce the influence of competition on plant growth. Although EAS biomass per unit area was not significantly affected by fungicide treatment, and the soil fungi effect had no impact on exotic LAS, it is possible that soil fungi influenced other traits that we did not measure, which also contribute to competitive strength. In the context of indirect effects of parasites on invasions, Dunn et al. (2012) distinguished between density-mediated indirect effects, which affect the survival or reproduction of the competitive partner, and trait-mediated indirect effects, which arise through induced changes in morphology, life history, or physiology. The potential of trait changes to generate various indirect effects has also been acknowledged in previous studies (Abrams, 1995; Werner & Peacor, 2003).

Furthermore, the results align with those observed for the competition effect. Although the competition effect on the establishment of native LAS was intensified by fungal reduction, exotic LAS were not significantly affected. For the competition effect on the per capita biomass of LAS, the pattern was reversed: the fungal reduction strengthened the competition effect on exotic LAS, whereas the effect on native LAS remained unchanged. This supports our assumption that native LAS respond to competition primarily with reduced establishment, whereas exotic LAS are more inhibited in their biomass production. As a result, intensified competition due to fungal reduction affects different stages of life in native and exotic species accordingly.

Conclusions

Our results highlight the key roles of both competition and soil fungi, independently and interactively, in shaping priority effects. LAS performance was influenced not only by direct soil fungi effects, but also indirectly through altered competition dynamics. Interestingly, biomass differences between native and exotic EAS emerged only in the fourth year, underlining the importance of timing in plant interactions. Furthermore, comparing competition effects with and without taking biomass into account suggests that the competitive effects of native and exotic species are mediated by different mechanisms. Future research should examine how the arrival timing of species influences origin-related differences. In scenarios of simultaneous arrival, biomass effects may be reduced, and origin-specific, biomass-independent factors could dominate, potentially favouring native species establishment with exotic rather than native competitors. However, given that plant-soil interactions are context dependent, shaped by environmental conditions and soil biota composition, our findings should be interpreted within this ecological framework. A logical next step would be to explore these dynamics under different environmental conditions and climate change scenarios, ideally over multiple years, to enhance generalisability.

Acknowledgements

We sincerely thank Ines Merbach and the entire team at the UFZ Field Experimental Station in Bad Lauchstädt for their practical support during the experiment. We also appreciate the assistance of Benjamin Bischoff, Angie Buchold, Yolanda Cacares, Henriette Christel, Ingmar Gaberle, Katrin Kittlaus, Kevin Kožić, Alfred Lochner, Tim Meier, Niclas Mehre, Annika Müller, Birgit Müller, Adrian Schaar, Robin Schmidt, Markus Seidler, Antonia Stürmer, Tobias Proß, Caroline Plos, Julia Rieger, Linda Rehfeldt, and Ina Vogler. Special thanks to Ralf Gründling for drone images of the experimental site and to Uwe Braun for identifying the leaf fungi we collected. We are grateful to Susanne Lachmuth for her valuable input on statistical analyses and to Helge Bruelheide, the Department of Community Ecology at UFZ, and the Plant Ecology Group at MLU for their constructive feedback on data analysis and the manuscript outline. We also thank Gabriele Rada for creating the schematic illustrations. Finally, we thank Michael Köhler for his comments on the manuscript. Moreover, N.E. acknowledges funding by the German Research Foundation (DFG, FZT 118, 202548816; Ei 862/29-1). Chat GPT-4 was used to translate individual sentences of the manuscript.

Supplementary material (S2)

Competition- and soil fungi-mediated priority effects differ between native and exotic European grassland plants

Authors: Julia Dieskau, Isabell Hensen, Nico Eisenhauer, Harald Auge

Journal: *Journal of Ecology* (submitted)

Timeline

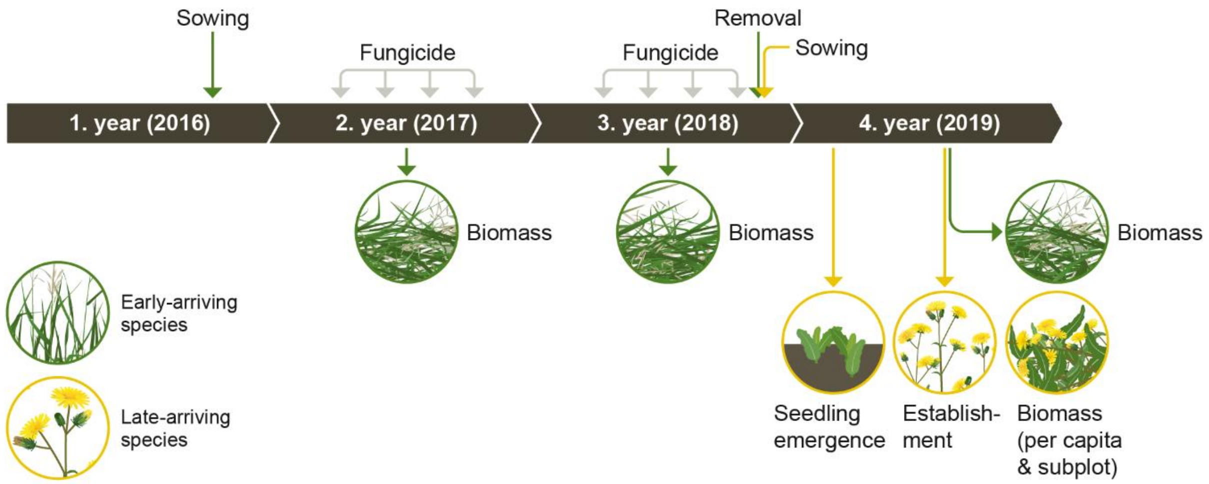


Figure S 2.1: Schematic representation of the temporal sequence of the experiment, including the different treatments and the measured plant performance variables.

Germination experiment

To ensure uniform establishment of all early-arriving species and compensate for differences in their germination behaviour, a germination experiment was conducted to calculate the required seed material for the main experiment. Initially, artificial cold stratification was performed by storing all seeds at 5°C in a refrigerator for three weeks. Subsequently, sets of 4 x 40 seeds were placed on filter paper in petri dishes filled with demineralized water. The temperature cycle was set to 20/10°C, with a light cycle of 12 hours light and 12 hours dark. Every 2-3 days, the seeds were checked, and as soon as the radicle penetrated the testa, a seed was recorded as germinated. After 45 days, the overall germination rate and the cumulative germination (%) were determined (Table S 2.1).

Table S 2.1: Number of germinated seeds for all 12 experimental species. Displayed are the number of germinated seeds for all four replicates, each with 40 sown seeds, as well as the total across all replicates for each of the six experimental weeks and the cumulative germination rate. Seeds of a species from different origins were analysed separately.

Week **Species**	**1**	**2**	**3**	**4**	**5**	**6**	**Cumulative germination (%)**
Arrhenaterum elatius							
Replicate 1	13	7	1	1	0	0	55.00
Replicate 2	8	10	5	0	1	2	65.00
Replicate 3	8	10	1	1	0	3	57.50
Replicate 4	10	8	1	1	2	2	60.00
Sum	39	35	8	3	3	7	59.38
Cynodon dactylon							
Replicate 1	1	4	10	0	1	2	45.00
Replicate 2	0	10	5	1	0	2	45.00
Replicate 3	0	7	0	3	1	6	42.50
Replicate 4	0	5	5	5	1	3	47.50
Sum	1	26	20	9	3	13	45.00
Dactylis glomerata							
Replicate 1	20	10	0	0	0	0	75.00
Replicate 2	7	12	2	1	0	0	55.00
Replicate 3	0	0	0	0	0	0	0.00
Replicate 4	0	0	0	0	0	0	0.00
Sum	27	22	2	1	0	0	32.50
Daucus carota							
Replicate 1	19	14	0	0	0	0	82.50
Replicate 2	12	11	0	0	0	0	57.50
Replicate 3	10	15	0	0	0	0	62.50
Replicate 4	18	6	0	0	0	0	60.00
Sum	59	46	0	0	0	0	65.63
Echinops sphaerocephalus							
Replicate 1	37	0	0	0	0	0	92.50
Replicate 2	35	2	0	1	0	0	95.00
Replicate 3	35	3	0	1	0	0	97.50
Replicate 4	38	0	2	0	0	0	100.00
Sum	145	5	2	2	0	0	96.25
Lolium multiflorum							
Replicate 1	34	2	0	0	0	0	90.00
Replicate 2	33	1	0	0	0	0	85.00
Replicate 3	33	0	0	0	0	0	82.50
Replicate 4	29	0	0	0	0	0	72.50
Sum	129	3	0	0	0	0	82.50
Medicago falcata							
Replicate 1	5	1	2	0	1	1	25.00
Replicate 2	3	1	1	0	0	1	15.00
Replicate 3	7	0	0	1	0	0	20.00
Replicate 4	3	1	1	2	0	0	17.50
Sum	18	3	4	3	1	2	19.38

Medicago x varia (collected by Saale Saaten Stolle)							
Replicate 1	13	0	0	0	0	0	32.50
Replicate 2	8	1	0	1	0	1	27.50
Replicate 3	12	0	0	1	0	0	32.50
Replicate 4	10	2	2	0	0	0	35.00
Sum	43	3	2	2	0	1	31.88
Medicago x varia (collected by the authors)							
Replicate 1	22	0	1	0	0	0	57.50
Replicate 2	16	1	0	0	0	0	42.50
Replicate 3	15	1	2	0	0	0	45.00
Replicate 4	18	1	0	1	0	0	50.00
Sum	71	3	3	1	0	0	48.75
Onobrychis viciifolia							
Replicate 1	29	5	1	0	0	0	87.50
Replicate 2	29	2	1	1	0	0	82.50
Replicate 3	30	1	1	0	0	0	80.00
Replicate 4	23	6	0	0	0	0	72.50
Sum	111	14	3	1	0	0	80.63
Picris hieracioides							
Replicate 1	26	4	0	0	0	1	77.50
Replicate 2	28	3	1	0	0	0	80.00
Replicate 3	21	5	0	1	0	0	67.50
Replicate 4	9	14	0	0	0	0	57.50
Sum	84	26	1	1	0	1	70.63
Pimpinella peregrina (collected by the authors in Großkorbetha)							
Replicate 1	31	6	3	0	0	0	100.00
Replicate 2	27	9	0	1	0	0	92.50
Replicate 3	22	12	0	0	2	0	90.00
Replicate 4	25	13	0	0	0	0	95.00
Sum	105	40	3	1	2	0	94.38
Pimpinella peregrina (collected by the authors in Leipzig Plagwitz)							
Replicate 1	38	0	0	0	0	0	95.00
Replicate 2	37	1	0	0	0	0	95.00
Replicate 3	37	2	0	1	0	0	100.00
Replicate 4	37	3	0	0	0	0	100.00
Sum	149	6	0	1	0	0	97.50
Securigera varia							
Replicate 1	6	2	3	4	5	2	55.00
Replicate 2	6	2	0	8	3	2	52.50
Replicate 3	7	6	1	2	2	2	50.00
Replicate 4	10	3	1	8	0	3	62.50
Sum	29	13	5	22	10	9	55.00

Climate data

Table S 2.2: Temperature (mean annual and mean monthly temperature in °C, measured 2 m above the ground) and precipitation (sum of annual and monthly precipitation in mm) for the experimental years (2016-2019) and the long-term average (1896-2013); data from Deutscher Wetterdienst (DWD) Climate Data Center (CDC) 2024.

Year		**2016**	**2017**	**2018**	**2019**	**Long-term average**
Mean annual temperature		10.5	10.5	10.8	11.2	8.9
Sum annual precipitation		437.2	403.2	254.0	353.2	486.4
Mean monthly temperature	January	1.0	-1.5	4.2	1.2	0.0
	February	3.9	3.1	-1.6	4.7	0.6
	March	4.7	8.0	2.2	7.5	4.1
	April	8.5	8.2	12.9	10.0	8.3
	May	14.6	15.2	13.0	12.0	13.2
	June	18.6	18.6	18.9	21.6	16.3
	July	20.2	19.5	21.5	20.1	18.1
	August	19.1	19.2	21.6	20.6	17.5
	September	18.4	14.1	16.2	15.0	14.0
	October	9.3	12.3	10.9	11.6	9.1
	November	4.4	6.0	5.2	5.8	4.2
	December	2.8	3.7	4.7	4.2	1.1
Monthly sum of precipitation	January	22.9	16.7	33.6	31.9	26.1
	February	42.7	19.5	2.1	3.4	23.2
	March	26.5	33.4	41.9	24.7	29.4
	April	24.3	24.4	33.4	16.4	34.7
	May	21.2	45	13.2	50.3	52.6
	June	80.2	40	14.7	27.2	59.4
	July	67.3	56.4	11.4	24.6	66.7
	August	32.9	67.5	7.8	21.1	57.7
	September	19.1	22.1	30.8	48.3	39.4
	October	52	31	10.8	53.4	36.0
	November	34.8	31.6	11.2	29.7	32.6
	December	13.3	15.6	43.1	22.2	28.6

General soil characterisation at the beginning of the experiment

In May of the second experimental year (2017), soil samples were collected from the pathways between the plots for a general site characterisation. These samples were taken from 27 locations across the entire area using a Pürckhauer auger at a depth of 0–20 cm. The samples were analysed separately for the depths of 0–10 cm and 10–20 cm. At each location, three subsamples were collected and pooled for analysis. After air-drying, the samples were sieved using a 2 mm sieve to remove small stones and plant roots. We measured the pH following Blakemore (1987) and analysed the phosphorous content (following the Egner−Riehm (DL) method). The remaining soil was dried for 72 hours at 80 °C and subsequently ground in an oscillating mill (MM 400, Retsch, Haan, Germany) until they became a homogeneous powder. Five milligrams of the soil powder were used to measure soil C and N gas-chromatographically with the Dumas method (Vario EL Cube, Elementar Analysensysteme, Langenselbold, Germany), from which we further calculated the carbon to nitrogen ratio (soil C:N ratio). Furthermore, we used atomic absorption spectroscopy (AAS vario®6, Analytik Jena) to determine the content of soil phosphorus, calcium, potassium, iron, and magnesium (soil P, Ca, K, Fe, Mg), cation exchange capacity and base saturation (Table S 2.3).

Table S 2.3: Soil characteristics measured from soil samples collected in May of the second experimental year (2017) at 28 locations along the pathways between plots, distributed across the entire experimental site, from 0–10 cm and 10–20 cm soil depth. Presented are the mean and coefficient of variation (CV), as well as the values averaged across both soil depths (total).

	0-10cm soil depth		**10-20cm soil depth**		**Total**	
Variable	Mean	CV	Mean	CV	Mean	CV
pH_{KCl}	6.39	0.04	6.41	0.03	6.4	0.03
Nitrogen (%)	0.18	0.06	0.17	0.05	0.17	0.05
Carbon (%)	2	0.06	2.01	0.05	2.01	0.06
C/N ratio	11.45	0.03	11.49	0.03	11.47	0.03
Phosphorus (µg/g soil)	132.66	0.16	165.62	0.14	149.14	0.19
Magnesium ([µmol IE/g)	0.02	0.18	0.02	0.17	0.02	0.19
Calcium (µmol IE /g)	0.28	0.08	0.29	0.05	0.28	0.07
Potassium (µmol IE /g)	0.01	0.38	0.01	0.35	0.01	0.38
Hydrogen (µmol IE /g)	0	0.61	0.01	0.47	0	0.54
Cec (µmol IE /g)	0.32	0.08	0.32	0.05	0.32	0.07

Biomass of early-arriving species across years

In the second (July 2017), third (June 2018), and fourth (July 2019) experimental years, the aboveground biomass of the early-arriving species (EAS) was measured. This was done by placing two 50 × 20 cm frames outside the central 1 m² of each plot and clipping all biomass within the frames at a height of 2 cm. The collected biomass was sorted into target species and weeds and afterwards dried separately at 60°C for 72 hours before being weighed. Subsequently, the EAS aboveground biomass (Figure S 2.2) and total aboveground biomass (Figure S 2.3) for each EAS and year was calculated.

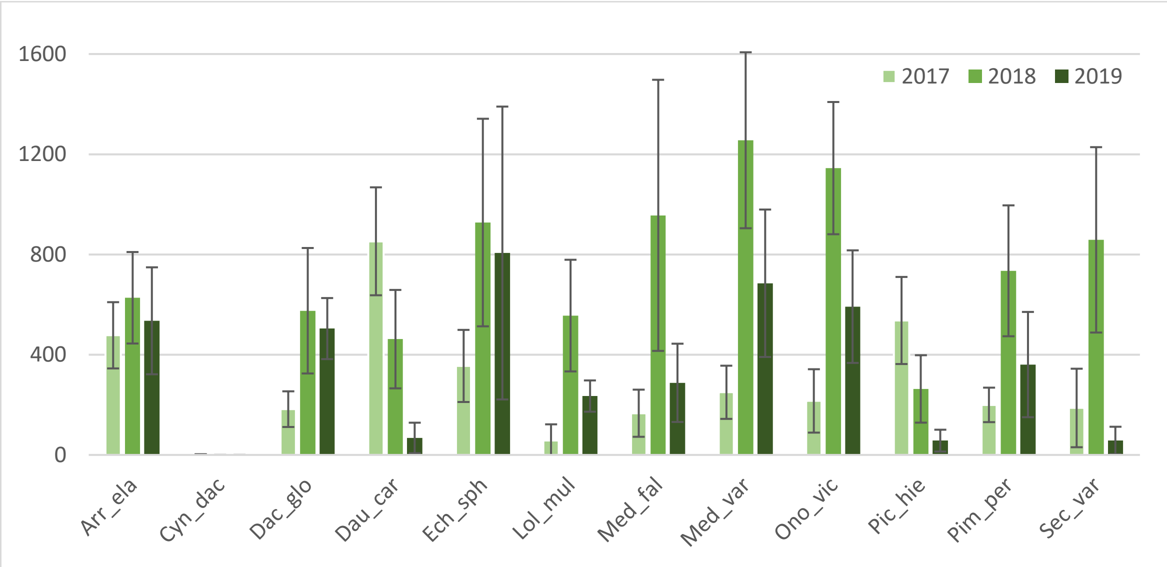


Figure S 2.2: Dry aboveground biomass of early-arriving species in the second (July 2017), third (June 2018) and fourth (July 2019) experimental year on plots without herbicide treatment. Given are mean values and standard deviations.

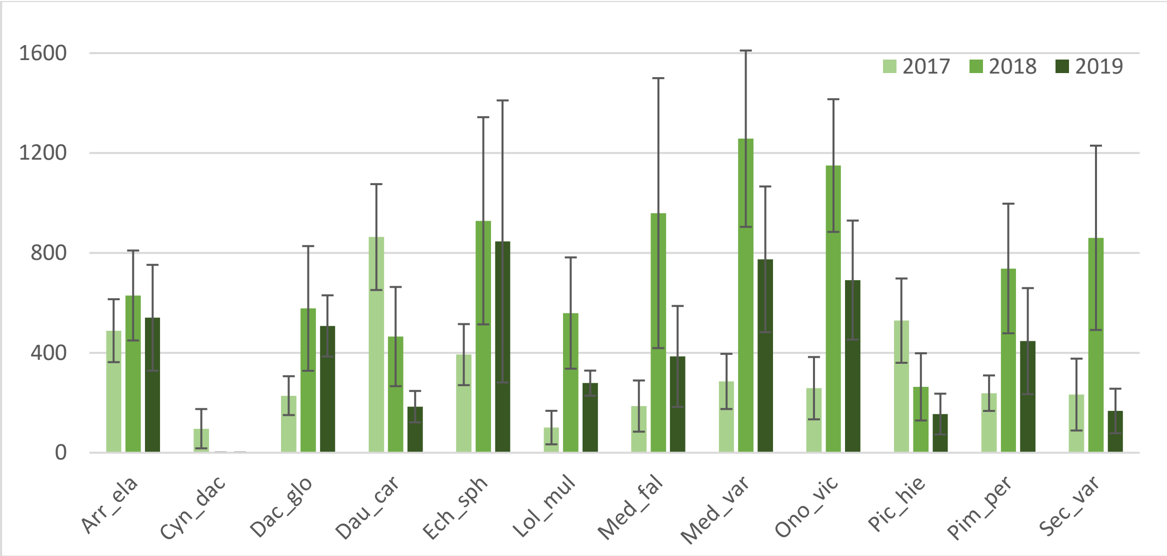


Figure S 2.3: Total aboveground biomass of early-arriving species in the second (July 2017), third (June 2018) and fourth (July 2019) experimental year on plots without herbicide treatment. Given are mean values and standard deviations.

Effects of fungicide treatment on soil characteristics

To investigate potential direct and indirect effects of fungicide application on soil characteristics, soil samples were collected in the third (April 2018) and fourth (April 2019) experimental years for the analysis of abiotic and biotic soil properties. For this purpose, three soil samples per plot were taken outside the central 1 m² using a Pürckhauer auger at a depth of 0–10 cm and pooled for analysis. The analysis of abiotic soil properties followed the procedures described above under "General soil characterisation at the beginning of the experiment." To analyse the response of soil microorganisms, including basal respiration (µl O_2 h^{-1} g^{-1} soil dry weight), microbial biomass (µg Cmic g^{-1} soil dry weight), and specific respiration (µl O_2 mg $Cmic^{-1}$ h^{-1}), soil samples were sieved through a 2 mm mesh to remove small stones and plant roots. An automated O_2-uptake method was used, in which glucose was added as a carbon substrate to measure the respiratory response of soil microorganisms, following established protocols that were used before (Dieskau et al. 2025a; Eisenhauer et al. 2010; Sünnemann et al. 2021a; for details of the method see Scheu 1992).

The statistical analyses were conducted using SAS (Proc GLM, SAS 9.04). Only plots that were not treated with herbicide were included in the statistical analysis. We fitted a model including fungicide (with or without), EAS origin (native or exotic), and all possible interactions. Response variables included phosphorus content, potassium content, nitrogen content, carbon content, C/N ratio, pH value, basal respiration, microbial biomass (Cmic), and specific respiration (qO_2). Random effects included the block, EAS plant functional group (PFG), EAS nested in EAS origin, interaction of removal x EAS nested in EAS origin.

The results show that in the third experimental year (2018), the examined soil variables were not affected by either the fungicide treatment or the origin of the EAS (Table S 2.4). However, in the fourth experimental year, the nitrogen content on fungicide-treated plots (0.172 ± 0.002 %, mean ± standard error) was significantly lower compared to untreated plots Similarly, the carbon content on fungicide-treated plots (2.066 ± 0.016 %) was also significantly lower compared to untreated plots (2.116 ± 0.016 %).

Table S 2.4: Results of the mixed effects model analysis of the fungicide application (fungicide), the origin of the early-arriving species (EAS), and their interactions on the phosphorus content, potassium content, nitrogen content, carbon content, C/N ratio, pH value, basal respiration, microbial biomass (Cmic), and specific respiration (qO_2) of soil taken in 0-10 cm depth in the third (April 2018) and fourth (April 2019) experimental year. Only plots without herbicide treatment were included in the analysis. Degrees of freedom of numerator (df Num) and denominator (df Den), F-statistics (F) and significance values (p) are provided. Bold numbers indicate significant main effects or interactions ($p < 0.05$).

	2018				2019			
	df Num	df Den	F	p	df Num	df Den	F	p
Phosphorus								
Fungicide	1	9	3.43	0.097	1	9	1.00	0.343
EAS origin	1	7	2.36	0.168	1	7	0.03	0.873
Fungicide x EAS Origin	1	9	0.04	0.848	1	9	2.89	0.124
Potassium								
Fungicide	1	9	0.21	0.659	1	9	1.93	0.198
EAS origin	1	7	1.96	0.204	1	7	0.23	0.647
Fungicide x EAS Origin	1	9	0.01	0.921	1	9	0.00	0.987
Nitrogen								
Fungicide	1	9	0.28	0.608	1	9	5.48	**0.044**
EAS origin	1	7	1.91	0.209	1	7	2.67	0.146
Fungicide x EAS Origin	1	9	0.00	0.998	1	9	3.75	0.085
Carbon								
Fungicide	1	9	0.58	0.465	1	9	5.29	**0.047**
EAS origin	1	7	0.05	0.838	1	7	5.07	0.059
Fungicide x EAS Origin	1	9	0.11	0.746	1	9	0.10	0.760
C/N ratio								
Fungicide	1	9	2.63	0.140	1	9	0.19	0.672

EAS origin	1	7	1.68	0.236	1	7	2.58	0.152
Fungicide x EAS Origin	1	9	0.16	0.701	1	9	4.96	0.053
pH_{KCl}								
Fungicide	1	9	1.89	0.203	1	9	0.82	0.390
EAS origin	1	7	0.07	0.794	1	7	0.04	0.840
Fungicide x EAS Origin	1	9	0.36	0.562	1	9	0.01	0.919
Basal respiration								
Fungicide	1	9	3.06	0.114	1	9	0.05	0.824
EAS origin	1	7	1.40	0.276	1	7	1.60	0.247
Fungicide x EAS Origin	1	9	0.23	0.641	1	9	0.22	0.649
Microbial biomass (Cmic)								
Fungicide	1	9	0.39	0.548	1	9	0.67	0.433
EAS origin	1	7	3.77	0.093	1	7	0.03	0.870
Fungicide x EAS Origin	1	9	1.51	0.251	1	9	0.24	0.638
Specific respiration (qO_2)								
Fungicide	1	9	2.08	0.183	1	9	0.38	0.552
EAS origin	1	7	0.08	0.789	1	7	1.23	0.304
Fungicide x EAS Origin	1	9	1.45	0.260	1	9	0.47	0.511

Efficiency of herbicide treatment

To test the efficiency of the herbicide, we compared the biomass of early-arriving species (EAS) and the total biomass including weeds in the fourth experimental year (July 2019) between plots with and without herbicide treatment. For biomass sampling, a 0.2 × 0.5 m frame was randomly placed on each plot, and all plants within the frame were cut at a height of 2 cm. EAS and weeds were then separated, and the EAS biomass was dried at 60°C for 72 hours before being weighed.

The statistical analyses were conducted using SAS (Proc GLM, SAS 9.04). To test whether the biomass of EAS was indeed reduced on plots with herbicide treatment compared to those without, we fitted a model including removal (with or without herbicide treatment), EAS origin (native or exotic), and all possible interactions (Proc GLM with lognormal distribution). The aboveground biomass of EAS and the total biomass on the plots without fungicide treatment of EAS served as the response variables. To address zero values in EAS biomass and total biomass, the smallest non-zero value was added to all values for each variable. Random effects included the block, EAS plant functional group (PFG), EAS nested in EAS origin, interaction of removal x EAS nested in EAS origin.

The results show that the aboveground biomass of EAS was significantly reduced on plots with herbicide treatment (3.25 ± 0.72 g/m², mean ± standard error) compared to untreated plots (5.35 ± 0.71 g/m²), indicating that the herbicide treatment did not completely remove the EAS but substantially reduced their aboveground biomass. In contrast, the total biomass was not affected by the removal treatment because biomass of spontaneously invading plant species (that were able to establish in addition to sown LAS) was higher on plots with herbicide treatment, just like the biomass of sown LAS. However, the EAS biomass and the total biomass on plots with exotic EAS (EAS biomass: 4.90 ± 0.73 g/m²; total biomass: 5.95 ± 0.16 g/m²) was greater than on plots with native EAS (EAS biomass: 3.71 ± 0.71 g/m²; total biomass: 5.34 ± 0.15 g/m²; Table S 2.5). For EAS biomass, however, this effect was only marginally significant.

Table S 2.5: Results of the mixed effects model analysis of the herbicide application (removal), the origin of the early-arriving species (EAS), and their interactions on the aboveground biomass of EAS and the total biomass in the fourth experimental year (July 2019). Only plots without fungicide treatment were included in the analysis. Degrees of freedom of numerator (df Num) and denominator (df Den), F-statistics (F) and significance values (p) are provided. Bold numbers indicate significant main effects or interactions ($p < 0.05$).

Response variable	df Num	df Den	F	p
EAS biomass				
Removal	1	9	17.86	**0.002**
EAS origin	1	7	5.54	0.051
Removal x EAS origin	1	9	0.14	0.714
Total biomass				
Removal	1	9	2.23	0.169
EAS origin	1	7	7.56	**0.029**
Removal x EAS origin	1	9	0.99	0.347

Effects of herbicide treatment on abiotic soil characteristics

To investigate potential direct and indirect effects of herbicide application on abiotic soil characteristics, soil samples were collected in the fourth experimental year (April 2019). For this purpose, three soil samples per plot were taken outside the central 1 m² using a Pürckhauer auger at a depth of 0–10 cm and pooled for analysis. The analysis of abiotic soil properties followed the procedures described above under "General soil characterisation at the beginning of the experiment.". The statistical analyses were conducted using SAS (Proc GLM, SAS 9.04). Only plots that were not treated with fungicide were included in the statistical analysis. We fitted a model including removal (with or without herbicide application), EAS origin (native or exotic), and all possible interactions. Response variables included phosphorus content, potassium content, nitrogen content, carbon content, C/N ratio, and pH value. Random effects included the block, EAS plant functional group (PFG), EAS nested in EAS origin, and interaction of removal x EAS nested in EAS origin.

The results show that the potassium content was significantly increased on plots with herbicide (7.859 ± 0.659 µmol IE/g, mean ± standard error) application compared to those without (6.799 ± 0.659µmol ie/g; Table S 2.6).

Table S 2.6: Results of the mixed effects model analysis of the herbicide application (removal), the origin of the early-arriving species (EAS), and their interactions on the phosphorus content, potassium content, nitrogen content, carbon content, C/N ratio, and pH value of soil taken in 0-10 cm depth in the fourth experimental year (April 2019). Only plots without fungicide treatment were included in the analysis. Degrees of freedom of numerator (df Num) and denominator (df Den), F-statistics (F) and significance values (p) are provided. Bold numbers indicate significant main effects or interactions ($p < 0.05$).

Response variable	df Num	df Den	F	p
Phosphorus				
Removal	1	9	0.52	0.489
EAS origin	1	7	0.03	0.874
Removal x EAS Origin	1	9	0.37	0.560
Potassium				
Removal	1	9	33.59	**<0.001**
EAS origin	1	7	0.23	0.647
Removal x EAS Origin	1	9	0.18	0.678
Nitrogen				
Removal	1	9	1.91	0.201
EAS origin	1	7	2.54	0.155
Removal x EAS Origin	1	9	1.26	0.291
Carbon				
Removal	1	9	0.07	0.794
EAS origin	1	7	4.96	0.061
Removal x EAS Origin	1	9	2.59	0.142
C/N ratio				
Removal	1	9	2.36	0.159
EAS origin	1	7	2.46	0.161
Removal x EAS Origin	1	9	1.24	0.294
pH_{KCl}				
Removal	1	9	2.63	0.140
EAS origin	1	7	0.04	0.840
Removal x EAS Origin	1	9	1.72	0.222

Effects of herbicide treatment on biotic soil characteristics

To investigate potential direct and indirect effects of herbicide application on the soil community, soil samples were collected six weeks after the herbicide treatment (August 2018) from two plots per block per early-arriving species that were not treated with fungicide. For this purpose, three soil samples per plot were taken outside the central 1 m^2 using a Pürckhauer auger at a depth of 0–10 cm and pooled for analysis. After each sampling, the materials used were cleaned and disinfected. The soil was sieved using a 2 mm sieve to remove small stones and plant roots and afterwards stored for a few days at 8°C for analysis of the response of soil microorganisms, including basal respiration (µl O_2 h-1 g-1 soil dry weight), microbial biomass (µg Cmic g−1 soil dry weight), and specific respiration (µl O_2 mg cmic-1 h-1). For this purpose, we used an automated O_2-uptake method involving the addition of glucose as a carbon substrate to measure the respiratory response of soil microorganisms, as done before (Dieskau et al. 2025a; Eisenhauer et al. 2010; Sünnemann et al. 2021a; for details of the method see Scheu 1992). The statistical analyses were conducted using SAS (Proc GLM, SAS 9.04). We fitted a model including removal (with or without herbicide application), EAS origin (native or exotic), and all possible interactions. Response variables included basal respiration, specific respiration (qO_2), and microbial biomass (Cmic). Random effects included the block, EAS plant functional group (PFG), EAS nested in EAS origin, interaction of removal x EAS nested in EAS origin.

The results show that none of the examined variables were significantly affected by the herbicide treatment (Table S 2.7), indicating that the herbicide application had no impact on soil biota activity.

Table S 2.7: Results of the mixed effects model analysis of the herbicide application (removal), the origin of the early-arriving species (EAS), and their interactions on the basal respiration, specific respiration (qO_2), and microbial biomass (Cmic) of soil taken in 0-10 cm depth six weeks after the herbicide application (August 2018). Only plots without fungicide treatment were included in the analysis. Degrees of freedom of numerator (df Num) and denominator (df Den), F-statistics (F) and significance values (p) are provided. Bold numbers indicate significant main effects or interactions ($p < 0.05$).

Response variable	df Num	df Den	F	p
Basal respiration				
Removal	1	9	0.26	0.622
EAS origin	1	7	0.36	0.569
Removal x EAS origin	1	9	0.48	0.504
Specific respiration (qO_2)				
Removal	1	9	0.66	0.436
EAS origin	1	7	0.74	0.418
Removal x EAS origin	1	9	0.55	0.476
Microbial biomass (Cmic)				
Removal	1	9	0.31	0.591
EAS origin	1	7	0.03	0.870
Removal x EAS origin	1	9	0.04	0.838

Subplot biomass

In July of the fourth experimental year (2019), established adult individuals were cut to a height of 2 cm. The three subplots per LAS per plot were pooled and dried at 60°C for 48 hours for a determination of the mean subplot biomass per late-arriving species per plot. The competition effects, soil fungi effects, and the role of soil fungi in competition effects were calculated as described in the main manuscript.

The results show that in the model where the biomass of the early-arriving species (EAS) was explicitly considered, the subplot biomass was not influenced by any of the explanatory variables for the competition effect (Table S 2.8). The model that did not explicitly consider the EAS biomass produced the same results. The same applies to the soil fungi effect (Table S 2.9).

Table S 2.8: Mixed effects model analysis results showing the effects of the early-arriving species origin (origin EAS), late-arriving species origin (origin LAS), the aboveground biomass of early-arriving species in the last experimental year (biomass), and their interactions on the competition effect ($LRR_{CE|-F}$=ln(+C-F/-C-F)) on LAS subplot biomass of adult individuals. The fungicide × EAS origin and fungicide × LAS origin interactions are decomposed into simple main effects of fungicide on each origin. Degrees of freedom of numerator (df Num) and denominator (df Den), F-statistics (F) and significance values (p) are provided. Bold numbers indicate significant main effects or interactions ($p < 0.05$).

Competition effect ($LRR_{CE|-F}$) on LAS subplot biomass

Response variable	df Num	df Den	F	p
EAS origin	1	7	0.01	0.936
LAS origin	1	7	0.70	0.430
biomass	1	214	0.12	0.724
EAS origin x LAS origin	1	84	0.69	0.408
biomass x EAS origin	1	214	1.42	0.235
biomass x LAS origin	1	214	0.38	0.536
biomass x EAS origin x LAS origin	1	214	0.15	0.699

Table S 2.9: Mixed effects model analysis results showing the effects of the early-arriving species origin (EAS origin), late-arriving species origin (LAS origin), and their interactions on the soil fungi effect ($LRR_{FE|-C}$=ln(-C+F/-C-F)) on LAS subplot biomass of adult individuals. Degrees of freedom of numerator (df Num) and denominator (df Den), F-statistics (F) and significance values (p) are provided. Bold numbers indicate significant main effects or interactions ($p < 0.05$).

Soil fungi effect ($LRR_{FE|-C}$) on LAS subplot biomass

Response variable	df Num	df Den	F	p
EAS origin	1	7	0.28	0.614
LAS origin	1	7	0.29	0.608
EAS origin x LAS origin	1	84	2.02	0.159

The analysis of the competition effect with and without fungicide treatment revealed that the inhibiting competition effect on subplot biomass was significantly stronger on plots with fungicide treatment (-0.368 ± 0.129, mean ± standard error) compared to plots without fungicide treatment (-0.189 ± 0.129, Table S 2.10). Furthermore, we found that the inhibiting competition effect of native and exotic EAS on subplot biomass was significantly stronger on fungicide-treated plots (native: -0.368 ± 0.136, exotic: -0.367 ± 0.138) compared to untreated plots (native: -0.171 ± 0.126, exotic: -0.207 ± 0.138), which did not differ significantly from zero. The inhibiting competition effect on native and exotic EAS was stronger on plots with fungicide treatment (native: -0.303 ± 0.141, exotic: -0.432 ± 0.147), while it did not differ significantly from zero on plots without fungicide treatment (native: -0.133 ± 0.141, exotic: -0.244 ± 0.147).

Table S 2.10: Mixed effects model analysis results showing the effects of the early-arriving species origin (EAS origin), late-arriving species origin (LAS origin), soil fungi reduction (fungicide), and their interactions on the competition effect (LRR_{CE}=ln(+C-F/-C-F)) on LAS subplot biomass of adult individuals. The fungicide × EAS origin and fungicide × LAS origin interactions are decomposed into simple main effects of fungicide on each origin. Degrees of freedom of numerator (df Num) and denominator (df Den), F-statistics (F) and significance values (p) are provided. Bold numbers indicate significant main effects or interactions ($p < 0.05$).

Competition effect (LRR_{CE}) on LAS subplot biomass

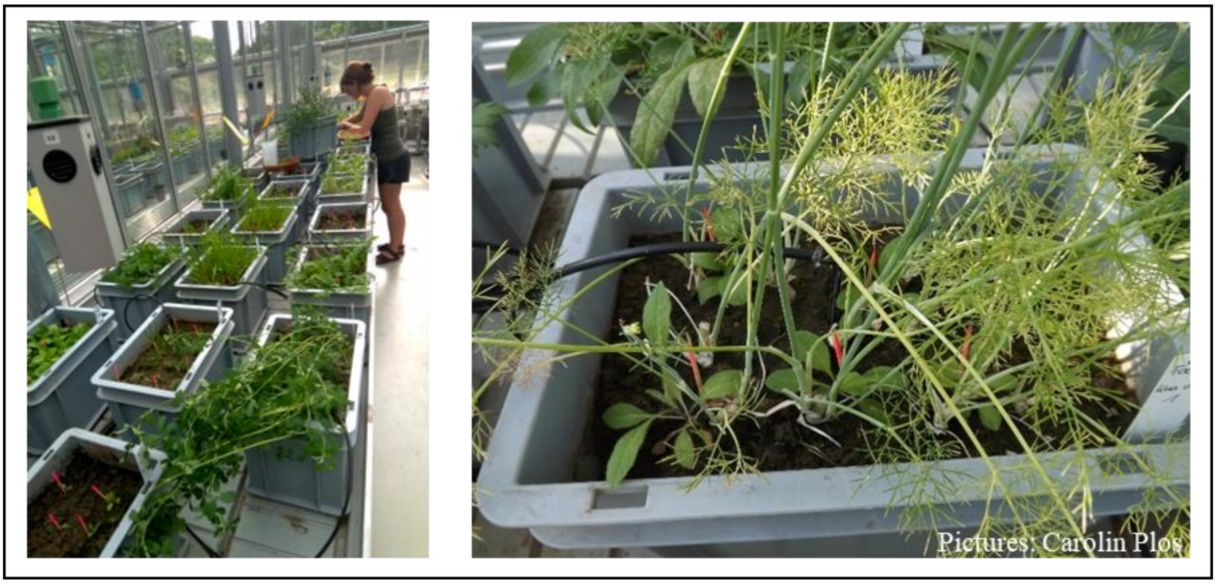
Response variable	df Num	df Den	F	p
EAS origin	1	7	0.05	0.834
LAS origin	1	7	1.00	0.351
fungicide	1	9	14.33	**0.004**
EAS origin x LAS origin	1	84	0.38	0.540
EAS origin x fungicide	1	9	0.22	0.653
fungicide | exotic	1	9	6.19	**0.035**
fungicide | native	1	9	11.22	**0.009**
LAS origin x fungicide	1	9	0.04	0.847
fungicide | exotic	1	9	7.58	**0.022**
fungicide | native	1	9	7.57	**0.022**
EAS origin x LAS origin x fungicide	1	88	2.07	0.154

Chapter 3

Phylogenetic relationships and plant life stage but not biogeographic history mediate priority effects of European grassland plants

This chapter is published in *Journal of Ecology* as:

Dieskau, J., Hensen, I., Eisenhauer, N., Gaberle, I., Durka, W., Lachmuth, S., & Auge, H. (2024). Phylogenetic relationships and plant life stage but not biogeographic history mediate priority effects of European grassland plants. *Journal of Ecology*, 112(9), 2007–2017. https://doi.org/10.1111/1365-2745.14373



Abstract

1. The timing and order of species arrival have been shown to be a significant factor in the assembly of biotic communities. Therefore, an understanding of priority effects, meaning the effect of an early-arriving species on a later-arriving, one can help us to better predict community assembly processes. However, little is known about the role of phylogenetic distance in priority effects and how they are mediated by the biogeographic history and the life stages of interacting species.
2. To shed light on the role of phylogenetic distance in priority effects, we conducted a multispecies greenhouse experiment. We created 10 allopatric and 10 sympatric species pairs each, representing a phylogenetic distance gradient between early- and late-arriving species from 5 to 270 Myr in evolutionary history and tested the priority effect of early-arriving species on the late-arriving species at multiple life stages.
3. We found evidence of stronger competition between closely related species, as late-arriving plants produced less aboveground biomass when the phylogenetic distance was low. However, priority effects varied across the development of late-arriving plants, as there were no effects on seedling emergence and survival, independent of phylogenetic distance. Regardless of phylogenetic distance, the pairs of allopatric and sympatric species did not differ in their responses.
4. *Synthesis*: While many studies have produced contradictory results regarding the effect of phylogenetic distance on plant-plant interactions, our study provides experimental evidence that priority effects can be stronger when phylogenetic distance is small. This effect was independent of biogeographic history but varied across different life stages of late-arriving plants. The dependence of the effect of phylogenetic distance on the life stage of late-arriving species highlights the importance of the timing of interactions for the assembly of plant communities, which could also have significant implications for the fields of invasion and restoration ecology.

Introduction

Intraspecific and interspecific plant-plant interactions affect the assembly of plant communities in complex and diverse ways (Chase, 2003a; Götzenberger et al., 2012; HilleRisLambers et al., 2012; Fukami, 2015; Larson & Funk, 2016; Rolhauser & Pucheta, 2017). Among other factors, the timing and order of species arrival appears to play a significant role in the outcome of community assembly processes and previous studies investigated these so-called “priority effects” in a wide range of terrestrial and aquatic ecosystems (Chase, 2003b; Fukami et al., 2010; Klingbeil & Willig, 2016; Toju et al., 2018; Dunck et al., 2021). However, despite a strongly increasing interest in priority effects, they continue to be an underrepresented topic in community assembly research (Fukami, 2015). In this study, we follow a broad definition of priority effects as the impact of an early-arriving species on a late-arriving species, occasionally referred to as historical contingency (Fukami, 2015; Zou & Rudolf, 2023). However, we are aware of other, narrower definitions according to Modern Coexistence Theory, which reserves the term for cases in which the outcome of species interactions depends on the order of arrival (Ke & Letten, 2018; Grainger et al., 2019).

The net effect of the early-arriving plant on the late-arriving plant can be positive, neutral, or negative and is based on a variety of mechanisms. First, early-arriving species can change the biotic and abiotic environmental conditions (Connell & Slatyer, 1977; Debray et al., 2022), for example, through the microclimate they create or through plant-soil feedback, where one plant species alters the soil conditions in a way that induces feedback on the performance of the species itself and/or on other species (Grman & Suding, 2010; Heinen et al., 2020; Delory et al., 2021). Second, the previous reduction of shared resources by the early-arriving species (space, nutrients, light, water, etc.) can lead to asymmetric competition, both aboveground and belowground (Körner et al., 2008; Weidlich et al., 2017) and hamper the establishment, survival, productivity, and reproduction of the late-arriving species.

As evolutionary relationships have been generally shown to play an important role in the outcome of species interactions, they might be a helpful predictor of the strength of priority effects. The *competition relatedness* hypothesis (Cahill et al., 2008) states that closely related species compete more intensely with each other than with distantly related competitors and goes back to Darwin's observation that 'the struggle will generally be more severe between species of the same genus, when they come into competition with each other than between species of distinct genera' (Darwin, 1859). This assumption has been supported by many studies (reviewed by Dayan & Simberloff, 2005). One mechanism behind this phenomenon may be that closely related species are ecologically more similar and therefore have more similar niches, resulting in stronger priority effects among species with higher resource use overlap (Vannette & Fukami, 2014). Considering Chase and Leibold's (2003, p. 15) definition of a niche, the strength of competition for resources should increase with niche similarity, ultimately decreasing the probability of closely related species to coexist, as predicted by the *limiting similarity* hypothesis (MacArthur & Levins, 1967). As ecologically relevant traits have been shown to often be phylogenetically conserved (Prinzing et al., 2001; Wiens et al., 2018), phylogenetic distances between higher plants can indicate their ecological differences and allow predictions about their interactions. However, although many studies found a clear association between phylogenetic distance and the outcome of species interactions (Violle et al., 2011; Verdú et al. 2012; Cadotte, 2013; Germain et al., 2016; Sheppard et al., 2018), others did not (Cahill et al., 2008; Narwani et al., 2013; Fritschie et al., 2014; Godoy et al., 2014; Fitzpatrick et al., 2017). These contradictory results might be caused by a number of biological and methodological factors such as inappropriate phylogenies, skewed distributions of phylogenetic distances, absence of sufficient niche spaces, or ignoring models of trait evolution (reviewed in Cadotte et al., 2017).

Studies testing the importance of phylogenetic relationships in priority effects are rare, and so far show no clear trend either. Although studies involving other organisms, such as yeast species in the floral nectar of shrubs (Peay et al., 2011) or bacteria (Tan et al., 2012), have often found that priority effects are stronger between closer relatives, the results of studies in plants are less clear. Castro et al. (2014) for example carried out a set of manipulative experiments in which they controlled the phylogenetic distance of a colonising species (*Lactuca sativa*) with five assemblages of plants (the recipient communities) and found that neither the mean phylogenetic distance between *Lactuca* and the members of each assemblage nor the mean phylogenetic distance to the nearest neighbour affected the performance of the late-arriving plants (germination, growth, flowering, survival, and *Lactuca* recruitment). Sheppard et al. (2018) found that the success of the establishment of recently introduced species in permanent grasslands throughout France was positively affected by the phylogenetic relatedness to native species and previous invaders.

One reason why phylogenies do not always predict ecological differences among species is that sympatric species may have evolved trait differences fostering coexistence, which can override phylogenetic effects (Cadotte et al. 2017). Thus, the effect of phylogenetic distance on priority effects might depend on the biogeographic history of early- and late-arriving species. While allopatric species did not have the opportunity to interact with each other because of geographic or habitat barriers, co-occurring sympatric species may have competed for the same resources in the past. Such interspecific competition can influence evolutionary trajectories through selection for greater niche divergence (Brown & Wilson, 1956; Schluter, 2000; Silvertown, 2004; Symonds & Elgar, 2004; Tobias et al., 2014; Weber et al., 2016) and, as a consequence, even closely related species can differ substantially and show larger niche difference than expected based on their phylogeny (Schluter, 1994; Davies et al., 2007; Nuismer & Harmon, 2015; Staples et al., 2016). How a history of sympatry can lead to evolutionary changes in species traits that increase niche differentiation, has been previously discussed on an intraspecific level (e.g. Aarssen & Turkington 1985; Hart et al., 2019; Sakarchi & Germain 2023) as well as on an interspecific level (e.g. Thorpe et al. 2011; Germain et al. 2016).

Furthermore, the role of phylogenetic distance for the strength of priority effects could also differ for different life cycle components of the late-arriving plants (for simplicity, referred to as life stage hereafter). Unfortunately, the seedling stage is often ignored in trait-based analyses (Larson et al., 2016), and evidence for phylogenetic signal in seedling traits is not unequivocal (Husáková et al., 2018). However, seedlings may have environmental requirements and thus niches distinct from those of conspecific adults due to ontogenetic niche shifts (Parish & Bazzaz, 1985; Lyons & Barnes, 1998; Miriti, 2006; Müller et al., 2018). Therefore, the importance of phylogeny for the priority effect should increase as late-arriving species mature from the seedling stage to the adult stage, whereby closely related species become ecologically more similar to the adult early-arriving species.

However, we are not aware of any studies investigating the influence of biogeographic history and the life stage of late-arriving species on the impact of phylogenetic distance on priority effects. To address this critical knowledge gap, we conducted a greenhouse study that investigated the role of phylogenetic distance for the priority effect of an early-arriving species on the establishment and performance of a late-arriving species. To analyse the influence of biogeographic history, we used interactions with 10 allopatric pairs (i.e., early-arriving species exotic and late-arriving species native to Germany) and 10 sympatric pairs (i.e., early- and late-arriving species native to Germany) of biennial and perennial European grassland species of different families and functional groups, spanning a gradient of phylogenetic distance. We tested the following hypotheses: (1) The priority effect of an early-arriving plant on a late-arriving plant of another species increases with decreasing phylogenetic distance between them due to higher ecological similarity. (2) The importance of phylogenetic distance for priority effects is more pronounced in allopatric than in sympatric species pairs as co-occurring closely related species have evolved niche differences which reduce competition. (3) The significance of phylogenetic distance for priority effects increases, as closely related late-arriving plants age, and become more ecologically similar to early-arriving adult plants.

Methods

Species Selection

We conducted a multispecies greenhouse experiment investigating the net priority effect of native and exotic early-arriving species on native late-arriving species across different life stages of the latter. Sympatric pairs of early- and late-arriving species were represented by two species native to central German grassland communities, and allopatric pairs by the same late-arriving species and an exotic early-arriving species, resulting in a species triplet (Figure 3.1). However, it is crucial to emphasise that within the experiment, only species pairs engaged in direct interactions, not triplets. All the species selected for the experiment were forbs, legumes, and grasses that occur in central German grasslands. Most of our exotic species were introduced to Germany around the 19th century (see Table S 3.1 in the supplementary information for a complete list of the native and exotic species used, their taxonomic affiliation, life span, and minimum residence time).

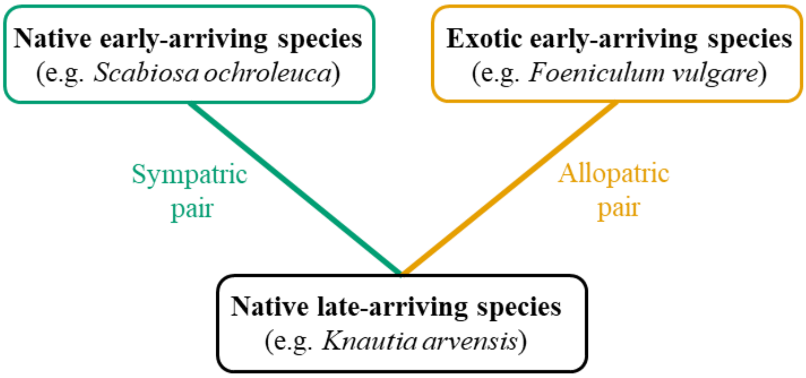


Figure 3.1: Scheme of a triplet of species (here exemplary triplet T01) consisting of two native and one exotic species, representing a pair of sympatric species and a pair of allopatric species.

To explicitly test for the interactive effects of phylogenetic distance and biogeographic history, we adopted the approach of Germain et al. (2016). We created 10 triplets, each representing a gradient in phylogenetic distance between early- and late-arriving species, encompassing up to 270 Myr of evolutionary history since their last common ancestor (see Table S 3.2 in the supplementary information for phylogenetic distance and shared community types among paired species). To ensure comparability among sympatric and allopatric species pairs within a triplet, we strived to select similar distances for the exotic-native and the native-native species pairs within each triplet. Moreover, to prevent systematic bias and ensure phylogenetic independence among triplets, we made efforts to minimise overlapping branches (Germain et al., 2016). In the few cases where this was not completely feasible, we minimised the lengths of the overlapping branches (Figure 3.2).

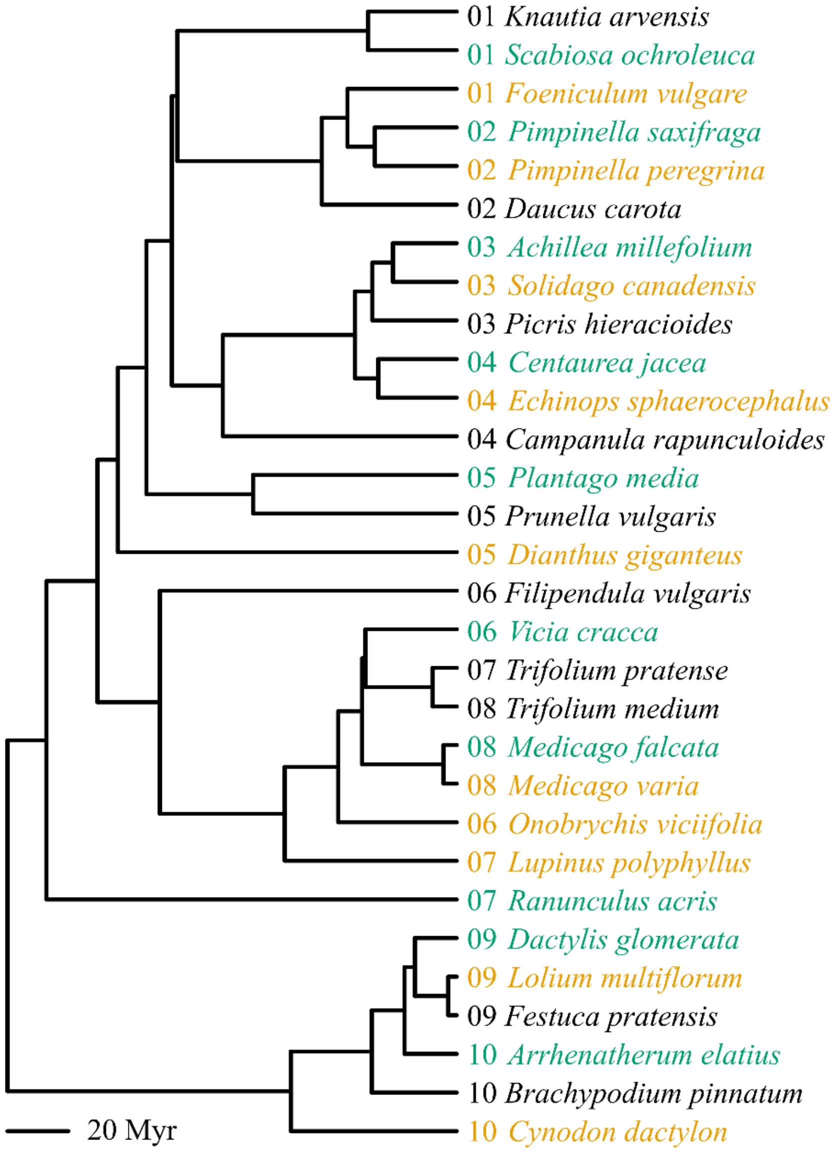


Figure 3.2: Phylogenetic tree of all experimental species with their triplet number (01-10) and origin (green = native early-arriving species; yellow = exotic early-arriving species; black = native late-arriving species). Phylogenetic distances were extracted from the Daphne data set (Durka & Michalski, 2012).

Phylogenetic distances were extracted from the Daphne data set (Durka & Michalski, 2012). Species missing in the phylogeny (*Dianthus giganteus*) were substituted by the most closely related congener. We purchased seeds for most species from local seed suppliers and collected seeds for *Dianthus giganteus* and *Pimpinella peregrina* ourselves in summer 2016 in central Germany (see supplementary information).

Setup and design

In early December 2017, we seeded 100 seeds of each of the 20 early-arriving species in 10 L boxes (L: 27, W: 17, H: 22cm). The boxes were provided with drainage holes at the bottom to prevent waterlogging. To facilitate realistic interactions between plants and soil, including soil biota, we used unsterilised chernozem soil instead of potting soil, which is often sterilised and less representative in terms of their chemical, physical, and soil biotic properties. Chernozem soil is the predominant soil type in Central German dry regions and thus representative of the grasslands in that region. We used the top layer of sieved soil from a site of the UFZ experimental station in Bad Lauchstädt, where none of our experimental species had previously established (for more detailed information regarding soil conditions, see Altermann et al., 2005). To ensure a uniform distribution of soil among all boxes, the soil was thoroughly mixed before the experiment. *Lupinus polyphyllus* was covered with 1-2 cm of soil, whereas the other species were seeded on the soil surface. To accelerate germination, we covered the boxes with transparent foil until germination reached 25% (5 to 28 days, depending on the species). For each of the 10 native and 10 exotic early-arriving species, we prepared four replicate boxes, which resulted in 80 boxes. Furthermore, we prepared four control boxes without early-arriving plants for each late-arriving species, using the same soil and keeping them free of any spontaneously occurring seedlings, resulting in an additional 40 boxes. Thus, we had a total of 120 boxes. In January 2018, the early-arriving species plants were reduced to 12 individuals per box and, when necessary, replanted from seedling trays during the first two weeks. The boxes were distributed in four greenhouse cabins, each cabin representing a block containing one replicate of each early-arriving species or of an empty control box, respectively. Within each cabin, boxes were randomly assigned to two greenhouse benches. Throughout the experimental period, plants were irradiated with additional light from 7 am to 7 pm to standardise light conditions within the cabins. The temperatures ranged from 15 ° C at night to 20 ° C during the day. Each box was watered from the top approximately every one to four days, depending on its individual requirements. The requirements varied among plant species due to their different biomasses and were assessed by estimating soil moisture by touching the substrate. The exceptionally high biomass production of the species pair *Trifolium medium* growing in *Medicago x varia*, along with the associated evapotranspiration, caused such intense soil drying that a gap formed between the box wall and the substrate. As a result, water flowed through the drainage holes, leading to extreme drought, and preventing soil rehydration. Consequently, this pair of species was excluded from the analysis. In all other pairs of species, the soil remained moist enough to absorb the supplied water, so there was no drought stress there.

After two months of growth, the plants were cut 4 cm above the soil surface using a scissor to simulate mowing, which is typical for central European grasslands. To maximize the duration for the early-arriving plants to grow and to develop plant-soil feedback, an additional two months were allocated for their growth. This extended period allowed the formation of a dense stand of adult plants, including some flowering individuals, before the plants were cut again. Two days after that, the late-arriving species were seeded in the four-month-old monocultures of the early-arriving species, as well as in the empty control boxes (100 seeds/box). Every week, emerging and dying seedlings were counted and used for the calculation of total seedling emergence and seedling survival. Averaged between all species, the median germination time (t50) was reached after an average of 22 days, at which 50% of all germinated seeds had germinated (t50 min=14.0, mean=21.8, max=28.0). As we are interested in the priority effect of early-arriving plants on late-arriving plants, we have tried to minimize intraspecific competition between late-arriving plants and reduced them to six seedlings per box. Some individuals of early- and late-arriving species were attacked by mildew, insects, and mites. Therefore, we treated all plants with an insecticide (0.5 ml/l Karate Zeon, Syngenta Agro GmbH, Maintal, Germany) and, where necessary, also with an acaricide (2% Spruzit Schädlingsfrei, W. Neudorff GmbH KG, Emmerthal, Germany). Three months after sowing, the late-arriving plants reached the adult stage and were partially flowering. To prevent nutrient deficiencies as well as senescence of flowering plants, late-arriving plants were counted, and aboveground biomass harvested and dried (72 h at 70°C) for the calculation of the mean aboveground biomass per capita for each box.

Statistical analyses

For each box of each sympatric or allopatric species pair, we calculated the mean seedling emergence, seedling survival, and mean aboveground biomass per survivor of the late-arriving species. To quantify the magnitude and direction of priority effects, we related seedling emergence, seedling survival, and aboveground biomass of adult late-arriving plants grown in boxes with early-arriving plants to the respective data in control boxes using log response ratios (LRR) based on mean values across the four replicate boxes (Hedges et al., 1999). The application of LRRs facilitated the comparison of plant performance in various ontogenetic stages, encompassing both binary metrics such as seedling emergence and survival and continuous variables such as biomass. Positive LRR values indicate a facilitative priority effect of early-arriving plants on late-arriving plants (better performance of late-arriving plants in the respective interspecific treatment), while negative values indicate an inhibitory priority effect (better performance of late-arriving plants in control boxes).

To test whether the effects of phylogenetic distance depended on the biogeographic history and differed among the life stages of the late-arriving species, we initially fitted a model that contained phylogenetic distance (PD; centred and scaled), biogeographic history (BH; allopatric vs. sympatric pairs), life stage (LS; seedling emergence, seedling survival, and aboveground biomass) and all possible interactions as explanatory variables and LRRs of the late-arriving species as response variable (using the package lmerTest in R, version 4.2.0, R Core Team, 2017; Kuznetsova et al., 2017). The random effects comprised identity of the early-arriving species nested in identity of the late-arriving species (since late-arriving species had been sown into both a native and an exotic early-arriving species). The random effect of the late-arriving species included a random intercept and a random slope to account for the nonindependence in LRR differences between the life stages of each late-arriving species. The random effect of the early-arriving species included only a random intercept. The significance of fixed effects was tested using the Wald type III test.

Furthermore, we calculated two additional models to investigate the priority effects on the three life stages in more detail. First, we investigated whether the priority effect generally differed between the different life stages. For this purpose, we fitted a model with BH, LS and their interaction as explanatory variables and LRRs of the late-arriving species as response variable using the same random effects as significance tests as in the initial model. Life stage effects were subjected to Tukey's post hoc tests to identify significant differences among them. Furthermore, we used the emmeans command from the emmeans package (Lenth et al., 2018) with the above model to assess whether the mean values per life stage significantly deviated from zero.

Second, we calculated separate models for seedling emergence, seedling survival, and aboveground biomass and analysed the effects of PD, BH and the interaction of PD x BH on LRRs of the late-arriving species. To account for the identity of the respective late-arriving species (that were sown into both native and exotic early-arriving species) we included the late-arriving species as random intercept term. All models were tested for normal distribution of residuals through visual inspection of model diagnostic plots.

It is important to note that variation in priority effects among our species pairs is partly due to species-specific properties. However, this does not imply that species-specific competitive ability is confounded with phylogenetic distance and biogeographic history, creating a spurious correlation with priority effects. Due to our procedure of randomly selecting early-arriving species and establishing species pairs, variation in competitive ability among species adds to other sources of random experimental error. This increases unexplained residual variance in our models. While an outlier, such as a super competitor or a particularly weak competitor, could potentially influence the relationships between phylogenetic distance or biogeographic history and priority effects, careful inspection of our data points did not reveal any influential observations.

Results

The mixed-effects models evaluating the effects of phylogenetic distance, biogeographic history and life stages demonstrated a significant influence of life stage and the interaction of phylogenetic distance and life stage on the log response ratio (LRR) of late-arriving plants, serving as a measure of the priority effects (Table 3.1). Subsequent analysis of the mixed-effects model that included only biogeographic history and life stages disclosed significant variations between life stages (Figure 3.3).

Table 3.1: Results of the mixed-effects model analysis for the effects of phylogenetic distance, biogeographic history, life stage, and their interactions on the log response ratios (LRR) of late-arriving plants. Bold p-values indicate significant main effects or interactions ($p < 0.05$).

Log response ratio (LRR)

	Chi²	df	p-value
Intercept	0.6	1	0.442
Phylogenetic distance	0.1	1	0.816
Biogeographic history	0.0	1	0.987
Life stage	179.2	2	**<0.001**
Phylogenetic distance x Biogeographic history	0.0	1	0.891
Phylogenetic distance x Life stage	12.0	2	**0.002**
Biogeographic history x Life stage	0.0	2	0.989
Phylogenetic distance x Biogeographic history x Life stage	0.2	2	0.897

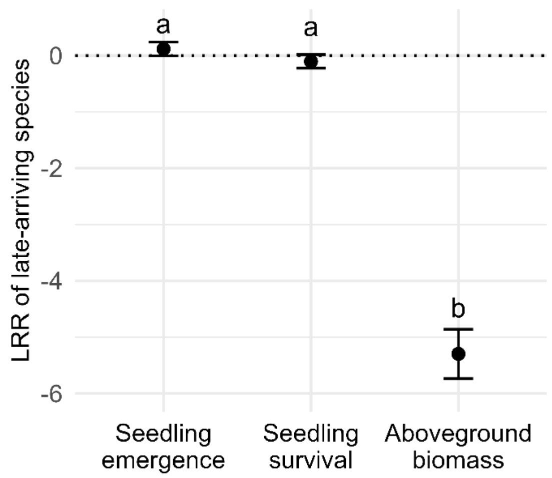


Figure 3.3: Log response ratios (LRR) for late-arriving species, depicting the priority effect across various life stages ($Chi^2=130.1$; df=2; p<0.001, n=19). Negative LRR values signify an inhibitory priority effect, while positive values indicate a facilitative effect of early-arriving plants on late-arriving ones. Significant differences are denoted by small letters on top of the symbols, determined through Tukey post hoc analysis. The LRRs for seedling emergence (t=0.957; df=8.71; p=0.716) and survival (t=-0.865; df=8.71; p=0.770) did not significantly differ from zero. However, the LRR for aboveground biomass was significantly negative (t=-12.096; df=8.99; p=<0.001).

The priority effect on the early stages of seedling emergence and survival did not exhibit statistically significant differences from zero. However, the log response ratio (LRR) for the aboveground biomass of the late-arriving species was significantly negative, indicating an inhibitory priority effect. This suggests that late-arriving adult plants produced less aboveground biomass when sown in boxes with previously established early-arriving plants compared to those sown in control boxes.

Examinations through separate mixed-effects models for distinct life stages revealed that the early phases of late-arriving plants, namely seedling emergence and survival, remained unaffected by the phylogenetic distance to their respective early-arriving species (Figure S 3.1 in the supplementary information). However, there was an inhibitory effect of early-arriving plants on the aboveground biomass of late-arriving plants that decreased with phylogenetic distance between them, represented by a significant positive correlation between the phylogenetic distance and the LRR of the aboveground biomass of the late-arriving species (Figure 3.4). On the contrary, the biogeographic history did not have a significant effect in any of the mixed-effects models we analysed, either individually or in interaction (Table 3.1).

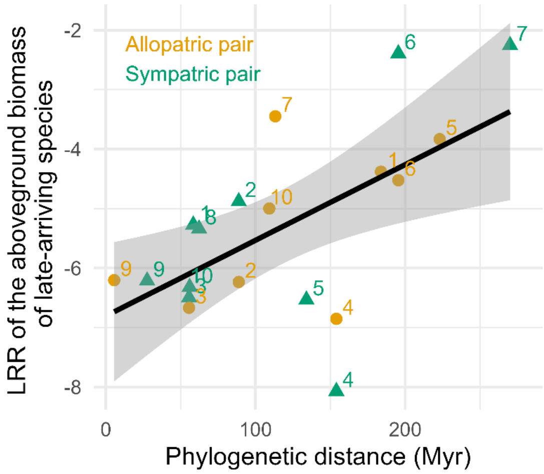


Figure 3.4: Relationship between the phylogenetic distance among early- and late-arriving species and the log response ratios (LRR) for aboveground biomass in late-arriving adult plants (Chi²=3.9; df=1; p=0.0497), as a measure of the priority effect. Negative LRR values signify an inhibitory priority effect, while positive values indicate a facilitative effect of early-arriving plants on late-arriving ones. Each data point for the species pairs is labelled with the triplet number (1-10). Sympatric species pairs are represented by green triangles and allopatric species pairs by yellow circles.

Discussion

This study investigates the role of phylogenetic distance in priority effects at multiple life stages of late-arriving plants and how this relationship is affected by the biogeographic history of the early- and late-arriving species. In line with our hypotheses, the results indicate that the aboveground biomass of late-arriving adult plants was more strongly inhibited when they were growing with closely related early-arriving species compared to distantly related ones. However, this effect could not be demonstrated for the earlier stages of seedling emergence and survival, indicating that the impact of phylogenetic distance on priority effects depends on the life stage of the late-arriving plants. Regardless of the phylogenetic distance and contrary to our hypothesis, the pairs of allopatric and sympatric species did not differ in their interaction.

Inhibitory priority effects are stronger between closely related species

In accordance with our hypothesis, the inhibitory effect of early-arriving plants on the aboveground biomass of late-arriving plants decreased with the phylogenetic distance. This is in line with the widespread assumption that closely related species are ecologically more similar, have similar niches, and, consequently, compete more intensely with each other (Dayan and Simberloff, 2005). This finding suggests that the phylogenetic distance may serve as a valuable proxy for trait dissimilarity where the labour-intensive measurement of an extensive set of traits is not feasible. Furthermore, the metric potentially captures ecological processes beyond the scope of trait measurements.

Our results are in part contradictory to some other studies which found no effect of phylogenetic distance on plant-plant interactions (see, e.g., Cahill et al., 2008; Narwani et al., 2013; Fritschie et al., 2014; Godoy et al., 2014; Fitzpatrick et al., 2017). An explanation for the contrasting findings could be the timing of arrival of the interacting species. Compared to simultaneously arriving species, early-arriving plants in our experiment had a longer time to modify environmental conditions and inhibit late-arriving plants, possibly through mechanisms like the accumulation of pathogens, a reduction of shared nutrients or a spatial occupation above- and belowground. These mechanisms could have compelled late-arriving plants, for instance, to extend their roots deeper into the soil (see, e.g., Mueller et al., 2013).

We suggest that the predictive power of the phylogenetic distance depends significantly on whether the ecologically relevant traits for a particular question are phylogenetically conserved.

It is important to consider that niches are multidimensional and that different aspects can be conserved or diversified within a clade (Wiens et al., 2018). Therefore, claims regarding conserved or labile niches are study-specific and outcomes are likely to vary under different environmental conditions. We assume, for example, that competition for nutrients is notably stronger in our greenhouse experiment than it might be in the field, as plants were growing in pots at high densities and without additional fertilisation. Recent advances in our understanding of coexistence (Chesson, 2000; Adler et al., 2007) state that competitive exclusion can occur when niche differences are small relative to differences in competitive ability. Both differences are expressions of trait value differences among species, which may or may not exhibit a phylogenetic signal, resulting in contrasting effects on relatedness patterns. As a result, competition can lead to the elimination of more distantly related plants when niche differences are small (Mayfield & Levine, 2010). Overall, we conclude that more work is needed to understand in which systems, and under which conditions the phylogenetic distance could be used as an alternative or additional predictor for priority effects.

No effect of biogeographic history on priority effects and the importance of phylogenetic distance

Contrary to our expectations, there were no differences in priority effects between pairs of allopatric and sympatric species, nor could we find an interaction effect of biogeographic history and phylogenetic distance. There are several plausible explanations for these findings. For instance, despite the relatively short residence time (most exotic species were introduced in the 19th century), native and exotic species might have rapidly coadapted to each other, much like native pairs.

Another explanation could be the lack of any evolutionary process that have led to niche divergence between closely related native species used in our experiment. Functional traits and thus certain niche dimensions can be highly conserved and thus may experience only weak selection (Peterson et al., 1999; Thorpe et al., 2011). A high level of phenotypic plasticity could have made evolutionary adaptation redundant. Furthermore, there could have been a lack of intense and close interactions between our sympatric species pairs in the past or interactions with extremely strong competitors that might have led to extinction of the less competitive sympatric population rather than adaptation (Case & Taper, 2000). In addition, there are indications that the duration of evolutionary history might be crucial. Zee & Fukami (2018) emphasise that sympatric evolution can also cause populations to become similar in competitive ability. They highlight that in contrast to niche divergence, such trait convergence has been demonstrated to evolve when species interact over longer time periods (see, e.g., Miller et al., 2010; Tobias et al., 2014).

Furthermore, it is possible that niche divergence occurred between our pairs of sympatric native species, but it was not observable within the constraints of our experimental setting. Greenhouse experiments allow us to control and analyse the role of biotic and abiotic conditions in plant-plant interactions on small scales, but at the same time it is impossible to simulate exactly the conditions under which plants are growing in their natural communities. As evolutionary consequences of plant-plant interactions can be highly context-specific, it is conceivable that the consequences of adaptive niche divergence cannot be observed in an experimental setting with different environmental conditions (see, e.g., Chanway et al., 1988; Lau, 2006).

The importance of phylogenetic distance and the strength of priority effects differ across life stages of late-arriving species

In accordance with our hypothesis, the effect of phylogenetic distance on priority effects differed among the investigated life stages of the late-arriving species. Regardless of phylogenetic distance, there was no priority effect on seedling emergence and survival of late-arriving plants. This is in line with the assumption that seedlings are less influenced by competition for nutrients (Primack & Kang, 1989) and are primarily affected by microclimatic environmental conditions (Donohue et al., 2001), which are independent of phylogenetic distance. Furthermore, early-arriving plants deplete nutrients not only before the arrival of late-arriving plants but also throughout their development, leading to increased competition for resources among adult individuals. However, the lack of effect on seedling emergence and the lack of influence of phylogenetic distance should be interpreted with caution, as the simulated mowing of early-arriving plants two days before sowing may have affected the germination of late-arriving plants, possibly through reduced shading and the associated microclimatic changes. On the contrary, we assume that the survival rate was minimally, if at all, influenced by the simulated mowing, as the early-arriving plants regrew very rapidly and most of the seedlings emerged only after three weeks. It is also conceivable that the effects of phylogenetic distance were overshadowed by a strong asymmetric competition between early-arriving adult plants and seedlings of the late-arriving plants. Given that previous studies have shown the significant role of facilitation in early life stages (Miriti, 2006), it is also possible that any inhibitory competition effects were offset by facilitative processes, ultimately leading to a neutral net priority effect. For example, Dudenhöffer et al. (2018) found that the effect of soil biota changed from positive in the juvenile life stages of plants to neutral or negative in the adult life stages of plants. In addition, we cannot completely exclude the possibility that the phylogenetic distance had an impact on the net priority effect on seedling emergence and survival due to potential offset mechanisms that have cancelled each other out. Furthermore, it is possible that seedlings from late-arriving plants are less inhibited by soil pathogens accumulated in the rhizosphere of early-arriving plants compared to adult individuals from late-arriving plants due to their shallower root systems and the resulting spatial separation of roots.

The priority effect on the aboveground biomass of the late-arriving plants was negative in all cases, indicating that late-arriving plants consistently produced less aboveground biomass when growing with their respective early-arriving plants compared to empty control boxes. This supports the hypothesis that early-arriving adult plants exert a stronger inhibitory effect on late-arriving plants in the same life stage because of their higher ecological similarity, as predicted by the *limiting similarity* hypothesis (MacArthur & Levins, 1967). Furthermore, the inhibitory priority effect on the aboveground biomass of late-arriving plants decreased with phylogenetic distance. These results suggest that the *competition-relatedness* hypothesis (Cahill et al., 2008) might be primarily relevant to interactions among mature plants. While we could not examine all life stages in our experiment, future studies could delve into the impact on reproductive phases and elucidate how the priority effect evolves across the life cycle of perennial species and successive generations of biennial species.

Conclusions

While many studies have produced contradictory results regarding the effect of phylogenetic distance on plant-plant interactions, we were able to demonstrate that inhibitory priority effects on the aboveground productivity of late-arriving plants can be mediated by the phylogenetic distance between early- and late-arriving plants. However, priority effects did not differ between pairs of allopatric and sympatric species. Our findings could have significant implications for the fields of invasion and restoration ecology. Restoration experiments, for example, could benefit from increasing the phylogenetic distances between neighbouring plants, as recommended by Verdú et al. (2012). However, we do not know how persistent the priority effects we observed are. For a better understanding of priority effects, future studies should therefore prioritise investigating the persistence of priority effects as well as the impact of varying time intervals between arrival events on the mechanisms that mediate the influence of phylogenetic distance. Furthermore, we recommend including the modification of arrival order, including simultaneous arrival as a control, as done, for example, by Delory et al. (2019a), and to differentiate between 'frequency-dependent' and 'trait-dependent' priority effects, as recommended by Zou and Rudolf (2023), to combine theory and empiricism in the study of priority effects.

Acknowledgements

We acknowledge the use of data drawn from the Daphne data set. We thank Ines Merbach and the entire team of Field Experimental Station of the UFZ at Bad Lauchstädt, and Niclas Mehre, Carolin Plos and Julia Rieger for practical support during the experiment. We are grateful to Alfred Lochner, Tobias Proß and Tim Walther for helpful support with laboratory analysis. Katrin Kittlaus and Birgit Müller provided valuable assistance in the acquaintance of seed material and support during the experiment. Nico Eisenhauer gratefully acknowledges the support of iDiv funded by the German Research Foundation (DFG– FZT 118, 202548816).

Supplementary material (S3)

Phylogenetic relationships and plant life stage but not biogeographic history mediate priority effects of European grassland plants

Authors: Julia Dieskau, Isabell Hensen, Nico Eisenhauer, Ingmar Gaberle, Walter Durka, Susanne Lachmuth, Harald Auge

Journal: *Journal of Ecology*

Species list

Table S 3.1: Species list with triplet number (T01-T10), role in the experiment (NL = native late-arriving species; NE = native early-arriving species; EE = exotic early-arriving species), family, lifespan, invasion status, minimum residence time (MRT) for exotic species, seed source (RH=Rieger-Hofmann GmbH, Blaufelden-Raboldshausen; Stolle=Saalesaaten Stolle, Halle; Sch=Samen Schwarzenberger, Völs). Invasion status was assessed according to Bundesamt für Naturschutz (2023) and Nehring et al. (2013), and lifespan sociology and minimum residence time was extracted from Bundesamt für Naturschutz (2023) and Seebens (2020).

Species	Triplet	Role in experi-ment	Family	Lifespan	Invasion status	MRT (y)	Seed source
Achillea millefolium L.	T03	NE	Asteraceae	polycarpic perennial	-	-	RH
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	T10	NE	Poaceae	polycarpic perennial	-	-	Stolle
Brachypodium pinnatum (L.) P. Beauv.	T10	NL	Poaceae	monocarpic perennial	-	-	Stolle
Campanula rapunculoides L.	T04	NL	Campanu-laceae	biennial, polycarpic perennial	-	-	RH
Centaurea jacea L.	T04	NE	Asteraceae	annual, biennial, polycarpic perennial	-	-	Stolle
Cynodon dactylon (L.) Pers.	T10	EE	Poaceae	polycarpic perennial	established	305	Sch
Dactylis glomerata L.	T09	NE	Poaceae	polycarpic perennial	-	-	RH
Daucus carota L.	T02	NL	Apiaceae	polycarpic perennial	-	-	Stolle
Dianthus giganteus d'Urv.	T05	EE	Caryo-phyllaceae	polycarpic perennial	established	31	The authors (Groß-korbetha)
Echinops sphaerocephalus L.	T04	EE	Asteraceae	polycarpic perennial	established	185	Stolle
Festuca pratensis Huds.	T09	NL	Poaceae	polycarpic perennial	-	-	RH
Filipendula vulgaris Moench	T06	NL	Rosaceae	polycarpic perennial	-	-	Stolle
Foeniculum vulgare Mill.	T01	EE	Apiaceae	polycarpic perennial	established	197	Stolle
Knautia arvensis (L.) Coult.	T01	NL	Capri-foliaceae	polycarpic perennial	-	-	Stolle

Lolium multiflorum Lam.	T09	EE	Poaceae	polycarpic perennial	established	203	Stolle
Lupinus polyphyllus Lindl.	T07	EE	Fabaceae	polycarpic perennial	established	137	Sch
Medicago falcata L.	T08	NE	Fabaceae	biennial, monocarpic perennial	-	-	Stolle
Medicago x varia Martyn	T08	EE	Fabaceae	polycarpic perennial	established	198	RH
Onobrychis viciifolia Scop	T06	EE	Fabaceae	polycarpic perennial	established	96	RH
Picris hieracioides L.	T03	NL	Asteraceae	polycarpic perennial	-	-	Stolle
Pimpinella peregrina L.	T02	EE	Apiaceae	polycarpic perennial	casual	17	The authors (Leipzig)
Pimpinella saxifraga L.	T02	NE	Apiaceae	biennial, monocarpic perennial	-	-	Stolle
Plantago media L.	T05	NE	Planta-ginaceae	polycarpic perennial	-	-	Stolle
Prunella vulgaris L.	T05	NL	Lamiaceae	polycarpic perennial	-	-	Stolle
Ranunculus acris L.	T07	NE	Ranuncu-laceae	polycarpic perennial	-	-	RH
Scabiosa ochroleuca L.	T01	NE	Capri-foliaceae	polycarpic perennial	-	-	Stolle
Solidago canadensis L.	T03	EE	Asteraceae	polycarpic perennial	established	175	Stolle
Trifolium medium L.	T08	NL	Fabaceae	polycarpic perennial	-	-	Stolle
Trifolium pratense L.	T07	NL	Fabaceae	polycarpic perennial	-	-	RH
Vicia cracca L.	T06	NE	Fabaceae	polycarpic perennial	-	-	RH

Table S 3.2: Species pairs and the respective triplet according to experimental design, phylogenetic distance within species pair, and shared community types according to biolflor.de (Klotz, Kühn & Durka 2002). (Community types: 1… Fescue-brome communities of dry and semi-dry grasslands; 2… Commercially used grasslands; 3… Eusiberian ruderal mugwort and thistles communities, and couch-grasslands; 4… Thermophilous and mesophilous forest grassland ecotones; 5… Nitrophilous tall herb communities.)

Early-arriving species	Late-arriving species	Triplet	Phylogenetic distance (myr)	Shared community types
Foeniculum vulgare	*Knautia arvensis*	T01	183.8	3
Scabiosa ochroleuca	*Knautia arvensis*	T01	58.4	1, 3
Pimpinella peregrina	*Daucus carota*	T02	88.8	1
Pimpinella saxifraga	*Daucus carota*	T02	88.8	1
Solidago canadensis	*Picris hieracioides*	T03	55.6	2, 3
Achillea millefolium	*Picris hieracioides*	T03	55.6	1, 2, 3
Echinops sphaerocephalus	*Campanula rapunculoides*	T04	154	-
Centaurea jacea	*Campanula rapunculoides*	T04	154	4
Dianthus giganteus	*Prunella vulgaris*	T05	223	1
Plantago media	*Prunella vulgaris*	T05	134	1, 2
Onobrychis viciifolia	*Filipendula vulgaris*	T06	195.4	1, 2
Vicia cracca	*Filipendula vulgaris*	T06	195.4	2
Lupinus polyphyllus	*Trifolium pratense*	T07	113.2	2
Ranunculus acris	*Trifolium pratense*	T07	270	2
Medicago varia	*Trifolium medium*	T08	62.3	-
Medicago falcata	*Trifolium medium*	T08	62.3	4
Lolium multiflorum	*Festuca pratensis*	T09	5.6	2
Dactylis glomerata	*Festuca pratensis*	T09	27.6	1, 2, 5
Cynodon dactylon	*Brachypodium pinnatum*	T10	109.2	2
Arrhenatherum elatius	*Brachypodium pinnatum*	T10	56	1, 2, 4

Association between the phylogenetic distance and LRR for seedling emergence and survival

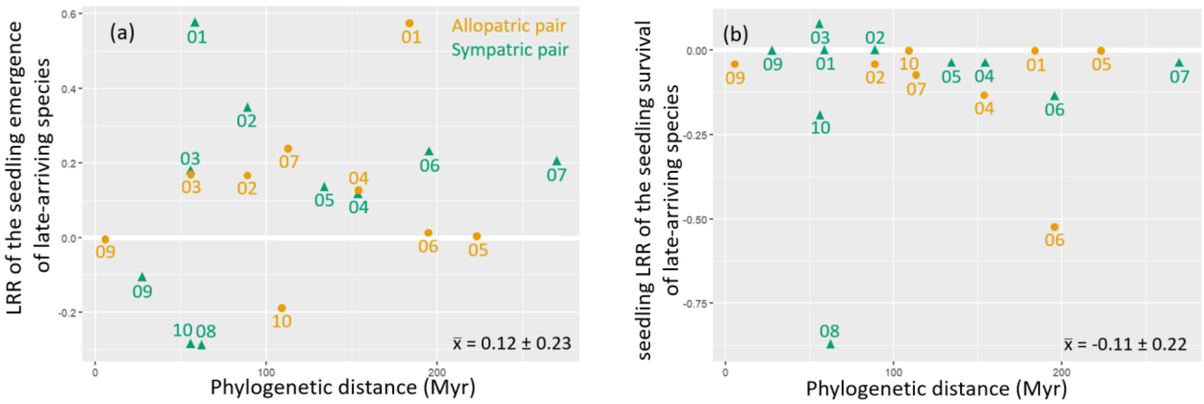


Figure S 3.1: Non-significant association between the phylogenetic distance among early- and late-arriving species and the log response ratios (LRRs) for a) seedling emergence and b) seedling survival in late-arriving adult plants, serving as an indicator of priority effect magnitude. Negative LRR values signify an inhibitory priority effect, while positive values indicate a facilitative effect of early-arriving plants on late-arriving ones. Each data point for the species pairs is labelled with the triplet number (01-10). Sympatric species pairs are represented by green triangles, and allopatric species pairs by yellow circles.

Chapter 4

Plant-soil feedback in European grasslands is phylogenetically independent but affected by plant species origin

This chapter is published in *Journal of Plant Ecology* as:

Dieskau, J., Hensen, I., Eisenhauer, N., Lachmuth, S., & Auge, H. (2025). Plant-soil feedback in European grasslands is phylogenetically independent but affected by plant species origin. *Journal of Plant Ecology*, rtaf021. https://doi.org/10.1093/jpe/rtaf021

Abstract

Interspecific plant-soil feedback (PSF), the influence of soil conditioned by one plant species on another, are key to ecosystem processes but remain challenging to predict due to complex factors like species origin and phylogenetic relatedness. These aspects are underexplored, limiting our understanding of the mechanisms driving PSFs and their broader implications for ecosystem functioning and species coexistence. To shed light on the role of plant species origin and phylogenetic distance in interspecific PSFs, we conducted a greenhouse experiment with 10 native responding species and soils conditioned by 10 native and 10 exotic species resulting in 20 species pairs. These pairs represented a range of phylogenetic distances between both species, spanning up to 270 million years of evolutionary history since their last common ancestor. Conditioning by both native and exotic species reduced biomass production, with stronger inhibition observed for native-conditioned soils. Native-conditioned soils also exhibited lower phosphorus levels, higher basal and specific respiration, and greater cation exchange capacity, base saturation, and magnesium content compared to exotic-conditioned soils. Contrary to expectations, phylogenetic distance did not influence PSFs, regardless of conditioning species origin. Our findings suggest that co-evolution drives native plants to foster microbial communities with low carbon-use efficiency, highlighting soil biota's critical role in PSFs. This advances our understanding of interactions between plant species origin and microbial communities and underlines the importance of microbial management for promoting native species and controlling invasives. The lack of phylogenetic distance effects aligns with prior studies, indicating evolutionary relatedness alone does not reliably predict PSF outcomes.

Introduction

Interactions between plants and the soil system are crucial for ecosystem functioning (Wardle et al., 2004). For example, they play a critical role in the invasion success of exotic plant species (Inderjit & van der Putten, 2010), the succession of plant communities (Kardol et al., 2006), as well as the diversity and productivity of terrestrial ecosystems (van der Heijden et al., 2008). The effect of soil influenced by an early-arriving species (hereafter referred to as conditioning species) on the performance of a later-arriving species (hereafter referred to as responding species) is also known as interspecific or heterospecific plant-soil feedback (hereafter referred to as interspecific PSF; van der Putten et al., 2013). Their strength and direction depend on various biotic and abiotic factors, which can act simultaneously, leading to either a positive or negative net effect, or potentially cancelling each other out, resulting in a neutral outcome.

Underlying mechanisms may include the accumulation of pathogenic or mutualistic soil biota (Bever, 2003), the release of allelopathic substances (Hierro & Callaway, 2003), and other soil chemical changes, such as in pH, soil moisture, and nutrient levels (Ehrenfeld et al., 2005), induced by the conditioning species. Since the interactions between plants and soil properties seem to depend on various factors, predicting the outcome of interspecific PSFs remains a challenge.

Interactions between plants and soil can depend, for example, on the origin of the species involved. Native and exotic species often differ in their resource-use strategies, resulting in altered nutrient cycling and availability (Vilà et al., 2011), and may thus differ in their PSFs on the responding species. Furthermore, plants can release allelopathic substances to which coexisting species in their native range are adapted. Conversely, species in new distribution areas may not yet be adapted to these substances and therefore may be more strongly negatively affected (Callaway & Aschehoug, 2000). In invasion biology, this phenomenon is known as the *novel weapons* hypothesis (Callaway & Ridenour, 2004). Based on this hypothesis, we would expect that the interspecific PSFs of exotic species on native species are more negative than those of native species. Moreover, compared to native species, exotic species may form different associations with soil mutualists, such as mycorrhizal fungi (Reinhart & Callaway, 2006), or accumulate fewer specialised soil pathogens and herbivores (Mitchell & Power, 2003). According to the *enemy release* hypothesis (ERH; Keane & Crawley, 2002; Wolfe, 2002; Mitchell & Power, 2003; Brian & Catford, 2023), exotic conditioning species are expected to accumulate significantly fewer soil-borne pathogens and herbivores compared to native ones. This is proposed to result in a less negative or even positive net PSF on native responding species compared to native conditioning species. However, research investigating the ERH has predominantly focused on interactions occurring aboveground (e.g. Memmott et al., 2000; Wolfe, 2002; Liu & Stiling, 2006) and there is only a limited number of experimental studies examining the ERH from a belowground perspective (but see Andonian, et al. 2012; Gundale et al., 2014; Müller et al., 2016; Broadbent et al., 2018; Dieskau et al., 2020; Nuske et al., 2021). Due to the variety of mechanisms influenced by the origin of species, we assume that the interspecific PSF differs between native and exotic species. However, because these mechanisms can have opposing effects, predicting the direction of the net effect can be challenging. Therefore, more research is needed to clarify which processes are predominant under different conditions.

The identity of the involved plant species and their relatedness can also play a significant role, as plants induce species-specific modifications in soils and react to these changes in a species-specific way (Bever, 1994; Ehrenfeld et al., 2005). Many studies found that the PSF of a species on itself is often negative (Bever, 1994; Mangan et al., 2010). Assuming that ecologically relevant plant traits are highly conserved (Senior et al., 2018) and correlate with phylogenetic distance, we can expect this effect to decrease with increasing phylogenetic distance between the involved plant species. This decrease is likely due to fewer shared specialised soil-borne pathogens (Gilbert & Webb, 2007) and a reduction in the overlap in resource requirements (Godoy et al., 2014). Research indicating that closely related plant species can indeed share (specialised) natural enemies and resources (Gilbert & Webb, 2007) supports the assumption that plants tend to perform less well in soils previously cultivated by closely related species. However, despite the significantly increased interest in belowground processes over the past decades, only a limited number of studies have explicitly tested whether phylogenetic relatedness is a useful predictor for PSFs, and these studies have produced contradictory results. While Liu et al. (2012), Anacker et al. (2014), Münzbergová & Šurinová (2015), and Kempel et al. (2018) found evidence supporting a relationship between phylogenetic relatedness and the strength of PSFs, Mehrabi and Tuck (2015) did not.

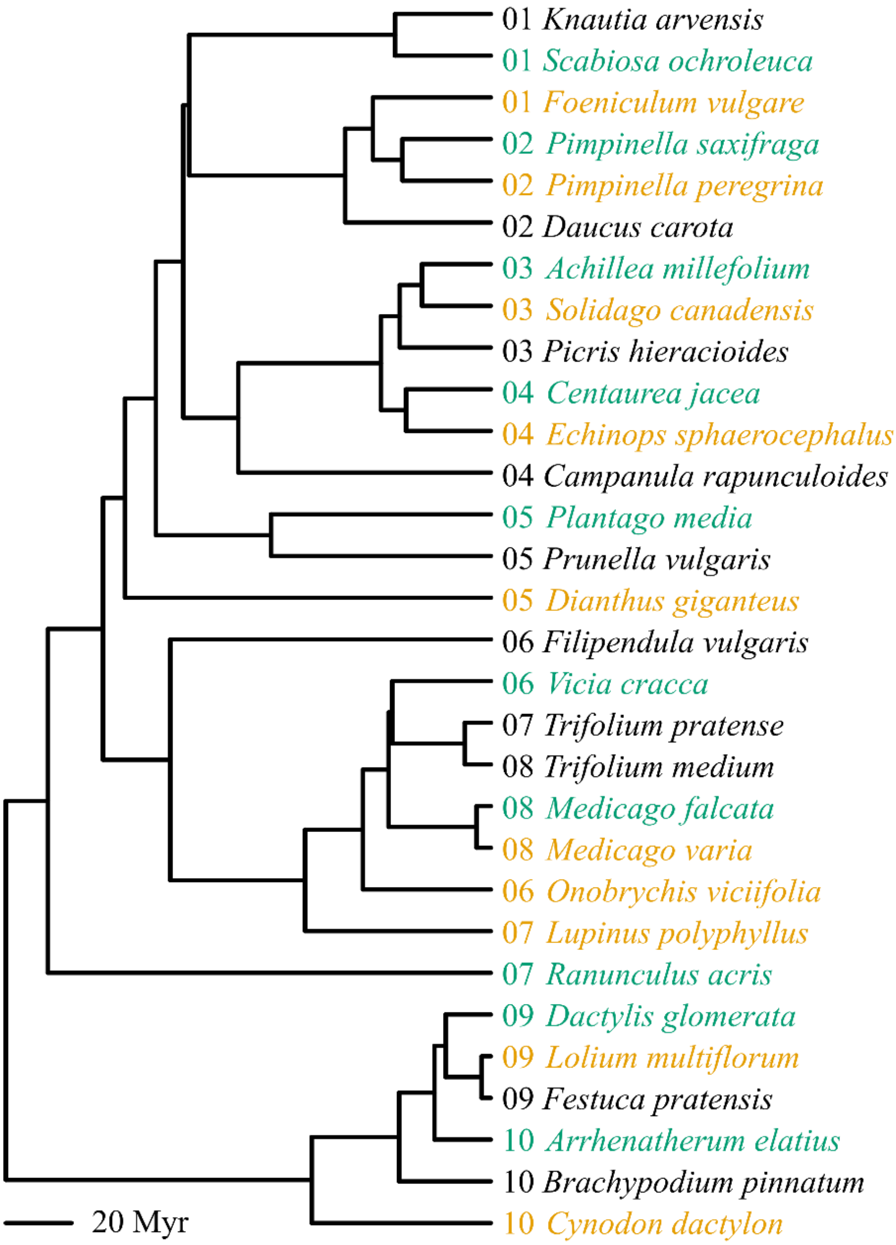
To address these research gaps in PSFs, we conducted a greenhouse experiment to investigate the role of origin and phylogenetic distance in interspecific PSFs. We analysed interactions within 20 plant species pairs, consisting of 10 responding species native to Germany, paired with 10 other native and 10 exotic conditioning species. These pairs comprised biennial and perennial European grassland species from various families and functional groups, covering a range of phylogenetic distances between conditioning and responding species. Based on the knowledge gaps mentioned above, this experiment aims to investigate the following questions: Firstly, does the origin of the conditioning species (native/exotic) influence differences in abiotic and biotic soil conditions and the strength and direction of the interspecific PSF on native responding species. Secondly, does the strength of interspecific PSF decrease as the phylogenetic distance between conditioning and responding species increases? Thirdly, is the phylogenetic signal weaker for exotic conditioning species compared to native ones, possibly due to their release from specialised soil biota?

Methods

Design and species selection

To investigate the role of origin and phylogenetic distance in interspecific PSFs, we conducted a multispecies greenhouse experiment at the UFZ experimental station in Bad Lauchstädt. We analysed the growth of 10 native plant species from central German grassland communities, following an approach by Germain et al. (2016) that we recently applied in another study (Dieskau et al., 2024a). Each of these 10 species was paired with one additional native and one exotic conditioning species (most of our exotic species were introduced to Germany around the 19th century. See Table S 4.1 for a complete list of the native and exotic species used, their taxonomic affiliation, life span, and minimum residence time). This resulted in 20 plant species pairs (either native-native or exotic-native), comprising a total of 30 different species, including forbs, legumes, and grasses. These species pairs represented a range of phylogenetic distances between the conditioning and the responding species, spanning up to 270 million years of evolutionary history since their last common ancestor (see Table S 4.2 for phylogenetic distance and shared community types among paired species). This design enabled us to explore the interactive effects of origin and phylogenetic distance. To ensure comparability of origins, we aimed to select conditioning species with similar distances to their respective native or exotic counterparts. Moreover, to prevent systematic bias and ensure phylogenetic independence among species pairs, we made efforts to minimise overlapping branches (Germain et al., 2016). In the few cases where this was not completely feasible, we minimised the lengths of the overlapping branches (Figure 4.1). Phylogenetic distances were extracted from the Daphne data set (Durka & Michalski, 2012). One species (*Dianthus giganteus*) was missing in the data set and was substituted by the most closely related congener (*Dianthus carthusianorum*) to construct the phylogeny. We purchased seeds for most species from local seed suppliers and collected seeds for *Dianthus giganteus* and *Pimpinella peregrina* ourselves in summer 2016 in central Germany.

Figure 4.1: Phylogenetic tree of all experimental species with their species pair number (01-10) and origin (green = native conditioning species; yellow = exotic conditioning species; black = native responding species; modified after Dieskau et al., 2024a). Phylogenetic distances were extracted from the Daphne data set (Durka & Michalski, 2012).



Experimental setup

Conditioning phase

The experiment started in December 2017 with the soil conditioning phase. For this purpose, 100 seeds of each of the 10 native and 10 exotic conditioning species were sown in 10 L boxes (L: 27, W: 17, H: 22cm) with two replicates per species, resulting in 40 boxes. The boxes were equipped with drainage holes at the bottom to prevent waterlogging. To meet the specific germination requirements (previously tested in a separate germination experiment, data not shown), *Lupinus polyphyllus* seeds were covered with 1-2 cm of soil, whereas the seeds of the other species were sown on the soil surface. To accelerate germination, we covered the boxes with transparent foil until germination reached 25% (5 to 28 days, depending on the species). Since potting soil is often sterilised and less representative in terms of chemical, physical, and soil biotic properties, we decided to use the top layer of sieved unsterilised chernozem soil. Chernozem is the predominant soil type in Central German dry regions and thus representative of the grasslands in the region where seeds had been collected (for more detailed information regarding soil conditions, see Altermann et al., 2005). The soil used was sourced from a site at the UFZ experimental station in Bad Lauchstädt (51.3917°N, 11.8779°E), which had been cultivated as arable land for over 125 years, including regular weed control, ensuring that none of our experimental species had previously established there. Before the experiment, the soil was thoroughly mixed to ensure uniform distribution across all boxes. Additionally, we prepared two control boxes per responding species with soil that was not conditioned, using the same soil and keeping them free of any spontaneously occurring seedlings, resulting in an additional 20 boxes. Thus, we had a total of 60 boxes. These were placed into two greenhouse cabins, each of them representing one replicate. Within the greenhouse cabin, boxes were randomly assigned to two greenhouse benches. Throughout the experimental period, plants were exposed to additional light from 7 am to 7 pm to standardise light conditions within the cabins. The temperatures ranged from 15°C at night to 20°C during the day. Each box was watered from the top approximately every one to four days, depending on its individual requirements. The requirements varied among plant species due to their different biomasses and were assessed by estimating soil moisture by touching the substrate. After two months of growth, the plants were trimmed 4 cm above the soil surface with scissors to simulate mowing, a common management practice in central European grasslands. An additional two months were added to maximise the time during which the plants could condition the soil. This extended period facilitated the establishment of a dense stands of mature plants, including some flowering individuals.

Assessment of abiotic and biotic soil conditions

Four months after sowing, three soil samples per box were taken to gain insight into some of the abiotic and biotic soil changes caused by the different species. Samples were taken in 0-5cm depth using a spoon, sieved using a 2 mm sieve to remove small stones and plant roots and afterwards divided into two plastic bags. One sample was stored for a few days at 8°C for analysis of the response of soil microorganisms, including basal respiration (µl O_2 h-1 g-1 soil dry weight), microbial biomass (µg Cmic g−1 soil dry weight), and specific respiration (µl O_2 mg cmic-1 h-1). For this purpose, we used an automated O_2-uptake method involving the addition of glucose as a carbon substrate to measure the respiratory response of soil microorganisms, as done before (Eisenhauer et al., 2010; Sünnemann et al., 2021a; for details of the method see Scheu, 1992). The other sample was air-dried and stored at room temperature. We measured the pH following Blakemore (1987) and analysed the phosphorous content (following the Egner−Riehm (DL) method). The remaining soil was dried for 72 hours at 80 °C and subsequently ground in an oscillating mill (MM 400, Retsch, Haan, Germany) until they became a homogeneous powder. Five milligrams of the soil powder were used to measure soil C and N gas-chromatographically with the Dumas method (Vario EL Cube, Elementar Analysensysteme, Langenselbold, Germany), from which we further calculated the carbon to nitrogen ratio (soil C:N ratio). Furthermore, we used atomic absorption spectroscopy (AAS vario®6, Analytik Jena) to determine the content of soil phosphorus, calcium, potassium, iron, and magnesium (soil P, Ca, K, Fe, Mg), cation exchange capacity and base saturation.

Response phase

The soil from the two replicates of each conditioning species and the controls was pooled and transferred into 1-liter pots. Each responding species was allocated to one pot with soil conditioned by a native species, to one pot with soil conditioned by an exotic species, and to one control pot with unconditioned soil. This setup was replicated four times, resulting in a total of 120 pots. Pots were distributed across four greenhouse cabins, each cabin representing a block containing one replicate. Within each cabin, pots were randomised across two greenhouse benches. The responding species were sown with 40 seeds per pot. To avoid competition, seedlings were thinned to one individual after two weeks, and any subsequently emerging seedlings were removed every two days. To prevent the exchange of soil biota between the pots and the leaching of nutrients from top watering, pots were positioned on saucers and watered from beneath as needed every one to five days. Three months after sowing, the responding plants reached the adult stage and were partially flowering. Subsequently, aboveground biomass of responding plants was harvested and dried (72 h at 70°C) for the calculation of the aboveground biomass for each pot.

Statistical analysis

To quantify the magnitude and direction of interspecific PSFs, we related the aboveground biomass of adult responding plants grown in conditioned pots to those in control pots. We used log response ratios (LRR) based on mean values across the four replicate pots for these comparisons (Hedges et al., 1999). The use of LRR provides a statistically robust measure to determine the strength and direction of PSFs relative to unconditioned soil. Positive LRR values indicate a facilitative PSF (higher aboveground biomass of responding plants in conditioned soil), while negative values indicate an inhibitory PSF (higher aboveground biomass of responding plants in control pots).

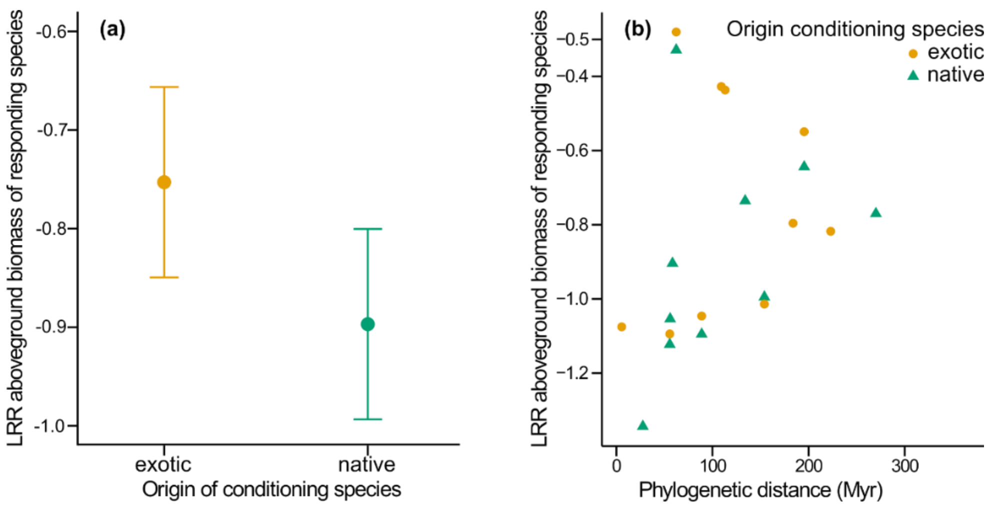
To test the effects of origin and phylogenetic distance on the PSF, we fitted a linear mixed effects model that contained the origin of the conditioning species (native or exotic), phylogenetic distance between conditioning and responding species (PD; centred and scaled) and all possible interactions as explanatory variables. LRRs of the aboveground biomass of responding species were used as response variable (using the package lmerTest in R, version 4.2.0, R Core Team, 2017; Kuznetsova et al., 2017). Since each responding species was sown into soil conditioned by a native and into soil conditioned by an exotic species, the responding species were treated as a random effect in the model. The significance of fixed effects was tested using the Wald type III test. In addition, we used the emmeans command from the emmeans package (Lenth et al., 2022) with the above model to assess whether the mean values per origin significantly deviated from zero.

Subsequently, we compared soils conditioned by native and exotic species in terms of their abiotic and biotic properties. To reduce the complexity of our soil data and account for correlations among abiotic soil characteristics, we conducted a principal component analysis (PCA) using the vegan package (Oksanen et al., 2021) in R (version 3.4.0, R Development Core Team, 2013). This analysis included C:N ratio, pH value, base saturation, cation exchange capacity, microbial biomass, and the content of nitrogen, carbon, magnesium, and phosphorus. To compare the effects of native and exotic species on soil properties, we fitted four different models that contained origin of the conditioning species as explanatory variable and either the first PCA axis (PC1), the second PCA axis (PC2), basal respiration, microbial biomass or specific respiration as responding variables.

Results

The mixed-effects models investigating the effect of origin and phylogenetic distance revealed a significant influence of plant species origin on the interspecific PSF. Conditioning by species of both origins showed an inhibitory PSF on the aboveground biomass of the responding species compared to the unconditioned control. This inhibitory effect was significantly stronger when the soil was conditioned by native species compared to exotic species (Figure 4.2a, Table 4.1).

Figure 4.2: Log response ratios (LRR) for the aboveground biomass of responding species as a measure of the PSF in response to (a) soil conditioned by native (green) and exotic (orange) species; and (b) soil conditioned by native (green triangles) and exotic (orange dots) species of different phylogenetic distance to the native responding species. It should be noted that the effect of phylogenetic distance and the interaction between phylogenetic distance and origin are not significant. Negative LRR values indicate an inhibitory PSF of conditioned soil compared to unconditioned soil, while positive values indicate a facilitative effect. The LRRs in response to native (t=-9.529; df=11.5; p=<0.001) and exotic (t=-7.988; df=11.5; p=<0.001) conditioning species were both significantly negative.



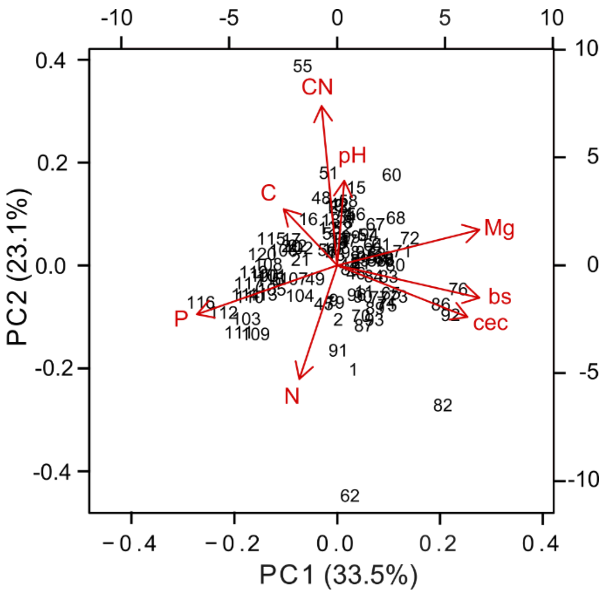
Furthermore, the LRR of the responding species' aboveground biomass showed no correlation with phylogenetic distance (Figure 4.2b), nor was there a significant interaction between phylogenetic distance and origin (Table 4.1). Figure 4.2b shows greater data point dispersion at small phylogenetic distances, suggesting higher variability in aboveground biomass LRR among closely related species compared to distantly related ones. However, we did not statistically test this relationship.

Table 4.1: Results of the mixed-effects model analysis assessing the impact of conditioning species origin, phylogenetic distance between conditioning and responding species, and their interactions on the log response ratios (LRR) of aboveground biomass of responding species as a measure of the PSF. Bold p-values indicate significant main effects or interactions ($p < 0.05$).

Log response ratio (LRR) for aboveground biomass			
	Chi^2	d.f.	*P*
(Intercept)	60.8	1	<0.001
Origin	4.0	1	**0.046**
Phylogenetic distance	0.1	1	0.791
Origin x Phylogenetic distance	0.4	1	0.549

The first two PCA axes of soil abiotic conditions collectively explained 56.6% of the variance in soil abiotic properties. The first axis (PC1, 33.5% of variation) correlated positively with base saturation, cation exchange capacity, and magnesium content, and negatively with phosphorus content; the second axis (PC2, 23.1% of variation) correlated positively with C:N ratio and pH (Figure 4.3).

Figure 4.3: PCA ordination diagram of 1st and 2nd axis. Letters refer to soil characteristics (N=nitrogen content, C=carbon content, CN=CN ratio, Mg=magnesium content, P=phosphorus content, pH= pH value, bs=base saturation, cec= cation exchange capacity). Numbers and arrows refer to recorded variables. The first and second principal components (PC1 and PC2) accounted for 33.5% and 23.1% of the total variation, respectively.

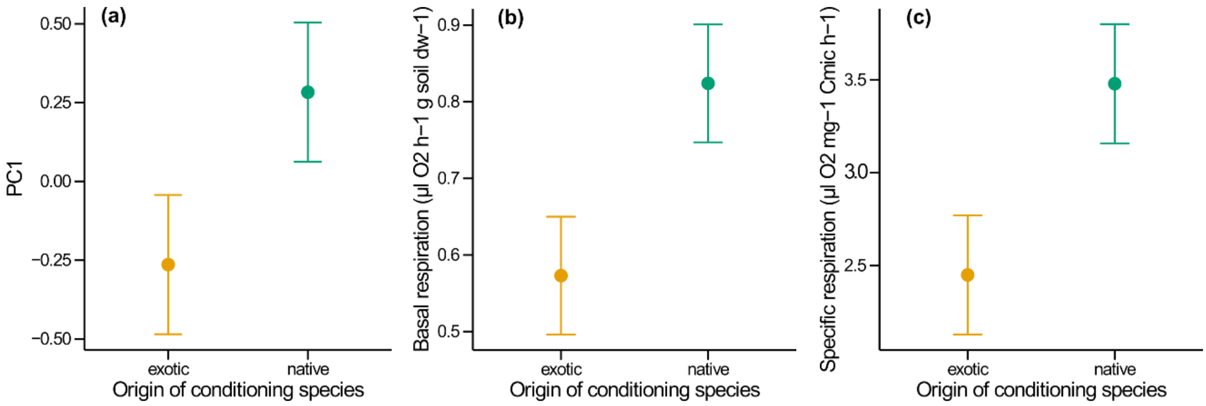


Native species conditioning led to higher values for PC1 compared to exotic species (Figure 4.4a; marginally significant), while PC2 showed no difference between the two origins (Table 4.2). Basal respiration (Figure 4.4b) and specific respiration (Figure 4.4c) attained significantly lower values for soil conditioned by exotic species compared to soil conditioned by native species (Table 4.2). Microbial biomass did not differ between native and exotic species.

Table 4.2: Results of the mixed-effects model analysis assessing the impact of the conditioning species origin on abiotic, including (A) first (PC1) and (B) second (PC2) axes of a Principal Component Analysis (PCA)) and biotic soil conditions, including (C) basal respiration, (D) microbial biomass and (E) specific respiration. Bold p-values indicate significant main effects ($p < 0.05$).

	d.f.	*F*	*P*
(A) PC1			
(Intercept)	1	1.43	0.248
Origin	1	3.06	0.097
Residuals	18		
(B) PC2			
(Intercept)	1	0.01	0.925
Origin	1	0.1	0.752
Residuals	18		
(C) Basal respiration			
(Intercept)	1	55.63	<0.001
Origin	1	5.32	**0.033**
Residuals	18		
(D) Microbial biomass			
(Intercept)	1	117.19	<0.001
Origin	1	0.01	0.906
Residuals	18		
(E) Specific respiration			
(Intercept)	1	58.41	<0.001
Origin	1	5.05	**0.037**
Residuals	18		

Figure 4.4: Effects of soil conditioned by native and exotic species on (a) the first axis (PC1) of a Principal Component Analysis (PCA) of abiotic soil characteristics (see Figure 4.3 for the PCA ordination diagram), (b) the basal respiration, and (c) the specific respiration. PC1 explains 33.5% of the variation in soil abiotic properties and correlates negatively with phosphorus content, and positively with base saturation, cation exchange capacity, and magnesium content.



Discussion

We investigated the significance of origin and phylogenetic distance between conditioning and responding species for interspecific PSFs. In general, soil conditioning by native and exotic species had an inhibitory effect on the productivity of the responding species. This effect was stronger for native conditioning species. Furthermore, the effect of native and exotic conditioning species on abiotic and biotic soil properties differed. Soil conditioned by native species exhibited higher basal respiration and greater specific respiration. Additionally, it showed higher values on the first principal component axis (PC1), indicating lower phosphorus content but higher base saturation, cation exchange capacity, and magnesium content compared to soil conditioned by exotic species. Contrary to our expectation, phylogenetic distance appeared to have no significant influence on the interspecific PSF, irrespective of the origin of the conditioning species.

PSFs of exotic conditioning species are less inhibitive

The results of our study indicate that the effect of soil conditioning by both native and exotic species had an inhibitory impact on the production of aboveground biomass of the responding species. Our finding is consistent with other studies that have observed interspecific PSFs, particularly in grasslands, to have negative impacts on plant growth (Petermann et al., 2008;

Maron et al., 2016). This negative net effect suggests that the impact of inhibitory mechanisms, such as those mediated by soil pathogens or the release of allelopathic substances, outweighs potential positive effects, such as those arising from soil mutualists. In our experiment, it is also quite possible that nutrient depletion contributed to the inhibitory net effects. Although the chernozem soil we used is relatively nutrient-rich, it is possible that nutrient limitation became increasingly important over the seven-month experimental period, as no additional fertiliser was applied and the PSF of the conditioning species was calculated in relation to empty control boxes that showed no plant-related changes in soil nutrient content.

As expected, the net effect differed between native and exotic conditioning species. Conditioning by native species had a more pronounced inhibitory effect on the biomass production of responding species compared to exotic species. One possible explanation is that the microbial activity and community composition may vary depending on the origin of the conditioning species. This assumption is supported by our finding of a higher basal respiration and specific respiration in soils conditioned by native species compared to those conditioned by exotic species. This suggests that co-evolutionary processes may have caused native plant species to foster microbial communities more strongly dominated by fast-growing, high-metabolism microbes exhibiting elevated respiration rates, in contrast to those associated with exotic species. While a high basal respiration indicates higher microbial activity, a high specific respiration value suggests that microbes are allocating a larger proportion of carbon resources to maintenance respiration rather than biomass production (e.g. Eisenhauer et al., 2013). When both values are increased, this indicates that plant species promote higher overall microbial activity but under conditions that hinder efficient microbial carbon utilisation. However, it is important to note that other factors may have also contributed to the observed differences. Stress, such as nutrient imbalances and microbial nutrient limitations, could have increased both basal respiration (due to higher metabolic demands) and specific respiration, as microbes redirect energy to maintain cellular functions rather than growth and reproduction (Eisenhauer et al., 2010). Furthermore, native plant species may have produced root exudates or litter with high-quality carbon substrates, which could stimulate microbial activity and elevate basal respiration.

Our results are consistent with other studies that have also demonstrated differences in microbial communities in soils conditioned by native and exotic plant species (Kourtev et al., 2002; Upton et al., 2020). Checinska Sielaff et al. (2018), for instance, found that native and exotic grasslands primarily differed in the structure and function of soil fungal community composition, and these differences were correlated with varying phosphorus mineralisation rates. This aligns with our finding that soils conditioned by native species exhibited marginally significantly lower levels of plant-available phosphorus compared to those conditioned by exotic species. This difference may have contributed to the stronger suppressive PSF observed in soils conditioned by native species in our study. While other studies have found that not only native but also exotic plant species can accumulate generalist pathogens shared with native species (e.g. Waller et al., 2021), our data are more in line with the *enemy release* hypothesis (ERH; Keane & Crawley, 2002; Brian & Catford, 2023) and suggest that co-evolutionary processes may have driven a stronger specialisation of soil pathogens toward plant species of the same origin. This could result in the accumulation of not only distinct specialised soil pathogens but also varying degrees of generalist soil pathogens as generalist soil organisms can also influence variations in PSFs when their effects and accumulation rates differ between plant species (Cortois et al., 2016; Semchenko et al., 2022; Wilschut et al., 2023). However, it must be considered that the observed differences may not necessarily result from a less inhibitory effect of exotic conditioning species, but from promoting mechanisms. As our focus was on capturing the overall net interspecific PSF, we are unable to conclusively determine the processes underlying the differing interspecific PSFs of native and exotic conditioning species in our experiment.

PSF independent of phylogenetic distance

Contrary to our hypothesis and the findings of Liu et al. (2012), Anacker et al. (2014), Münzbergová and Šurinová (2015), and Kempel et al. (2018), the phylogenetic distance did not influence the strength of the interspecific PSF in our experiment, regardless of the origin of the conditioning species. Although there appears to be a trend aligning with our expectation of a stronger positive correlation between the performance of the responding species and phylogenetic distance for native conditioning species, this relationship was not statistically significant. We suggest that effects not accounted for by phylogeny may have overridden any phylogenetic effects, as the PSF varied largely even at small phylogenetic distances. Our results therefore suggest that phylogenetic distance does not have any decisive influence on how strongly the performance of the responding species is affected by soil conditioning. A possible explanation for this could be that the traits critical for PSFs are highly plasticity and are not sufficiently phylogenetically conserved. This interpretation is also supported by a meta-analysis by Mehrabi and Tuck (2015) of all available pairwise PSF experiments conducted over two decades, involving 133 plant species in 329 pairwise interactions. They found that the sign and magnitude of PSFs were not explained by the phylogenetic distance between interacting species. This result was consistent across different life forms, life cycles, provenances, and phylogenetic scales.

We still caution against concluding that phylogenetic distance generally does not play a role in interspecific PSFs. We do not assume that the conditioning phase was too short to produce effects of phylogeny, as it was evidently sufficient to generate differences between native and exotic species. However, it is possible that opposing effects may cancel each other out. For example, closely related responding species might be more inhibited by pathogens accumulated by conditioning species, yet simultaneously possess better defences against allelopathic effects. Depending on which mechanism is more pronounced, there could be varying degrees of deviation in either direction, which would align with our observation of higher variability at smaller phylogenetic distances. For a clearer distinction between these mechanisms, studies involving inoculation and sterilisation would be necessary. In addition, plant–microbe interactions are influenced by various environmental factors, making them highly context-dependent. These factors can include soil type, moisture levels, temperature, nutrient availability (van der Putten et al., 2013). Our findings support the assumption that the phylogenetic distance between conditioning and responding species may not be a reliable predictor of interspecific PSFs across different environmental contexts.

Conclusion

We investigated whether native and exotic conditioning species differ in their interspecific PSFs on native responding species. Our findings reveal that PSFs were consistently negative, with the effect being significantly stronger for native conditioning species than for exotic ones. This stronger negative impact of native species likely stems from the activity and accumulation of local soil microorganisms, further emphasising the importance of soil biota for interspecific PSFs. The marginally lower phosphorus availability in soils conditioned by native species also supports the hypothesis that native plants may exert stronger nutrient depletion effects, possibly through differential interactions with soil microorganisms involved in nutrient cycling or competition for limited resources. These findings have important implications for strategies aimed at promoting native plant species and controlling invasive species. For instance, during the restoration of degraded ecosystems, soil microorganisms could be deliberately utilised to enhance the growth of native species while suppressing that of invasive species. However, since nutrient limitations tend to be more pronounced in greenhouse settings without additional fertiliser than in natural field conditions, it should be noted that these results are only partially transferable. Future studies should therefore test the ERH with a focus on belowground processes, conducting more detailed investigations to differentiate the underlying mechanisms. The absence of an influence of phylogenetic distance on the PSF in our study and others suggests that analysing phylogenetic relationships among the involved plant species is insufficient to predict the direction and strength of interspecific PSFs.

Acknowledgement

We acknowledge the use of data drawn from the Daphne data set. We thank Ines Merbach and the entire team of Field Experimental Station of the UFZ at Bad Lauchstädt, and Niclas Mehre, Carolin Plos and Julia Rieger for practical support during the experiment. We are grateful to Alfred Lochner, Tobias Proß and Tim Walther for helpful support with laboratory analysis. Katrin Kittlaus and Birgit Müller provided valuable assistance in the acquaintance of seed material and support during the experiment. Chat GPT-4 was used to translate individual sentences of the manuscript. The authors declare that there is no conflict of interest regarding the publication of this manuscript.

Supplementary material (S4)

Plant-soil feedback in European grasslands is phylogenetically independent but affected by plant species origin

Authors: Julia Dieskau, Isabell Hensen, Nico Eisenhauer, Susanne Lachmuth, Harald Auge

Journal: *Journal of Plant Ecology*

Species list

Table S 4.1: Species list with triplet number (T01-T10), role in the experiment (NR = native responding species; NC = native conditioning species; EC = exotic conditioning species), family, lifespan, invasion status, minimum residence time (MRT) for exotic species. Invasion status was assessed according to Bundesamt für Naturschutz (2023) and Nehring et al. (2013), and lifespan sociology and minimum residence time was extracted from Bundesamt für Naturschutz (2023) and Seebens (2020); modified after Dieskau et al. (2024a).

Species	Triplet	Role in experi-ment	Family	Lifespan	Invasion status	MRT (y)
Achillea millefolium L.	T03	NC	Asteraceae	polycarpic perennial	-	-
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	T10	NC	Poaceae	polycarpic perennial	-	-
Brachypodium pinnatum (L.) P. Beauv.	T10	NR	Poaceae	monocarpic perennial	-	-
Campanula rapunculoides L.	T04	NR	Campanulaceae	biennial, polycarpic perennial	-	-
Centaurea jacea L.	T04	NC	Asteraceae	annual, biennial, polycarpic perennial	-	-
Cynodon dactylon (L.) Pers.	T10	EC	Poaceae	polycarpic perennial	established	305
Dactylis glomerata L.	T09	NC	Poaceae	polycarpic perennial	-	-
Daucus carota L.	T02	NR	Apiaceae	polycarpic perennial	-	-
Dianthus giganteus d'Urv.	T05	EC	Caryo-phyllaceae	polycarpic perennial	established	31
Echinops sphaerocephalus L.	T04	EC	Asteraceae	polycarpic perennial	established	185
Festuca pratensis Huds.	T09	NR	Poaceae	polycarpic perennial	-	-
Filipendula vulgaris Moench	T06	NR	Rosaceae	polycarpic perennial	-	-
Foeniculum vulgare Mill.	T01	EC	Apiaceae	polycarpic perennial	established	197
Knautia arvensis (L.) Coult.	T01	NR	Caprifoliaceae	polycarpic perennial	-	-
Lolium multiflorum Lam.	T09	EC	Poaceae	polycarpic perennial	established	203
Lupinus polyphyllus Lindl.	T07	EC	Fabaceae	polycarpic perennial	established	137
Medicago falcata L.	T08	NC	Fabaceae	biennial, monocarpic perennial	-	-
Medicago x varia Martyn	T08	EC	Fabaceae	polycarpic perennial	established	198
Onobrychis viciifolia Scop	T06	EC	Fabaceae	polycarpic perennial	established	96
Picris hieracioides L.	T03	NR	Asteraceae	polycarpic perennial	-	-

Pimpinella peregrina L.	T02	EC	Apiaceae	polycarpic perennial	casual	17
Pimpinella saxifraga L.	T02	NC	Apiaceae	biennial, monocarpic perennial	-	-
Plantago media L.	T05	NC	Plantaginaceae	polycarpic perennial	-	-
Prunella vulgaris L.	T05	NR	Lamiaceae	polycarpic perennial	-	-
Ranunculus acris L.	T07	NC	Ranunculaceae	polycarpic perennial	-	-
Scabiosa ochroleuca L.	T01	NC	Caprifoliaceae	polycarpic perennial	-	-
Solidago canadensis L.	T03	EC	Asteraceae	polycarpic perennial	established	175
Trifolium medium L.	T08	NR	Fabaceae	polycarpic perennial	-	-
Trifolium pratense L.	T07	NR	Fabaceae	polycarpic perennial	-	-
Vicia cracca L.	T06	NC	Fabaceae	polycarpic perennial	-	-

Table S 4.2: Species pairs and the respective triplet according to experimental design, phylogenetic distance within species pair, and shared community types according to biolflor.de (Klotz et al., 2002). (Community types: 1… Fescue-brome communities of dry and semi-dry grasslands; 2… Commercially used grasslands; 3… Eusiberian ruderal mugwort and thistles communities, and couch-grasslands; 4… Thermophilous and mesophilous forest grassland ecotones; 5… Nitrophilous tall herb communities.). Adapted from Dieskau et al. (2024a).

Conditioning species	**Responding species**	**Triplet**	**Phylogenetic distance (myr)**	**Shared community types**
Foeniculum vulgare	*Knautia arvensis*	T01	183.8	3
Scabiosa ochroleuca	*Knautia arvensis*	T01	58.4	1, 3
Pimpinella peregrina	*Daucus carota*	T02	88.8	1
Pimpinella saxifraga	*Daucus carota*	T02	88.8	1
Solidago canadensis	*Picris hieracioides*	T03	55.6	2, 3
Achillea millefolium	*Picris hieracioides*	T03	55.6	1, 2, 3
Echinops sphaerocephalus	*Campanula rapunculoides*	T04	154	-
Centaurea jacea	*Campanula rapunculoides*	T04	154	4
Dianthus giganteus	*Prunella vulgaris*	T05	223	1
Plantago media	*Prunella vulgaris*	T05	134	1, 2
Onobrychis viciifolia	*Filipendula vulgaris*	T06	195.4	1, 2
Vicia cracca	*Filipendula vulgaris*	T06	195.4	2
Lupinus polyphyllus	*Trifolium pratense*	T07	113.2	2
Ranunculus acris	*Trifolium pratense*	T07	270	2
Medicago varia	*Trifolium medium*	T08	62.3	-
Medicago falcata	*Trifolium medium*	T08	62.3	4
Lolium multiflorum	*Festuca pratensis*	T09	5.6	2
Dactylis glomerata	*Festuca pratensis*	T09	27.6	1, 2, 5
Cynodon dactylon	*Brachypodium pinnatum*	T10	109.2	2
Arrhenatherum elatius	*Brachypodium pinnatum*	T10	56	1, 2, 4

Chapter 5

Synthesis

Summary of results

In this thesis, I explore how priority effects in European grassland plant communities are shaped by both the origin of early- and late-arriving species and their phylogenetic relationships. Chapters 2, 3, and 4 examine how these factors influence the mechanisms of priority effects via direct competition and PSF, as well as their interaction. By combining controlled glasshouse experiments with a manipulative field experiment, the thesis draws robust conclusions about priority effects under ecologically realistic conditions, while also elucidating the underlying mechanisms in detail (see Figure 5.1 for a graphical summary of the results).

In **Chapter 2**, I found that competition- and soil fungi-mediated priority effects consistently inhibited both the establishment and biomass production of late-arriving species. Exotic species exhibited higher overall biomass, and biomass production of early-arriving species contributed to competition effects. Nevertheless, competition effects did not differ between native and exotic species, suggesting that additional factors beyond biomass influence these interactions. Moreover, soil fungi-mediated priority effects were generally more inhibitory for native late-arriving species compared to exotic ones and the presence of soil fungi reduced the overall strength of competition effects.

In **Chapter 3**, I found that net priority effects were consistently negative when present, and their strength increased with decreasing phylogenetic distance between early- and late-arriving species. Notably, this pattern was evident only in the biomass production of late-arriving species, and not in earlier developmental stages such as seedling emergence or survival. Furthermore, allopatric and sympatric species pairs showed no significant differences in their responses, regardless of their phylogenetic relatedness.

In **Chapter 4**, I found that PSF-mediated priority effects were generally inhibitory but independent of phylogenetic distance between early- and late-arriving species. However, priority effects varied depending on the origin of the early-arriving species, with stronger inhibition observed in soils conditioned by native species. Moreover, several soil variables differed between soils conditioned by native and exotic species.

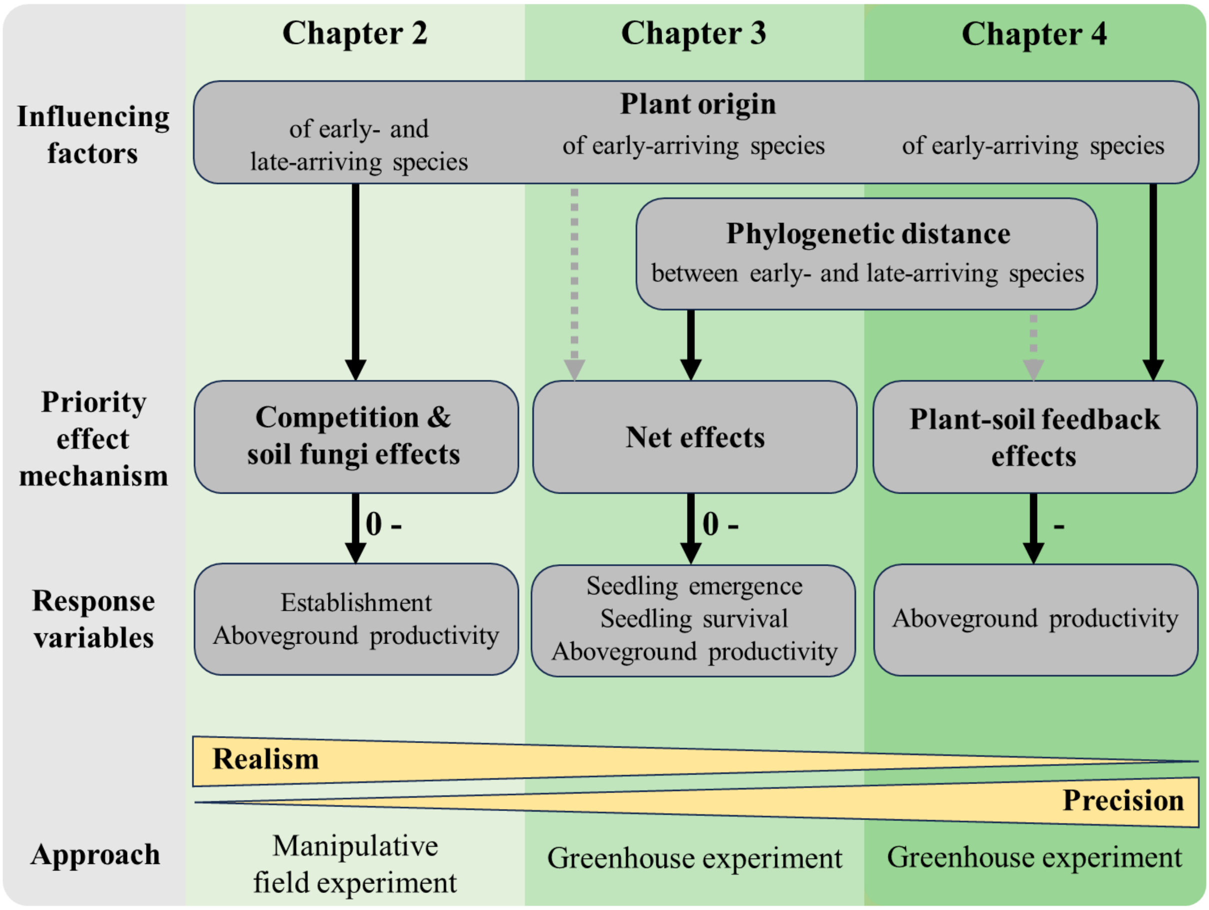


Figure 5.1: Graphical summary of the results of my thesis, based on Figure 1.2. Black arrows with solid lines indicate effects for which evidence was found, whereas grey arrows with dashed lines indicate effects for which no evidence was found. Symbols next to the arrows indicate the direction of priority effects mediated by the different mechanisms (- represents inhibitory effects and 0 represents neutral effects).

General discussion

Competition and plant-soil feedback as drivers of negative priority effects

Priority effects in grassland plant communities arise from the complex interplay between aboveground and belowground competitive dynamics and PSFs (Alonso-Crespo et al., 2025; Dostál, 2021; Lekberg et al., 2018; Senthilnathan & D'Andrea, 2024; Uricchio et al., 2019). Together, these abiotic and biotic interactions mediate the extent to which early-arriving species influence the establishment and performance of later-arriving species (Gillhaussen et al., 2014; Weidlich et al., 2021; Yan et al., 2024). My results indicate that priority effects in the studied grassland system are predominantly negative. For example, findings from my controlled greenhouse experiment (Chapter 3) show that, wherever a net priority effect was observed, it was negative, with the presence of an early-arriving species inhibiting the biomass production of late-arriving species. These results are consistent with a growing body of research reporting predominantly negative priority effects in temperate grassland ecosystems (e.g. Ferenc et al., 2021; Stuble & Souza, 2016; van Steijn et al., 2025; Wilsey et al., 2015).

My results further indicate that both direct competition and PSF, jointly contribute to the observed negative net priority effects. Competition-mediated priority effects are inherently inhibitory, as also demonstrated in my field experiment (Chapter 2). This inhibitory effect is even more pronounced under sequential compared to simultaneous arrival (van Steijn et al., 2025). The emergence of positive priority effects would therefore require particularly strong facilitative niche modifications to overcome these suppressive interactions (Fukami, 2015). However, irrespective of the experimental context and the mechanism studied, early-arriving species consistently reduced the performance of later-arriving species when effects were observed. For example, both interspecific PSF (Chapter 4) and soil fungal interactions as a subcomponent of PSF (Chapter 2) contributed negatively to the performance of later-arriving species. This pattern aligns with previous findings that interspecific PSFs often have inhibitory effects (e.g. Maron et al. 2016; Lekberg et al. 2018; Xue et al. 2018; Rallo et al. 2023), suggesting that early-arriving species can modify the belowground environment in ways that further suppress the success of late-arriving species.

Interestingly, the effects of competition- and PSF-mediated priority effects appear to be not merely additive, but synergistic. In line with previous findings that soil fungi can mitigate the intensity of competition (e.g. Bennett & Cahill 2016; McHaffie & Maherali, 2020; Stanescu & Maherali, 2016), I found that the presence of soil fungi reduced the overall strength of competitive interactions, likely due to their inhibitory effects on early-arriving species (Chapter 2). These results highlight the importance of considering not only direct competition and modifications to the belowground environment, but also the relative strength of intraspecific versus interspecific PSFs. Moreover, there is a need for increased focus on understanding the relative importance of PSFs versus direct competition, particularly given that their influence is highly context-dependent (Crawford et al., 2019; Huangfu et al., 2022; Lekberg et al., 2018). Integrating these aspects into future research could enhance our understanding of how priority effects influence assembly outcomes in plant communities.

The role of evolutionary relatedness in shaping priority effect mechanisms

The strength of the net priority effect in my study was negatively correlated with the phylogenetic distance between early- and late-arriving species, with inhibitory effects being strongest among closely related species (Chapter 3). In contrast, PSFs showed no such relationship with phylogenetic distance (Chapter 4). Given that both experiments shared the same design and species pool, the observed pattern in net priority effects is more likely attributable to direct competitive interactions than to PSFs. These findings align with prior research suggesting that closely related species tend to compete more intensely (Anacker & Strauss, 2016; Burns & Strauss, 2011; Castillo et al., 2010; Feng & van Kleunen, 2016; Valiente-Banuet & Verdú, 2008), thereby lending support to the concepts of niche conservatism (Wiens & Graham, 2005) and competitive exclusion among phylogenetic relatives (Webb et al., 2002).

Nevertheless, the relationship between phylogenetic relatedness and competition is complex and context-dependent. For example, stressful, resource-limited conditions can influence competitive interactions between distantly related plant species in both directions (Williams et al., 2021; Zhang et al., 2016, 2017), whereas in resource-rich environments, competition among closely related species tends to intensify (Burns & Strauss, 2011; Williams et al., 2021). Furthermore, the shift from competition to facilitation under stress may depend on additional factors, such as mutualistic relationships (e.g., with mycorrhizal fungi) and specific ecological strategies, rather than phylogenetic distance alone (Zhang et al., 2016, 2017). Moreover, several studies have found only weak or inconsistent patterns, with functional traits frequently emerging as more reliable predictors of competitive outcomes than evolutionary relatedness (Cahill et al., 2008; Feng & van Kleunen, 2016; Godoy et al., 2014; Verdú et al., 2012; Williams et al., 2021). Traits such as plant height, leaf area, and root architecture may more directly mediate competitive dynamics and thus offer a more mechanistic understanding of species interactions (Cahill et al., 2008; Feng & van Kleunen, 2016).

Furthermore, the role of arrival order in shaping the relationship between phylogenetic distance and competition strength remains understudied. Some evidence indicates that the temporal dynamics introduced by priority effects can override phylogenetic signals (Godoy et al., 2014; Valiente-Banuet & Verdú, 2008), while other studies suggest that influence of competitive traits can be intensified when species arrive sequentially rather than simultaneously (van Steijn et al., 2025). Such conflicting findings in the literature might be explained by ontogenetic niche shifts (Auffret et al., 2010; Miriti, 2006; Parish & Bazzaz, 1985; Wegasie et al., 2021), whereby trait similarity becomes important only at later, adult stages. For example, in my experiment, phylogenetic distance had no detectable effect on early life stages such as seedling emergence and survival, whereas closely related late-arriving species experienced significantly greater reductions in biomass at the adult stage compared to distantly related ones (Chapter 3).

Plant species origin as a mediator of priority effect mechanisms

Contrary to initial expectations, the net priority effects observed in the greenhouse experiment (Chapter 3) did not differ significantly between native and exotic early-arriving species. A similar pattern emerged for the competition effect in the field experiment (Chapter 2), which also showed no clear difference between native and exotic species. However, when biomass was included as a covariate, native early-arriving species exhibited stronger competition effects. This suggests that the competitive effect of exotic species is largely attributable to their rapid biomass accumulation, a well-documented pattern (Funk & Vitousek, 2007; Pyšek & Richardson, 2007), whereas native species may rely more on alternative strategies such as stress tolerance, specialised mutualisms, or chemical defences to sustain competitive performance (Burns & Strauss, 2011; Callaway et al., 2004; Fridley et al., 2007). The biogeographic history of early- and late-arriving species did also not appear to influence the relationship between phylogenetic distance and priority effects (Chapter 3), suggesting that co-occurring sympatric species pairs did not undergo evolutionary trajectories shaped by stronger selection for niche divergence compared to allopatric species pairs.

In the PSF experiment (Chapter 4), I found that the inhibitory effect of soil conditioning by early-arriving species was significantly stronger when the early-arriving species were native. Likewise, in the field experiment (Chapter 2), native late-arriving species were more negatively affected by accumulated soil fungi than their exotic counterparts. Together, these findings suggest that exotic species may experience reduced pathogen accumulation or weaker negative PSFs compared to natives. This provides clear support for the widely recognised *enemy release* hypothesis (Keane & Crawley, 2002; Mitchell & Power, 2003). Similar findings have also been reported in other studies demonstrating that introduced species escape their natural belowground enemies (Dawson & Schrama, 2016; Reinhart & Callaway, 2006). The greater aboveground biomass of exotic species observed in the fourth year of the field experiment may also suggest that, as a result of release from specialist enemies, exotic species evolve to shift resources from defence to growth and competition—consistent with the *evolution of increased competitive ability* (EICA) hypothesis (Blossey & Notzold, 1995). However, my study design did not explicitly test this hypothesis. Recent meta-analyses have revealed mixed evidence for the EICA hypothesis but have also contributed to a more nuanced understanding of the underlying processes (Bossdorf et al., 2005; Callaway et al., 2022; Felker-Quinn et al., 2013; Rotter & Holeski, 2018). Overall, while the core trade-off proposed by the EICA hypothesis holds in certain contexts, it is now seen as just one component of a broader invasion framework (Bossdorf et al., 2005; Felker-Quinn et al., 2013). Future studies should experimentally assess defence-related trade-offs under controlled conditions to elucidate the potential relevance of this mechanism in interaction with PSF and interspecific competition.

Additional support for temporal and functional differentiation between native and exotic species is provided by the field experiment (Chapter 2). Here, competition primarily suppressed the establishment of late-arriving native species, whereas late-arriving exotic species were more strongly limited in their biomass production. This highlights the importance of developmental stage and, consequently, timing in determining the outcomes of competitive interactions (Fukami, 2015). Native species may be particularly vulnerable to early priority effects, especially when exotic species establish rapidly and dominate resource uptake, a pattern well documented in invasion ecology (Dickson et al., 2012; Tilman, 2004; Wilsey et al., 2015). In contrast, exotic species, though initially advantaged, may eventually face diminishing returns, potentially due to density-dependent effects, self-shading, or delayed biotic interactions such as the accumulation of soil pathogens (Bever et al., 2015; Dawson & Schrama, 2016; Mitchell & Power, 2003). Overall, these findings highlight the need to integrate both above- and belowground mechanisms and to account for temporal dynamics when studying plant invasions and community assembly.

Practical implications for restoration and invasion management

The findings from my studies provide valuable implications for the restoration and management of temperate grasslands, particularly regarding invasive species control. The consistent observation that priority effects were negative whenever present highlights the critical role of species arrival order in shaping community composition and dynamics. Research demonstrates that even slight variations in the timing of species arrival can have enduring impacts on plant community structure, potentially leading to the establishment of alternative stable states and significantly influencing the dynamics of both native and exotic species (Helsen et al., 2016; Martin & Wilsey, 2012; Mudrák et al., 2018; Roscher et al., 2009; Švamberková et al., 2019; Ulrich et al., 2016; Weidlich et al., 2021; Werner et al., 2016). This underscores the importance of strategically managing the timing of species introductions for successful restoration efforts.

Moreover, results from the field experiment (Chapter 2) indicate that native late-arriving species are more vulnerable to competition during early establishment stages, whereas exotic species face greater suppression in biomass production at later, adult stages. Additionally, soil fungi exerted an inhibitory effect on the establishment of native late-arriving species. This suggests distinct windows of vulnerability and potentially different underlying competitive mechanisms, as has been documented in previous studies (Abraham et al., 2009; Corbin & D'Antonio, 2004; Gioria et al., 2018; Mordecai et al., 2015). Together, these insights highlight the necessity of aligning restoration interventions with critical life-history stages of target species (Andel & Aronson, 2012; Harzé et al., 2018; Larson et al., 2015; Winkler et al., 2024). Strategies that promote native establishment before exotics, such as priority seeding (Dickson et al., 2012; Vaughn & Young, 2015; Werner et al., 2016; Young et al., 2015), high-density sowing (Carter & Blair, 2012; Nemec et al., 2013; Reinhardt Adams & Galatowitsch, 2008; Schuster et al., 2018; Yannelli et al., 2018), or removal of undesirable vegetation prior to sowing (Cox & Allen, 2008; D'Antonio & Meyerson, 2002; Johnson et al., 2018; Tognetti & Chaneton, 2012), can help overcome early-stage vulnerabilities and reduce invasion success by enabling natives to preempt resources and accumulate biomass (Delory et al., 2019a; Hess et al., 2022; Yannelli et al., 2020).

On sites that have already been invaded, early intervention is broadly recognised as an effective strategy and can substantially improve the success of management efforts (Blumenthal et al., 2005; D'Antonio & Meyerson, 2002; Grman et al., 2013; Hobbs & Harris, 2001). This is also supported by my findings from the field experiment (Chapter 2), where exotic early-arriving species exhibited significantly greater aboveground biomass only in the fourth year, suggesting that their competitive strength increases over time. Since greater biomass contributed substantially to the competitive strength of exotic species, reducing their biomass (Lishawa et al., 2015; Ramula, 2020) and limiting their access to light and other resources early after arrival (Funk & McDaniel, 2010; Jones et al., 2015) may prove essential in mitigating their dominance once established.

The negative correlation between the strength of the inhibitory net priority effect and phylogenetic distance (Chapter 3) suggests that considering phylogenetic relatedness when assembling native communities on restoration sites may enhance resistance to invasion. Maximising phylogenetic distance among native species may not only reduce intra-community competition but also increase the likelihood that the native community includes species with low phylogenetic distance to, and therefore stronger competitive effects against, invading exotic species. However, recent experimental and observational studies have shown that greater phylogenetic diversity may sometimes correlate with increased, rather than reduced, invasive species abundance (Ernst et al., 2022, 2023; Zhang et al., 2024c). These findings may reflect that invasive species closely related to the established native community are initially limited in their ability to establish but ultimately impose greater competitive pressure on native species once established. This underscores the importance of targeted monitoring of exotic species that are closely related to native species and may, following a prolonged lag phase, develop strongly invasive dynamics. However, meta-analyses and field experiments suggest that invasion resistance is more strongly governed by resource availability and key functional traits of resident species, such as tall, highly competitive grasses, than by phylogenetic distance alone (Bennett et al., 2014; Ernst et al., 2022, 2023; Li et al., 2022; Zhang et al., 2024c). Promoting competitive native species capable of producing high biomass may therefore be a more reliable and effective restoration strategy (Csákvári et al., 2023; Yannelli et al., 2020).

In sum, effective restoration and invasive species management should employ a combination of strategies to promote long-term ecosystem resilience. While priority effects offer valuable tools for steering community assembly, their successful application requires context-specific approaches and long-term studies to fully realise their potential and mitigate unintended consequences (Martin & Wilsey, 2012; Weidlich et al., 2021; Werner et al., 2016).

Limitations and perspectives for future research

Following the broader definition of priority effects (Alonso-Crespo et al., 2025; Grman & Suding, 2010), I assessed the performance of my experimental species when arriving late by comparing it to their performance in monoculture. This approach provides insights into the inhibitory or facilitative effects of early-arriving species and enables a nuanced examination of the underlying mechanisms (Delory et al., unpublished manuscript). However, the observed differences reflect the impact of the presence of early arrivals and cannot be attributed unequivocally to arrival order. To disentangle the specific effects of arrival order, future studies should include an additional control treatment involving simultaneous arrival, a design that is indeed increasingly employed in experimental studies on priority effects (e.g. Alonso-Crespo et al., 2023; Gillhaussen et al., 2014; Kardol et al., 2013b; Ploughe et al., 2020; van Steijn et al., 2025).

Furthermore, most research on priority effects has predominantly focused on inhibitory outcomes (Stroud et al., 2024). However, it is important to consider that the balance between competition and facilitation is environment-dependent, as predicted by the *stress-gradient* hypothesis (SGH; Bertness & Callaway, 1994). There is growing evidence that in certain ecosystems, particularly those characterised by harsh environmental conditions such as deserts or alpine regions, facilitative priority effects may play a significant role (Castro et al., 2004; Holzapfel & Mahall, 1999). Moreover, they may gain increasing importance in the future as a consequence of climate change, which is expected to lead to more stressful environmental conditions in European grasslands (Carozzi et al., 2022; Trnka et al., 2021). To date, only a limited number of studies have explored priority effects across a broad spectrum of ecosystems (reviewed in Weidlich et al., 2021), leading to an incomplete understanding of the prevalence and ecological relevance of facilitative priority effects (Stroud et al., 2024). Additionally, the narrow definition of priority effects used in some ecological frameworks, such as Tilman's consumer-resource model (R*) (Tilman, 1982) and modern coexistence theory, which construes them strictly as inhibitory processes arising from positive frequency-dependent population dynamics, may be overly restrictive (Ke & Letten, 2018; Stroud et al., 2024). Future research should therefore place greater emphasis on incorporating facilitative interactions into ecological theory and on conducting studies of priority effects across a broader range of ecosystems.

Moreover, most experiments on priority effects have focused exclusively on pairwise interactions. However, ecological outcomes in natural communities typically emerge from complex, context-dependent interactions among multiple species (Bairey et al., 2016; Gibbs et al., 2022; Mougi, 2024; Mougi & Kondoh, 2012). As such, reliance on two-species designs may limit the generalisability of findings, highlighting the need to incorporate more complex, multispecies approaches in future research (Fukami, 2015; Fukami & Nakajima, 2011; Levine et al., 2017).

Additionally, little is known about the importance of the length of time intervals between arrival events. Most studies on priority effects, particularly greenhouse experiments, investigate unrealistically short time intervals (e.g. Gillhaussen et al., 2014; Kardol et al., 2013b; van Steijn et al., 2025) and, if at all, compare only two or three different arrival times (e.g. Durbecq et al., 2023; Gillhaussen et al., 2014; van Steijn et al., 2025; but see Kardol et al., 2013b). To improve our understanding of their ecological significance, future studies should ideally employ a continuous, temporally staggered design in which late-arriving species are introduced at multiple time points.

The environmental dependence of priority effects adds an additional layer of complexity to community assembly. Since species vary in their sensitivity to environmental conditions (Bohnert et al., 1995; Mareri et al., 2022) and in their phenology (Liu et al., 2021; Sporbert et al., 2022; Zettlemoyer et al., 2019) and, the strength and direction of priority effects are likely modulated by interannual variability, drought events, as observed in my field experiment during the third and fourth years, and site-specific factors (Alonso-Crespo et al., 2025; Cleland & Wolkovich, 2024; Cobon et al., 2017; Schwieger et al., 2025; Wang et al., 2020; Zhao et al., 2023). This context dependence underscores the importance of experimental designs that span environmental gradients (e.g. Grainger et al., 2019; Leopold et al., 2015) and include replication across multiple years (e.g. Alonso-Crespo et al., 2025; Stuble et al., 2017).

Although seasonal priority effects may be especially relevant under climate change scenarios, their long-term persistence remains poorly understood. To date, only a limited number of studies, primarily in temperate grasslands, have examined priority effects over multiple years (but see Collinge & Ray, 2009; Martin & Wilsey, 2012, 2014; Werner et al., 2016; Wohlwend et al., 2019; Young et al., 2017; reviewed in Weidlich et al., 2021), suggesting that such effects can persist for several years under field conditions. However, the duration and strength of these effects were highly variable, leaving a substantial knowledge gap regarding their temporal stability and broader ecological significance.

Future research should overcome these limitations by incorporating more realistic community compositions and environmental conditions, varying species arrival intervals, and integrating trait-based frameworks within long-term field experiments. This approach will better capture the ecological relevance and practical implications of priority effects across diverse ecosystems, while addressing all facets of the trade-off triangle between realism, precision, and generality (Morin, 1998).

Concluding remarks

This thesis provides a comprehensive analysis of priority effects mediated by competition and PSF, and how these interactions are shaped by the origin and phylogenetic relatedness of early- and late-arriving species. As such, it makes a significant contribution to our understanding of the mechanisms underpinning priority effects in European grasslands. I demonstrate that priority effects in this system are predominantly inhibitory, with both competition and PSFs contributing to this outcome. Moreover, the effects of these two mechanisms appear not merely additive but interactive, underscoring the importance of examining them jointly. Another key finding is that inhibitory net priority effects were stronger among closely related species, driven primarily by competitive interactions rather than PSFs. However, as this relationship was evident only when interacting species were at the same life stage, it suggests that phylogenetic relatedness may play a less important role under sequential arrival compared to simultaneous arrival. Consequently, focusing on functional traits related to competitive interactions rather than phylogenetic distance per se may provide a more effective framework for investigating priority effects. Furthermore, I demonstrated that plant origin influences both competition-mediated priority effects and PSFs. Exotic species produced greater biomass, which substantially contributed to their competitive strength. In contrast, native species were comparatively more vulnerable during early life stages, with their competitive strength driven by mechanisms beyond biomass production. These findings provide valuable insights for ecological restoration and invasive species management. By employing a combination of greenhouse and field experiments, I was able to address both ecological realism and experimental precision. Future research should build on this approach by placing greater emphasis on the generalisability of findings, for instance through replication of field experiments across different regions and years. The results of my thesis suggest that integrating trait-based frameworks, dynamic arrival scenarios, and experiments involving multispecies interactions are now necessary to further advance our understanding of the mechanisms and ecological consequences of priority effects.

References

Aarssen, L. W., & Turkington, R. (1985). Biotic specialization between neighbouring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. *Journal of Ecology*, 73(2), 605–614. https:// doi. org/ 10. 2307/ 2260497

Abraham, J. K., Corbin, J. D., & D'Antonio, C. M. (2009). California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. In A. G. Valk (Ed.), *Herbaceous Plant Ecology* (pp. 81–92). Springer Netherlands. http://www.springerlink.com/content/k824p7344505567j/abstract/

Abrams, P. A. (1995). Implications of Dynamically Variable Traits for Identifying, Classifying, and Measuring Direct and Indirect Effects in Ecological Communities. *The American Naturalist*, 146(1), 112–134. https://doi.org/10.1086/285789

Adler, P. B., HilleRisLambers, J., & Levine, J. M. (2007). A niche for neutrality. *Ecology Letters*, 10(2), 95–104. https:// doi. org/ 10. 1111/j. 1461-0248. 2006. 00996. x

Agrawal, A. A., Kotanen, P. M., Mitchell, C. E., Power, A. G., Godsoe, W., & Klironomos, J. (2005). Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology*, 86(11), Article 11. https://doi.org/10.1890/05-0219

Alford, R. A., & Wilbur, H. M. (1985). Priority Effects in Experimental Pond Communities: Competition between *Bufo* and *Rana*. *Ecology*, 66(4), 1097–1105. https://doi.org/10.2307/1939161

Allan, E., Jenkins, T., Fergus, A. J. F., Roscher, C., Fischer, M., Petermann, J., Weisser, W. W., & Schmid, B. (2013). Experimental plant communities develop phylogenetically overdispersed abundance distributions during assembly. *Ecology*, 94(2), 465–477. https://doi.org/10.1890/11-2279.1

Alonso-Crespo, I. M., Weidlich, E. W. A., Temperton, V. M., & Delory, B. M. (2023). Assembly history modulates vertical root distribution in a grassland experiment. *Oikos*, 2023(1), e08886. https://doi.org/10.1111/oik.08886

Alonso-Crespo, I. M., Temperton, V. M., Fichtner, A., Niemeyer, T., Schloter, M., & Delory, B. M. (2025). Exploring Priority and Year Effects on Plant Diversity, Productivity and Vertical Root Distribution: First Insights From a Grassland Field Experiment. *Journal of Vegetation Science*, 36(2), e70026. https://doi.org/10.1111/jvs.70026

Altermann, M., Rinklebe, J., Merbach, I., Körschens, M., Langer, U., & Hofmann, B. (2005). Chernozem—Soil of the Year 2005. *Journal of Plant Nutrition and Soil Science*, 168(6), 725–740. https://doi.org/10.1002/jpln.200521814

Anacker, B. L., Klironomos, J. N., Maherali, H., Reinhart, K. O., & Strauss, S. Y. (2014). Phylogenetic conservatism in plant-soil feedback and its implications for plant abundance. *Ecology Letters*, 17(12), Article 12. https://doi.org/10.1111/ele.12378

Anacker, B. L., & Strauss, S. Y. (2016). Ecological similarity is related to phylogenetic distance between species in a cross-niche field transplant experiment. *Ecology*, 97(7), 1807–1818. https://doi.org/10.1890/15-1285.1

Andel, J. van, & Aronson, J. (2012). Restoration Ecology: The New Frontier. *John Wiley & Sons*.

Andonian, K., Hierro, J. L., Khetsuriani, L., Becerra, P. I., Janoyan, G., Villareal, D., Cavieres, L. A., Fox, L. R., & Callaway, R. M. (2012). Geographic mosaics of plant–soil microbe interactions in a global plant invasion. *Journal of Biogeography*, 39(3), Article 3. https://doi.org/10.1111/j.1365-2699.2011.02629.x

Audino, L. D., Murphy, S. J., Zambaldi, L., Louzada, J., & Comita, L. S. (2017). Drivers of community assembly in tropical forest restoration sites: Role of local environment, landscape, and space. *Ecological Applications*, 27(6), 1731–1745. https://doi.org/10.1002/eap.1562

Auffret, A. G., Meineri, E., Bruun, H. H., Ejrnæs, R., & Graae, B. J. (2010). Ontogenetic niche shifts in three *Vaccinium* species on a sub-alpine mountain side. *Plant Ecology & Diversity*, 3(2), 131–139. https://doi.org/10.1080/17550874.2010.498063

Bairey, E., Kelsic, E. D., & Kishony, R. (2016). High-order species interactions shape ecosystem diversity. *Nature Communications*, 7(1), 12285. https://doi.org/10.1038/ncomms12285

Babai, D., Jánó, B., & Molnár, Z. (2021). In the trap of interacting indirect and direct drivers: The disintegration of extensive, traditional grassland management in Central and Eastern Europe. *Ecology and Society*, 26(4). https://doi.org/10.5751/ES-12679-260406

Bais, H. P., Vepachedu, R., Gilroy, S., Callaway, R. M., & Vivanco, J. M. (2003). Allelopathy and Exotic Plant Invasion: From Molecules and Genes to Species Interactions. *Science*, 301(5638), Article 5638. https://doi.org/10.1126/science.1083245

Bauer, J. T., Mack, K. M. L., & Bever, J. (2015). Plant-soil feedbacks as drivers of succession: Evidence from remnant and restored tallgrass prairies. *Ecosphere*, 6, 1–12. https://doi.org/10.1890/ES14-00480.1

Beckman, N. G., Dybzinski, R., & Tilman, D. (2023). Short-term plant–soil feedback experiment fails to predict outcome of competition observed in long-term field experiment. *Ecology*, 104(2), e3883. https://doi.org/10.1002/ecy.3883

Bell, T., Freckleton, R. P., & Lewis, O. T. (2006). Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters*, 9(5), Article 5. https://doi.org/10.1111/j.1461-0248.2006.00905.x

Bennett, J. A., & Cahill, J. F. (2016). Fungal effects on plant–plant interactions contribute to grassland plant abundances: Evidence from the field. *Journal of Ecology*, 104(3), Article 3. https://doi.org/10.1111/1365-2745.12558

Bennett, J. A., Stotz, G. C., & Cahill Jr., J. F. (2014). Patterns of phylogenetic diversity are linked to invasion impacts, not invasion resistance, in a native grassland. *Journal of Vegetation Science*, 25(6), 1315–1326. https://doi.org/10.1111/jvs.12199

Berg, G., & Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology*, 68(1), 1–13. https://doi.org/10.1111/j.1574-6941.2009.00654.x

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bever, J. D. (1994). Feeback between Plants and Their Soil Communities in an Old Field Community. *Ecology*, 75(7), Article 7. https://doi.org/10.2307/1941601

Bever, J. D., Westover, K. M., & Antonovics, J. (1997). Incorporating the Soil Community into Plant Population Dynamics: The Utility of the Feedback Approach. *Journal of Ecology*, 85(5), Article 5. https://doi.org/10.2307/2960528

Bever, J. D. (2003). Soil community feedback and the coexistence of competitors: Conceptual frameworks and empirical tests. *New Phytologist*, 157(3), Article 3. https://doi.org/10.1046/j.1469-8137.2003.00714.x

Bever, J. D., Dickie, I. A., Facelli, E., Facelli, J. M., Klironomos, J., Moora, M., Rillig, M. C., Stock, W. D., Tibbett, M., & Zobel, M. (2010). Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution*, 25(8), 468–478. https://doi.org/10.1016/j.tree.2010.05.004

Bever, J. D., Mangan, S. A., & Alexander, H. M. (2015). Maintenance of Plant Species Diversity by Pathogens. *Annual Review of Ecology, Evolution, and Systematics*, 46(1), 305–325. https://doi.org/10.1146/annurev-ecolsys-112414-054306

Bezemer, T. M., Lawson, C. S., Hedlund, K., Edwards, A. R., Brook, A. J., Igual, J. M., Mortimer, S. R., & van Der Putten, W. H. (2006). Plant species and functional group effects on abiotic and microbial soil properties and plant–soil feedback responses in two grasslands. *Journal of Ecology*, 94(5), 893–904. https://doi.org/10.1111/j.1365-2745.2006.01158.x

Blakemore, L. C. (1987). Methods for chemical analysis of soils. *N.Z.Soil Bureau Scientific Report*, 80, 71–76.

Blonder, B. W., Lim, M. H., & Godoy, O. (2024). Predicting and Prioritising Community Assembly: Learning Outcomes via Experiments. *Ecology Letters*, 27(10), e14535. https://doi.org/10.1111/ele.14535

Blossey, B., & Notzold, R. (1995). Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants: A Hypothesis. *Journal of Ecology*, 83(5), Article 5. https://doi.org/10.2307/2261425

Blumenthal, D. M., Jordan, N. R., & Svenson, E. L. (2005). Effects of prairie restoration on weed invasions. *Agriculture, Ecosystems & Environment*, 107(2), 221–230. https://doi.org/10.1016/j.agee.2004.11.008

Bohnert, H. J., Nelson, D. E., & Jensen, R. G. (1995). Adaptations to Environmental Stresses. *The Plant Cell*, 7(7), 1099–1111. https://doi.org/10.1105/tpc.7.7.1099

Bonser, S. P., & Reader, R. J. (1995). Plant Competition and Herbivory in Relation to Vegetation Biomass. *Ecology*, 76(7), 2176–2183. https://doi.org/10.2307/1941691

Bossdorf, O., Auge, H., Lafuma, L., Rogers, W. E., Siemann, E., & Prati, D. (2005). Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, 144(1), Article 1. https://doi.org/10.1007/s00442-005-0070-z

Bossdorf, O. (2013). Enemy release and evolution of increased competitive ability: At last, a smoking gun! *New Phytologist*, 198(3), 638–640. https://doi.org/10.1111/nph.12265

Brandt, A. J., Seabloom, E. W., & Hosseini, P. R. (2009). Phylogeny and provenance affect plant–soil feedbacks in invaded California grasslands. *Ecology*, 90(4), 1063–1072. https://doi.org/10.1890/08-0054.1

Brian, J. I., & Catford, J. A. (2023). A mechanistic framework of enemy release. *Ecology Letters*, 26(12), 2147–2166. https://doi.org/10.1111/ele.14329

Broadbent, A. A. D., Stevens, C. J., Ostle, N. J., & Orwin, K. H. (2018). Biogeographic differences in soil biota promote invasive grass response to nutrient addition relative to co-occurring species despite lack of belowground enemy release. *Oecologia*, 186(3), 611–620. https://doi.org/10.1007/s00442-018-4081-y

Brown, W. L., & Wilson, E. O. (1956). Character displacement. *Systematic Zoology*, 5(2), 49–64. https:// doi. org/ 10. 2307/ 2411924

Brown, V. K., & Gange, A. C. (1990). Insect Herbivory Insect Below Ground. In M. Begon, A. H. Fitter, & A. Macfadyen (Eds.), *Advances in Ecological Research* (Vol. 20, pp. 1–58). Academic Press. https://doi.org/10.1016/S0065-2504(08)60052-5

Bundesamt für Naturschutz (ed.) (2023) *Floraweb*. https://www.floraweb.de. 07.08.2023.

Bünemann, E. K., Schwenke, G. D., & Zwieten, L. V. (2006). Impact of agricultural inputs on soil organisms - A review. *Soil Research*, 44(4), Article 4. https://doi.org/10.1071/SR05125

Burdon, J. J., & Chilvers, G. A. (1982). Host Density as a Factor in Plant Disease Ecology. *Annual Review of Phytopathology*, 20(Volume 20,), 143–166. https://doi.org/10.1146/annurev.-py.20.090182.001043

Burns, J. H., & Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences*, 108(13), 5302–5307. https://doi.org/10.1073/pnas.1013003108

Byun, C. (2023). Role of priority effects in invasive plant species management: Early arrival of native seeds guarantees the containment of invasion by Giant ragweed. *Ecology and Evolution*, 13(3), e9940. https://doi.org/10.1002/ece3.9940

Cadotte, M. W. (2013). Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 110(22), 8996–9000. https:// doi. org/ 10. 1073/ pnas. 13016 85110

Cadotte, M. W., Davies, T. J., & Peres-Neto, P. R. (2017). Why phylogenies do not always predict ecological differences. *Ecological Monographs*, 87(4), 535–551. https:// doi. org/ 10. 1002/ ecm. 1267

Cahill, J. F., Kembel, S. W., Lamb, E. G., & Keddy, P. A. (2008). Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology, Evolution and Systematics*, 10(1), 41–50. https:// doi. org/ 10. 1016/j. ppees. 2007. 10. 001

Callaway, R. M., & Aschehoug, E. T. (2000). Invasive Plants Versus Their New and Old Neighbors: A Mechanism for Exotic Invasion. *Science*, 290(5491), Article 5491. https://doi.org/10.1126/science.290.5491.521

Callaway, R. M., & Ridenour, W. M. (2004). Novel weapons: Invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, 2(8), Article 8. https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

Callaway, R. M., Thelen, G. C., Rodriguez, A., & Holben, W. E. (2004). Soil biota and exotic plant invasion. *Nature*, 427(6976), Article 6976. https://doi.org/10.1038/nature02322

Callaway, R. M., Lucero, J. E., Hierro, J. L., & Lortie, C. J. (2022). The EICA is dead? Long live the EICA! *Ecology Letters*, 25(10), 2289–2302. https://doi.org/10.1111/ele.14088

Callaway, R., Pal, R., Schaar, A., Hooper, D., Auge, H., Hensen, I., Kožić, K., Lekberg, Y., Nagy, D., Selke, J., Thoma, A., Träger, S., Rosche, C. (2025). Exotic invasive plant species increase primary productivity, but not in their native ranges. *Ecology Letters*. Manuscript accepted

Carozzi, M., Martin, R., Klumpp, K., & Massad, R. (2022). Effects of climate change in European croplands and grasslands: Productivity, greenhouse gas balance and soil carbon storage. *Biogeosciences*. https://doi.org/10.5194/bg-19-3021-2022

Carter, D. L., & Blair, J. M. (2012). High richness and dense seeding enhance grassland restoration establishment but have little effect on drought response. *Ecological Applications*, 22(4), 1308–1319. https://doi.org/10.1890/11-1970.1

Case, T. J., & Taper, M. L. (2000). Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *The American Naturalist*, 155, 583–605. https:// doi. org/ 10. 1086/303351

Casper, C. W., DuPre, M. E., McLeod, M. L., Bunn, R. A., Maron, J. L., Ramsey, P. W., & Lekberg, Y. (2024). Negative plant–soil feedback influences a dominant seeded species, Western yarrow (*Achillea millefolium*), in grassland restoration. *Restoration Ecology*, 32(8), e14271. https://doi.org/10.1111/rec.14271

Castillo, J. P., Verdú, M., & Valiente-Banuet, A. (2010). Neighborhood phylodiversity affects plant performance. *Ecology*, 91(12), 3656–3663. https://doi.org/10.1890/10-0720.1

Castro, J., Zamora, R., Hódar, J. A., Gómez, J. M., & Gómez-Aparicio, L. (2004). Benefits of Using Shrubs as Nurse Plants for Reforestation in Mediterranean Mountains: A 4-Year Study. *Restoration Ecology*, 12(3), 352–358. https://doi.org/10.1111/j.1061-2971.2004.0316.x

Castro, S. A., Escobedo, V. M., Aranda, J., & Carvallo, G. O. (2014). Evaluating Darwin's naturalization hypothesis in experimental plant assemblages: Phylogenetic relationships do not determine colonization success. *PLOS ONE*, 9(8), e105535. https:// doi. org/ 10. 1371/journ al. pone. 0105535

Catano, C. P., Groves, A. M., & Brudvig, L. A. (2023). Community assembly history alters relationships between biodiversity and ecosystem functions during restoration. *Ecology*, 104(2), e3910. https://doi.org/10.1002/ecy.3910

Cavender-Bares, J., Keen, A., & Miles, B. (2006). Phylogenetic Structure of Floridian Plant Communities Depends on Taxonomic and Spatial Scale. *Ecology*, 87(sp7), S109–S122. https://doi.org/10.1890/0012-9658(2006)87[109:PSOFPC]2.0.CO;2

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12(7), 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Chanway, C. P., Holl, F. B., & Turkington, R. (1988). Genotypic coadaptation in plant growth promotion of forage species by *Bacillus polymyxa*. *Plant and Soil*, 106(2), 281–284. https:// doi. org/ 10. 1007/ BF023 71225

Chase, J. M., & Leibold, M. A. (2003). Ecological niches: Linking classical and contemporary approaches. *University of Chicago Press*. https:// doi. org/ 10. 7208/ chica go/ 97802 26101 811. 001. 0001

Chase, J. M. (2003a). Community assembly: When should history matter? *Oecologia*, 136(4), 489–498. https:// doi. org/ 10. 1007/ s00442-003-1311-7

Chase, J. M. (2003b). Experimental evidence for alternative stable equilibria in a benthic pond food web. *Ecology Letters*, 6(8), 733–741. https:// doi. org/ 10. 1046/j. 1461-0248.2003. 00482. x

Chase, J. M. (2010). Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science*, 328(5984), Article 5984. https://doi.org/10.1126/science.1187820

Checinska Sielaff, A., Upton, R. N., Hofmockel, K. S., Xu, X., Polley, H. W., & Wilsey, B. J. (2018). Microbial community structure and functions differ between native and novel (exotic-dominated) grassland ecosystems in an 8-year experiment. *Plant and Soil*, 432(1), 359–372. https://doi.org/10.1007/s11104-018-3796-1

Cheng, C., Gundale, M., Li, B., & Wu, J. (2024). Deciphering the drivers of plant-soil feedbacks and their context-dependence: A meta-analysis. *Plant and Soil*. https://doi.org/10.1007/s11104-024-06922-1

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.

Cleland, E. E., Esch, E., & McKinney, J. (2015). Priority effects vary with species identity and origin in an experiment varying the timing of seed arrival. *Oikos*, 124(1), Article 1 https://doi.org/10.1111/oik.01433

Cleland, E. E., & Wolkovich, E. M. (2024). Effects of Phenology on Plant Community Assembly and Structure. *Annual Review of Ecology, Evolution, and Systematics*, 55(Volume 55, 2024), 471–492. https://doi.org/10.1146/annurev-ecolsys-102722-011653

Cobon, D., Baethgen, W., Landman, W., Williams, A., Archer, E., Johnston, P., Malherbe, J., Maluleke, P., Kgakatsi, I., Davis, P., Hatfield, J., & Sivakumar, M. (2017). Agroclimatology in Grasslands. https://doi.org/10.2134/agronmonogr60.2016.0013

Collinge, S. K., & Ray, C. (2009). Transient patterns in the assembly of vernal pool plant communities. *Ecology*, 90(12), Article 12. https://doi.org/10.1890/08-2155.1

Connell, J. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations*.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, 111(982), 1119–1144. https:// doi.org/ 10. 1086/ 283241

Corbin, J. D., & D'Antonio, C. M. (2004). Competition Between Native Perennial and Exotic Annual Grasses: Implications for an Historical Invasion. *Ecology*, 85(5), Article 5. https://doi.org/10.1890/02-0744

Cortois, R., Schröder-Georgi, T., Weigelt, A., van der Putten, W. H., & De Deyn, G. B. (2016). Plant–soil feedbacks: Role of plant functional group and plant traits. *Journal of Ecology*, 104(6), 1608–1617. https://doi.org/10.1111/1365-2745.12643

Cox, R. D., & Allen, E. B. (2008). Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. *Journal of Applied Ecology*, 45(2), 495–504. https://doi.org/10.1111/j.1365-2664.2007.01437.x

Crawford, K. M., Bauer, J. T., Comita, L. S., Eppinga, M. B., Johnson, D. J., Mangan, S. A., Queenborough, S. A., Strand, A. E., Suding, K. N., Umbanhowar, J., & Bever, J. D.

(2019). When and where plant-soil feedback may promote plant coexistence: A meta-analysis. *Ecology Letters*, 22(8), 1274–1284. https://doi.org/10.1111/ele.13278

Csákvári, E., Sáradi, N., Berki, B., Csecserits, A., Csonka, A. C., Reis, B. P., Török, K., Valkó, O., Vörös, M., & Halassy, M. (2023). Native species can reduce the establishment of invasive alien species if sown in high density and using competitive species. *Restoration Ecology*, 31(5), e13901. https://doi.org/10.1111/rec.13901

D'Antonio, C., & Meyerson, L. A. (2002). Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis. *Restoration Ecology*, 10(4), 703–713. https://doi.org/10.1046/j.1526-100X.2002.01051.x

Daisog, H., Sbrana, C., Cristani, C., Moonen, A.-C., Giovannetti, M., & Bàrberi, P. (2012). Arbuscular mycorrhizal fungi shift competitive relationships among crop and weed species. *Plant and Soil*, 353(1), 395–408. https://doi.org/10.1007/s11104-011-1040-3

Darwin, C. (1859). On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life. *John Murray*, London.

Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, 14(4), Article 4. https://doi.org/10.1111/j.1461-0248.2011.01596.x

Davies, J., Meiri, S., Barraclough, T. G., & Gittleman, J. L. (2007). Species co-existence and character divergence across carnivores. *Ecology Letters*, 10(2), 146–152. https:// doi. org/ 10. 1111/j. 1461-0248.2006. 01005. x

Davis, M. A., Thompson, K., & Philip Grime, J. (2005). Invasibility: The local mechanism driving community assembly and species diversity. *Ecography*, 28(5), 696–704. https://doi.org/10.1111/j.2005.0906-7590.04205.x

Dawson, W., Fischer, M., & van Kleunen, M. (2011). The maximum relative growth rate of common UK plant species is positively associated with their global invasiveness. *Global Ecology and Biogeography*, 20(2), 299–306. https://doi.org/10.1111/j.1466-8238.2010.00599.x

Dawson, W., & Schrama, M. (2016). Identifying the role of soil microbes in plant invasions. *Journal of Ecology,* 104(5), Article 5. https://doi.org/10.1111/1365-2745.12619

Dayan, T., & Simberloff, D. (2005). Ecological and community-wide character displacement: The next generation. *Ecology Letters*, 8(8), 875–894. https:// doi. org/ 10. 1111/j. 1461-0248.2005. 00791. x

De Long, J. R., Heinen, R., Steinauer, K., Hannula, S. E., Huberty, M., Jongen, R., Vandenbrande, S., Wang, M., Zhu, F., & Bezemer, T. M. (2019a). Taking plant–soil feedbacks to the field in a temperate grassland. *Basic and Applied Ecology*, 40, 30–42. https://doi.org/10.1016/j.baae.2019.08.001

De Long, J. R., Fry, E. L., Veen, G. F., & Kardol, P. (2019b). Why are plant–soil feedbacks so unpredictable, and what to do about it? *Functional Ecology*, 33(1), 118–128. https://doi.org/10.1111/1365-2435.13232

De Long, J. R., Heinen, R., Heinze, J., Morriën, E., Png, G. K., Sapsford, S. J., Teste, F. P., & Fry, E. L. (2023). Plant-soil feedback: Incorporating untested influential drivers and reconciling terminology. *Plant and Soil*, 485(1), 7–43. https://doi.org/10.1007/s11104-023-05908-9

Debray, R., Herbert, R. A., Jaffe, A. L., Crits-Christoph, A., Power, M. E., & Koskella, B. (2022). Priority effects in microbiome assembly. *Nature Reviews Microbiology*, 20(2), 109–121. https:// doi. org/ 10. 1038/s4157 9-021-00604-w

Decaëns, T. (2010). Macroecological patterns in soil communities. *Global Ecology and Biogeography*, 19(3), 287–302. https://doi.org/10.1111/j.1466-8238.2009.00517.x

Delory, B. M., Little, C. J., Marton, H., Halliday, F. W., Stiver, I., Sarneel, J. M., van Steijn, T. L.H., Barnes, E. M., Grainger, T. N., de Meester, L., Dieskau, J., Kardol, P., Knight, T. M., Ladouceur, E., Ojima, M. N., Roscher, C., Stroud, J. T., Temperton, V.M., Werner, C. M., Fukami, T. Quantifying priority effects (manuscript in preparation).

Delory, B. M., Weidlich, E. W. A., Kunz, M., Neitzel, J., & Temperton, V. M. (2019a). The exotic species *Senecio inaequidens* pays the price for arriving late in temperate European grassland communities. *Oecologia*, 191(3), 657–671. https:// doi. org/ 10. 1007/ s0044 2-019-04521-x

Delory, B. M., Weidlich, E. W. A., Gillhaussen, P. von, & Temperton, V. M. (2019b). When history matters: The overlooked role of priority effects in grassland overyielding. *Functional Ecology*, 0(0), Article 0. https://doi.org/10.1111/1365-2435.13455

Delory, B. M., Schempp, H., Spachmann, S. M., Störzer, L., van Dam, N. M., Temperton, V. M., & Weinhold, A. (2021). Soil chemical legacies trigger species-specific and context-dependent root responses in later arriving plants. *Plant, Cell & Environment*, 44(4), 1215–1230. https:// doi. org/ 10. 1111/ pce. 13999

Diamond, J. M. (1975). Assembly of species communities. *Ecology and Evolution of Communities*, 342–444.

Dickson, T. L., Hopwood, J. L., & Wilsey, B. J. (2012). Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biological Invasions*, 14(12), Article 12. https://doi.org/10.1007/s10530-012-0257-2

Dieskau, J., Bruelheide, H., Gutknecht, J., & Erfmeier, A. (2020). Biogeographic differences in plant–soil biota relationships contribute to the exotic range expansion of *Verbascum thapsus*. *Ecology and Evolution*, 10(23), 13057–13070. https://doi.org/10.1002/ece3.6894

Dieskau, J., Hensen, I., Eisenhauer, N., Gaberle, I., Durka, W., Lachmuth, S., & Auge, H. (2024a). Phylogenetic relationships and plant life stage but not biogeographic history mediate priority effects of European grassland plants. *Journal of Ecology*, 112(9), 2007–2017. https://doi.org/10.1111/1365-2745.14373

Dieskau, J., Hensen, I., Eisenhauer, N., Gaberle, I., Durka, W., Lachmuth, S., & Auge, H. (2024b). 'Phylogenetic relationships and plant life stage but not biogeographical history mediate priority effects of European grassland plants' (version 1.0) [dataset]. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. https://doi. org/ 10. 25829/ idiv. 3548-bz7p93

Dieskau, J., Hensen, I., Eisenhauer, N., Lachmuth, S., & Auge, H. (2025a). Plant-soil feedback in European grasslands is phylogenetically independent but affected by plant species origin. *Journal of Plant Ecology*, rtaf021. https://doi.org/10.1093/jpe/rtaf021

Dieskau, J., Hensen, I., Eisenhauer, N., Gaberle, I., Durka, W., Lachmuth, S., & Auge, H. (2025b). Phylogeny and Plant Origin in Plant-Soil Feedbacks (Version 1.0). German

Centre for Integrative Biodiversity Research. https://doi. org/10.25829/idiv.3583-p235q9

Dieskau, J., Hensen, I., Eisenhauer, N., & Auge, H. Competition- and soil fungi-mediated priority effects differ between native and exotic European grassland plants. *Journal of Ecology*, (manuscript under review)

Donohue, K., Hammond Pyle, E., Messiqua, D., Shane Heschel, M., & Schmitt, J. (2001). Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. *Evolution*, 55(4), 692–702. https:// doi. org/10. 1111/j. 0014-3820.2001. tb008 05. x

Dostál, P. (2021). The temporal development of plant-soil feedback is contingent on competition and nutrient availability contexts. *Oecologia*, 196(1), 185–194. https://doi.org/10.1007/s00442-021-04919-6

Drake, J. A., Staelens, P., & Kridler, C. (2013). Fifty years of invasion ecology: A concerto in seven parts. *Biological Invasions*, 15(10), 2359–2361. https://doi.org/10.1007/s10530-013-0450-y

Drenovsky, R., & James, J. (2007). A Basis for Relative Growth Rate Differences Between Native and Invasive Forb Seedlings. *Rangeland Ecology and Management*. https://collected.jcu.edu/biol-facpub/32

Drenovsky, R. E., Grewell, B. J., D'Antonio, C. M., Funk, J. L., James, J. J., Molinari, N., Parker, I. M., & Richards, C. L. (2012). A functional trait perspective on plant invasion. *Annals of Botany*, 110(1), Article 1. https://doi.org/10.1093/aob/mcs100

Dudenhöffer, J.-H., Ebeling, A., Klein, A. M., & Wagg, C. (2018). Beyond biomass: Soil feedbacks are transient over plant life stages and alter fitness. *Journal of Ecology*, 106(1), 230–241. https:// doi. org/ 10.1111/ 1365-2745.12870

Duell, E., Zaiger, K., Bever, J., & Wilson, G. (2019). Climate Affects Plant-Soil Feedback of Native and Invasive Grasses: Negative Feedbacks in Stable but Not in Variable Environments. *Frontiers in Ecology and Evolution*. https://doi.org/10.3389/fevo.2019.00419

Dunck, B., Rodrigues, L., Lima-Fernandes, E., Cássio, F., Pascoal, C., & Cottenie, K. (2021). Priority effects of stream eutrophication and assembly history on beta diversity across aquatic consumers, decomposers and producers. *Science of the Total Environment*, 797, 149106. https:// doi. org/ 10. 1016/j. scito tenv. 2021. 149106

Dunn, A. M., Torchin, M. E., Hatcher, M. J., Kotanen, P. M., Blumenthal, D. M., Byers, J. E., Coon, C. A. C., Frankel, V. M., Holt, R. D., Hufbauer, R. A., Kanarek, A. R., Schierenbeck, K. A., Wolfe, L. M., & Perkins, S. E. (2012). Indirect effects of parasites in invasions. *Functional Ecology*, 26(6), 1262–1274. https://doi.org/10.1111/j.1365-2435.2012.02041.x

Durbecq, A., Bischoff, A., Buisson, É., Corcket, E., & Jaunatre, R. (2023). Using priority effects for grassland restoration: Sequential sowing can promote subordinate species. *Applied Vegetation Science*. https://doi.org/10.1111/avsc.12748

Durka, W., & Michalski, S. G. (2012). Daphne: A dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, 93(10), 2297–2297. https://doi.org/10.1890/12-0743.1

Ehrenfeld, J. G., Ravit, B., & Elgersma, K. (2005). Feedback in the Plant-Soil System. *Annual Review of Environment and Resources*, 30(1), Article 1. https://doi.org/10.1146/annurev.energy.30.050504.144212

Eisenhauer, N., Beßler, H., Engels, C., Gleixner, G., Habekost, M., Milcu, A., Partsch, S., Sabais, A. C. W., Scherber, C., Steinbeiss, S., Weigelt, A., Weisser, W. W., & Scheu, S. (2010). Plant diversity effects on soil microorganisms support the singular hypothesis. *Ecology*, 91(2), 485–496. https://doi.org/10.1890/08-2338.1

Eisenhauer, N., Dobies, T., Cesarz, S., Hobbie, S. E., Meyer, R. J., Worm, K., & Reich, P. B. (2013). Plant diversity effects on soil food webs are stronger than those of elevated CO2 and N deposition in a long-term grassland experiment. *Proceedings of the National Academy of Sciences*, 110(17), 6889–6894. https://doi.org/10.1073/pnas.1217382110

Ejrnæs, R., Bruun, H. H., & Graae, B. J. (2006). Community Assembly in Experimental Grasslands: Suitable Environment or Timely Arrival? *Ecology*, 87(5), 1225–1233. https://doi.org/10.1890/0012-9658(2006)87[1225:CAIEGS]2.0.CO;2

Ellison, A. M., & Rabinowitz, D. (1989). Effects of Plant Morphology and Emergence Time on Size Hierarchy Formation in Experimental Populations of Two Varieties of Cultivated Peas (*Pisum sativum*). *American Journal of Botany*, 76(3), 427–436. https://doi.org/10.1002/j.1537-2197.1989.tb11331.x

Elton, C. S. (1946). Competition and the Structure of Ecological Communities. *Journal of Animal Ecology*, 15(1), 54–68. https://doi.org/10.2307/1625

Elton, C. S. (2000). The Ecology of Invasions by Animals and Plants. *University of Chicago Press*.

Eppinga, M. B., Rietkerk, M., Dekker, S. C., De Ruiter, P. C., van der Putten, W. H., & van der Putten, W. H. (2006). Accumulation of local pathogens: A new hypothesis to explain exotic plant invasions. *Oikos*, 114(1), Article 1. https://doi.org/10.1111/j.2006.0030-1299.14625.x

Ernst, A. R., Barak, R. S., Hipp, A. L., Kramer, A. T., Marx, H. E., & Larkin, D. J. (2022). The invasion paradox dissolves when using phylogenetic and temporal perspectives. *Journal of Ecology*, 110(2), 443–456. https://doi.org/10.1111/1365-2745.13812

Ernst, A. R., Barak, R. S., Glasenhardt, M.-C., Kramer, A. T., Larkin, D. J., Marx, H. E., Kamakura, R. P., & Hipp, A. L. (2023). Dominant species establishment may influence invasion resistance more than phylogenetic or functional diversity. *Journal of Applied Ecology*, 60(12), 2652–2664. https://doi.org/10.1111/1365-2664.14534

Eviner, V. T., & Hawkes, C. V. (2008). Embracing Variability in the Application of Plant–Soil Interactions to the Restoration of Communities and Ecosystems. *Restoration Ecology*, 16(4), 713–729. https://doi.org/10.1111/j.1526-100X.2008.00482.x

Facelli, E., & Facelli, J. M. (2002). Soil phosphorus heterogeneity and mycorrhizal symbiosis regulate plant intra-specific competition and size distribution. *Oecologia*, 133(1), 54–61. https://doi.org/10.1007/s00442-002-1022-5

Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences*, 100(15), 8916–8920. https://doi.org/10.1073/pnas.1033107100

Felker-Quinn, E., Schweitzer, J. A., & Bailey, J. K. (2013). Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). *Ecology and Evolution*, 3(3), Article 3. https://doi.org/10.1002/ece3.488

Felsenstein, J. (1985). Phylogenies and the Comparative Method. *The American Naturalist*, 125(1), 1–15. https://doi.org/10.1086/284325

Feng, Y., & van Kleunen, M. (2016). Phylogenetic and functional mechanisms of direct and indirect interactions among alien and native plants. *Journal of Ecology*, 104(4), 1136–1148. https://doi.org/10.1111/1365-2745.12577

Ferenc, V., Merkert, C., Zilles, F., & Sheppard, C. S. (2021). Native and alien species suffer from late arrival, while negative effects of multiple alien species on natives vary. *Oecologia*, 197(1), 271–281. https://doi.org/10.1007/s00442-021-05017-3

Fischer, D. G., Chapman, S. K., Classen, A. T., Gehring, C. A., Grady, K. C., Schweitzer, J. A., & Whitham, T. G. (2014). Plant genetic effects on soils under climate change. *Plant and Soil*, 379(1), 1–19. https://doi.org/10.1007/s11104-013-1972-x

Fitzpatrick, C. R., Gehant, L., Kotanen, P. M., & Johnson, M. T. J. (2017). Phylogenetic relatedness, phenotypic similarity and plant–soil feedbacks. *Journal of Ecology*, 105(3), 786–800. https:// doi. org/ 10.1111/ 1365-2745.12709

Fragata, I., Costa-Pereira, R., Kozak, M., Majer, A., Godoy, O., & Magalhães, S. (2022). Specific sequence of arrival promotes coexistence via spatial niche pre-emption by the weak competitor. *Ecology Letters*, 25(7), 1629–1639. https://doi.org/10.1111/ele.14021

Freckleton, R. P., & Watkinson, A. R. (2001). Asymmetric competition between plant species. *Functional Ecology*, 15(5), 615–623. https://doi.org/10.1046/j.0269-8463.2001.00558.x

Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., Stohlgren, T. J., Tilman, D., & Holle, B. V. (2007). The Invasion Paradox: Reconciling Pattern and Process in Species Invasions. *Ecology*, 88(1), 3–17. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Fritschie, K. J., Cardinale, B. J., Alexandrou, M. A., & Oakley, T. H. (2014). Evolutionary history and the strength of species interactions: Testing the phylogenetic limiting similarity hypothesis. *Ecology*, 95(5), 1407–1417. https:// doi. org/ 10. 1890/ 13-0986.1

Fukami, T., Dickie, I. A., Paula Wilkie, J., Paulus, B. C., Park, D., Roberts, A., Buchanan, P. K., & Allen, R. B. (2010). Assembly history dictates ecosystem functioning: Evidence from wood decomposer communities. *Ecology Letters*, 13(6), 675–684. https:// doi. org/ 10. 1111/j.1461-0248.2010. 01465. x

Fukami, T., & Nakajima, M. (2011). Community assembly: Alternative stable states or alternative transient states? *Ecology Letters*, 14(10), 973–984. https://doi.org/10.1111/j.1461-0248.2011.01663.x

Fukami, T. (2015). Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46(1), 1–23. https://doi. org/ 10. 1146/ annur ev-ecolsys-110411-160340

Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, 446(7139), 1079–1081. https://doi.org/10.1038/nature05719

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology & Evolution*, 23(12), 695–703. https://doi.org/10.1016/j.tree.2008.07.013

Funk, J. L., & McDaniel, S. (2010). Altering Light Availability to Restore Invaded Forest: The Predictive Role of Plant Traits. *Restoration Ecology*, 18(6), 865–872. https://doi.org/10.1111/j.1526-100X.2008.00515.x

Geisen, S., ten Hooven, F. C., Kostenko, O., Snoek, L. B., & van der Putten, W. H. (2021). Fungal root endophytes influence plants in a species-specific manner that depends on plant's growth stage. *Journal of Ecology*, 109(4), 1618–1632. https://doi.org/10.1111/1365-2745.13584

Gensollen, T., Iyer, S. S., Kasper, D. L., & Blumberg, R. S. (2016). How colonization by microbiota in early life shapes the immune system. *Science*, 352(6285), 539–544. https://doi.org/10.1126/science.aad9378

Germain, R. M., Weir, J. T., & Gilbert, B. (2016). Species coexistence: Macroevolutionary relationships and the contingency of historical interactions. *Proceedings of the Royal Society* B, 283(1827), 20160047. https:// doi. org/ 10. 1098/ rspb. 2016. 0047

Gibbs, T., Levin, S. A., & Levine, J. M. (2022). Coexistence in diverse communities with higher-order interactions. *Proceedings of the National Academy of Sciences*, 119(43), e2205063119. https://doi.org/10.1073/pnas.2205063119

Gilbert, G. S., & Webb, C. O. (2007). Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences*, 104(12), 4979–4983. https://doi.org/10.1073/pnas.0607968104

Gille, C. E., Finnegan, P. M., Hayes, P. E., Ranathunge, K., Burgess, T. I., de Tombeur, F., Migliorini, D., Dallongeville, P., Glauser, G., & Lambers, H. (2024). Facilitative and competitive interactions between mycorrhizal and nonmycorrhizal plants in an extremely phosphorus-impoverished environment: Role of ectomycorrhizal fungi and native oomycete pathogens in shaping species coexistence. *New Phytologist*, 242(4), 1630–1644. https://doi.org/10.1111/nph.19489

Gillhaussen, P. von, Rascher, U., Jablonowski, N. D., Plückers, C., Beierkuhnlein, C., & Temperton, V. M. (2014). Priority Effects of Time of Arrival of Plant Functional Groups Override Sowing Interval or Density Effects: A Grassland Experiment. *PLOS ONE*, 9(1), e86906. https://doi.org/10.1371/journal.pone.0086906

Gioria, M., Pyšek, P., & Osborne, B. A. (2018). Timing is everything: Does early and late germination favor invasions by herbaceous alien plants? *Journal of Plant Ecology*, 11(1), 4–16. https://doi.org/10.1093/jpe/rtw105

Gleason, H. A. (1927). Further Views on the Succession-Concept. *Ecology*, 8(3), 299–326. https://doi.org/10.2307/1929332

Godoy, O., Kraft, N. J. B., & Levine, J. M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, 17(7), Article 7. https://doi.org/10.1111/ele.12289

Godoy, O., Soler-Toscano, F., Portillo, J. R., & Langa, J. A. (2024). The assembly and dynamics of ecological communities in an ever-changing world. *Ecological Monographs*, 94(4), e1633. https://doi.org/10.1002/ecm.1633

Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. (2012). Ecological assembly rules in plant communities—Approaches, patterns and prospects. *Biological Reviews*, 87(1), 111–127. https:// doi. org/ 10. 1111/j.1469-185X.2011. 00187. x

Grainger, T. N., Letten, A. D., Gilbert, B., & Fukami, T. (2019). Applying modern coexistence theory to priority effects. *Proceedings of the National Academy of Sciences of the United States of America*, 116(13), 6205–6210. https:// doi. org/ 10. 1073/ pnas. 18031 22116

Grime, J. P. (2006). Plant Strategies, Vegetation Processes, and Ecosystem Properties. *John Wiley & Sons.*

Grman, E., & Suding, K. N. (2010). Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology*, 18(5), 664–670. https:// doi. org/10. 1111/j. 1526-100X.2008. 00497. x

Grman, E., Bassett, T., & Brudvig, L. A. (2013). Confronting contingency in restoration: management and site history determine outcomes of assembling prairies, but site characteristics and landscape context have little effect. *Journal of Applied Ecology*, 50(5), 1234–1243. https://doi.org/10.1111/1365-2664.12135

Grotkopp, E., & Rejmanek, M. (2007). High seedling relative growth rate and specific leaf area are traits of invasive species: Phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany*, 94, 526–532. https://doi.org/10.3732/ajb.94.4.526

Gundale, M. J., Kardol, P., Nilsson, M.-C., Nilsson, U., Lucas, R. W., & Wardle, D. A. (2014). Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. *New Phytologist*, 202(2), Article 2. https://doi.org/10.1111/nph.12699

Gundale, M. J., & Kardol, P. (2021). Multi-dimensionality as a path forward in plant-soil feedback research. *Journal of Ecology*, 109(10), 3446–3465. https://doi.org/10.1111/1365-2745.13679

Halbritter, A. H., Carroll, G. C., Güsewell, S., & Roy, B. A. (2012). Testing assumptions of the enemy release hypothesis: Generalist versus specialist enemies of the grass *Brachypodium sylvaticum*. *Mycologia*, 104(1), 34–44. https://doi.org/10.3852/11-071

Handley, R. J., Steinger, T., Treier, U. A., & Müller-Schärer, H. (2008). Testing the Evolution of Increased Competitive Ability (EICA) Hypothesis in a Novel Framework. *Ecology*, 89(2), 407–417. https://doi.org/10.1890/07-0160.1

Harmon, G. D., & Stamp, N. E. (2002). Relative Size Early in Population Development Determines Reproductive Status of Individual *Erodium cicutarium* Plants. *The American Midland Naturalist*, 147(1), 32–43. https://doi.org/10.1674/0003-0031(2002)147[0032:RSEIPD]- 2.0.CO;2

Hart, S. P., Turcotte, M. M., & Levine, J. M. (2019). Effects of rapid evolution on species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 116(6), 2112–2117. https://doi. org/ 10. 1073/ pnas. 18162 98116

Harzé, M., Monty, A., Boisson, S., Pitz, C., Hermann, J., Kollmann, J., & Mahy, G. (2018). Towards a population approach for evaluating grassland restoration—A systematic review. *Restoration Ecology,* 26(2), 227–234. https://doi.org/10.1111/rec.12663

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 36(1), 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80(4), 1150–1156. https:// doi. org/ 10. 1890/ 0012-9658(1999) 080[1150: TMAORR]2.0. CO; 2

Heinen, R., Hannula, S. E., de Long, J. R., Huberty, M., Jongen, R., Kielak, A., Steinauer, K., Zhu, F., & Bezemer, T. M. (2020). Plant community composition steers grassland vegetation via soil legacy effects. *Ecology Letters*, 23(6), 973–982. https:// doi. org/ 10. 1111/ele. 13497

Helsen, K., Hermy, M., & Honnay, O. (2016). A test of priority effect persistence in semi-natural grasslands through the removal of plant functional groups during community assembly. *BMC Ecology*, 16, 22. https://doi.org/10.1186/s12898-016-0077-9

Hersh, M. H., Vilgalys, R., & Clark, J. S. (2012). Evaluating the impacts of multiple generalist fungal pathogens on temperate tree seedling survival. *Ecology*, 93(3), 511–520. https://doi.org/10.1890/11-0598.1

Hess, M. C. M., Mesléard, F., & Buisson, E. (2019). Priority effects: Emerging principles for invasive plant species management. *Ecological Engineering*, 127, 48–57. https://doi.org/10.1016/j.ecoleng.2018.11.011

Hess, M. C. M., Mesléard, F., Young, T. P., de Freitas, B., Haveneers, N., & Buisson, E. (2022). Altering native community assembly history influences the performance of an annual invader. *Basic and Applied Ecology*, 59, 70–81. https://doi.org/10.1016/j.baae.2022.01.004

Hierro, J. L., & Callaway, R. M. (2003). Allelopathy and exotic plant invasion. *Plant and Soil*, 256(1), Article 1. https://doi.org/10.1023/A:1026208327014

Higgins, S. I., & Richardson, D. M. (2014). Invasive plants have broader physiological niches. *Proceedings of the National Academy of Sciences*, 111(29), 10610–10614. https://doi.org/10.1073/pnas.1406075111

HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43(1), 227–248. https:// doi. org/ 10. 1146/ annur ev-ecolsys-110411-160411

Hobbs, R. J., & Harris, J. A. (2001). Restoration Ecology: Repairing the Earth's Ecosystems in the New Millennium. *Restoration Ecology*, 9(2), 239–246. https://doi.org/10.1046/j.1526-100x.2001.009002239.x

Hodge, A., & Fitter, A. H. (2013). Microbial mediation of plant competition and community structure. *Functional Ecology*, 27(4), 865–875. https://doi.org/10.1111/1365-2435.12002

Hoeksema, J. D., Chaudhary, V. B., Gehring, C. A., Johnson, N. C., Karst, J., Koide, R. T., Pringle, A., Zabinski, C., Bever, J. D., Moore, J. C., Wilson, G. W. T., Klironomos, J. N., & Umbanhowar, J. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13(3), 394–407. https://doi.org/10.1111/j.1461-0248.2009.01430.x

Holzapfel, C., & Mahall, B. E. (1999). Bidirectional Facilitation and Interference Between Shrubs and Annuals in the Mojave Desert. *Ecology*, 80(5), 1747–1761. https://doi.org/10.1890/0012-9658(1999)080[1747:BFAIBS]2.0.CO;2

Hopkins, J. R., & Bennet, A. E. (2024). Fire effects on soil biota alter the strength and direction of plant-soil feedbacks between *Schizachyrium scoparium* (Michx.) Nash and *Rudbeckia hirta* L. *Plant and Soil*. https://doi.org/10.1007/s11104-024-06585-y

Huangfu, C., Zhang, L., & Hui, D. (2022). Density-dependent plant-soil feedbacks of two plant species affected by plant competition. *Science of The Total Environment*, 807, 150908. https://doi.org/10.1016/j.scitotenv.2021.150908

Husáková, I., Weiner, J., & Münzbergová, Z. (2018). Species traits and shoot–root biomass allocation in 20 dry-grassland species. *Journal of Plant Ecology*, 11(2), 273–285. https:// doi. org/ 10. 1093/ jpe/rtw143

Inderjit, & Putten, W. H. van der. (2010). Impacts of soil microbial communities on exotic plant invasions. *Trends in Ecology & Evolution*, 25(9), 512–519. https://doi.org/10.1016/j.tree.2010.06.006

Inderjit, Wardle, D. A., Karban, R., & Callaway, R. M. (2011). The ecosystem and evolutionary contexts of allelopathy. *Trends in Ecology & Evolution*, 26(12), 655–662. https://doi.org/10.1016/j.tree.2011.08.003

Inderjit, & Cahill, J. F. (2015). Linkages of plant–soil feedbacks and underlying invasion mechanisms. *AoB PLANTS*, 7, plv022. https://doi.org/10.1093/aobpla/plv022

James, J. J., & Drenovsky, R. E. (2007). A Basis for Relative Growth Rate Differences Between Native and Invasive Forb Seedlings. *Rangeland Ecology & Management*, 60(4), Article 4. https://doi.org/10.2111/1551-5028(2007)60[395:ABFRGR]2.0.CO;2

Janzen, D. H. (1970). Herbivores and the Number of Tree Species in Tropical Forests. *The American Naturalist*, 104(940), Article 940.

Jia, Y., van der Heijden, M. G. A., Wagg, C., Feng, G., & Walder, F. (2021). Symbiotic soil fungi enhance resistance and resilience of an experimental grassland to drought and nitrogen deposition. *Journal of Ecology*, 109(9), 3171–3181. https://doi.org/10.1111/1365-2745.13521

Johnson, D. P., Catford, J. A., Driscoll, D. A., & Gibbons, P. (2018). Seed addition and biomass removal key to restoring native forbs in degraded temperate grassland. *Applied Vegetation Science*, 21(2), 219–228. https://doi.org/10.1111/avsc.12352

Johnson, N. C., Graham, J.-H., & Smith, F. A. (1997). Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytologist*, 135(4), Article 4. https://doi.org/10.1046/j.1469-8137.1997.00729.x

Jones, R. O., Chambers, J. C., Board, D. I., Johnson, D. W., & Blank, R. R. (2015). The role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass (*Bromus tectorum*). *Ecosphere*, 6(7), art107. https://doi.org/10.1890/ES14-00285.1

Kandeler, E., Gebala, A., Boeddinghaus, R. S., Müller, K., Rennert, T., Soares, M., Rousk, J., & Marhan, S. (2019). The mineralosphere – Succession and physiology of bacteria and fungi colonising pristine minerals in grassland soils under different land-use intensities. *Soil Biology and Biochemistry*, 136, 107534. https://doi.org/10.1016/j.soilbio.2019.107534

Kardol, P., Bezemer, T. M., & van der Putten, W. H. (2006). Temporal variation in plant–soil feedback controls succession. *Ecology Letters*, 9(9), Article 9. https://doi.org/10.1111/j.1461-0248.2006.00953.x

Kardol, P., De Deyn, G. B., Laliberté, E., Mariotte, P., & Hawkes, C. V. (2013a). Biotic plant–soil feedbacks across temporal scales. *Journal of Ecology*, 101(2), Article 2. https://doi.org/10.1111/1365-2745.12046

Kardol, P., Souza, L., & Classen, A. T. (2013b). Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos*, 122(1), Article 1. https://doi.org/10.1111/j.1600-0706.2012.20546.x

Kardol, P., Yang, T., Arroyo, D. N., & Teste, F. P. (2023). Plant-soil feedback in the 'real world': How does fire fit into all of this? *Plant and Soil*, 485(1), 91–102. https://doi.org/10.1007/s11104-022-05778-7

Ke, P.-J., & Letten, A. D. (2018). Coexistence theory and the frequency-dependence of priority effects. *Nature Ecology & Evolution*, 2(11), 1691–1695. https:// doi. org/ 10. 1038/ s4155 9-018-0679-z

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17(4), Article 4. https://doi.org/10.1016/S0169-5347(02)02499-0

Kempel, A., Rindisbacher, A., Fischer, M., & Allan, E. (2018). Plant soil feedback strength in relation to large-scale plant rarity and phylogenetic relatedness. *Ecology*, 99(3), 597–606. https://doi.org/10.1002/ecy.2145

Klingbeil, B. T., & Willig, M. R. (2016). Community assembly in temperate forest birds: Habitat filtering, interspecific interactions and priority effects. *Evolutionary Ecology*, 30(4), 703–722. https:// doi. org/ 10.1007/ s1068 2-016-9834-7

Klironomos, J. N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, 417(6884), Article 6884. https://doi.org/10.1038/417067a

Klotz, S., Kühn, I., Durka, W. (eds.) (2002). BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. *Schriftenreihe für Vegetationskunde* 38. Bonn: Bundesamt für Naturschutz.

Korell, L., Schmidt, R., Bruelheide, H., Hensen, I., & Auge, H. (2016). Mechanisms driving diversity–productivity relationships differ between exotic and native communities and are affected by gastropod herbivory. *Oecologia*, 180(4), 1025–1036. https://doi.org/10.1007/s00442-015-3395-2

Körner, C., Stöcklin, J., Reuther-Thiébaud, L., & Pelaez-Riedl, S. (2008). Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist*, 177(3), 698–705. https:// doi. org/ 10. 1111/j. 1469-8137.2007. 02287. x

Kourtev, P. S., Ehrenfeld, J. G., & Häggblom, M. (2002). Exotic plant species alter the microbial community structure and function in the soil. *Ecology*, 83(11), Article 11. https://doi.org/10.1890/0012-9658(2002)083[3152:EPSATM]2.0.CO;2

Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science*, 322(5901), 580–582. https://doi.org/10.1126/science.1160662

Kulmatiski, A., Beard, K. H., Stevens, J. R., & Cobbold, S. M. (2008). Plant–soil feedbacks: A meta-analytical review. *Ecology Letters*, 11(9), Article 9. https://doi.org/10.1111/j.1461-0248.2008.01209.x

Kulmatiski, A., Beard, K. H., Norton, J. M., Heavilin, J. E., Forero, L. E., & Grenzer, J. (2017). Live long and prosper: Plant–soil feedback, lifespan, and landscape abundance covary. *Ecology*, 98(12), 3063–3073. https://doi.org/10.1002/ecy.2011

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26. https:// doi. org/ 10. 18637/ jss. v082. i13

Lance, A. C., Carrino-Kyker, S. R., Burke, D. J., & Burns, J. H. (2020). Individual Plant-Soil Feedback Effects Influence Tree Growth and Rhizosphere Fungal Communities in a Temperate Forest Restoration Experiment. *Frontiers in Ecology and Evolution*, 7. https://doi.org/10.3389/fevo.2019.00500

Lankau, R. A. (2012). Coevolution between invasive and native plants driven by chemical competition and soil biota. *Proceedings of the National Academy of Sciences*, 109(28), 11240–11245. https://doi.org/10.1073/pnas.1201343109

Larson, J. E., Sheley, R. L., Hardegree, S. P., Doescher, P. S., & James, J. J. (2015). Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. *Journal of Applied Ecology*, 52(1), 199–209. https://doi.org/10.1111/1365-2664.12350

Larson, J. E., & Funk, J. L. (2016). Regeneration: An overlooked aspect of trait-based plant community assembly models. *Journal of Ecology*, 104(5), 1284–1298. https:// doi. org/ 10. 1111/ 1365-2745.12613

Lau, J. A. (2006). Evolutionary responses of native plants to novel community members. *Evolution*, 60(1), 56–63. https:// doi. org/ 10.1111/j. 0014-3820.2006. tb010 81. x

Lekberg, Y., Bever, J. D., Bunn, R. A., Callaway, R. M., Hart, M. M., Kivlin, S. N., Klironomos, J., Larkin, B. G., Maron, J. L., Reinhart, K. O., Remke, M., & Putten, W. H. van der. (2018). Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. *Ecology Letters*, 21(8), Article 8. https://doi.org/10.1111/ele.13093

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. Emmeans: Estimated marginal means, aka least-squares means. R package Version 1 (2018). Preprint at (2021). https:// CRAN. R-project. org/ packa geemmeans

Lenth, R. (2022). emmeans: Estimated Marginal Means, Aka Least- Squares Means. R package version 1.7. 2.

Leopold, D. R., Tanentzap, A. J., Lee, W. G., Heenan, P. B., & Fukami, T. (2015). Evolutionary priority effects in New Zealand alpine plants across environmental gradients. *Journal of Biogeography*, 42(4), 729–737. https://doi.org/10.1111/jbi.12441

Lepinay, C., Vondráková, Z., Dostálek, T., & Münzbergová, Z. (2018). Duration of the conditioning phase affects the results of plant-soil feedback experiments via soil chemical properties. *Oecologia*, 186(2), Article 2. https://doi.org/10.1007/s00442-017-4033-y

Letcher, S. G. (2010). Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B: Biological Sciences*, 277(1678), 97–104. https://doi.org/10.1098/rspb.2009.0865

Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, 7(10), Article 10. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Levine, J. M., Bascompte, J., Adler, P. B., & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546(7656), Article 7656. https://doi.org/10.1038/nature22898

Li, S., Jia, P., Fan, S., Wu, Y., Liu, X., Meng, Y., Li, Y., Shu, W., Li, J., & Jiang, L. (2022). Functional traits explain the consistent resistance of biodiversity to plant invasion under nitrogen enrichment. *Ecology Letters*, 25(4), 778–789. https://doi.org/10.1111/ele.13951

Liang, M., Shi, L., Burslem, D. F. R. P., Johnson, D., Fang, M., Zhang, X., & Yu, S. (2021). Soil fungal networks moderate density-dependent survival and growth of seedlings. *New Phytologist*, 230(5), 2061–2071. https://doi.org/10.1111/nph.17237

Lishawa, S. C., Lawrence, B. A., Albert, D. A., & Tuchman, N. C. (2015). Biomass harvest of invasive *Typha* promotes plant diversity in a Great Lakes coastal wetland. *Restoration Ecology*, 23(3), 228–237. https://doi.org/10.1111/rec.12167

Liu, H., & Stiling, P. (2006). Testing the enemy release hypothesis: A review and meta-analysis. Biological Invasions, 8(7), Article 7. https://doi.org/10.1007/s10530-005-5845-y

Liu, Q., Pang, Z., Liu, Y., Fallah, N., Hu, C., Lin, W., & Yuan, Z. (2023). Rhizosphere Fungal Dynamics in Sugarcane during Different Growth Stages. *International Journal of Molecular Sciences*, 24(6), Article 6. https://doi.org/10.3390/ijms24065701

Liu, S., García-Palacios, P., Tedersoo, L., Guirado, E., van der Heijden, M. G. A., Wagg, C., Chen, D., Wang, Q., Wang, J., Singh, B. K., & Delgado-Baquerizo, M. (2022). Phylotype diversity within soil fungal functional groups drives ecosystem stability. *Nature Ecology & Evolution*, 6(7), 900–909. https://doi.org/10.1038/s41559-022-01756-5

Liu, X., Liang, M., Etienne, R. S., Wang, Y., Staehelin, C., & Yu, S. (2012). Experimental evidence for a phylogenetic Janzen–Connell effect in a subtropical forest. *Ecology Letters*, 15(2), 111–118. https://doi.org/10.1111/j.1461-0248.2011.01715.x

Liu, X., Steinauer, K., van der Veen-van Wijk, K., & Bezemer, T. M. (2025). Zooming in on the temporal dimensions of plant–soil feedback: Plant sensitivity and microbial dynamics. *Journal of Ecology,* 113(1), 39–52. https://doi.org/10.1111/1365-2745.14435

Liu, Y., Li, G., Wu, X., Niklas, K. J., Yang, Z., & Sun, S. (2021). Linkage between species traits and plant phenology in an alpine meadow. *Oecologia*, 195(2), 409–419. https://doi.org/10.1007/s00442-020-04846-y

Lowry, E., Rollinson, E. J., Laybourn, A. J., Scott, T. E., Aiello-Lammens, M. E., Gray, S. M., Mickley, J., & Gurevitch, J. (2013). Biological invasions: A field synopsis, systematic review, and database of the literature. *Ecology and Evolution*, 3(1), 182–196. https://doi.org/10.1002/ece3.431

Lucero, J. E., Schaffner, U., Asadi, G., Bagheri, A., Rajabov, T., & Callaway, R. M. (2019). Enemy release from the effects of generalist granivores can facilitate *Bromus tectorum* invasion in the Great Basin Desert. *Ecology and Evolution*, 9(15), 8490–8499. https://doi.org/10.1002/ece3.5314

Lundberg, D. S., Lebeis, S. L., Paredes, S. H., Yourstone, S., Gehring, J., Malfatti, S., Tremblay, J., Engelbrektson, A., Kunin, V., Rio, T. G. del, Edgar, R. C., Eickhorst, T., Ley, R. E., Hugenholtz, P., Tringe, S. G., & Dangl, J. L. (2012). Defining the core *Arabidopsis thaliana* root microbiome. *Nature*, 488(7409), 86–90. https://doi.org/10.1038/nature11237

Lyons, T. M., & Barnes, J. D. (1998). Influence of plant age on ozone resistance in Plantago major. *The New Phytologist*, 138(1), 83–89. https://doi. org/ 10. 1046/j. 1469-8137.1998. 00879. x

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101(921), 377–385. https:// doi. org/ 10. 1086/ 282505

Maestre, F. T., Delgado-Baquerizo, M., Jeffries, T. C., Eldridge, D. J., Ochoa, V., Gozalo, B., Quero, J. L., García-Gómez, M., Gallardo, A., Ulrich, W., Bowker, M. A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitán, J., Gutiérrez, J. R., Huber-Sannwald, E., Jankju, M., … Singh, B. K. (2015). Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proceedings of the National Academy of Sciences*, 112(51), 15684–15689. https://doi.org/10.1073/pnas.1516684112

Malmstrom, C. M., McCullough, A. J., Johnson, H. A., Newton, L. A., & Borer, E. T. (2005). Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrasses. *Oecologia*, 145(1), 153–164. https://doi.org/10.1007/s00442-005-0099-z

Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M. L., Valencia, M. C., Sanchez, E. I., & Bever, J. D. (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466(7307), Article 7307. https://doi.org/10.1038/nature09273

Mareri, L., Parrotta, L., & Cai, G. (2022). Environmental Stress and Plants. *International Journal of Molecular Sciences*, 23(10), Article 10. https://doi.org/10.3390/ijms23105416

Maron, J. L., Marler, M., Klironomos, J. N., & Cleveland, C. C. (2011). Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecology Letters*, 14(1), Article 1. https://doi.org/10.1111/j.1461-0248.2010.01547.x

Maron, J. L., Laney Smith, A., Ortega, Y. K., Pearson, D. E., & Callaway, R. M. (2016). Negative plant-soil feedbacks increase with plant abundance, and are unchanged by competition. *Ecology*, 97(8), 2055–2063. https://doi.org/10.1002/ecy.1431

Martin, F. M., Perotto, S., & Bonfante, P. (2000). Mycorrhizal Fungi: A Fungal Community at the Interface Between Soil and Roots. *The Rhizosphere*. CRC Press.

Martin, L. M., & Wilsey, B. J. (2012). Assembly history alters alpha and beta diversity, exotic–native proportions and functioning of restored prairie plant communities. *Journal of Applied Ecology*, 49(6), 1436–1445. https://doi.org/10.1111/j.1365-2664.2012.02202.x

Martin, L. M., & Wilsey, B. J. (2014). Native-species seed additions do not shift restored prairie plant communities from exotic to native states. *Basic and Applied Ecology*, 15(4), 297–304. https://doi.org/10.1016/j.baae.2014.05.007

Martin, P. R., & Ghalambor, C. K. (2023). A Case for the "Competitive Exclusion–Tolerance Rule" as a General Cause of Species Turnover along Environmental Gradients. *The American Naturalist*, 202(1), 1–17. https://doi.org/10.1086/724683

Massot, M., Clobert, J., Lecomte, J., & Barbault, R. (1994). Incumbent Advantage in Common Lizards and their Colonizing Ability. *Journal of Animal Ecology*, 63(2), 431–440. https://doi.org/10.2307/5560

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13(9), 1085–1093. https:// doi. org/ 10. 1111/j. 1461-0248.2010. 01509. x

McCarthy-Neumann, S., & Kobe, R. K. (2019). Site Soil-Fertility and Light Availability Influence Plant-Soil Feedback. *Frontiers in Ecology and Evolution*, 7. https://doi.org/10.3389/fevo.2019.00383

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McHaffie, M. B., & Maherali, H. (2020). Variation in mycorrhizal growth response influences competitive interactions and mechanisms of plant species coexistence. *Oecologia*, 192(3), 755–765. https://doi.org/10.1007/s00442-020-04609-9

McLeod, M. L., Cleveland, C. C., Lekberg, Y., Maron, J. L., Philippot, L., Bru, D., & Callaway, R. M. (2016). Exotic invasive plants increase productivity, abundance of ammonia-oxidizing bacteria and nitrogen availability in intermountain grasslands. *Journal of Ecology*, 104(4), 994–1002. https://doi.org/10.1111/1365-2745.12584

Mehrabi, Z., & Tuck, S. L. (2015). Relatedness is a poor predictor of negative plant–soil feedbacks. *New Phytologist*, 205(3), 1071–1075. https://doi.org/10.1111/nph.13238

Memmott, J., Fowler, S. V., Paynter, Q., Sheppard, A. W., & Syrett, P. (2000). The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecologica*, 21(3), Article 3. https://doi.org/10.1016/S1146-609X(00)00124-7

Merges, D., Bálint, M., Schmitt, I., Böhning-Gaese, K., & Neuschulz, E. L. (2018). Spatial patterns of pathogenic and mutualistic fungi across the elevational range of a host plant. *Journal of Ecology*, 106(4), 1545–1557. https://doi.org/10.1111/1365-2745.12942

Merrild, M. P., Ambus, P., Rosendahl, S., & Jakobsen, I. (2013). Common arbuscular mycorrhizal networks amplify competition for phosphorus between seedlings and established plants. *New Phytologist*, 200(1), 229–240. https://doi.org/10.1111/nph.12351

Michalet, R., Delerue, F., & Liancourt, P. (2023). Disentangling the effects of biomass and productivity in plant competition. *Ecology*, 104(1), e3851. https://doi.org/10.1002/ecy.3851

Milici, V. R., Ballesteros, J., & Bagchi, R. (n.d.). High soil moisture triggers negative plant–soil feedbacks in a tropical forest. *Functional Ecology*, n/a(n/a). https://doi.org/10.1111/1365-2435.70007

Miller, T. E. (1987). Effects of emergence time on survival and growth in an early old-field plant community. *Oecologia*, 72(2), 272–278. https://doi.org/10.1007/BF00379278

Miller, T. E., & Powell, E. (2010). When can competition for resources lead to ecological equivalence? *Evolutionary Ecology Research*, 12(7), 843-854.

Miller-Pierce, M. R., & Preisser, E. L. (2012). Asymmetric priority effects influence the success of invasive forest insects. *Ecological Entomology*, 37(5), 350–358. https://doi.org/10.1111/j.1365-2311.2012.01371.x

Mills, K. E., & Bever, J. D. (1998). Maintenance of diversity within plant communities: Soil pathogens as agents of negative feedback. *Ecology*, 79(5), Article 5. https://doi.org/10.1890/0012-9658(1998)079[1595:MODWPC]2.0.CO;2

Miriti, M. N. (2006). Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, 94(5), 973–979. https:// doi. org/10. 1111/j. 1365-2745.2006. 01138. x

Mitchell, C. E., & Power, A. G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature*, 421(6923), Article 6923. https://doi.org/10.1038/nature01317

Mittelbach, G. G., & McGill, B. J. (2019). Community Ecology. *Oxford University Press*.

Montesinos, D. (2022). Fast invasives fastly become faster: Invasive plants align largely with the fast side of the plant economics spectrum. *Journal of Ecology*, 110(5), 1010–1014. https://doi.org/10.1111/1365-2745.13616

Mordecai, E. A., Molinari, N. A., Stahlheber, K. A., Gross, K., & D'Antonio, C. (2015). Controls over native perennial grass exclusion and persistence in California grasslands invaded by annuals. *Ecology*, 96(10), 2643–2652. https://doi.org/10.1890/14-2023.1

Mori, A. S., Shiono, T., Koide, D., Kitagawa, R., Ota, A. T., & Mizumachi, E. (2013). Community assembly processes shape an altitudinal gradient of forest biodiversity. *Global Ecology and Biogeography*, 22(7), 878–888. https://doi.org/10.1111/geb.12058

Morin, P. (1998). Realism, precision, and generality in experimental ecology. *Experimental Ecology*. Issues and Perspectives, 50–70.

Mougi, A., & Kondoh, M. (2012). Diversity of Interaction Types and Ecological Community Stability. *Science*, 337(6092), 349–351. https://doi.org/10.1126/science.1220529

Mougi, A. (2024). Dual species interaction and ecological community stability. *Ecology*, 105(3), e4251. https://doi.org/10.1002/ecy.4251

Mudrák, O., Fajmon, K., Jongepierová, I., & Prach, K. (2018). Mass effects, clonality, and phenology but not seed traits predict species success in colonizing restored grasslands. *Restoration Ecology*, 26(3), 489–496. https://doi.org/10.1111/rec.12588

Mueller, K. E., Tilman, D., Fornara, D. A., & Hobbie, S. E. (2013). Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. *Ecology*, 94(4), 787–793. https://doi. org/ 10. 1890/ 12-1399.1

Müller, G., Horstmeyer, L., Rönneburg, T., van Kleunen, M., & Dawson, W. (2016). Alien and native plant establishment in grassland communities is more strongly affected by disturbance than above- and below-ground enemies. *Journal of Ecology*, 104(5), Article 5. https://doi.org/10.1111/1365-2745.12601

Müller, L.-L. B., Albach, D. C., & Zotz, G. (2018). Growth responses to elevated temperatures and the importance of ontogenetic niche shifts in Bromeliaceae. *New Phytologist*, 217(1), 127–139. https:// doi. org/10. 1111/ nph. 14732

Münzbergová, Z., & Šurinová, M. (2015). The importance of species phylogenetic relationships and species traits for the intensity of plant-soil feedback. *Ecosphere*, 6(11), art234. https://doi.org/10.1890/ES15-00206.1

Murillo-Rincón, A. P., Kolter, N. A., Laurila, A., & Orizaola, G. (2017). Intraspecific priority effects modify compensatory responses to changes in hatching phenology in an amphibian. *Journal of Animal Ecology,* 86(1), 128–135. https://doi.org/10.1111/1365-2656.12605

Murray, B. R., & Phillips, M. L. (2010). Investment in seed dispersal structures is linked to invasiveness in exotic plant species of south-eastern Australia. *Biological Invasions*, 12(7), 2265–2275. https://doi.org/10.1007/s10530-009-9637-7

Najberek, K., Solarz, W., Pusz, W., Patejuk, K., & Olejniczak, P. (2020). Two sides of the same coin: Does alien *Impatiens balfourii* fall into an ecological trap after releasing from enemies? *Environmental and Experimental Botany*, 176, 104103. https://doi.org/10.1016/j.envexpbot.2020.104103

Narwani, A., Alexandrou, M. A., Oakley, T. H., Carroll, I. T., & Cardinale, B. J. (2013). Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, 16(11), 1373–1381. https:// doi.org/ 10. 1111/ ele. 12182

Ndiribe, C., Pellissier, L., Antonelli, S., Dubuis, A., Pottier, J., Vittoz, P., Guisan, A., & Salamin, N. (2013). Phylogenetic plant community structure along elevation is lineage specific. *Ecology and Evolution*, 3(15), 4925–4939. https://doi.org/10.1002/ece3.868

Nehring, S., Kowarik, I., Rabitsch, W., Essl F. (eds.) (2013). Naturschutzfachliche Invasivitätsbewertungen für in Deutschland wild lebende gebietsfremde Gefäßpflanzen. *BfN-Skripten* 352. Bundesamt für Naturschutz. Bonn - Bad Godesberg.

Nemec, K. T., Allen, C. R., Helzer, C. J., & Wedin, D. A. (2013). Influence of Richness and Seeding Density on Invasion Resistance in Experimental Tallgrass Prairie Restorations. *Ecological Restoration*, 31(2), 168–185. https://doi.org/10.3368/er.31.2.168

Nuismer, S. L., & Harmon, L. J. (2015). Predicting rates of interspecific interaction from phylogenetic trees. *Ecology Letters*, 18(1), 17–27. https:// doi. org/ 10. 1111/ ele. 12384

Nuland, M. E., Wooliver, R., Pfennigwerth, A. A., Read, Q. D., Ware, I. M., Mueller, L. O., Fordyce, J., Schweitzer, J., & Bailey, J. (2016). Plant–soil feedbacks: Connecting ecosystem ecology and evolution. *Functional Ecology*, 30, 1032–1042. https://doi.org/10.1111/1365-2435.12690

Nuske, S. J., Fajardo, A., Nuñez, M. A., Pauchard, A., Wardle, D. A., Nilsson, M.-C., Kardol, P., Smith, J. E., Peltzer, D. A., Moyano, J., & Gundale, M. J. (2021). Soil biotic and abiotic effects on seedling growth exhibit context-dependent interactions: Evidence from a multi-country experiment on *Pinus contorta* invasion. *New Phytologist*, 232(1), 303–317. https://doi.org/10.1111/nph.17449

Oksanen J, Blanchet FG, Friendly M, et al. (2022). vegan: Community Ecology Package. R package version 2.6-4. https:// CRAN.R-project.org/package=vegan

Orwin, K. H., Buckland, S. M., Johnson, D., Turner, B. L., Smart, S., Oakley, S., & Bardgett, R. D. (2010). Linkages of plant traits to soil properties and the functioning of temperate grassland. *Journal of Ecology*, 98(5), 1074–1083. https://doi.org/10.1111/j.1365-2745.2010.01679.x

Palma, E., Vesk, P. A., White, M., Baumgartner, J. B., & Catford, J. A. (2021). Plant functional traits reflect different dimensions of species invasiveness. *Ecology*, 102(5), e03317. https://doi.org/10.1002/ecy.3317

Pan, Y., Wu, Y., Li, X., Zeng, J., & Lin, X. (2019). Continuing Impacts of Selective Inhibition on Bacterial and Fungal Communities in an Agricultural Soil. *Microbial Ecology*, 78(4), 927–935. https://doi.org/10.1007/s00248-019-01364-0

Parish, J. a. D., & Bazzaz, F. A. (1985). Ontogenetic niche shifts in old-field annuals. *Ecology*, 66(4), 1296–1302. https:// doi. org/ 10. 2307/1939182

Pearson, D. E., Ortega, Y. K., Eren, Ö., & Hierro, J. L. (2018). Community Assembly Theory as a Framework for Biological Invasions. *Trends in Ecology & Evolution*, 33(5), 313–325. https://doi.org/10.1016/j.tree.2018.03.002

Peay, K. G., Belisle, M., & Fukami, T. (2011). Phylogenetic relatedness predicts priority effects in nectar yeast communities. *Proceedings of the Royal Society of London B: Biological Sciences*, 279, 749–758. https:// doi. org/ 10. 1098/ rspb. 2011. 1230

Peay, K. G., Baraloto, C., & Fine, P. V. A. (2013). Strong coupling of plant and fungal community structure across western Amazonian rainforests. *The ISME Journal*, 7(9), 1852–1861. https://doi.org/10.1038/ismej.2013.66

Perea, R., & Gil, L. (2014). Shrubs facilitating seedling performance in ungulate-dominated systems: Biotic versus abiotic mechanisms of plant facilitation. *European Journal of Forest Research*, 133(3), 525–534. https://doi.org/10.1007/s10342-014-0782-x

Petermann, J. S., Fergus, A. J. F., Turnbull, L. A., & Schmid, B. (2008). Janzen-Connell Effects Are Widespread and Strong Enough to Maintain Diversity in Grasslands. *Ecology*, 89(9), Article 9. https://doi.org/10.1890/07-2056.1

Peterson, A. T., Soberón, J., & Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, 285(5431), 1265–1267. https:// doi. org/ 10. 1126/ science. 285. 5431. 1265

Phillips, H. R. P., Cameron, E. K., Eisenhauer, N., Burton, V. J., Ferlian, O., Jin, Y., Kanabar, S., Malladi, S., Murphy, R. E., Peter, A., Petrocelli, I., Ristok, C., Tyndall, K., Putten, W. van der, & Beaumelle, L. (2024). Global changes and their environmental stressors have a significant impact on soil biodiversity - A meta-analysis. *Science*, 27(9). https://doi.org/10.1016/j.isci.- 2024.110540

Ploughe, L. W., Carlyle, C. N., & Fraser, L. H. (2020). Priority effects: How the order of arrival of an invasive grass, *Bromus tectorum*, alters productivity and plant community structure when grown with native grass species. *Ecology and Evolution*, 10(23), 13173–13181. https://doi.org/10.1002/ece3.6908

Pouteau, R., Munoz, F., & Birnbaum, P. (2019). Disentangling the processes driving tree community assembly in a tropical biodiversity hotspot (New Caledonia). *Journal of Biogeography*, 46(4), 796–806. https://doi.org/10.1111/jbi.13535

Primack, R. B., & Kang, H. (1989). Measuring fitness and natural selection in wild plant populations. *Annual Review of Ecology and Systematics*, 20(1), 367–396. https:// doi. org/ 10. 1146/ annur ev. es. 20. 110189.002055

Prinzing, A., Durka, W., Klotz, S., & Brandl, R. (2001). The niche of higher plants: Evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 268(1483), 2383–2389. https:// doi. org/ 10. 1098/ rspb. 2001. 1801

Pyšek, P., & Richardson, D. M. (2007). Traits Associated with Invasiveness in Alien Plants: Where Do we Stand? In W. Nentwig (Ed.), *Biological Invasions* (Vol. 193, pp. 97–125).

Springer Berlin Heidelberg. http://www.springerlink.com/content/r787144nv7680252/abstract/

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing. http:// www. r-project.org

Rallo, P., Hannula, S. E., ten Hooven, F. C., Verhoeven, K. J. F., Kammenga, J., & van der Putten, W. H. (2023). Inter- and intraspecific plant-soil feedbacks of grass species. *Plant and Soil*, 486(1), 575–586. https://doi.org/10.1007/s11104-023-05893-z

Ramula, S. (2020). Annual mowing has the potential to reduce the invasion of herbaceous *Lupinus polyphyllus*. *Biological Invasions*, 22(10), 3163–3173. https://doi.org/10.1007/s10530-020-02316-3

Rees, M., Childs, D. Z., & Freckleton, R. P. (2012). Assessing the role of competition and stress: A critique of importance indices and the development of a new approach. *Journal of Ecology*, 100(3), 577–585. https://doi.org/10.1111/j.1365-2745.2011.01946.x

Reinhardt Adams, C., & Galatowitsch, S. M. (2008). The transition from invasive species control to native species promotion and its dependence on seed density thresholds. *Applied Vegetation Science,* 11(1), 131–138. https://doi.org/10.1111/j.1654-109X.2008.tb00211.x

Reinhart, K. O., & Callaway, R. M. (2006). Soil biota and invasive plants. *New Phytologist*, 170(3), Article 3. https://doi.org/10.1111/j.1469-8137.2006.01715.x

Restrepo-Carvajal, I. C., Manhães, A., Pantaleão, L. C., Moraes, L. F. D. de, Mantuano, D., & Sansevero, J. (2024). Testing for priority effects of tree plantings on natural regeneration in restoration sites in the Brazilian Atlantic Forest. *Applied Vegetation Science*. https://doi.org/10.1111/avsc.12768

Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J., & Pigliucci, M. (2006). Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters, 9(8), Article 8. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Richardson, D. M., & Pyšek, P. (2008). Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, 14(2), Article 2. https://doi.org/10.1111/j.1472-4642.2007.00464.x

Rolhauser, A. G., & Pucheta, E. (2017). Directional, stabilizing, and disruptive trait selection as alternative mechanisms for plant community assembly. *Ecology*, 98(3), 668–677. https:// doi. org/ 10. 1002/ecy. 1713

Rolo, V., Plieninger, T., & Moreno, G. (2013). Facilitation of holm oak recruitment through two contrasted shrubs species in Mediterranean grazed woodlands. *Journal of Vegetation Science*, 24(2), 344–355. https://doi.org/10.1111/j.1654-1103.2012.01458.x

Roscher, C., Temperton, V. M., Buchmann, N., & Schulze, E.-D. (2009). Community assembly and biomass production in regularly and never weeded experimental grasslands. *Acta Oecologica*, 35(2), 206–217. https://doi.org/10.1016/j.actao.2008.10.003

Ross, M. A., & Harper, J. L. (1972). Occupation of Biological Space During Seedling Establishment. *Journal of Ecology*, 60(1), 77–88. https://doi.org/10.2307/2258041

Rotter, M. C., & Holeski, L. M. (2018). A meta-analysis of the evolution of increased competitive ability hypothesis: Genetic-based trait variation and herbivory resistance trade-offs. *Biological Invasions,* 20(9), 2647–2660. https://doi.org/10.1007/s10530-018-1724-1

Sakarchi, J., & Germain, R. M. (2023). The evolution of competitive ability. *The American Naturalist*, 201(1), 1–15. https:// doi. org/ 10. 1086/722234

Sarneel, J. M., Kardol, P., & Nilsson, C. (2016). The importance of priority effects for riparian plant community dynamics. *Journal of Vegetation Science*, 27(4), Article 4. https://doi.org/10.1111/jvs.12412

SAS Institute Inc. 2013. SAS/STAT® 13.1 User's Guide. SAS Institute Inc., Cary, NC, USA.

Schädler, M., Jung, G., Brandl, R., & Auge, H. (2004). Secondary succession is influenced by belowground insect herbivory on a productive site. *Oecologia*, 138(2), 242–252. https://doi.org/10.1007/s00442-003-1425-y

Scheu, S. (1992). Automated measurement of the respiratory response of soil microcompartments: Active microbial biomass in earthworm faeces. *Soil Biology and Biochemistry*, 24(11), 1113–1118. https://doi.org/10.1016/0038-0717(92)90061-2

Schluter, D. (1994). Experimental evidence that competition promotes divergence in adaptive radiation. *Science*, 266(5186), 798–801. https:// doi. org/ 10. 1126/ scien ce. 266. 5186. 798

Schluter, D. (2000). Ecological character displacement in adaptive radiation. *The American Naturalist*, 156(S4), S4–S16. https:// doi. org/ 10.1086/ 303412

Schmidt, R., Deising, H. B., Hensen, I., Schädler, M., & Auge, H. (2020). Natural enemies do not contribute to negative frequency-dependence in native and exotic grassland plants. *Perspectives in Plant Ecology, Evolution and Systematics*, 46, 125565. https://doi.org/10.1016/j.ppees.2020.125565

Schroeder, J. W., Martin, J. T., Angulo, D. F., Arias-Del Razo, I., Barbosa, J. M., Perea, R., Sebastián-González, E., & Dirzo, R. (2019). Host plant phylogeny and abundance predict root-associated fungal community composition and diversity of mutualists and pathogens. *Journal of Ecology*, 107(4), 1557–1566. https://doi.org/10.1111/1365-2745.13166

Schuster, M. J., Wragg, P. D., & Reich, P. B. (2018). Using revegetation to suppress invasive plants in grasslands and forests. *Journal of Applied Ecology*, 55(5), 2362–2373. https://doi.org/10.1111/1365-2664.13195

Schwieger, S., Dorrepaal, E., Petit Bon, M., Vandvik, V., le Roux, E., Strack, M., Yang, Y., Venn, S., van den Hoogen, J., Valiño, F., Thomas, H. J. D., te Beest, M., Suzuki, S., Petraglia, A., Myers-Smith, I. H., Munir, T. M., Michelsen, A., Løkken, J. O., Li, Q., … Sarneel, J. M. (2025). Environmental Conditions Modulate Warming Effects on Plant Litter Decomposition Globally. *Ecology Letters*, 28(1), e70026. https://doi.org/10.1111/ele.70026

Seebens, H. (ed.) (2020). Alien Species First Records. https://zenodo.org/records/3690742. 07.08.2023.

Semchenko, M., Saar, S., & Lepik, A. (2014). Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. *New Phytologist*, 204(3), Article 3. https://doi.org/10.1111/nph.12930

Semchenko, M., Leff, J. W., Lozano, Y. M., Saar, S., Davison, J., Wilkinson, A., Jackson, B. G., Pritchard, W. J., De Long, J. R., Oakley, S., Mason, K. E., Ostle, N. J., Baggs, E. M., Johnson, D., Fierer, N., & Bardgett, R. D. (2018). Fungal diversity regulates plant-

soil feedbacks in temperate grassland. *Science Advances*, 4(11), eaau4578. https://doi.org/10.1126/sciadv.aau4578
Semchenko, M., Barry, K. E., de Vries, F. T., Mommer, L., Moora, M., & Maciá-Vicente, J. G. (2022). Deciphering the role of specialist and generalist plant–microbial interactions as drivers of plant–soil feedback. *New Phytologist*, 234(6), 1929–1944. https://doi.org/10.1111/nph.18118
Senior, J. K., Potts, B. M., O'Reilly-Wapstra, J. M., Bissett, A., Wooliver, R. C., Bailey, J. K., Glen, M., & Schweitzer, J. A. (2018). Phylogenetic trait conservatism predicts patterns of plant-soil feedback. *Ecosphere*, 9(10), e02409. https://doi.org/10.1002/ecs2.2409
Senthilnathan, A., & D'Andrea, R. (2024). Coexistence of Competing Plants Under Plant-Soil Feedback. *Ecology Letters*, 27 9. https://doi.org/10.1111/ele.14503
Shealy, N. G., Yoo, W., & Byndloss, M. X. (2021). Colonization resistance: Metabolic warfare as a strategy against pathogenic Enterobacteriaceae. *Current Opinion in Microbiology*, 64, 82–90. https://doi.org/10.1016/j.mib.2021.09.014
Sheppard, C. S., Carboni, M., Essl, F., Seebens, H., DivGrass Consortium, & Thuiller, W. (2018). It takes one to know one: Similarity to resident alien species increases establishment success of new invaders. *Diversity and Distributions*, 24(5), 680–691. https:// doi. org/ 10.1111/ ddi. 12708
Silva, I. A., & Batalha, M. A. (2009). Phylogenetic overdispersion of plant species in southern Brazilian savannas. *Brazilian Journal of Biology*, 69, 843–849. https://doi.org/10.1590/S1519-69842009000400011
Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & Evolution*, 19(11), 605–611. https:// doi. org/ 10. 1016/j. tree. 2004.09. 003
Singh, K., Sobuj, N., & Byun, C. (2024). Native plants do not benefit from arriving early, but invasives pay to arrive late. *Ecological Indicators*, 166, 112453. https://doi.org/10.1016/j.ecolind.2024.112453
Smit, C., Vandenberghe, C., den Ouden, J., & Müller-Schärer, H. (2007). Nurse plants, tree saplings and grazing pressure: Changes in facilitation along a biotic environmental gradient. *Oecologia*, 152(2), 265–273. https://doi.org/10.1007/s00442-006-0650-6
Smith, L. M., & Reynolds, H. L. (2015). Plant–soil feedbacks shift from negative to positive with decreasing light in forest understory species. *Ecology*, 96(9), 2523–2532. https://doi.org/10.1890/14-2150.1
Smith, S. E., & Read, D. J. (2010). Mycorrhizal Symbiosis. *Academic Press*.
Sotomayor, D. A., & Lortie, C. J. (2015). Indirect interactions in terrestrial plant communities: Emerging patterns and research gaps. *Ecosphere*, 6(6), art103. https://doi.org/10.1890/ES14-00117.1
Sporbert, M., Jakubka, D., Bucher, S. F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Mašková, T., Primack, R. B., Rosche, C., Shah, M. A., Stevens, A.-D., … Römermann, C. (2022). Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. *New Phytologist*, 235(6), 2199–2210. https://doi.org/10.1111/nph.18345

Stadler, J., Klotz, S., Brandl, R., & Knapp, S. (2017). Species richness and phylogenetic structure in plant communities: 20 years of succession. *Web Ecology*, 17(2), 37–46. https://doi.org/10.5194/we-17-37-2017

Stanescu, S., & Maherali, H. (2016). Arbuscular mycorrhizal fungi alter the competitive hierarchy among old-field plant species. *Oecologia*, 183, 479–491. https://doi.org/10.1007/s00442-016-3771-6

Staples, T. L., Dwyer, J. M., Loy, X., & Mayfield, M. M. (2016). Potential mechanisms of coexistence in closely related forbs. *Oikos*, 125(12), 1812–1823. https:// doi. org/ 10. 1111/ oik. 03180

Stroud, J. T., Delory, B. M., Barnes, E. M., Chase, J. M., Meester, L. D., Dieskau, J., Grainger, T. N., Halliday, F. W., Kardol, P., Knight, T. M., Ladouceur, E., Little, C. J., Roscher, C., Sarneel, J. M., Temperton, V. M., Steijn, T. L. H. van, Werner, C. M., Wood, C. W., & Fukami, T. (2024). Priority effects transcend scales and disciplines in biology. *Trends in Ecology & Evolution*, 0(0). https://doi.org/10.1016/j.tree.2024.02.004

Stuble, K. L., & Souza, L. (2016). Priority effects: Natives, but not exotics, pay to arrive late. *Journal of Ecology*, 104(4), 987–993. https://doi.org/10.1111/1365-2745.12583

Stuble, K. L., Fick, S. E., & Young, T. P. (2017). Every restoration is unique: Testing year effects and site effects as drivers of initial restoration trajectories. *Journal of Applied Ecology*, 54(4), 1051–1057. https://doi.org/10.1111/1365-2664.12861

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, 19(1), 46–53. https://doi.org/10.1016/j.tree.2003.10.005

Suding, K. N., Stanley Harpole, W., Fukami, T., Kulmatiski, A., MacDougall, A. S., Stein, C., & van der Putten, W. H. (2013). Consequences of plant–soil feedbacks in invasion. *Journal of Ecology*, 101(2), 298–308. https://doi.org/10.1111/1365-2745.12057

Sünnemann, M., Siebert, J., Reitz, T., Schädler, M., Yin, R., & Eisenhauer, N. (2021a). Combined effects of land-use type and climate change on soil microbial activity and invertebrate decomposer activity. *Agriculture, Ecosystems & Environment*, 318, 107490. https://doi.org/10.1016/j.agee.2021.107490

Sünnemann, M., Alt, C., Kostin, J. E., Lochner, A., Reitz, T., Siebert, J., Schädler, M., & Eisenhauer, N. (2021b). Low-intensity land-use enhances soil microbial activity, biomass and fungal-to-bacterial ratio in current and future climates. *Journal of Applied Ecology*, 58(11), 2614–2625. https://doi.org/10.1111/1365-2664.14004

Švamberková, E., Doležal, J., & Lepš, J. (2019). The legacy of initial sowing after 20 years of ex-arable land colonisation. *Oecologia*, 190(2), 459–469. https://doi.org/10.1007/s00442-019-04415-y

Svoboda, P., Lindström, E. S., Ahmed Osman, O., & Langenheder, S. (2018). Dispersal timing determines the importance of priority effects in bacterial communities. *The ISME Journal*, 12(2), 644–646. https://doi.org/10.1038/ismej.2017.180

Symonds, M. R. E., & Elgar, M. A. (2004). Species overlap, speciation and the evolution of aggregation pheromones in bark beetles. *Ecology Letters*, 7(3), 202–212. https:// doi. org/ 10. 1111/j. 1461-0248.2004.00571. x

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., & Milberg, P. (2018). Similar effects of different mowing frequencies on the conservation value of semi-natural grasslands in Europe. *Biodiversity and Conservation*, 27(10), 2451–2475. https://doi.org/10.1007/s10531-018-1562-6

Tan, J., Pu, Z., Ryberg, W. A., & Jiang, L. (2012). Species phylogenetic relatedness, priority effects, and ecosystem functioning. *Ecology*, 93(5), 1164–1172. https:// doi. org/ 10. 1890/ 11-1557.1

Thonis, A., & Akçakaya, H. R. (2024). Experimental evidence that competition strength scales with ecological similarity: A case study using Anolis lizards. *Oecologia*, 204(3), 451–465. https://doi.org/10.1007/s00442-023-05507-6

Thorpe, A. S., Aschehoug, E. T., Atwater, D. Z., & Callaway, R. M. (2011). Interactions among plants and evolution. *Journal of Ecology*, 99(3), 729–740. https:// doi. org/ 10. 1111/j. 1365-2745.2011. 01802. x

Tilman, D. (1982). Resource Competition and Community Structure. *Princeton University Press*.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences*, 101(30), 10854–10861. https://doi.org/10.1073/pnas.0403458101

Tobias, J. A., Cornwallis, C. K., Derryberry, E. P., Claramunt, S., Brumfield, R. T., & Seddon, N. (2014). Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*, 506(7488), 359–363. https:// doi. org/ 10. 1038/ natur e12874

Tognetti, P. M., & Chaneton, E. J. (2012). Invasive exotic grasses and seed arrival limit native species establishment in an old-field grassland succession. *Biological Invasions*, 14(12), 2531–2544. https://doi.org/10.1007/s10530-012-0249-2

Toju, H., Vannette, R. L., Gauthier, M. P. L., Dhami, M. K., & Fukami, T. (2018). Priority effects can persist across floral generations in nectar microbial metacommunities. *Oikos*, 127(3), 345–352. https://doi. org/ 10. 1111/ oik. 04243

Torres, A., Rodríguez-Cabal, M. A., & Núñez, M. A. (2022). Do not come late to the party: Initial success of nonnative species is contingent on timing of arrival of co-occurring nonnatives. *Biological Invasions*, 24(2), 557–573. https://doi.org/10.1007/s10530-021-02660-y

Trnka, M., Balek, J., Semenov, M., Semerádová, D., Bělínová, M., Hlavinka, P., Olesen, J., Eitzinger, J., Schaumberger, A., Zahradníček, P., Kopecky, D., & Žalud, Z. (2021). Future agroclimatic conditions and implications for European grasslands. *Biologia Plantarum*, 64, 865–880. https://doi.org/10.32615/BP.2021.005

Ulrich, W., Zaplata, M. K., Winter, S., Schaaf, W., Fischer, A., Soliveres, S., & Gotelli, N. J. (2016). Species interactions and random dispersal rather than habitat filtering drive community assembly during early plant succession. *Oikos*, 125(5), 698–707. https://doi.org/10.1111/oik.02658

Upton, R. N., Checinska Sielaff, A., Hofmockel, K. S., Xu, X., Polley, H. W., & Wilsey, B. J. (2020). Soil depth and grassland origin cooperatively shape microbial community co-occurrence and function. *Ecosphere*, 11(1), e02973. https://doi.org/10.1002/ecs2.2973

Uricchio, L. H., Daws, S. C., Spear, E. R., & Mordecai, E. A. (2019). Priority Effects and Nonhierarchical Competition Shape Species Composition in a Complex Grassland Community. *The American Naturalist*, 193(2), 213–226. https://doi.org/10.1086/701434

Valiente-Banuet, A., & Verdú, M. (2008). Temporal shifts from facilitation to competition occur between closely related taxa. *Journal of Ecology*, 96(3), 489–494. https://doi.org/10.1111/j.1365-2745.2008.01357.x

Valverde, T., Bongers, F., Vega, E., Gallego-Mahecha, M. del M., & Martínez-Ramos, M. (2021). Demographic differentiation among pioneer tree species during secondary succession of a Neotropical rainforest. *Journal of Ecology*, 109, 3572–3586. https://doi.org/10.1111/1365-2745.13738

van de Voorde, T. F. J., van der Putten, W. H., & Martijn Bezemer, T. (2011). Intra- and interspecific plant–soil interactions, soil legacies and priority effects during old-field succession. *Journal of Ecology*, 99(4), Article 4. https://doi.org/10.1111/j.1365-2745.2011.01815.x

van der Heijden, M. G. A., Bardgett, R. D., & Van Straalen, N. M. (2008). The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, 11(3), Article 3. https://doi.org/10.1111/j.1461-0248.2007.01139.x

van der Heijden, M. G. A., & Horton, T. R. (2009). Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology*, 97(6), 1139–1150. https://doi.org/10.1111/j.1365-2745.2009.01570.x

van der Putten, W. H., & Peters, B. A. M. (1997). How soil-borne pathogens may affect plant competition. *Ecology*, 78(6), Article 6. https://doi.org/10.1890/0012-9658(1997)078[1785:HSBPMA]2.0.CO;2

van der Putten, W. H., & van der Stoel, C. D. (1998). Plant parasitic nematodes and spatio-temporal variation in natural vegetation. *Applied Soil Ecology*, 10(3), 253–262. https://doi.org/10.1016/S0929-1393(98)00124-3

van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., van de Voorde, T. F. J., & Wardle, D. A. (2013). Plant–soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, 101(2), Article 2. https://doi.org/10.1111/1365-2745.12054

van Geel, M., Jacquemyn, H., Plue, J., Saar, L., Kasari, L., Peeters, G., van Acker, K., Honnay, O., & Ceulemans, T. (2018). Abiotic rather than biotic filtering shapes the arbuscular mycorrhizal fungal communities of European seminatural grasslands. *New Phytologist*, 220(4), 1262–1272. https://doi.org/10.1111/nph.14947

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13(2), 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

van Steijn, T. L. H., Kardol, P., Jansson, R., Tjäder, J., & Sarneel, J. M. (2025). Priority effects can be explained by competitive traits. *Ecology*, 106(1), e4528. https://doi.org/10.1002/ecy.4528

Vannette, R. L., & Fukami, T. (2014). Historical contingency in species interactions: Towards niche-based predictions. *Ecology Letters*, 17(1), 115–124. https:// doi. org/ 10. 1111/ ele. 12204

Vaughn, K. J., & Young, T. P. (2015). Short-term priority over exotic annuals increases the initial density and longer-term cover of native perennial grasses. *Ecological Applications*, 25(3), 791–799. https://doi.org/10.1890/14-0922.1

Venail, P. A., Narwani, A., Fritschie, K., Alexandrou, M. A., Oakley, T. H., & Cardinale, B. J. (2014). The influence of phylogenetic relatedness on species interactions among freshwater green algae in a mesocosm experiment. *Journal of Ecology*, 102(5), 1288–1299. https://doi.org/10.1111/1365-2745.12271

Verdú, M., Gómez-Aparicio, L., & Valiente-Banuet, A. (2012). Phylogenetic relatedness as a tool in restoration ecology: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 279(1734), 1761–1767. https:// doi. org/ 10. 1098/ rspb. 2011. 2268

Vilà, M., Maron, J. L., & Marco, L. (2005). Evidence for the enemy release hypothesis in *Hypericum perforatum*. *Oecologia*, 142(3), 474–479. https://doi.org/10.1007/s00442-004-1731-z

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14(7), Article 7. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), Article 5. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Violle, C., Nemergut, D. R., Pu, Z., & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, 14(8), 782–787. https:// doi. org/ 10. 1111/j. 1461-0248.2011. 01644. x

Vivanco, J. M., Bais, H. P., Stermitz, F. R., Thelen, G. C., & Callaway, R. M. (2004). Biogeographical variation in community response to root allelochemistry: Novel weapons and exotic invasion. *Ecology Letters*, 7(4), Article 4. https://doi.org/10.1111/j.1461-0248.2004.00576.x

Von Holle, B. (2005). Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. *Journal of Ecology*, 93(1), 16–26. https://doi.org/10.1111/j.0022-0477.2004.00946.x

Waller L, Allen W, Black A, et al. (2021). Asymmetric pathogen spillover favors exotic plants over natives. *Authorea* https:// doi.org/10.22541/au.162064926.63740751/v1

Wandrag, E. M., Bates, S. E., Barrett, L. G., Catford, J. A., Thrall, P. H., van der Putten, W. H., & Duncan, R. P. (2020). Phylogenetic signals and predictability in plant–soil feedbacks. *New Phytologist*, 228(4), 1440–1449. https://doi.org/10.1111/nph.16768

Wang, Y., Niu, X., Zhao, L., Liang, C., Miao, B., Zhang, Q., Zhang, J., Schmid, B., & Ma, W. (2020). Biotic stability mechanisms in Inner Mongolian grassland. *Proceedings of the Royal Society B: Biological Sciences*, 287(1928), 20200675. https://doi.org/10.1098/rspb.2020.0675

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Putten, W. H. van der, & Wall, D. H. (2004). Ecological Linkages Between Aboveground and Belowground Biota. *Science*, 304(5677), Article 5677. https://doi.org/10.1126/science.1094875

Waring, B. G., Álvarez-Cansino, L., Barry, K. E., Becklund, K. K., Dale, S., Gei, M. G., Keller, A. B., Lopez, O. R., Markesteijn, L., Mangan, S., Riggs, C. E., Rodríguez-Ronderos, M. E., Segnitz, R. M., Schnitzer, S. A., & Powers, J. S. (2015). Pervasive and strong effects of plants on soil chemistry: A meta-analysis of individual plant 'Zinke' effects.

Proceedings of the Royal Society B: Biological Sciences, 282(1812), 20151001. https://doi.org/10.1098/rspb.2015.1001

Warneke, C. R., Yelenik, S. G., & Brudvig, L. A. (2023). Fire modifies plant–soil feedbacks. *Ecology*, 104(5), e3994. https://doi.org/10.1002/ecy.3994

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and Community Ecology. *Annual Review of Ecology and Systematics*, 33(1), 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Weber, M. G., Mitko, L., Eltz, T., & Ramírez, S. R. (2016). Macroevolution of perfume signalling in orchid bees. *Ecology Letters*, 19(11), 1314–1323. https:// doi. org/ 10. 1111/ ele. 12667

Wegasie, M. O., Klanderud, K., Totland, Ø., & Eldegard, K. (2021). Ontogenetic niche shifts in a locally endangered tree species (Olea europaea subsp. cuspidata) in a disturbed forest in Northern Ethiopia: Implications for conservation. *PLOS ONE*, 16(9), e0256843. https://doi.org/10.1371/journal.pone.0256843

Weidlich, E. W. A., Von Gillhaussen, P., Delory, B. M., Blossfeld, S., Poorter, H., & Temperton, V. M. (2017). The importance of being first: Exploring priority and diversity effects in a grassland field experiment. *Frontiers in Plant Science*, 7. https:// doi. org/ 10. 3389/ fpls. 2016. 02008

Weidlich, E. W. A., Nelson, C. R., Maron, J. L., Callaway, R. M., Delory, B. M., & Temperton, V. M. (2021). Priority effects and ecological restoration. *Restoration Ecology*, 29(1), e13317. https://doi.org/10.1111/rec.13317

Weiher, E., & Keddy, P. A. (1995). Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. *Oikos*, 74(1), 159–164. https://doi.org/10.2307/3545686

Weiner, J. (1990). Asymmetric competition in plant populations. *Trends in Ecology & Evolution*, 5(11), 360–364. https://doi.org/10.1016/0169-5347(90)90095-U

Weremijewicz, J., & Janos, D. P. (2013). Common mycorrhizal networks amplify size inequality in *Andropogon gerardii* monocultures. *New Phytologist*, 198(1), 203–213. https://doi.org/10.1111/nph.12125

Weremijewicz, J., Sternberg, L. da S. L. O., & Janos, D. P. (2016). Common mycorrhizal networks amplify competition by preferential mineral nutrient allocation to large host plants. *New Phytologis*t, 212(2), 461–471. https://doi.org/10.1111/nph.14041

Werner, C. M., Vaughn, K. J., Stuble, K. L., Wolf, K., & Young, T. P. (2016). Persistent asymmetrical priority effects in a California grassland restoration experiment. *Ecological Applications*, 26(6), 1624–1632. https://doi.org/10.1890/15-1918.1

Werner, E. E., & Peacor, S. D. (2003). A Review of Trait-Mediated Indirect Interactions in Ecological Communities. *Ecology*, 84(5), 1083–1100. https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Wiens, J. J., & Graham, C. H. (2005). Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics*, 36(1), Article 1. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Jonathan Davies, T., Grytnes, J. A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., & Stephens, P. R. (2018). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, 13, 1310–1324. https:// doi. org/ 10. 1111/j. 1461-0248.2010. 01515. x

Wilfahrt, P., Halliday, F., & Heckman, R. W. (2019). Priority effects, consumer pressure, and soil resources independently alter plant diversity and resource strategies during a multi-year successional field experiment. *bioRxiv.* https://doi.org/10.1101/722264

Williams, E. W., Zeldin, J., Semski, W. R., Hipp, A. L., & Larkin, D. J. (2021). Phylogenetic distance and resource availability mediate direction and strength of plant interactions in a competition experiment. *Oecologia*, 197(2), 459–469. https://doi.org/10.1007/s00442-021-05024-4

Wilschut, R. A., Hume, B. C. C., Mamonova, E., & van Kleunen, M. (2023). Plant–soil feedback effects on conspecific and heterospecific successors of annual and perennial Central European grassland plants are correlated. *Nature Plants*, 9(7), 1057–1066. https://doi.org/10.1038/s41477-023-01433-w

Wilsey, B. J., & Wayne Polley, H. (2006). Aboveground productivity and root–shoot allocation differ between native and introduced grass species. *Oecologia*, 150(2), 300–309. https://doi.org/10.1007/s00442-006-0515-z

Wilsey, B. J., Teaschner, T. B., Daneshgar, P. P., Isbell, F. I., & Polley, H. W. (2009). Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecology Letters*, 12(5), 432–442. https://doi.org/10.1111/j.1461-0248.2009.01298.x

Wilsey, B. J., Barber, K., & Martin, L. M. (2015). Exotic grassland species have stronger priority effects than natives regardless of whether they are cultivated or wild genotypes. *New Phytologist*, 205(2), Article 2. https://doi.org/10.1111/nph.13028

Winkler, D. E., Garbowski, M., Kožić, K., Ladouceur, E., Larson, J., Martin, S., Rosche, C., Roscher, C., Slate, M. L., & Korell, L. (2024). Facilitating comparable research in seedling functional ecology. *Methods in Ecology and Evolution*, 15(3), 464–476. https://doi.org/10.1111/2041-210X.14288

Wohlwend, M. R., Schutzenhofer, M. R., & Knight, T. M. (2019). Long-term experiment manipulating community assembly results in favorable restoration outcomes for invaded prairies. *Restoration Ecology*, 27(6), 1307–1316. https://doi.org/10.1111/rec.13006

Wolfe, B. E., & Klironomos, J. N. (2005). Breaking New Ground: Soil Communities and Exotic Plant Invasion. *BioScience*, 55(6), Article 6. https://doi.org/10.1641/0006-3568(2005)055[0477:BNGSCA]2.0.CO;2

Wolfe, L. M. (2002). Why Alien Invaders Succeed: Support for the Escape-from-Enemy Hypothesis. *The American Naturalist*, 160(6), Article 6. https://doi.org/10.1086/343872

Woodward, J. A., & Bonett, D. G. (1991). Simple main effects in factorial designs. *Journal of Applied Statistics*, 18(2), 255–264. https://doi.org/10.1080/02664769100000019

Xi, N., McCarthy-Neumann, S., Feng, J., Wu, H., Wang, W., & Semchenko, M. (2023). Light availability and plant shade tolerance modify plant–microbial interactions and feedbacks in subtropical trees. *New Phytologist*, 238(1), 393–404. https://doi.org/10.1111/nph.18737

Xu, J., Zhang, Y., Liu, S., Chai, Y., Dang, H., Yue, M., Liu, X., & Guo, Y. (2021). Patterns of diversity and community assembly change across local to regional scales: An evidence of deterministic assembly processes along resource availability gradient at temperate forest. *Ecological Indicators*, 132, 108261. https://doi.org/10.1016/j.ecolind.2021.108261

Xue, W., Bezemer, T. M., & Berendse, F. (2018). Density-dependency and plant-soil feedback: Former plant abundance influences competitive interactions between two grassland plant species through plant-soil feedbacks. *Plant and Soil*, 428(1), 441–452. https://doi.org/10.1007/s11104-018-3690-x

Yan, X., Li, X., & Jin, K. (2024). Priority effects of forbs arriving early: The role of root interaction and asymmetric competition. *Ecological Processes*, 13(1), 4. https://doi.org/10.1186/s13717-024-00483-y

Yannelli, F. A., Karrer, G., Hall, R., Kollmann, J., & Heger, T. (2018). Seed density is more effective than multi-trait limiting similarity in controlling grassland resistance against plant invasions in mesocosms. *Applied Vegetation Science*, 21(3), 411–418. https://doi.org/10.1111/avsc.12373

Yannelli, F. A., MacLaren, C., & Kollmann, J. (2020). Moving Away From Limiting Similarity During Restoration: Timing of Arrival and Native Biomass Are Better Proxies of Invasion Suppression in Grassland Communities. *Frontiers in Ecology and Evolution*, 8. https://www.frontiersin.org/articles/10.3389/fevo.2020.00238

Young, T. P., Zefferman, E. P., Vaughn, K. J., & Fick, S. (2015). Initial success of native grasses is contingent on multiple interactions among exotic grass competition, temporal priority, rainfall and site effects. *AoB PLANTS*, 7, plu081. https://doi.org/10.1093/aobpla/plu081

Young, T. P., Stuble, K. L., Balachowski, J. A., & Werner, C. M. (2017). Using priority effects to manipulate competitive relationships in restoration. *Restoration Ecology*, 25(S2), S114–S123. https://doi.org/10.1111/rec.12384

Zee, P. C., & Fumaki, T. (2018). Priority effects are weakened by a short, but not long, history of sympatric evolution. *Proceedings of the Royal Society B: Biological Sciences*, 285(1871), 20171722. https:// doi. org/10. 1098/ rspb. 2017. 1722

Zettlemoyer, M. A., Schultheis, E. H., & Lau, J. A. (2019). Phenology in a warming world: Differences between native and non-native plant species. *Ecology Letters*, 22(8), 1253–1263. https://doi.org/10.1111/ele.13290

Zhang, H., Xu, J., Meng, W., Li, Z., Ni, Y., Li, W., Chen, H., Zhang, X., Yuan, H., & Wang, Z. (2024a). Positive interactions in shaping neighborhood diversity during secondary forests recovery: Revisiting the classical paradigm. *Forest Ecology and Management*. https://doi.org/10.1016/j.foreco.2023.121586

Zhang, J., Ai, Z., Xu, H., Liu, H., Wang, G., Deng, L., Liu, G., & Xue, S. (2021). Plant-microbial feedback in secondary succession of semiarid grasslands. Science of The Total Environment, 760, 143389. https://doi.org/10.1016/j.scitotenv.2020.143389

Zhang, L., Mi, X., & Shao, H. (2016). Phylogenetic Relatedness Influences Plant Interspecific Interactions Across Stress Levels in Coastal Ecosystems: *A Meta-Analysis. Estuaries and Coasts*, 39(6), 1669–1678. https://doi.org/10.1007/s12237-016-0104-2

Zhang, L., Wang, B., & Qi, L. (2017). Phylogenetic relatedness, ecological strategy, and stress determine interspecific interactions within a salt marsh community. *Aquatic Sciences*, 79(3), 587–595. https://doi.org/10.1007/s00027-017-0519-2

Zhang, L., Zuo, Q., Cai, H., Li, S., Shen, Z., & Song, T. (2024b). Fungicides reduce soil microbial diversity, network stability and complexity in wheat fields with different disease resistance. *Applied Soil Ecology*, 201, 105513. https://doi.org/10.1016/j.apsoil.2024.105513

Zhang, L., Chi, X., Sun, M., Chen, X., Lan, S., Zhang, Y., Su, X., Tang, C., & Wang, Q. (2024c). Native shrub and plant diversity mitigate plant invasion in eastern China's humid grasslands. *Applied Vegetation Science*, 27(4), e70004. https://doi.org/10.1111/avsc.70004

Zhao, B., Stephenson, M. B., Awada, T., Volesky, J. D., Wardlow, B., Zhou, Y., & Shi, Y. (2023). Combined Long-Term Effects of Precipitation and Temperature Variability on Semi-Arid Grazed Grasslands of the Nebraska Sandhills: Implications for Resilience and Adaptive Grazing Management (SSRN Scholarly Paper 4357140). *Social Science Research Network*. https://doi.org/10.2139/ssrn.4357140

Zirbel, C. R., Bassett, T., Grman, E., & Brudvig, L. (2017). Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *Journal of Applied Ecology*, 54, 1070–1079. https://doi.org/10.1111/1365-2664.12885

Zou, H.-X., & Rudolf, V. H. W. (2023). Bridging theory and experiments of priority effects. *bioRxiv*, 2022.12.05.519211. https:// doi. org/ 10.1101/ 2022. 12. 05. 519211

Appendices

Author contributions

Deklaration der Beiträge von Autoren zur kumulativen Arbeit (entsprechend §7 (5) der Promotionsordnung der Naturwissenschaftlichen Fakultäten I, II und III der MLU).

Chapter 2

Dieskau, J., Hensen, I., Eisenhauer, N., & Auge, H. (unpublished manuscript). Competition- and soil fungi-mediated priority effects differ between native and exotic European grassland plants. *under review in Journal of Ecology*

	Julia Dieskau [81%]	Isabell Hensen [1,0%]	Nico Eisenhauer [1,0%]	Harald Auge [16,75%]
Entwurf (Design)	50%	2%	2%	46%
Umsetzung (Implementation)	99%	0%	0%	1%
Auswertung (Analysis)	80%	1%	1%	18%
Schreiben (Writing)	95%	1%	1%	3%

Chapter 3

Dieskau, J., Hensen, I., Eisenhauer, N., Gaberle, I., Durka, W., Lachmuth, S., & Auge, H. (2024a). Phylogenetic relationships and plant life stage but not biogeographic history mediate priority effects of European grassland plants. *Journal of Ecology*, 112(9), 2007–2017. https://doi.org/10.1111/1365-2745.14373

	Julia Dieskau [77%]	Isabell Hensen [1,25%]	Nico Eisenhauer [1,75%]	Ingmar Gaberle [2,25%]	Walter Durka [1,5%]	Susanne Lachmuth [1,75%]	Harald Auge [14%]
Entwurf (Design)	48%	3%	3%	0%	2%	0%	44%
Umsetzung (Implementation)	90%	0%	0%	9%	0%	0%	1%
Auswertung (Analysis)	80%	1%	5%	0%	3%	5%	6%
Schreiben (Writing)	90%	1%	1%	0%	1%	2%	5%

Chapter 4

Dieskau, J., Hensen, I., Eisenhauer, N., Lachmuth, S., & Auge, H. (2025a). Plant-soil feedback in European grasslands is phylogenetically independent but affected by plant species origin. *Journal of Plant Ecology*, rtaf021. https://doi.org/10.1093/jpe/rtaf021

	Julia Dieskau [81,25%]	Isabell Hensen [1,0%]	Nico Eisenhauer [1,0%]	Susanne Lachmuth [2,5%]	Harald Auge [14,75%]
Entwurf (Design)	50%	1%	1%	0%	48%
Umsetzung (Implementation)	100%	0%	0%	0%	0%
Auswertung (Analysis)	85%	1%	1%	8%	7%
Schreiben (Writing)	90%	2%	2%	2%	4%

Julia Dieskau (Datum)

Prof. Dr. Isabell Hensen (Datum)

Acknowledgement / Danksagung

First and foremost, I would like to sincerely thank my supervisors Isabell Hensen, Harald Auge, and Nico Eisenhauer. Their wholehearted support made this work possible in many ways. Dear Isabell, I am especially grateful for your continuous support – even during difficult times. You gave me the opportunity to gain experience in university teaching, offered encouraging feedback throughout the writing process, and connected me with motivated students for subprojects. Your support has been valuable to me in every respect. I also want to thank you for your willingness to extend my contract to the maximum duration possible. Dear Harald, I am deeply thankful for so many years of unwavering support – from practical help with seed collection and LAI measurements, to the planning and execution of experiments, and finally data analysis and writing. You have always been a role model, showing that science and humanity are not mutually exclusive. Thank you from the bottom of my heart – I could not have wished for a better supervisor. Dear Nico, I would like to especially thank you for your motivating, constructive, and exceptionally prompt feedback, as well as for the opportunity to conduct measurements in your lab. I am also grateful for your helpful advice regarding my career planning. My special thanks also go to Isabell Hensen, Harald Auge, and Viktoria Wagner for their willingness to review my dissertation.

A heartfelt thank you to the many dedicated helpers who supported me during fieldwork, in the greenhouse and in the lab: Benjamin Bischoff, Angie Buchold, Yolanda Cacares, Henriette Christel, Ingmar Gaberle, Katrin Kittlaus, Kevin Kožić, Alfred Lochner, Ines Mehrbach and her team, Niclas Mehre, Tim Meier, Annika Müller, Birgit Müller, Caroline Plos, Tobias Proß, Linda Rehfeldt, Julia Rieger, Adrian Schaar, Robin Schmidt, Markus Seidler, Antonia Stürmer, Tim Walther, Ina Vogler – without you, experiments of this scale would have been unthinkable. The long hours in the greenhouse were never dull thanks to your company. I am also grateful to Susanne Lachmuth for her valuable support with statistical analysis, and to Helge Bruelheide for his constructive feedback on the field experiment, as well as for the many stimulating discussions and career tips over lunch.

I would also like to extend my sincere thanks to my graduate school, yDiv, and especially to Nicole Sachmerda-Schulz, who was always approachable and attentive to the concerns of the doctoral researchers. You are an outstanding coordinator – a true role model whose example will be hard to follow. I am also thankful for the opportunity to participate in the “sPriority” group and for the engaging scientific exchange during the meetings, which greatly supported my dissertation work.

To all my colleagues in the Plant Ecology and Geobotany working groups – thank you for fostering such a wonderfully diverse and trusting atmosphere, where everyone is free to be themselves. This time would not have been the same without you. Tobi, thank you for your tireless willingness to help – even when it meant putting yourself second. Your support, both intellectually and practically, was crucial to me in many situations. A special thank you also goes to Caro, Yola, Sabrina, Marie and Kevin – for sharing my unfiltered emotions and always lifting me up when I needed it. In this context, I would also like to especially mention, Christoph, Arpad, Lina, Adrian, Christian, Maria, Weronika, Amanda, Susi, Gunnar and Mariem – thank you for being part of this journey.

Ein ganz besonderer Dank gilt meiner Familie für ihre beständige Unterstützung – soweit es ihre eigenen Kräfte erlaubten und oftmals darüber hinaus. Ihr habt mir stets den Rücken gestärkt und ohne euch wäre ich nicht, wer ich heute bin und wo ich heute bin. Durch die Gewissheit immer auf euch zählen zu können, konnte ich mich frei entfalten und meinen Weg gehen.

Zudem danke ich meinen Freunden, welche mir auch in herausfordernden Zeiten zur Seite standen, und mir geholfen haben wieder zurück zu mir und auch zurück zu meiner Doktorarbeit zu finden. In diesem Zusammenhang möchte ich insbesondere Yola, Sascha, Lydia, Lis, Adrian, Hanna, Satya, Katja, Wenzel und Aleks nennen. Und schließlich danke ich meinem wundervollen Sohn Jakob. Du hast meinem Leben eine neue Dimension von Sinnhaftigkeit geschenkt und wirst für immer einen unverrückbaren Platz in meinem Herzen haben.

Curriculum Vitae

Personal information

Name:	Julia Dieskau
Research profiles	https://orcid.org/0000-0002-2410-415X https://www.researchgate.net/profile/Julia-Dieskau?ev=hdr_xprf
Language Skills	German: native speaker English: fluent

Education & Employment

2016-Present **Research associate and PhD student**
Martin-Luther University Halle-Wittenberg
Institute of Biology, Geobotany and Botanical Garden
Working Group Plant Ecology, Prof. Dr. Isabell Hensen

Teaching Experience
Supervision of Bachelor's and Master's theses, practical exercises and lectures in plant identification, instruction in basic plant ecology field course, leading field excursions

Parental leave 12.2019-08.2021

2012-2016 **MA Biology**, Martin-Luther University Halle-Wittenberg
Modules included: **Habitat and population ecology, Nature Conservation, Plant Physiology**

Master thesis: The role of soil biota in the invasion process of *Verbascum thapsus* in New Zealand: A comparison of native and invasive populations. (1.0)

2012-2013 **Study abroad,** Lincoln University, New Zealand
Topic: "Comparison of native and invasive populations of *Verbascum thapsus* under UV and drought stress" as well as "Morphological differences in native and invasive *Verbascum thapsus* populations along an altitudinal gradient"

2009-2012 **BA Biology**, Martin-Luther University Halle-Wittenberg

Bachelor thesis: Adaptation of *Echium vulgare* to simulated UV-B stress: morphological and physiological comparison of native and invasive populations (1.0)

Methods and Skills

Soil and Plant Chemistry
Atomic Absorption Spectrometry (AAS), C/N elemental analysis, analysis of leaf chemistry (chlorophyll, carotenoids, anthocyanins, proline)

Statistics
(Generalized) linear models, linear mixed models, post hoc tests in R and SAS

Other Skills
Management of Vegetation Data and Geographic Information Systems Turboveg, Quantum GIS (QGIS), Certificate of competence for the use of plant protection products, content management systems, customer relationship management systems

---

Scholarships & Graduate Schools

2016-Present	Member in iDiv graduate school yDiv
2013-2015	German National Academic Foundation, *Studienstiftung des deutschen Volkes* (Study Scholarship)
2013	The Germany Scholarship from the German government for students with outstanding academic achievements (study scholarship)
2012	PROMOS Scholarship from the German Academic Exchange Service, DAAD (research scholarship for a project on invasive plant species in New Zealand)
2012	Scholarship from the Bayer Science & Education Foundation

---

Publications

Dieskau, J., et al. Competition- and soil fungi-mediated priority effects differ between native and exotic European grassland plants. Submitted to *Journal of Ecology*

Dieskau, J., et al. (2024): Plant-soil feedback in European grasslands is phylogenetically independent but affected by plant species origin. *Journal of Plant Ecology*

Dieskau, J., et al. (2024): Phylogenetic relationships and plant life stage but not biogeographic history mediate priority effects of European grassland plants. *Journal of Ecology*

Stroud, J. T., **et al**. (2024): Priority effects transcend scales and disciplines in biology. *Trends in Ecology & Evolution*

Dieskau J., Bruelheide H., Gutknecht J. & Erfmeier A. (2020): Biogeographic differences in plant-soil biota relationships contribute to the invasion of *Verbascum thapsus*. *Journal of Ecology and Evolution*

Conference contributions

2024	**Dieskau**, J., Hensen, I., Eisenhauer, N., Auge, H. (2024): Competition and soil fungi mediated priority effects in native and exotic European grassland plants. Oral presentation at iDiv Annual Conference, 2024, Leipzig
2023	**Dieskau**, J., Hensen, I., Eisenhauer, N., Gaberle, I., Durka, W., Lachmuth, S., Auge, H. (2024): Phylogenetic relationships mediate priority effects of European grassland plants. Oral presentation at Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Leipzig
2018	Gaberle I., **Dieskau J.,** Durka W., Hensen I., Auge H. (2018): Does phylogenetic relatedness affect the strength of priority effects in native and exotic grassland species? Poster presentation at iDiv Annual Conference, 2018, Leipzig
2017	**Dieskau J**., Auge H., Hensen I. (2017): How do priority effects and mutual invasibility of native and exotic grassland species affect plant community assembly? Poster presentation at iDiv Annual Conference, 2017, Leipzig
2015	**Dieskau, J**., Bruelheide, H., Erfmeier, A. (2015): Exotic *Verbascum thapsus* populations: interaction with novel soil biota communities in plant invasions? Poster presentation at 45th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Göttingen

Julia Dieskau, Halle (Saale) 17.07.2025

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Priority effects in European grassland plants – how plant origin and phylogeny affect competition and plant-soil feedback“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Julia Dieskau, Halle (Saale) 17.07.2025

"Blessed are they who never read a newspaper,
for they shall see Nature, and through her, God."

Henry David Thoreau to Parker Pillsbury (Thoreau 1861)