RESEARCH ARTICLE

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

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## Abstract

1. The timing and order of species arrival have been shown to be a significant factor in the assembly of biotic communities. Therefore, understanding priority effects, which refer to the impact of an early-arriving species on a later-arriving one, can help us better predict community assembly processes. However, little is known about the role of phylogenetic distance (PD) in priority effects and how they are mediated by the biogeographic history (BH) and the life stages (LSs) of interacting species.

2. To shed light on the role of PD in priority effects, we conducted a multispecies greenhouse experiment. We created 10 allopatric and 10 sympatric species pairs, representing a PD 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 LSs.

3. We found evidence of stronger competition between closely related species, as late-arriving plants produced less above-ground biomass when the PD 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 PD. Regardless of PD, 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 PD on plant–plant interactions, our study provides experimental evidence that priority effects can be stronger when PD is small. This effect was independent of BH but varied across different LSs of late-arriving plants. The dependence of the effect of PD on the LS 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.

## 1 | INTRODUCTION

Intraspecific and interspecific plant–plant interactions affect the assembly of plant communities in complex and diverse ways (Chase, 2003a; Fukami, 2015; Götzenberger et al., 2012; HilleRisLambers et al., 2012; 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; Dunck et al., 2021; Fukami et al., 2010; Klingbeil & Willig, 2016; Toju et al., 2018). 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 (Grainger et al., 2019; Ke & Letten, 2018).

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 feedbacks, 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 (Delory et al., 2021; Grman & Suding, 2010; Heinen et al., 2020). Second, the previous reduction of shared resources by the early-arriving species (space, nutrients, light, water, etc.) can lead to asymmetric competition, both above-ground and below-ground (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 (PDs) between higher plants can indicate their ecological differences and allow predictions about their interactions. However, although many studies found a clear association between PD and the outcome of species interactions (Cadotte, 2013; Germain et al., 2016; Sheppard et al., 2018; Verdú et al., 2012; Violle et al., 2011), others did not (Cahill et al., 2008; Fitzpatrick et al., 2017; Fritschie et al., 2014; Godoy et al., 2014; Narwani et al., 2013). These contradictory results might be caused by a number of biological and methodological factors such as inappropriate phylogenies, skewed distributions of PDs, 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 PD of a colonising species (*Lactuca sativa*) with five assemblages of plants (the recipient communities) and found that neither the mean PD between *Lactuca* and the members of each assemblage nor the mean PD 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 PD on priority effects might depend on the biogeographic

history (BH) 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 (Davies et al., 2007; Nuismer & Harmon, 2015; Schluter, 1994; 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. Germain et al., 2016; Thorpe et al., 2011).

Furthermore, the role of PD 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 & Funk, 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 (Lyons & Barnes, 1998; Miriti, 2006; Müller et al., 2018; Parish & Bazzaz, 1985). 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 BH and the life stage (LS) of late-arriving species on the impact of PD on priority effects. To address this critical knowledge gap, we conducted a greenhouse study that investigated the role of PD for the priority effect of an early-arriving species on the establishment and performance of a late-arriving species. To analyse the influence of BH, 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 PD. 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 PD between them due to higher ecological similarity. (2) The importance of PD 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 PD for priority effects increases, as closely related late-arriving plants age, and become more ecologically similar to early-arriving adult plants.
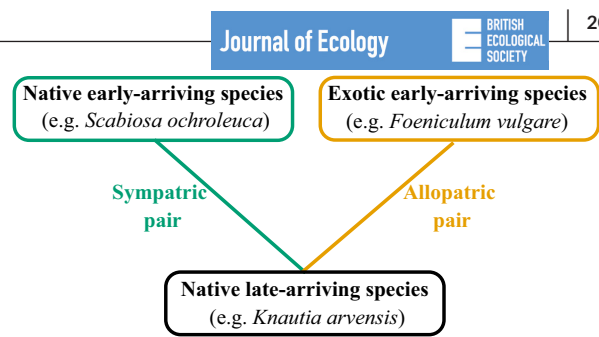


**FIGURE 1** Scheme of a triplet of species (here exemplary triplet T01) consisting of two native and one exotic species, representing a pair of sympatric species and a pair of allopatric species.

## 2 | METHODS

### 2.1 | 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 LSs 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 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 S1 for a complete list of the native and exotic species used, their taxonomic affiliation, life span and minimum residence time).

To explicitly test for the interactive effects of PD and BH, we adopted the approach of Germain et al. (2016). We created 10 triplets, each representing a gradient in PD between early- and late-arriving species, encompassing up to 270 Myr of evolutionary history since their last common ancestor (see Table S2 for PD 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 2). PDs 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 Supporting Information).
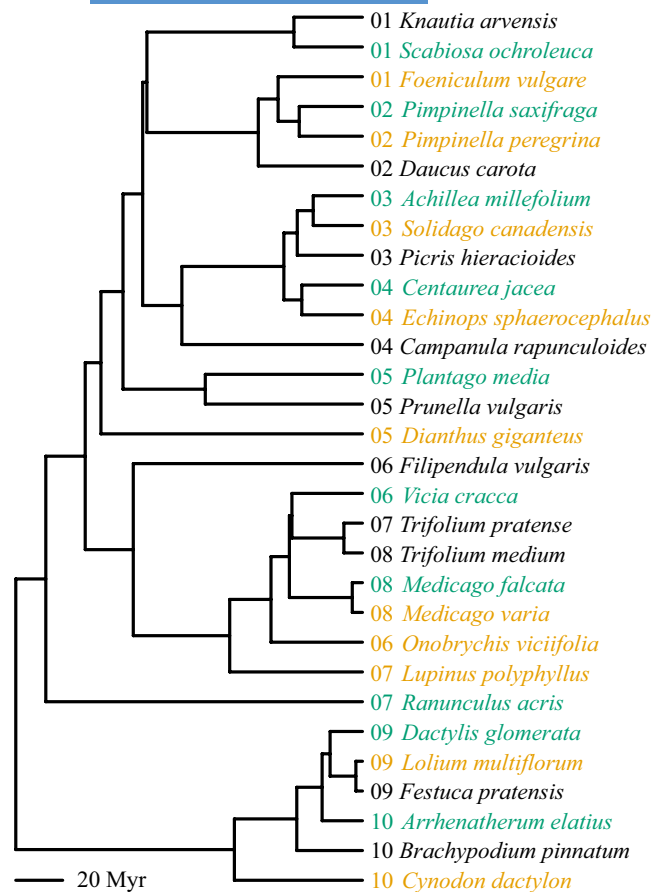
01 *Knautia arvensis*
01 *Scabiosa ochroleuca*
01 *Foeniculum vulgare*
02 *Pimpinella saxifraga*
02 *Pimpinella peregrina*
02 *Daucus carota*
03 *Achillea millefolium*
03 *Solidago canadensis*
03 *Picris hieracioides*
04 *Centaurea jacea*
04 *Echinops sphaerocephalus*
04 *Campanula rapunculoides*
05 *Plantago media*
05 *Prunella vulgaris*
05 *Dianthus giganteus*
06 *Filipendula vulgaris*
06 *Vicia cracca*
07 *Trifolium pratense*
08 *Trifolium medium*
08 *Medicago falcata*
08 *Medicago varia*
06 *Onobrychis viciifolia*
07 *Lupinus polyphyllus*
07 *Ranunculus acris*
09 *Dactylis glomerata*
09 *Lolium multiflorum*
09 *Festuca pratensis*
10 *Arrhenatherum elatius*
10 *Brachypodium pinnatum*
10 *Cynodon dactylon*

20 Myr

**FIGURE 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).

## 2.2 | 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: 22 cm). 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% (5–28 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 2 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 1–4 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×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 2 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 maximise the duration for the early-arriving plants to grow and to develop plant–soil feedbacks, an additional 2 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 4-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 minimise 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 above-ground biomass harvested and dried (72 h at 70°C) for the calculation of the mean above-ground biomass per capita for each box.

## 2.3 | Statistical analyses

For each box of each sympatric or allopatric species pair, we calculated the mean seedling emergence, seedling survival and mean above-ground biomass per survivor of the late-arriving species. To quantify the magnitude and direction of priority effects, we related seedling emergence, seedling survival and above-ground 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 PD depended on the BH and differed among the LSs of the late-arriving species, we initially fitted a model that contained PD (centred and scaled), BH (allopatric vs. sympatric pairs), LS (seedling emergence, seedling survival and above-ground 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, Kuznetsova et al., 2017; R Core Team, 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 LSs 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 LSs in more detail. First, we investigated whether the priority effect generally differed between the different LSs. 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. LS 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 LS significantly deviated from zero.

Second, we calculated separate models for seedling emergence, seedling survival and above-ground biomass and analysed the effects of PD, BH and the interaction of PD×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 PD and BH, 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 PD or BH and priority effects, careful inspection of our data points did not reveal any influential observations.

## 3 | RESULTS

The mixed-effects models evaluating the effects of PD, BH and LSs demonstrated a significant influence of LS and the interaction of PD and LS on the LRR of late-arriving plants, serving as a measure of the priority effects (Table 1).
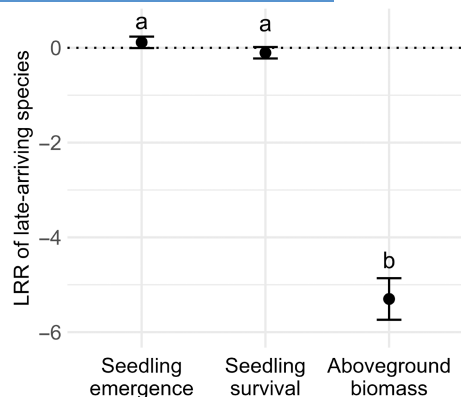
**TABLE 1** Results of the mixed-effects model analysis for the effects of phylogenetic distance, biogeographic history, life stage and their interactions on the log response ratios (LRR) of late-arriving plants. Bold $p$-values indicate significant main effects or interactions ($p < 0.05$).

| | LRR | | |
|---|---|---|---|
| | $\chi^2$ | 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 × biogeographic history | 0.0 | 1 | 0.891 |
| Phylogenetic distance × life stage | 12.0 | 2 | **0.002** |
| Biogeographic history × life stage | 0.0 | 2 | 0.989 |
| Phylogenetic distance × biogeographic history × life stage | 0.2 | 2 | 0.897 |

**FIGURE 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 above-ground biomass was significantly negative ($t = -12.096$; df $= 8.99$; $p < 0.001$).



**FIGURE 4** Relationship between the phylogenetic distance among early- and late-arriving species and the log response ratios (LRR) for above-ground biomass in late-arriving adult plants ($\chi^2 = 3.9$; 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.

Subsequent analysis of the mixed-effects model that included only BH and LSs disclosed significant variations between LSs (Figure 3). The priority effect on the early stages of seedling emergence and survival did not exhibit statistically significant differences from zero. However, the LRR for the above-ground biomass of the late-arriving species was significantly negative, indicating an inhibitory priority effect. This suggests that late-arriving adult plants produced less above-ground 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 LSs revealed that the early phases of late-arriving plants, namely seedling emergence and survival, remained unaffected by the PD to their respective early-arriving species (Figure S1). However, there was an inhibitory effect of early-arriving plants on the above-ground biomass of late-arriving plants that decreased with PD between them, represented by a significant positive correlation between the PD and the LRR of the above-ground biomass of the late-arriving species (Figure 4). On the contrary, the BH did not have a significant effect in any of the mixed-effects models we analysed, either individually or in interaction (Table 1).

# 4 | DISCUSSION

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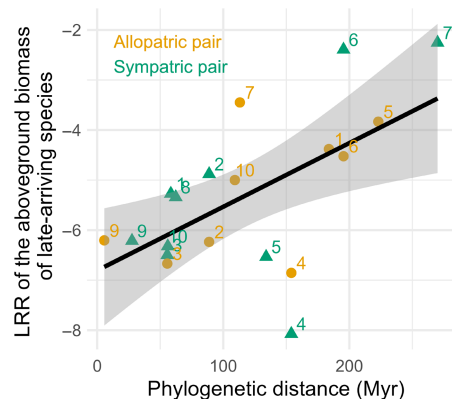
were growing with closely related early-arriving species compared to distantly related ones. However, this effect could not be demonstrated for the earlier stages of seedling emergence and survival, indicating that the impact of PD on priority effects depends on the LS of the late-arriving plants. Regardless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

## 4.1 | Inhibitory priority effects are stronger between closely related species

In accordance with our hypothesis, the inhibitory effect of early-arriving plants on the above-ground biomass of late-arriving plants decreased with the PD. 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 & Simberloff, 2005). This finding suggests that the PD 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 PD on plant–plant interactions (see, e.g. Cahill et al., 2008; Fitzpatrick et al., 2017; Fritschie et al., 2014; Godoy et al., 2014; Narwani et al., 2013). 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 PD 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 (Adler et al., 2007; Chesson, 2000) 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 PD could be used as an alternative or additional predictor for priority effects.

## 4.2 | No effect of BH on priority effects and the importance of PD

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 BH and PD. 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 and 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 & Powell, 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).

## 4.3 | The importance of PD and the strength of priority effects differ across LSs of late-arriving species

In accordance with our hypothesis, the effect of PD on priority effects differed among the investigated LSs of the late-arriving species. Regardless of PD, 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 PD. 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 PD should be interpreted with caution, as the simulated mowing of early-arriving plants 2 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 3 weeks. It is also conceivable that the effects of PD 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 LSs (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 LSs of plants to neutral or negative in the adult LSs of plants. In addition, we cannot completely exclude the possibility that the PD 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 above-ground biomass of the late-arriving plants was negative in all cases, indicating that late-arriving plants consistently produced less above-ground 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 LS because of their higher ecological similarity, as predicted by the limiting similarity hypothesis (Macarthur & Levins, 1967). Furthermore, the inhibitory priority effect on the above-ground biomass of late-arriving plants decreased with PD. 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 LSs 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.

## 5 | CONCLUSIONS

While many studies have produced contradictory results regarding the effect of PD on plant–plant interactions, we were able to demonstrate that inhibitory priority effects on the above-ground productivity of late-arriving plants can be mediated by the PD 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 PDs 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 PD. Furthermore, we recommend including the modification of arrival order, including simultaneous arrival as a control, as done, for example, by Delory et al. (2019), 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.

### AUTHOR CONTRIBUTIONS

Julia Dieskau, Harald Auge and Isabell Hensen conceived the ideas and designed methodology; Julia Dieskau and Ingmar Gaberle collected the data; Walter Durka provided the distance matrix and the phylogenetic tree; Julia Dieskau, Nico Eisenhauer and Susanne Lachmuth analysed the data; Julia Dieskau led the writing of the manuscript. Harald Auge, Isabell Hensen, Walter Durka, Nico Eisenhauer and Susanne Lachmuth contributed critically to the drafts and all authors gave final approval for publication.

### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14373.

### DATA AVAILABILITY STATEMENT

Raw data and metadata used to generate tables and figures are publicly available at the iDiv data repository: https://doi.org/10.25829/idiv.3548-bz7p93 (Dieskau et al., 2024).

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## SUPPORTING INFORMATION

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

**Figure S1.** Non-significant association between the phylogenetic distance among early- and late-arriving species and the log response ratios for (a) seedling emergence and (b) seedling survival in late-arriving adult plants, serving as an indicator of priority effect magnitude.

**Table S1.** Species list with triplet number (T01–T10), role in the experiment (EE, exotic early-arriving species; NE, native early-arriving species; NL, native late-arriving species), family, lifespan, invasion status, minimum residence time for exotic species, seed source (RH, Rieger-Hofmann GmbH, Blaufelden-Raboldshausen; Sch, Samen Schwarzenberger, Völs; Stolle, Saalesaaten Stolle, Halle).

**Table S2.** 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).