DOI: 10.1111/ddi.12708

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

It takes one to know one: Similarity to resident alien species increases establishment success of new invaders

Christine S. Sheppard[1] | Marta Carboni[2] | Franz Essl[3] | Hanno Seebens[4] | DivGrass Consortium | Wilfried Thuiller[2]

[1]Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany

[2]Univ. Grenoble Alpes, CNRS, UMR 5553, Laboratoire d'Écologie Alpine (LECA), Grenoble, France

[3]Division of Conservation, Vegetation and Landscape Ecology, University of Vienna, Wien, Austria

[4]Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany

Correspondence
Christine S. Sheppard, Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany.
Email: christine.sheppard@uni-hohenheim.de

Funding information
Austrian Science Fund, Grant/Award Number: I2086-B16; Agence Nationale de la Recherche, Grant/Award Number: ANR-13-EBID-0004; Deutsche Forschungsgemeinschaft, Grant/Award Number: SE 1891/2-1 and SH 924/1-1; Fondation pour la Recherche sur la Biodiversite

Editor: Petr Pysek

Abstract

Aim: Darwin's naturalization hypothesis states that dissimilarity to native species may benefit alien species establishment due to empty niches and reduced competition. We here add a new dimension to large-scale tests of community invasibility, investigating the role that previously established alien species play in facilitating or hindering new invasions in plant communities.

Location: Permanent grasslands across France (including mainland and Corsica), as a receding ecosystem of great conservation importance.

Methods: Focusing on 121 alien plant species occurring in 7,215 vegetation plots, we quantified biotic similarity between new invaders and resident alien species (i.e., alien species with longer residence times) based on phylogenetic and trait distances. Additionally, we calculated distances to native species for each alien species and plot. Using multispecies distribution models, we analysed the influence of these biotic similarity measures and additional covariates on establishment success (presence/absence) of new invaders.

Results: We found that biotic similarity to resident alien species consistently increased establishment success of more recently introduced species. Phylogenetic relatedness to previous invaders had an equally strong positive effect as relatedness to native species. Conversely, trait similarity to natives hindered alien establishment as predicted by Darwin's naturalization hypothesis. These results highlight that various mechanisms may act simultaneously to determine alien establishment success.

Main conclusions: Our results suggest that, with greater similarity among alien species, invasion success increases. Such a pattern may arise either due to actual facilitation among invaders or as a result of weaker competitive interactions among invaders than between native and alien species, leading to an indirect facilitative effect. Alternatively, recent environmental changes (e.g., eutrophication, climate change) may have added new environmental filters. Determining how initial invasions might pave the road for subsequent invasions is crucial for effective multispecies management decisions and contributes a new aspect to our understanding of community assembly.

KEYWORDS
alien species, biological invasion, biotic dissimilarity, community invasibility, Darwin's naturalization hypothesis, facilitation, functional trait distance, invasional interference, invasional meltdown, phylogenetic distance

1 | INTRODUCTION

Biological invasions as a major driver of global change pose a great threat to biodiversity (Lambertini et al., 2011). New invasions continue to arise, to some extent simply due to delayed responses to increasing socio-economic pressures having generated an invasion debt (Essl et al., 2011). In addition, new alien species are transported with increased global trade and new trade routes (Bradley et al., 2012; Seebens et al., 2015), and climate change can provide new opportunities for alien species to establish or spread (Sheppard, Burns, & Stanley, 2014; Walther et al., 2009). In view of this global accumulation of invaders (van Kleunen et al., 2015), it is crucial to better understand interactions among multiple alien species and their combined impacts on biodiversity.

To date, understanding what allows an alien species to establish and spread in the new range (i.e., to become invasive sensu Richardson, Pyšek, et al., 2000) has been a major research objective in ecology. In this quest, studies using a trait-based approach have shown that invasive species often share functional traits, such as high relative growth rates, high specific leaf area and smaller seed mass (Ordonez, Wright, & Olff, 2010; van Kleunen, Weber, & Fischer, 2010). These traits potentially distinguish them from native or non-invasive species and are thought to convey higher competitive ability leading to invasion success. Conversely, from the perspective of the native community, factors such as species diversity that potentially contribute to biotic resistance against invasions have received a lot of attention (Shea & Chesson, 2002). Because the ecological attributes that determine high performance are context-dependant, functional similarity among species may affect invasion success more than species richness and traits *per se* (Hooper & Dukes, 2010; Lemoine, Burkepile, & Parker, 2016; Marx, Giblin, Dunwiddie, & Tank, 2016; Ordonez, 2014). To quantify ecological differences (biotic dissimilarities) among species, two approaches have been used so far: phylogenetic and trait-based distances, which may describe different aspects of variation in function, niche and evolutionary history (Cadotte, Albert, & Walker, 2013). Phylogenetic relatedness describes evolutionary history, which is the basis for phenotypic variation and is thus used as a proxy for niche similarity (Mouquet et al., 2012; Webb, Ackerly, McPeek, & Donoghue, 2002). However, this assumption has been questioned (Mayfield & Levine, 2010; Thuiller et al., 2010), alternatively advocating for a trait-based approach (Gallien et al., 2015; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2015). Functional traits describe a species' physiology, morphology and life history strategy and thus provide a mechanistic link between fundamental biological processes and community dynamics, with the ability to achieve generalizations in community ecology (McGill et al., 2006).

Darwin originally proposed that alien species that have no close relatives in the introduced range should be more likely to establish (Darwin, 1859). This idea, coined Darwin's naturalization hypothesis (DNH), proposes that dissimilarity to native species may benefit alien species establishment due to empty niches, reduced competition or a lack of natural enemies (Darwin, 1859; Figure 1a). Conversely, Darwin also suggested that relatedness to the resident community should facilitate establishment due to similar adaptations to environmental conditions (environmental filtering). These two opposing hypotheses are jointly known as Darwin's naturalization conundrum (Diez, Sullivan, Hulme, Edwards, & Duncan, 2008; Thuiller et al., 2010). In line with the contradictory theory, empirical studies of the DNH have reported mixed results (Carboni et al., 2016; Diez et al., 2008; Park & Potter, 2013; Strauss, Webb, & Salamin, 2006). Furthermore, recent studies that considered functional similarity in addition to phylogenetic relatedness found contrasting results between the two approaches (Marx et al., 2016; Ordonez, 2014). However, all previous tests of the DNH and community invasibility, using either the standard phylogenetic approach or functional similarity, neglected the contribution of resident alien species to invasion success (Figure 1b).

In fact, in invasion biology, there has generally been a distinct lack of studies considering multiple invaders, especially for plant invasions; with a recent review finding that <6% of such studies explicitly tested interactions among invasive plant species (Kuebbing, Nuñez, & Simberloff, 2013). Across the few studies that did investigate interactions among plant invaders, negative and neutral interactions were found to be more common compared to positive ones (Kuebbing & Nuñez, 2015; with similar results also found for invasive animals; Jackson, 2015). Thus, direct or indirect antagonistic interactions may reduce invader performance ("invasional interference"; Yang, Ferrari, & Shea, 2011) or lead to transient invasions as one invader replaces another (Simberloff & Gibbons, 2004). However, positive interactions (i.e., facilitation) where two (or more) alien species benefit from each other's presence may also occur, which can lead to a scenario of "invasional meltdown" that corresponds to an increased rate of establishment or impacts of alien species (Simberloff, 2006; Simberloff & Von Holle, 1999). An example of facilitative interactions between invaders is given by Flory and Bauer (2014) who showed that the invasion by *Microstegium vimineum* indirectly facilitated a secondary invasion by *Alliara petiolata*, probably through its negative effect on native competitors of *A. petiolata* increasing resource availability. Clearly, improving our understanding of the type of interactions among multiple alien species is of great importance for management decisions (Kuebbing et al., 2013) and for building more relevant predictive models of future invasions.

In this study, we provide the first comprehensive test of whether similarity to resident alien species facilitates or hinders establishment of more invaders. We address this question using a massive vegetation plot data set for French permanent grasslands from which 121 alien species were identified (Carboni et al., 2016; Violle et al., 2015). In Europe, permanent grasslands are a receding ecosystem of great conservation importance. We quantify the influence of biotic similarity using relevant phylogenetic and trait-based distance metrics, while at the same time, accounting for other potential drivers (biotic similarities to native species, residence time, plot species richness and climatic variation) that may further influence the establishment success of alien species.

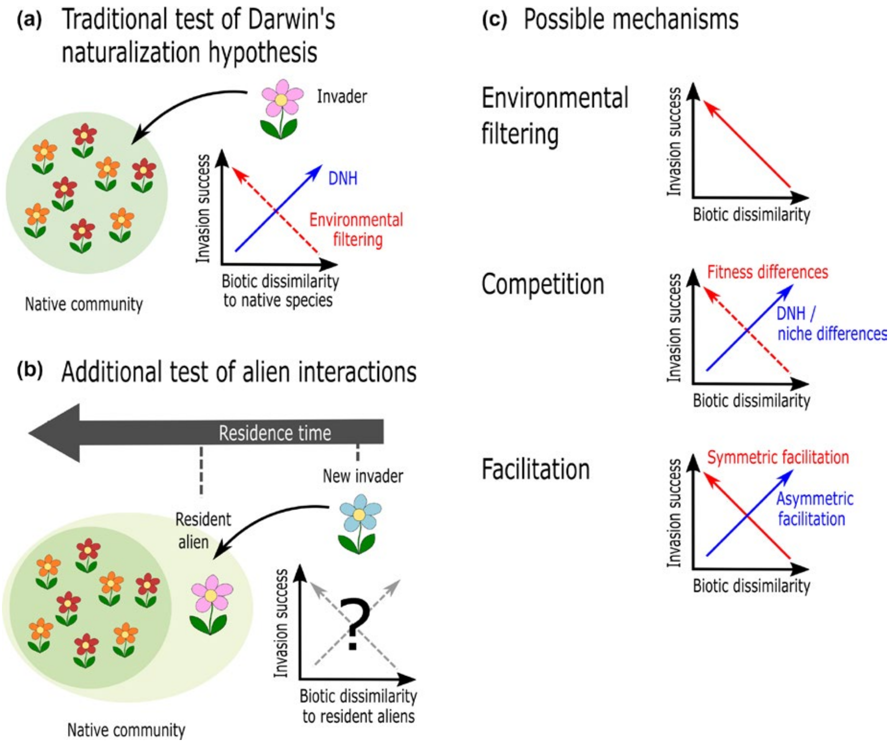

FIGURE 1 Traditional tests of Darwin's naturalization hypothesis (DNH) and our proposed extension, illustrating how biotic (phylogenetic and trait) dissimilarity influences invasion success of alien species in communities. (a) Studies so far have tested the DNH by considering biotic dissimilarity (specifically, phylogenetic distance) of a new invader to the native community: if invasion success increases with biotic dissimilarity, findings are interpreted as support of the DNH, whereas if it decreases, environmental filtering dominates. (b) With ongoing invasions, the temporal dimension of community invasibility needs to be considered: biotic dissimilarity of new invaders to alien species of longer residence times. (c) Possible mechanisms creating the patterns depicted in (a) and (b): environmental filtering may lead to decreased invasion success with biotic dissimilarity. If competition is the dominant mechanism, invasion success should increase with biotic dissimilarity as suggested by the DNH (empty niches). Conversely, increased success with decreasing dissimilarity may also result if fitness differences drive competition. If facilitation dominates, increased invasion success should be associated with lower dissimilarity in case of symmetric facilitation and higher dissimilarity in case of asymmetric facilitation. To shed light on which mechanisms apply, macroecological analyses should be complemented with an experimental approach, in which both phylogenetic and functional distances should be considered, and distances to both native and alien residents contrasted. [Colour figure can be viewed at wileyonlinelibrary.com]

2 | METHODS

2.1 | Study system: alien plant species invading French permanent grasslands

This study focused on investigating alien plant invasions in permanent grasslands across France (including Corsica), using the DivGrass database, a compilation of vegetation plot data (Violle et al., 2015). This database comprises 4,280 species occurring in more than 50,000 vegetation plots (25–100 m^2) covering four grassland types: dry calcareous grasslands, mountain grasslands, mesic grasslands and ruderal and trampled grasslands.

Of the 160 herbaceous alien species identified by Carboni et al. (2016) to have invaded these grasslands, 121 species were included in our study (with the remaining species excluded due to uncertainty regarding alien status, a lack of data on time of introduction or functional traits). The focal species' status was indicated as introduced according to the French National Inventory of the Natural Heritage database (https://inpn.mnhn.fr). Specifically, the species set included neophytes (introduced after 1492), but also 14 species that have long been cultivated but only more recently been recorded to have established in the wild. Given the uncertainty about their year of first record and invasion status, these 14 species were removed in a control analysis (see below). The complete set of 121 alien species occurred in 7,215 plots totalling 8,292 occurrences (with each species occurring in 1–2,646 plots and the maximum number of alien species per plot being seven; see Table S1). For each plot, we extracted climate information from the French meteorological model AURELHY (Bènichou & Le Breton, 1987), based on interpolated climate measurements over the period of 1971–2000 downscaled at 100 m resolution.

For the 121 alien species, we compiled the most up-to-date information on minimum residence time (MRT) to estimate the temporal sequence of establishment. These data were obtained from the Global Alien Species First Record Database (Seebens et al., 2017), providing information of the year an alien established species was first recorded in a region (here a country or subnational island). Where data for France (or if applicable, Corsica) were not available, MRT from an adjacent country was taken as a proxy (in most cases, this was Belgium, in some cases, Germany; Table S2). For 20 species that occur both in mainland France and in Corsica and for which MRT data were available for both regions, we used two separate MRT values for the mainland and island vegetation plots. Given the low prevalence of most alien species, national MRT was likely a reasonable proxy, as no mismatches between MRT and vegetation plot dates were found. MRT across the 121 species ranged from 6 to 517 years.

2.2 | Calculation of biotic dissimilarities: phylogenetic and trait-based metrics

To investigate whether biotic dissimilarity to resident alien species affects establishment of new invaders, for each species and plot, phylogenetic and trait distances to alien species of longer MRT were calculated. For phylogenetic distance, we calculated the cophenetic distance from the dated, molecular genus-level phylogeny described in Appendix S2 in Carboni et al. (2016). For the trait-based metrics, we used data on specific leaf area, plant maximum height at maturity and seed mass, extracted from databases (Carboni et al., 2016; Violle et al., 2015). Although these traits represent mean values across the global range of a species, an earlier study introducing the DivGrass database (Violle et al., 2015) showed high correlations between regionally collected traits in French permanent grasslands and traits obtained from the global database TRY (Kattge et al., 2011). Following the leaf-height-seed (LHS) plant ecology strategy scheme (Westoby, 1998), these traits describe important trade-offs between rapid growth and coping with disturbance. The few trait values that were missing for the alien species were imputed through multivariate imputation by chained equations (see Appendix S3 in Carboni et al., 2016). The three functional trait measures were then combined into one pairwise distance measure as the Euclidean distance over three standardized traits.

Based on these pairwise distances, for each alien species and for each plot, we calculated the minimum phylogenetic or trait distance to the nearest resident alien species (i.e., only alien species of longer MRT) as well as the mean phylogenetic or trait distance to all resident alien species. Similarly, we calculated the minimum and mean phylogenetic and trait distances of each alien species to all resident native species in each plot. Overall, 2,658 herbaceous native comparison species were present in the 7,215 plots where alien species occurred, of which 2,642 native species had data on phylogenetic relationships and 1,948 had data on traits to calculate distances. Additionally, we calculated the total plot species richness.

2.3 | Analysis of establishment success

Establishment success (presence/absence) of alien species was analysed in R (v 3.3.2 for Windows; R Core Team 2016), employing a generalized linear mixed model (GLMM) approach with a binomial error distribution and logit link, using the LME4 package (Bates, Maechler, Bolker, & Walker, 2014). Although 121 alien species were available to calculate biotic dissimilarities (see above), the analysis of establishment success was based on 74 focal species: those occurring in sites where resident alien species were present. A control analysis was carried out excluding 14 potentially archaeophytic species, resulting in 107 species to calculate biotic dissimilarities and 65 in the analysis of establishment success.

Instead of analysing alien species independently by building single species statistical models, we used a multispecies distribution model (multi-SDM) to estimate the joint probability of establishment of all alien species (Jamil, Ozinga, Kleyer, & ter Braak, 2013; Warton et al., 2015) in function of biotic dissimilarities and other covariates (MRT, species richness, climate). Multi-SDMs allow for rare species to be included, allowing a more accurate estimate of the mean community-level response (Ovaskainen & Soininen, 2011). This is of particular benefit in our study system where alien species prevalence is low in many cases. In the full model, fixed effects included minimum (or mean) phylogenetic distance to resident alien species, minimum (or mean) trait distance to resident alien species, minimum (or mean) phylogenetic distance to native species, minimum (or mean) trait distance to native species, MRT of the focal alien species, species richness of the plot, annual precipitation and mean annual temperature. We included MRT because the length of time a species has had to spread has been shown to greatly affect its establishment success (Lavoie, Shah, Bergeron, & Villeneuve, 2013; Pyšek et al., 2015; Williamson et al., 2009; Wilson et al., 2007). Species richness was used to describe potential differences among plots (e.g., competitive pressure, empty niche space, resource availability and hence also invasibility) using a quantitative measure. To account for general climatic variation among plots, we used annual precipitation and mean annual temperature as two non-correlated, integrative climatic variables shaping temperate grasslands (Cain, 1944). Random effects (varying intercepts) included species and plot. Pairwise Spearman rank correlations between explanatory variables were all below <0.7 (Table S3). All explanatory variables were centred and scaled by dividing by their standard deviation. The minimum adequate model was then obtained by individually removing the least significant variables and applying likelihood ratio tests. The variance explained (R^2) was calculated using the function rsquared.glmm in the package MuMIn (Nakagawa & Schielzeth, 2013). To compare models using minimum or mean biotic dissimilarity measures, differences in AIC (Akaike's information criterion) are reported. Residual spatial autocorrelation was checked for using Moran's I plots in the NCF package (Bjornstad, 2015; Figure S1).

In our model, we used presence–absence ("establishment success") of each species as a response variable. However, given the high number of plots available in the database (leading to many observed absences compared to presences), we used an absence-selection procedure to avoid including absence sites that were ecologically unreasonable due to (1) environmental suitability (habitat type), (2) time since introduction, or (3) dispersal limitations. To do so, absences were first filtered based on the grassland type (i.e., one of the following: dry calcareous grasslands, mountain grasslands, mesic grasslands and ruderal and trampled grasslands), meaning that only absences from the grassland types where the species could potentially occur (i.e., with at least one presence record) were considered in the models. Second, absences were only included in the models if the date the vegetation plot was sampled was more recent than the MRT of the focal species (notably, for presence points, no mismatch between MRT and vegetation plot date was detected). These two steps resulted in 1,071 presence (1–324 per species) and 77,857 absence records occurring in 6,915 plots (Figure S2, Table S4), which we used to run a first GLMM (referred to as the model using all absence data). In a third step, to account for dispersal limitation, the analysis was repeated only including those absences that fall within a given distance to presence sites, with a 100, 50 or 25 km radius around presence sites (Figure S2, Table S4). This was done to ensure that the results were robust when absences were only considered if the species was likely to have had the opportunity to disperse to the sites where it was recorded to be absent.

3 | RESULTS

We present results for the analyses that only included absences selected among vegetation plots occurring within a 50 km distance radius around presence plots (i.e., accounting for intermediate dispersal limitation; Table 1, Figures 2 and 3), but note that the results from the various analyses of establishment success were qualitatively very similar (Table S5).

Across all analyses, smaller phylogenetic and trait distances to resident alien species increased establishment success of new invaders (Figures 2, 3 and S4, Tables 1 and S5). Effect sizes of phylogenetic distance were similar across all models, but the effect size of trait distance was higher for models including only absences within a smaller radius around presence sites (and not significant in the models using all absence data, Table S5). A negative effect of phylogenetic distance on establishment success was also found with respect to native species (Figures 2 and 3). Conversely, mean trait distance to native species had a positive effect on establishment success: alien species were more likely to establish in plots where they were less similar to native species (Figure 3). For models using minimum distances, trait distances to native species were not significant (Table S5). As the calculations of dissimilarity measures were based on a small number of alien comparison species, values for minimum and mean phylogenetic or trait distances were generally very similar, whereas, for dissimilarities to native species, minimum distances were lower than mean distances (Figures S3 and S4).

All other explanatory variables were retained in the minimum adequate models (Table S5). Longer MRT increased establishment success (Figures 2, 3 and S4, Tables 1 and S5). Establishment success of alien species also increased with species richness and mean annual temperature and decreased with annual precipitation. The control analysis excluding 14 potentially archaeophytic species (long since cultivated but with more recent first record in the wild) showed qualitatively similar results, with stronger effects of alien trait distances (Figures S6 and S7, Table S6).

4 | DISCUSSION

Our analysis consistently showed that biotic similarity to resident alien species increased establishment success (measured as probability of presence) of new invaders at the vegetation plot level, regardless of whether a minimum or mean distance measure was used and whether all absences or only those within a given dispersal distance radius around presence sites were considered. As we discuss below, higher success with greater similarity among invaders may arise because similarity of new invaders to resident alien species

TABLE 1 Parameter estimates and standard errors (in parentheses) of the full and minimum adequate multispecies distribution models that included absences only within a distance radius of 50 km around presence sites. Significant explanatory variables (based on likelihood ratio tests) are indicated by $^{**}p < .01$; $^{***}p < .001$. R^2 (marginal R^2 and in parentheses conditional R^2) is indicated as well as AIC and differences in AIC (ΔAIC) compared to the model with the lowest AIC

	Minimum distances		Mean distances
Explanatory variable	Full model	Minimum adequate model	Full model = min. adequate model
Alien phylogenetic distance	−0.354 (0.043)***	−0.354 (0.043)***	−0.324 (0.044)***
Alien trait distance	−0.199 (0.072)***	−0.198 (0.069)**	−0.254 (0.072)***
Native phylogenetic distance	−0.332 (0.052)***	−0.331 (0.052)***	−0.265 (0.054)***
Native trait distance	0.006 (0.070)		0.354 (0.070)***
Minimum residence time	0.487 (0.116)***	0.487 (0.116)***	0.461 (0.119)***
Species richness	0.277 (0.033)***	0.277 (0.033)***	0.360 (0.032)***
Annual precipitation	−0.260 (0.045)***	−0.260 (0.045)***	−0.244 (0.045)***
Mean annual temperature	0.222 (0.046)***	0.222 (0.046)***	0.233 (0.047)***
R^2 (%)	17.2 (34.1)	17.2 (34.0)	14.5 (34.6)
AIC	6,913.3	6,911.3	6,928.5
ΔAIC	+2.0	0	+17.2

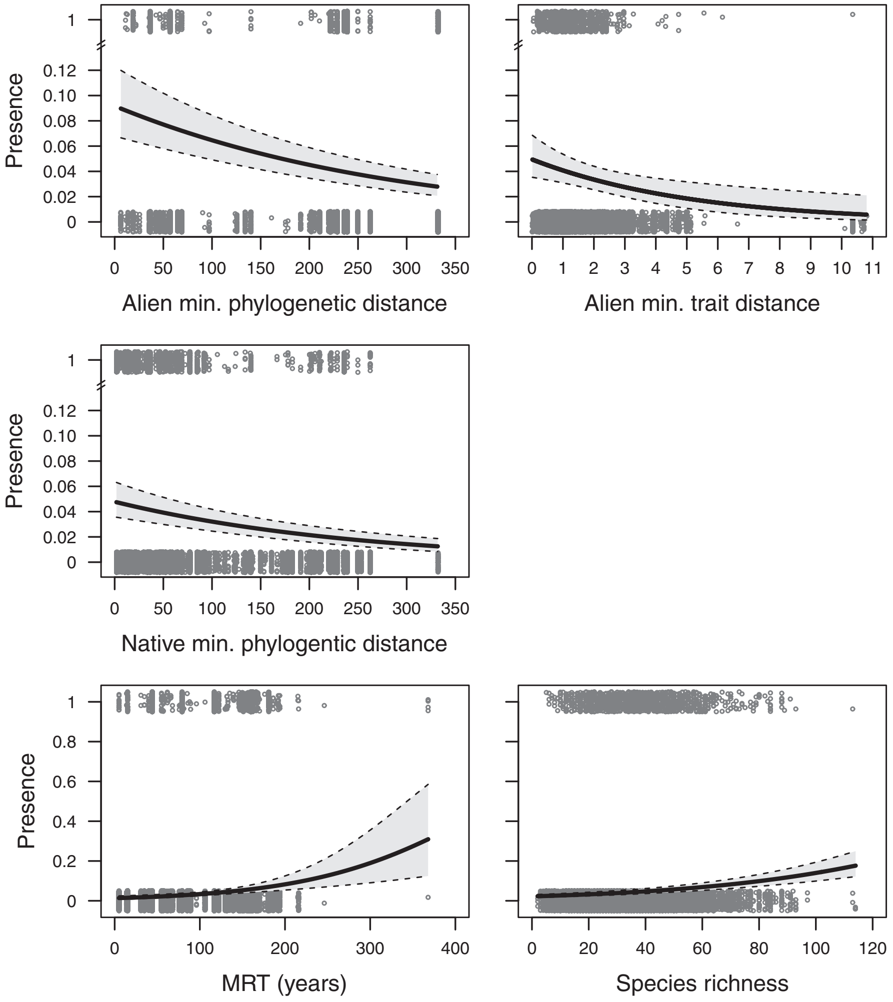

FIGURE 2 Joint modelled probability of alien establishment in function of *minimum* phylogenetic distance and *minimum* trait distance of new invaders to resident alien species (top row); *minimum* phylogenetic distance to native species (middle row); and minimum residence time (MRT) of the focal alien species and species richness per plot (bottom row). Model predictions (bold line) and 95% confidence intervals (light grey shaded area) are from the minimum adequate model that included absences only within a radius of 50 km around presence sites, with all other explanatory variables held at their median values. Actual data are jittered around 0 (absence) and 1 (presence) for better visibility

facilitates invasions, either directly or mediated via relative interaction strengths. Alternatively, such a pattern may arise as a result of fitness differences driving alien–alien competition or recent environmental changes (e.g., eutrophication, climate change) having added new abiotic filters. For biotic similarity to native species, conflicting results of phylogenetic versus trait distance were found, highlighting that various mechanisms may act simultaneously: although new invaders benefit from greater relatedness possibly indicating adaptation to the local environment, they succeed using different functional strategies than the natives (as suggested by the DNH).

4.1 | Mechanisms leading to the biotic similarities and invasion success patterns

Tests of the DNH have produced conflicting results, which led previous studies to discuss the importance of spatial scale (Carboni et al., 2016; Diez et al., 2008). At large spatial scales with low resolution, environmental filtering signals may mask signals of biotic interaction (Diez et al., 2008; Thuiller et al., 2010), as shown for example by the contrasting results of two studies in California that investigated phylogenetic relatedness of invasive alien species to the regional native community in comparison with non-invasive alien species (Park & Potter, 2013; Strauss et al., 2006). Our large-scale analysis is instead focused on interactions in realized species compositions at the fine resolution of vegetation plots of one broad ecosystem type (permanent grasslands) that are located across one country (France), and thus the DNH should more likely hold true. As we are specifically interested in biotic interactions, we further deliberately reduced potential effects of environmental filtering by only including absence records from grassland types where a species has been shown to occur, using limited dispersal distances and accounting for the influence of climatic variation among plots on establishment success.

While we did not expect a strong signal of environmental filtering, we found mixed results, with alien species more likely to establish in plots where they have closely related native species, but then being ecologically dissimilar to the natives based on traits. Such a result is in line with previous findings by Marx et al. (2016) and Ordonez (2014), suggesting that to successfully invade, alien species must be similar in certain aspects to pass environmental filters and yet functionally different enough to persist by exploiting empty niches. By considering biotic similarity to resident alien species in the community, our study adds a new and important dimension, the temporal sequence of invasions, to the challenge of resolving Darwin's naturalization conundrum (Figure 1b). Interestingly, our results showed that phylogenetic

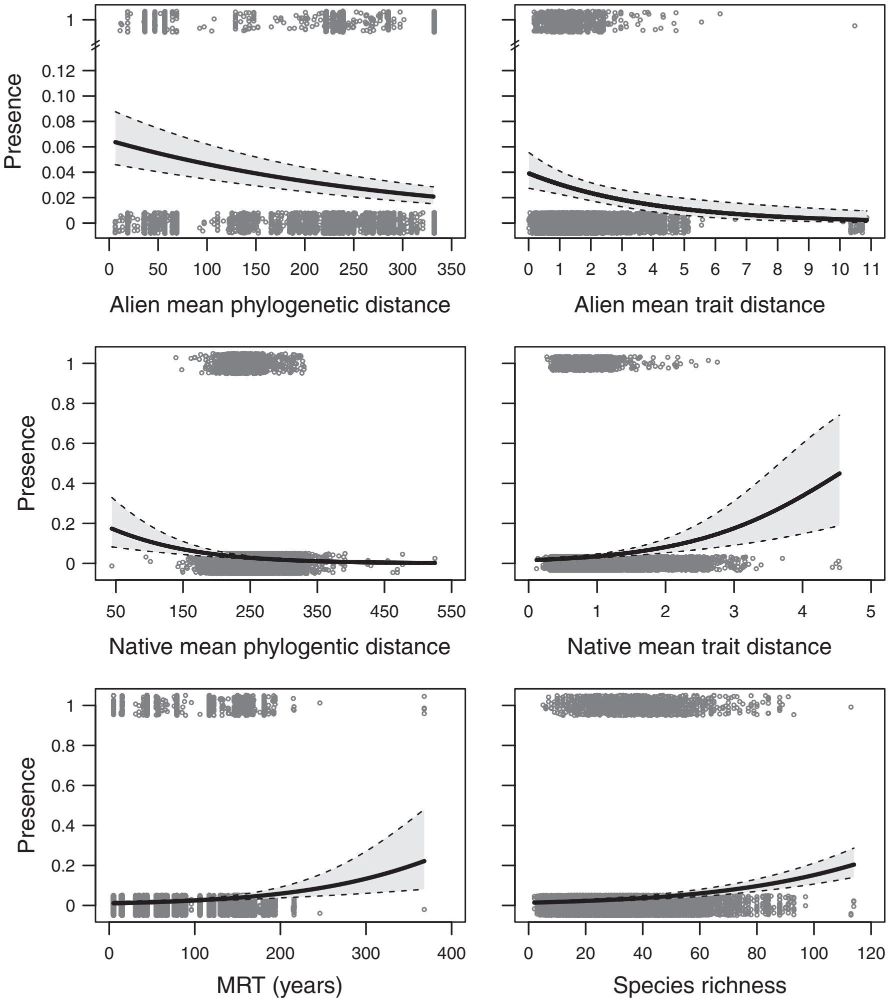

FIGURE 3 Joint modelled probability of alien establishment in function of mean phylogenetic distance and mean trait distance of new invaders to resident alien species (top row); mean phylogenetic and mean trait distance to native species (middle row); and minimum residence time (MRT) of the focal alien species and species richness per plot (bottom row). Model predictions (bold line) and 95% confidence intervals (light grey shaded area) are from the full model (= minimum adequate model) that included absences only within a radius of 50 km around presence sites, with all other explanatory variables held at their median values. Actual data are jittered around 0 (absence) and 1 (presence) for better visibility

distance to resident alien species had an equally strong negative effect on establishment success as distance to native species (although the two variables were not correlated, Figure S4), whereas results for trait distance to aliens opposed those for trait distance to natives.

These results thus suggest that while competition drives native–alien interactions in French grassland communities (resulting in functional dissimilarity), there is either no strong competition among aliens or possibly even facilitation (allowing similar species to coexist). Indeed, environmental filtering is unlikely to be the dominant mechanism driving the establishment of new invaders because if it was, we should find signatures for both alien–native and alien–alien functional patterns. However, if recent environmental change has added new filters (e.g., Bobbink et al., 2010), this could possibly explain similarity to resident aliens but not natives and potentially contribute to the observed patterns. More likely, however, we see two biotic mechanisms that may explain that invader similarity increases establishment success and which can lead to more invaders establishing even in the presence of other invaders (Kuebbing et al., 2013; van Kleunen et al., 2015). First, if the relative strength of competitive interactions between invaders is lower than between native and alien species, then such a scenario may indirectly facilitate establishment of more invaders (Kuebbing & Nuñez, 2016). A recent meta-analysis on plant interactions supports this idea, showing that the negative effect of alien plants on native species was double compared to on other alien plants (Kuebbing & Nuñez, 2016). If, due to a negative effect of the resident alien species on native species, the magnitude of an indirect positive effect experienced by the new invader is greater than the direct negative effect among invaders, overall, a facilitative effect results (Callaway & Walker, 1997).

Second, another possible explanation for our results is that actual facilitation could be relevant for alien plant–plant interactions, with the relative strength of facilitation more important with greater similarity among alien species (i.e., symmetric facilitation, Figure 1c). Although mutualisms between trophic levels have been well appreciated, facilitation within trophic levels has received less attention. Yet, McIntire and Fajardo (2014) pointed out that facilitation is a “ubiquitous driver of biodiversity”, and positive interactions such as facilitation or mutualisms may also influence invasion success (Mitchell et al., 2006). Hence, facilitation needs to be integrated into theory of community phylogenetics (Elias, Gompert, Willmott, & Jiggins, 2009). Understanding facilitative interactions could be highly relevant for invasions if invasional meltdowns may be a consequence (Simberloff, 2006; Simberloff & Von Holle, 1999). The magnitude of symmetric facilitation among co-occurring invaders (e.g., to what degree species may benefit from shared pollinators, seed dispersers or mycorrhizal fungi) is expected to increase with greater phylogenetic relatedness (Mitchell et al., 2006; Figure 1c), which could be particularly important when the invaders are different to the native species. For example, having close relatives in the community reduced pollen limitation of the annual plant *Lasthenia fremontii* (Sargent, Kembel, Emery, Forrestel, & Ackerly, 2011). Enhanced pollinator services could arise either just due to increased flower density or due to one alien species acting as a magnet species benefitting the other invader (Molina-Montenegro, Badano, & Cavieres, 2008).

Conversely, other facilitative mechanisms may more likely occur between more distantly related species (i.e., asymmetric facilitation, Figure 1c), as facilitation has been shown in some cases to lead to phylogenetic divergence (Valiente-Banuet & Verdú, 2007). Such conflicting patterns have also been discussed for competitive mechanisms, which may be either based on niche differences that favour coexistence or fitness differences that drive competitive exclusion (Chesson, 2000). Depending on the strength of the respective underlying mechanisms (i.e., niche overlap versus weaker competitor exclusion), trait divergence or convergence in a community may result (Kraft et al., 2015; Mayfield & Levine, 2010). Hence, elucidating the biotic interactions at play is particularly challenging. Indeed, if competitive interactions among aliens are driven by fitness differences rather than empty niches, establishment success of functionally different invaders could be reduced (i.e., exclusion of weaker alien competitors), providing yet another explanation for our observed pattern (Figure 1c). For example, for fish introductions in Swedish lakes, Henriksson, Wardle, Trygg, Diehl, and Englund (2016) showed that species with high invasion success also contributed high biotic resistance against further invasions (but without testing how this may be driven by biotic dissimilarities).

4.2 | Limitations to the interpretation of the analysis

Clearly, the numerous direct or indirect biotic interactions acting in concert, as well as the multitude of ways in which these mechanisms translate into biotic similarity indices (Figure 1c), make generalizations and predictions of invasion success inherently challenging. We note that results may depend on the indices used to quantify biotic similarity. Adding a trait-based approach to community phylogenetics will help disentangle mechanisms and contribute to deconstruct Darwin's naturalization conundrum (Marx et al., 2016). However, the opposing results for the effect of trait distance to native and alien species may depend on the specific traits selected. The traits we used are highly relevant to study community invasibility as they are related to competitive performance, but we note that SLA, plant height and seed mass have often been shown to differ between alien and native species (Ordonez et al., 2010; van Kleunen et al., 2010). For our study species of 121 alien and 1,948 native species with trait data, SLA did not differ across the two groups (with a median of 22.7 vs. 21.7 m^2/kg), but plant height (0.7 vs. 0.4 m) and seed mass (1.7 vs. 0.8 mg) were higher for alien compared to native species. Because establishment success is higher with functional distance to the native community, this suggests that such trait differentiation is important at the community level. However, similar or closely related native species could also have gone locally extinct as a consequence of invasion (as shown by Li et al., 2015; using time series data). Furthermore, we note that we used mean trait values, whereas ideally locally collected trait data would be preferable given recent debates on the importance of inter- versus intraspecific trait variability (e.g., Albert et al., 2012; Siefert et al., 2015; Violle et al., 2012). On a similar note, we acknowledge the constraint of lacking plot-scale invasion data. However, given that the regional MRTs we used span a large time period (500 years), local invasion sequence is likely following regional sequence in the majority of cases.

A central point to consider is that the effect of similarity on interaction strength and the general applicability of the positive effect of biotic similarity among invaders in French permanent grasslands may also depend on species numbers or abundance. Plant density affects the relative strength of competition and facilitation (Callaway & Walker, 1997). One example would be a positive effect of attracting shared pollinators, which at high densities may then become competitive (Yang et al., 2011). Hence, it may be beneficial to be similar as long as only few species are present (or only at low densities), but once there are many (or highly abundant), similarity may cease to be beneficial (this could potentially explain the negative effect of mean distance to native species, but positive effect to alien species). To test this idea, a more heavily invaded study system would need to be investigated. Within our study system, we assessed the potential influence of the number of alien species co-occurring per plot on the calculation of the distance measures: minimum distance to resident alien species decreases with the number of species the calculation is based on, and mean distance tends to increase with the variance tending to decrease; however, these trends are weak as indicated by the generally high standard deviation and they are similar across presence–absences sites (Figure S5). Thus, we consider our analysis to be robust to the calculation of dissimilarity measures, but note that our conclusions may not extrapolate to ecosystems with higher alien species richness.

Finally, although we found that biotic similarity to resident alien species increased establishment success, this may not hold true for other aspects of invader performance (as e.g., shown in the contrasting results of establishment success versus biomass production in an experimental study of invader interactions; Flory & Bauer, 2014) and should thus be further investigated in other studies. In a next step, to clearly link the observed patterns to processes and assess the relative importance of simultaneous interaction types, experimental tests are necessary (e.g., see Violle, Nemergut, Pu, & Jiang, 2011 for an example of a microcosm study on protists that confirmed increasing competition with decreasing phylogenetic distance). In an experimental setting, the number and density of invaders can be specifically manipulated and the influence of the choice of traits and various performance measures studied to better elucidate the mechanisms at play and test the hypotheses proposed in this study.

4.3 | Importance for conservation

Even given these limitations, our study raises some important issues concerning the management of plant invasions. MRT consistently had a strong effect on establishment success, as expected from results of previous studies (Lavoie et al., 2013; Pyšek et al., 2015; Williamson et al., 2009; Wilson et al., 2007). Indeed, if residence time is not accounted for, the role of traits may be overestimated (Pyšek et al., 2015). Notably, the strong effect of MRT on establishment success supports the well-established view that early control measures are most effective when managing biological invasions. However, as the reality of conservation involves multiple invaders, more studies are needed to address interactions among alien species and how these may affect their impacts (Kuebbing et al., 2013). Should resident alien species facilitate the invasion of further alien species, early control becomes even more crucial. In invasion ecology, there has been a focus towards biotic resistance and the role of natural enemies rather than positive interactions (Richardson, Allsopp, D'Antonio, Milton, & Rejmánek, 2000), which is in line with the general bias in ecological theory and empirical research in favour of competition as the dominant biotic interaction structuring communities. Yet, in addition to our main finding that invader similarity increases establishment success, we also found the surprising result that species richness per plot had a positive effect on establishment success of alien species, raising additional concern for conservation management. However, species richness itself is not as informative to elucidate potential mechanisms at play compared to descriptions of functional diversity and distance, and many of the same limitations as discussed above in regards to biotic dissimilarity measures apply. Also, we note that comparability of species richness among plots is limited because the plot sizes in our data set are not constant. However, this bias should be rather limited as varying plot sizes reflect the optimal sampling of homogeneous communities and experience with vegetation plots in European grasslands shows that few species are added beyond plot sizes of 25 m^2 (Dierschke, 1994). One explanation for the positive diversity–invasibility relationship is that even at this regional scale, environmental conditions may generally be more favourable in some plots compared to others, exceeding biotic resistance effects due to species richness. Another possible explanation is given by Bulleri, Bruno, and Benedetti-Cecchi (2008), however, who argue that such a pattern could arise because of a higher probability of including facilitators. Clearly, a better understanding of how both positive and negative biotic interactions (and specifically, the quantification of interaction strengths) shape communities is crucial for conservation. Better predictions of when facilitation among invaders and possibly even a case of invasional meltdown is likely and how it is determined by ecological attributes of the species involved will assist in directing management efforts most effectively.

5 | CONCLUSIONS

Following 500 years of species introductions around the globe and the ongoing arrival of new species facilitated by global change and trade, it is urgent to consider the effects of resident alien species on invasion success of subsequent invaders. Our study provides novel insights into how biotic similarity to resident alien species may affect new invaders. The generality of our principal finding that invader similarity may increase invasion success needs to be tested across other study systems. Inference of the actual ecological mechanisms at play is difficult from observed species associations, as various processes such as a multitude of biotic interactions and habitat requirements could produce these patterns. One hypothesis based on our results is that with greater invader similarity, invasion success increases possibly due to greater facilitation or relative interaction strengths leading to an overall facilitative effect. Whether this hypothesis applies or the suggested alternatives (competition driven by fitness differences or abiotic filtering based on recent environmental changes) should now be tested with an experimental approach to provide conclusive evidence. Determining how initial invasions pave the road for subsequent invasions contributes a new aspect to our understanding of community assembly and has important implications for multispecies management decisions and conservation of permanent grasslands.

ACKNOWLEDGEMENTS

We acknowledge the contribution of the DivGrass Consortium, who compiled the vegetation plot data used in this research, supported by the French Foundation for Research on Biodiversity (FRB; www.fondationbiodiversite.fr) in the context of the CESAB project "Assembling, analysing and sharing data on plant functional diversity to understand the effects of biodiversity on ecosystem functioning: a case study with French Permanent Grasslands" (DivGrass). C.S.S. and H.S. received funding from the German Research Foundation DFG (grants SH 924/1-1 and SE 1891/2-1). F.E. was supported by the Austrian Science Foundation FWF (grant I2086-B16). M.C., F.E. and W.T. acknowledge support by the ERA-Net BiodivERsA, with the national funders ANR (ANR-13-EBID-0004), DFG and FWF, part of the 2013 BiodivERsA call (project "WhoIsNext").

ORCID

Christine S. Sheppard http://orcid.org/0000-0002-7847-2310
Franz Essl http://orcid.org/0000-0001-8253-2112
Wilfried Thuiller http://orcid.org/0000-0002-5388-5274
Marta Carboni http://orcid.org/0000-0002-9348-4758
Hanno Seebens http://orcid.org/0000-0001-8993-6419

REFERENCES

Albert, C. H., de Bello, F., Boulangeat, I., Pellet, G., Lavorel, S., & Thuiller, W. (2012). On the importance of intraspecific variability for the quantification of functional diversity. *Oikos*, *121*, 116–126. https://doi.org/10.1111/j.1600-0706.2011.19672.x

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7. Retrieved from http://CRAN.R-project.org/package=lme4

Bènichou, P., & Le Breton, O. (1987). Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *La Météorologie*, *7*, 23–24.

Bjornstad, O. N. (2015). *ncf: Spatial nonparametric covariance functions*. R package version 1.1-6. Retrieved from https://CRAN.R-project.org/package=ncf

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., … De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*, 30–59. https://doi.org/10.1890/08-1140.1

Bradley, B. A., Blumenthal, D. M., Early, R., Grosholz, E. D., Lawler, J. J., Miller, L. P., … Olden, J. D. (2012). Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment*, *10*, 20–28. https://doi.org/10.1890/110145

Bulleri, F., Bruno, J. F., & Benedetti-Cecchi, L. (2008). Beyond competition: Incorporating positive interactions between species to predict ecosystem invasibility. *PLOS Biology*, *6*, e162. https://doi.org/10.1371/journal.pbio.0060162

Cadotte, M., Albert, C. H., & Walker, S. C. (2013). The ecology of differences: Assessing community assembly with trait and evolutionary distances. *Ecology Letters*, *16*, 1234–1244. https://doi.org/10.1111/ele.12161

Cain, S. A. (1944). *Foundations of plant geography*. New York, NY: Harper & Brothers Publishers.

Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation – a synthetic approach to interactions in plant communities. *Ecology*, *78*, 1958–1965. https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2

Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C., … Thuiller, W. (2016). What it takes to invade grassland ecosystems: Traits, introduction history and filtering processes. *Ecology Letters*, *19*, 219–229. https://doi.org/10.1111/ele.12556

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Darwin, C. R. (1859). *The origin of species*. London, UK: John Murray.

Dierschke, H. (1994). *Pflanzensoziologie – Grundlagen und Methoden*. Stuttgart, Germany: Verlag Eugen Ulmer.

Diez, J. M., Sullivan, J. J., Hulme, P. E., Edwards, G., & Duncan, R. P. (2008). Darwin's naturalization conundrum: Dissecting taxonomic patterns of species invasions. *Ecology Letters*, *11*, 674–681. https://doi.org/10.1111/j.1461-0248.2008.01178.x

Elias, M., Gompert, Z., Willmott, K., & Jiggins, C. (2009). Phylogenetic community ecology needs to take positive interactions into account. *Communicative & Integrative Biology*, *2*, 113–116. https://doi.org/10.4161/cib.7718

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hülber, K., Jarošík, V., … Pyšek, P. (2011). Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 203–207. https://doi.org/10.1073/pnas.1011728108

Flory, S. L., & Bauer, J. T. (2014). Experimental evidence for indirect facilitation among invasive plants. *Journal of Ecology*, *102*, 12–18. https://doi.org/10.1111/1365-2745.12186

Gallien, L., Mazel, F., Lavergne, S., Renaud, J., Douzet, R., & Thuiller, W. (2015). Contrasting the effects of environment, dispersal and biotic interactions to explain the distribution of invasive plants in alpine communities. *Biological Invasions*, *17*, 1407–1423. https://doi.org/10.1007/s10530-014-0803-1

Henriksson, A., Wardle, D. A., Trygg, J., Diehl, S., & Englund, G. (2016). Strong invaders are strong defenders – implications for the resistance of invaded communities. *Ecology Letters*, *19*, 487–494. https://doi.org/10.1111/ele.12586

Hooper, D. U., & Dukes, J. S. (2010). Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology*, *98*, 764–777. https://doi.org/10.1111/j.1365-2745.2010.01673.x

Jackson, M. C. (2015). Interactions among multiple invasive animals. *Ecology*, *96*, 2035–2041. https://doi.org/10.1890/15-0171.1

Jamil, T., Ozinga, W. A., Kleyer, M., & ter Braak, C. J. F. (2013). Selecting traits that explain species–environment relationships: A generalized linear mixed model approach. *Journal of Vegetation Science*, *24*, 988–1000. https://doi.org/10.1111/j.1654-1103.2012.12036.x

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., … Wirth, C. (2011). TRY: A global database of plant traits. *Global Change Biology*, *17*, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*, 592–599. https://doi.org/10.1111/1365-2435.12345

Kuebbing, S. E., & Nuñez, M. A. (2015). Negative, neutral, and positive interactions among nonnative plants: Patterns, processes, and management implications. *Global Change Biology*, *21*, 926–934. https://doi.org/10.1111/gcb.12711

Kuebbing, S. E., & Nuñez, M. A. (2016). Invasive non-native plants have a greater effect on neighbouring natives than other non-natives. *Nature Plants*, *2*, 16134. https://doi.org/10.1038/nplants.2016.134

Kuebbing, S. E., Nuñez, M. A., & Simberloff, D. (2013). Current mismatch between research and conservation efforts: The need to study co-occurring invasive plant species. *Biological Conservation*, *160*, 121–129. https://doi.org/10.1016/j.biocon.2013.01.009

Lambertini, M., Leape, J., Marton-Lefèvre, J., Mittermeier, R. A., Rose, M., Robinson, J. G., … Genovesi, P. (2011). Invasives: A major conservation threat. *Science*, *333*, 404–405. https://doi.org/10.1126/science.333.6041.404-b

Lavoie, C., Shah, M. A., Bergeron, A., & Villeneuve, P. (2013). Explaining invasiveness from the extent of native range: New insights from plant atlases and herbarium specimens. *Diversity and Distributions*, *19*, 98–105. https://doi.org/10.1111/ddi.12014

Lemoine, N. P., Burkepile, D. E., & Parker, J. D. (2016). Quantifying differences between native and introduced species. *Trends in Ecology & Evolution*, *31*, 372–381. https://doi.org/10.1016/j.tree.2016.02.008

Li, S., Cadotte, M. W., Meiners, S. J., Hua, Z., Shu, H., Li, J., & Shu, W. (2015). The effects of phylogenetic relatedness on invasion success and impact: Deconstructing Darwin's naturalisation conundrum. *Ecology Letters*, *18*, 1285–1292. https://doi.org/10.1111/ele.12522

Marx, H. E., Giblin, D. E., Dunwiddie, P. W., & Tank, D. C. (2016). Deconstructing Darwin's Naturalization Conundrum in the San Juan Islands using community phylogenetics and functional traits. *Diversity and Distributions*, *22*, 318–331. https://doi.org/10.1111/ddi.12401

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, *13*, 1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

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

McIntire, E. J. B., & Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*, *201*, 403–416. https://doi.org/10.1111/nph.12478

Mitchell, C. E., Agrawal, A. A., Bever, J. D., Gilbert, G. S., Hufbauer, R. A., Klironomos, J. N., … Vazquez, D. P. (2006). Biotic interactions and plant invasions. *Ecology Letters*, *9*, 726–740. https://doi.org/10.1111/j.1461-0248.2006.00908.x

Molina-Montenegro, M. A., Badano, E. I., & Cavieres, L. A. (2008). Positive interactions among plant species for pollinator service: Assessing the "magnet species" concept with invasive species. *Oikos*, *117*, 1833–1839. https://doi.org/10.1111/j.0030-1299.2008.16896.x

Mouquet, N., Devictor, V., Meynard, C. N., Munoz, F., Bersier, L.-F., Chave, J., … Thuiller, W. (2012). Ecophylogenetics: Advances and perspectives. *Biological Reviews*, *87*, 769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Ordonez, A. (2014). Functional and phylogenetic similarity of alien plants to co-occurring natives. *Ecology*, *95*, 1191–1202. https://doi.org/10.1890/13-1002.1

Ordonez, A., Wright, I. J., & Olff, H. (2010). Functional differences between native and alien species: A global-scale comparison. *Functional Ecology*, *24*, 1353–1361. https://doi.org/10.1111/j.1365-2435.2010.01739.x

Ovaskainen, O., & Soininen, J. (2011). Making more out of sparse data: Hierarchical modeling of species communities. *Ecology*, *92*, 289–295. https://doi.org/10.1890/10-1251.1

Park, D. S., & Potter, D. (2013). A test of Darwin's naturalization hypothesis in the thistle tribe shows that close relatives make bad neighbors. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 17915–17920. https://doi.org/10.1073/pnas.1309948110

Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., … Kühn, I. (2015). Naturalization of central European plants in North America: Species traits, habitats, propagule pressure, residence time. *Ecology*, *96*, 762–774. https://doi.org/10.1890/14-1005.1

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., & Rejmánek, M. (2000). Plant invasions — the role of mutualisms. *Biological Reviews*, *75*, 65–93. https://doi.org/10.1017/S0006323199005435

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Dane Panetta, F., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions*, *6*, 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Sargent, R. D., Kembel, S. W., Emery, N. C., Forrestel, E. J., & Ackerly, D. D. (2011). Effect of local community phylogenetic structure on pollen limitation in an obligately insect-pollinated plant. *American Journal of Botany*, *98*, 283–289. https://doi.org/10.3732/ajb.1000329

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., … Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, *21*, 4128–4140. https://doi.org/10.1111/gcb.13021

Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, *17*, 170–176. https://doi.org/10.1016/S0169-5347(02)02495-3

Sheppard, C. S., Burns, B. R., & Stanley, M. C. (2014). Predicting plant invasions under climate change: Are species distribution models validated by field trials? *Global Change Biology*, *20*, 2800–2814. https://doi.org/10.1111/gcb.12531

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419. https://doi.org/10.1111/ele.12508

Simberloff, D. (2006). Invasional meltdown 6 years later: Important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, *9*, 912–919. https://doi.org/10.1111/j.1461-0248.2006.00939.x

Simberloff, D., & Gibbons, L. (2004). Now you see them, now you don't! – Population crashes of established introduced species. *Biological Invasions*, *6*, 161–172. https://doi.org/10.1023/B:BINV.0000022133.49752.46

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, *1*, 21–32. https://doi.org/10.1023/A:1010086329619

Strauss, S. Y., Webb, C. O., & Salamin, N. (2006). Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 5841–5845. https://doi.org/10.1073/pnas.0508073103

Thuiller, W., Gallien, L., Boulangeat, I., De Bello, F., Münkemüller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: A quest for evidence. *Diversity and Distributions*, *16*, 461–475. https://doi.org/10.1111/j.1472-4642.2010.00645.x

Valiente-Banuet, A., & Verdú, M. (2007). Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, *10*, 1029–1036. https://doi.org/10.1111/j.1461-0248.2007.01100.x

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., … Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*, 100–103. https://doi.org/10.1038/nature14910

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

Violle, C., Choler, P., Borgy, B., Garnier, E., Amiaud, B., Debarros, G., … Viovy, N. (2015). Vegetation ecology meets ecosystem science: Permanent grasslands as a functional biogeography case study. *Science of the Total Environment*, *534*, 43–51. https://doi.org/10.1016/j.scitotenv.2015.03.141

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., … Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*, *27*, 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Violle, C., Nemergut, D. R., Pu, Z., & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, *14*, 782–787. https://doi.org/10.1111/j.1461-0248.2011.01644.x

Walther, G. R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., … Settele, J. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution*, *24*, 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology & Evolution*, *30*, 766–779. https://doi.org/10.1016/j.tree.2015.09.007

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

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227. https://doi.org/10.1023/A:1004327224729

Williamson, M., Dehnen-Schmutz, K., Kühn, I., Hill, M., Klotz, S., Milbau, A., … Pyšek, P. (2009). The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions*, *15*, 158–166. https://doi.org/10.1111/j.1472-4642.2008.00528.x

Wilson, J. R. U., Richardson, D. M., Rouget, M., Procheş, Ş., Amis, M. A., Henderson, L., & Thuiller, W. (2007). Residence time and potential range: Crucial considerations in modelling plant invasions. *Diversity and Distributions*, *13*, 11–22. https://doi.org/10.1111/j.1366-9516.2006.00302.x

Yang, S., Ferrari, M. J., & Shea, K. (2011). Pollinator behavior mediates negative interactions between two congeneric invasive plant species. *The American Naturalist*, *177*, 110–118. https://doi.org/10.1086/657433

BIOSKETCH

Christine S. Sheppard is a senior research associate at the University of Hohenheim, Germany, with research interests focused mainly on plant invasions. She combines various approaches including field and common garden experiments as well as macroecological analyses to investigate temporal or spatial dynamics of plant invasions, the effects of climate change on invasive species and biotic interactions among alien and native species.

Author contributions: C.S.S. conceived the idea with input from F.E.; M.C. and W.T. processed data on phylogeny, traits and climate; F.E. and H.S. contributed data on residence time; C.S.S. carried out the analysis, and all authors assisted with the interpretation; C.S.S. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Sheppard CS, Carboni M, Essl F, Seebens H, DivGrass Consortium, Thuiller W. It takes one to know one: Similarity to resident alien species increases establishment success of new invaders. *Divers Distrib*. 2018;24:680–691. https://doi.org/10.1111/ddi.12708