IS PHYLOGENETIC AND FUNCTIONAL TRAIT DIVERSITY A DRIVER
OR CONSEQUENCE OF GRASSLAND COMMUNITY ASSEMBLY?

Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities

Thomas Galland[1,2] | Guillaume Adeux[3,4] | Hana Dvořáková[1] | Anna E-Vojtkó[1,2] | Ildikó Orbán[5,6] | Michele Lussu[7] | Javier Puy[1] | Petr Blažek[1] | Vojtěch Lanta[2] | Jan Lepš[1,8] | Francesco de Bello[1,9] | Carlos Pérez Carmona[10] | Enrique Valencia[1,11] | Lars Götzenberger[1,2]

[1]Department of Botany, Faculty of Sciences, University of South Bohemia, České Budějovice, Czech Republic; [2]Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic; [3]AgroSup Dijon, INRA, Univ. Bourgogne Franche-Comté, Agroécologie, Dijon, France; [4]Institute of Life Sciences, Scuola Superiore Sant'Anna, Pisa, Italy; [5]Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös Loránd University, Budapest, Hungary; [6]Institute of Ecology and Botany, MTA Centre for Ecological Research, Vácrátót, Hungary; [7]Dipartimento di Scienze della Vita e dell'Ambiente Sezione Botanica, Università degli Studi di Cagliari, Cagliari, Italy; [8]Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic; [9]CIDE-CSIC, Valencia, Spain; [10]Institute of Ecology and Earth Sciences, Department of Botany, University of Tartu, Tartu, Estonia and [11]Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles, Spain

Correspondence
Thomas Galland
Email: galland.thom@gmail.com

Abstract

1. Functional and phylogenetic diversity (FD and PD respectively) of the resident community are expected to exert a key role in community resistance to colonization by surrounding species, and their establishment success. However, few studies have explored this topic experimentally or evaluated the interactive effects of these diversity measures.

2. We implemented a diversity experiment to disentangle the role of FD and PD by sowing mixtures of 6 species, drawn from a pool of 19 species naturally coexisting in central European mesic meadows. The mixtures were designed to cover four independent combinations of high and low FD and PD. Species covers were estimated in spring and late summer over two growing seasons. We then assessed the establishment success of colonizers as a function of their mean traits and phylogenetic distance to the resident (i.e. sown) communities, as well as the resistance of the resident communities to natural colonizers as a function of their functional and phylogenetic structure.

3. Results generally indicated a temporal shift regarding which trait values made a colonizer successful, from an acquisitive strategy in early stages to a more conservative trait syndrome in later stages.

4. FD decreased community resistance to natural colonization. However, PD tempered this effect: with high PD, FD was not significant, suggesting complementary information between these two components of biodiversity. On average,

colonizing species were more functionally distant from the resident species in sown communities with high functional diversity, i.e. those that were more colonized.

5. *Synthesis*. Our results confirm an interplay between FD and PD during community assembly processes, namely resistance to colonizers, suggesting that these two descriptors of biodiversity only partially overlap in their contribution to the overall ecological structure of a community. The hypothesis that higher FD increases resistance through a more complete use of resources was challenged. Results rather suggested that greater FD could provide an unsaturated functional trait space allowing functionally unique species to occupy it.

1 | INTRODUCTION

Shifts in species composition resulting from growing human influence and continuous climate change have brought new challenges to community ecology (Pecl et al., 2017). Natural community dynamics are driven by key processes such as the establishment of new species in the local resident communities (Kempel, Chrobock, Fischer, Rohr, & van Kleunen, 2013; Vítová & Lepš, 2011). While colonization can occur either from a regional species pool or by an invading alien species, the main questions remain roughly the same (Lanta & Lepš, 2008; Shea & Chesson, 2002): what makes a species a successful colonizer? What makes a community more resistant to colonization? Studies that aim at answering these questions could provide valuable knowledge on the biotic drivers influencing community assembly processes.

Community resistance to colonization has traditionally been attributed to high species richness. Species-rich communities are expected to resist colonization through a more complete use of resources (Elton, 1958). Increased resistance due to greater species richness has been repeatedly observed in communities where diversity was experimentally manipulated (Fargione, Brown, & Tilman, 2003; Fargione & Tilman, 2005; Kennedy et al., 2002; Van Ruijven, De Deyn, & Berendse, 2003). However, inconsistent and contradictory results have been shown both within natural (Robinson, Quinn, & Stanton, 1995) and experimental systems (Palmer & Maurer, 1997). Moreover, colonizers' diversity can also be positively correlated with resident community diversity, particularly at large scales (e.g. Stohlgren et al., 1999; reviewed by Fridley et al., 2007). Greater diversity of colonizers in richer regions can be explained by the covariation of biodiversity with extrinsic factors, e.g. resource heterogeneity (Naeem et al., 2000).

At the local scale, inconsistent results on the relationship between resistance to colonization and species richness, and the recognition that ecosystem processes depend on species' traits rather than species richness (Hooper et al., 2005) has led researchers to study community assembly processes through the lens of species'

functional traits and communities' functional structure. Functional structure is often characterized by two components: functional diversity (FD), i.e. the extent of functional trait dissimilarity between species, and traits of dominant species, reflected by community weighted mean (CWM; Violle et al., 2007). FD, in studies using a variety of estimators, has been shown to increase colonization resistance (Finn et al., 2013; Frankow-Lindberg, 2012; Lanta & Lepš, 2008; Schittko, Hawa, & Wurst, 2014; Suter, Hofer, & Lüscher, 2017), suggesting the importance of niche-based processes such as a more complementary use of available resources in functionally diverse communities. Other studies have found no evidence for the importance of processes such as complementarity or limiting similarity in colonization success (Bennett, Stotz, & Cahill, 2014; Letten, Keith, & Tozer, 2014), leading to inconsistent results among both experimental and observational studies. In this sense, measures of FD which reflect the uniqueness of species in a community (Ricotta et al., 2016) could provide a clearer picture of the relationship between colonization resistance and saturation of the functional trait space (Gurvich, Tecco, & Díaz, 2009; Loiola et al., 2018). At the same time, dominant species and their trait values could have a greater impact on resistance to colonization than species richness itself (Smith, Wilcox, Kelly, & Knapp, 2004) and could, therefore, be a useful predictor of resistance to colonization. However, dominant species can either increase or decrease resistance to colonization in a community. For example, high canopy cover increases competition for light, but also reduces stressful conditions by increasing soil moisture content (Smith et al., 2004). Assessing the functional structure of a community through both CWM and FD (Ricotta & Moretti, 2011) should allow to disentangle whether trait diversity or dominance (or both) are responsible for resistance to colonization in homogenous environmental conditions.

Measuring all the relevant functional traits to a given ecosystem function is often materially impossible, therefore, phylogenetic diversity has been proposed as a proxy, or complement, for unmeasured functional diversity (de Bello et al., 2017; Webb et al., 2002). Phylogenetic diversity summarizes the evolutionary

relationship between species (Faith, 1992). It is commonly used alone or in combination with FD under the hypothesis that closely related species are more similar than distant ones (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Loiola et al., 2018; Mace, Gittleman, & Purvis, 2003). However, to the best of our knowledge, few studies have measured the effect of PD on the success of individual-species colonization, and overall they yielded inconsistent results. For example, Whitfeld, Lodge, Roth, and Reich (2014) demonstrated a negative effect of higher PD on invading *Rhamnus cathartica*, whereas Bennett et al. (2014) showed that invading *Bromus inermis* was not restricted by high PD.

While numerous studies use PD as a proxy for FD, PD and FD are not necessarily correlated (Gerhold et al., 2011; Prinzing et al., 2008). This lack of correlation can be explained by the ability of PD to potentially capture unmeasured functional diversity (de Bello et al., 2017; Webb et al., 2002) and by the limitation of the phylogenetic approach to reflect traits with weak phylogenetic signal, i.e. which are less conserved over the phylogeny (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011). Therefore, several studies (Cadotte, 2013; Pavoine & Bonsall, 2011; Prinzing et al., 2008) have highlighted how a combination of phylogenetic and functional measures may paint a more complete picture of ecosystem functioning. Nevertheless, studies that test this approach experimentally are still rare (Feng, Fouqueray, & van Kleunen, 2018; Tan, Pu, Ryberg, & Jiang, 2015).

While resistance to colonization can be studied through traits and phylogeny of the resident community, it seems equally important to take into account the perspective of the colonizing species and the traits that enable them to successfully enter into already established communities (Roscher, Gerighausen, Schmid, & Schulze, 2015). Based on the limiting similarity theory, a successful colonizer should present functional traits that do not completely overlap with those of the resident community (Funk, Cleland, Suding, & Zavaleta, 2008). Several studies have tried to identify traits defining a successful colonizer but a review of these studies has highlighted some contradictions (see Pyšek & Richardson, 2007). This lack of consistency can partly be explained by interactions between different traits (Küster, Kühn, Bruelheide, & Klotz, 2008), by trait dissimilarity to resident species being more important for establishment success than specific traits values (Feng et al., 2018; Loiola et al., 2018), and by different traits values being advantageous at different stages of colonization or in different environments (Crawley, Harvey, & Purvis, 1996; Kempel et al., 2013; Van Kleunen, Dawson, & Maurel, 2015; Thompson, Hodgson, Grime, & Burke, 2001). Hence, different studies, both experimental and observational, might provide partially contrasting results. The possibility to combine trait and phylogenetic information on species can help to reveal processes underlying community assembly.

In addition to plant properties determining the outcome of colonization, environmental conditions such as nutrient availability, can modify ecosystem processes by affecting plant–plant interactions and community saturation. For instance Lepš (2014) showed that 15 years of fertilization in a central European oligotrophic meadow, led to increased competition between plants and species richness depletion by exclusion of subordinate species. In terms of colonization, lower nutrient availability was found to reduce establishment of colonizers (Fargione & Tilman, 2005) while higher levels of nitrate in the soil was found to increase the total abundance of colonizers in resident plant communities (Knops et al., 1999; Roscher et al., 2009; Thompson et al., 2001).

In our study, we combine trait-based and phylogeny-based measures, both from the resident communities' and from single colonizing species' perspective, in an attempt to provide a more complete understanding of the colonization process. We assessed the effects of different levels of FD, PD and fertilization on spontaneous colonization in experimental grassland communities with a fixed amount of sown species. The methodological approach leading to these contrasted levels of FD and PD also generated a gradient of saturation of phylogenetic and functional space. We recorded spontaneous colonization by unsown species and combined this vegetation data with species' traits and phylogeny data in order to address the following questions: (a) Which traits promote species colonization success? (b) Are the colonizing species filling empty functional and/or phylogenetic space of the resident community? (c) How does the functional and phylogenetic structure of the resident community affect resistance to colonization? Furthermore, through a fertilization treatment we investigated if the relations between traits and colonization depend on nutrient availability. We argue that such a multi-directional evaluation can help us to understand how ecological differences between species, in particular between colonizers and residents, can shape the colonization process.

2 | MATERIALS AND METHODS

2.1 | Experimental design and data collection

A sowing experiment was carried out on a mesic meadow 30 km southeast of Tábor, at an elevation of 660 m (Vysočina region, Czech Republic, 49.331N, 15.003E). The climate is temperate continental with an average annual temperature of 6.7°C and average annual precipitation of 759 mm (data from Černovice meteorological station, *c.* 4 km from the site). The study site is an abandoned crop field, last cultivated in 2001 and ploughed in 2014 prior to the experiment.

Information for five numerical and four categorical traits, related to the competitive ability and niche occupation of the species were obtained from the LEDA trait database (Kleyer et al., 2008) and BiolFlor (Kühn, Durka, & Klotz, 2004) for both the sown species and unsown (i.e. spontaneous colonizers) species. The continuous traits were canopy height (m), seed mass (mg), specific leaf area (SLA, mm^2/mg), leaf dry matter content (LDMC, mg/g) and length of flowering period (month 1–12). Categorical traits were Raunkiær's life form (T = Therophyte, G = Geophyte, H = Hemicryptophyte, and C = Chamaephyte), lifespan (a = annual, b = biennial and p = perennial), growth form (e = erosulate, leaves are separated by long internodes all along plant growth; h = hemirosette, plants combining a rosette and elongation phase; r = rosette, leaves are exclusively separated by short internodes) and nitrogen-fixing ability (1 = yes, 0 = no; the only nitrogen fixers present on our site were legumes).

The experimental set-up was a fully randomized factorial design with three factors: functional diversity (low and high), phylogenetic diversity (low and high) and fertilization (yes/no). Following the framework from Dias et al. (2013), we simulated all potential combinations of six species from a pool of 19 species (27,132 combinations). From the simulated combinations of species, we removed those with extreme CWM values (highest and lowest 10%) for the continuous traits. We also removed communities with more than 4 legumes or 4 grasses, in order to avoid an over-disproportionate dominance of functional or taxonomic groups in the communities (see Figure S1 for complete flowchart of community selection process). Then, we randomly selected four groups of 10 communities each, covering relatively extreme values of FD and PD with constant species richness (Table S2). In the low FD and low PD group, an additional constraint was set in the random selection of communities: one of the 10 communities had to contain 5 grasses in order to further increase the gradient of PD covered in the experiment.

Each of the 40 communities was sown on two randomly selected plots in the field, one fertilized and one unfertilized, in order to test the effect of nutrient availability. A concentrate of composted cow manure was applied at a rate of 2.2 t/ha (33 N, 55 P_2O_5, 33 K_2O) on each fertilized plot at the beginning of the growing season in March 2015, 2016 and 2017.

Each 1.5 × 1.5 m plot, separated by a 0.5 m buffer zone, was sown with a combination of 6 species obtained from a pool of 19 species naturally present in mesic meadows of the area (See Table S1 for sowing densities and trait values). Seeds were obtained from a local commercial provider (Planta Naturalis). In order to maximize the evenness in species abundance and considering that species with heavier seed generally establish better, the sown proportions of seeds from species with bigger seed mass were reduced. Specifically, the number of sown seed decreased linearly with the logarithm of seed mass (see details on the calculation of sown species proportion in Table S1). To ensure a good establishment of the sown communities, sowing took place twice in 2015, once in spring and once in autumn. In summer 2015, the entire field was mainly dominated by *Chenopodium album*; to avoid this species restricting the growth of sown communities, we weeded it from all the plots.

Vegetation sampling was carried out in 2016 and 2017 during May and September. Cover of sown and unsown species was visually estimated on a positively unbounded percentage scale in order to account for the different strata of vegetation. All species that were not sown in a particular plot were considered as colonizers, i.e. species present in the local seed bank and species disseminated from the surrounding area or from the other experimental plots. Another experiment running at the locality, together with marginal seed admixtures from the seed provider, provided some potential colonizers that do not belong to the local species pool (e.g. *Dianthus superbus*). Nevertheless, the vast majority of colonizers were naturally occurring species in the surrounding area. Species nomenclature follows the key to the flora of the Czech Republic (Kubát et al., 2002).

FD and PD of the sown communities were computed using Rao's index (Rao, 1982). It is important to note that, for a fixed amount of sown species and an expected even distribution of species cover (as in our experimental setup), this index is equivalent to a measure of species uniqueness (Ricotta et al., 2016). This measure of uniqueness (*U*) is the complement of functional redundancy (*R*), i.e. $R = 1 - U$ (Ricotta et al., 2016), where redundancy reflects the saturation of communities in terms of functional or phylogenetic space. In other words, communities with higher sown FD are less saturated in functional trait space because they are less redundant in their traits values.

For FD we considered seven different traits (lifespan and life form were excluded from diversity measures at the community level since all sown species were hemicryptophytes, therefore perennials; these traits were only used to characterize the unsown species and their functional distances from the sown communities; Table S1). The 'trova' function (de Bello, Carmona, Mason, Sebastia, & Lepš, 2013) was used to estimate the Gower dissimilarity between pairs of species. CWMs of the resident species were calculated as average trait values of the 6 sown species. To compute CWM, FD and PD, we considered species weights to be the same, as their initial proportion was intended to be equal (we also computed FD and CWMs for the observed communities, using observed species covers as weights, and generally obtained similar main results, see further below). Height, seed mass and SLA were ln-transformed prior to the calculation of indices to reduce skewness of the distribution. For categorical traits, CWM is equivalent to the proportion of species in each category. To calculate phylogenetic distances between species, we used a dated ultrametric supertree of European plant species, 'Daphne' (Durka & Michalski, 2012) and the function 'cophenetic' from the APE R package (Paradis, Claude, & Strimmer, 2004).

2.2 | Statistical analysis

2.2.1 | Functional traits promoting colonization success

All analyses were carried out with the R software version 3.3.2 (R Core Team, 20177). The colonization success of each species was estimated as the $\ln(x + 1)$ transformed sum of its cover over the 80 plots at each sampling time. All continuous traits were scaled around their mean and standardized by their standard deviation. Linear mixed-effect models (LMEM), as implemented in the NLME package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018), were used to identify which traits could best predict colonizing success with species identity included as a random factor. We first tested the effect of year, season and their interaction. Since only years had a significant effect and it only had two levels, it was included as an a priori covariate, i.e. fixed effect, in the models rather than as an additional random variable. Species traits, as well as their interaction with years, were first tested individually and then added sequentially (forward selection) to select the best predictive model through the Akaike information criterion (AIC). A drop of 2 AIC points was considered to significantly improve the model. When categorical variables were identified as significant predictors, post-hoc multiple comparisons were performed using the MULTCOMP package (Hothorn,

Bretz, & Westfall, 2008) to identify statistically different categories. In total, 110 species occurring in at least one plot within one sampling session were used in the analysis (resulting in 327 data points).

2.2.2 | Functional and phylogenetic distances between the colonizers and the resident community

The functional and phylogenetic distances between each of the colonizers and the resident communities were calculated as the mean of the 6 pairwise distances with the 6 sown species of each resident community, using the species pairwise distance matrix previously calculated (Gower distance on seven functional traits or cophenetic phylogenetic distance). Furthermore, for each plot, we averaged the distances obtained above for each of the colonizers in that plot (see below). For each species, LMEMs were used to evaluate the relationship between its cover ($\ln(x + 1)$ transformed) and its mean functional or phylogenetic distance (scaled and standardized) from the sown species in each plot, with plot identity included as a random factor. The strength of the relationship was derived from the estimate and variance explained only by the fixed factors (R^2_M, marginal R^2) using the MuMIn R package (Barton, 2018). In total, 79 species (those with at least 10 occurrences across the four sampling sessions) were used in the analysis. Fertilization, year and season had no significant effect and therefore were not included in the model.

Additionally, in order to compare the functional and phylogenetic distances of the set of colonizers in each plot across the different diversity treatments, we summarized the distance of the colonizers to the resident species as one mean value per plot (and per sampling time). This also provides a greater statistical power, because for several of the colonizers the number of observations was only slightly above 10 plots. These averaged functional and phylogenetic distances of the colonizers to the resident species were treated as response variable in a LMEM with diversity treatments as fixed predictor and plot identity as random factor.

2.2.3 | Functional and phylogenetic structure of the resident community and its resistance to colonization

Finally, we analysed to what extent the functional and phylogenetic structure of the resident community could predict the level of colonization by unsown species. The level of colonization was calculated as the $\ln(x + 1)$ transformed sum of unsown species cover in each plot and sampling session. LMEMs were used to assess the effect of different components of functional and phylogenetic structure (PD, FD over all traits, FD and CWM for individual traits), as well as fertilization, on the total cover of unsown species. Plot identity was included as a random factor and year as an a priori covariate. First, each predictor was tested individually, and then, forward selection based on AIC was applied on groups of predictors: (a) all individual FD, (b) all CWM and (c) all FD and CWM. This analysis included 320 measures, 80 plots sampled on four different occasions. We also considered the effect of observed FD, PD and CWMs of sown species on the abundance of colonizers, which were generally consistent with the one presented here. We argue that it is preferable to consider the values based on sown densities (i.e. all the sown species in equal proportions) because the realized community composition could already be a consequence of colonization (Roscher et al., 2013), thus leading to potential circularity in the analyses. Moreover, the sown species successfully established in almost all the plots. Out of the 80 communities, only 2 did not fulfil the sown species richness at least one time during the four sampling sessions. Therefore, the intended diversity levels are the relevant factors in our analyses.

3 | RESULTS

Over the 320 samples, 91 colonizing species were identified in addition to the 19 sown ones. The four most abundant unsown taxa were *Taraxacum* sect. *Ruderalia*, *Trifolium repens*, *Plantago lanceolata* and *Elytrigia repens* which represented, respectively, 21%, 9%, 9% and 8% of the total cover of unsown species. The average total cover occupied by colonizing species per plot increased from 18.4% (*SD* = 11.6) in 2016 to 30.9% (*SD* = 17.0) in 2017.

3.1 | Functional traits promoting colonization success

The results show a change in the traits of successful colonizers from 2016 to 2017 driven by a shift in successful species in the two seasons (Figure 1). The interaction effect with year was significant for five of the traits tested individually (Table S3). Perennial colonizers were generally more abundant than annuals and this difference increased in 2017 ($F_{2,214}$ = 15.27, p < .001; Figure 1a). Similar results were obtained with species lifeforms: hemicryptophytes significantly increased from 2016 to 2017, whereas therophytes decreased ($F_{3,213}$ = 13.27, p < .001; Figure 1b). In 2016, LDMC, SLA and flowering period length showed no relationship with colonization success, whereas in 2017 species with higher LDMC, lower SLA and shorter flowering period were more abundant (respectively $F_{1,215}$ = 13.27, p = .005; $F_{1,215}$ = 6.91, p = .010; $F_{1,215}$ = 25.53, p < .001; Figure 1d–f). Nitrogen-fixing colonizers were more abundant than non-nitrogen fixing colonizers and this relationship remained stable across the 2 years of sampling ($F_{1,215}$ = 1.73, p = .189; Figure 1c).

When all traits were combined into a single model, the only selected predictors in addition to year were nitrogen fixing ability, lifespan and the interaction between lifespan and year. In this final model, 16.2% of the variation in species colonization success was explained by the fixed predictors (Table 1).

3.2 | Functional and phylogenetic distances between the colonizers and the resident community

Fifteen unsown species presented a significant relationship between their abundance per plot and the mean distance (phylogenetic or functional) from the resident community, 13 of which were positive (Figure 2a). These species yielded significantly higher cover in the
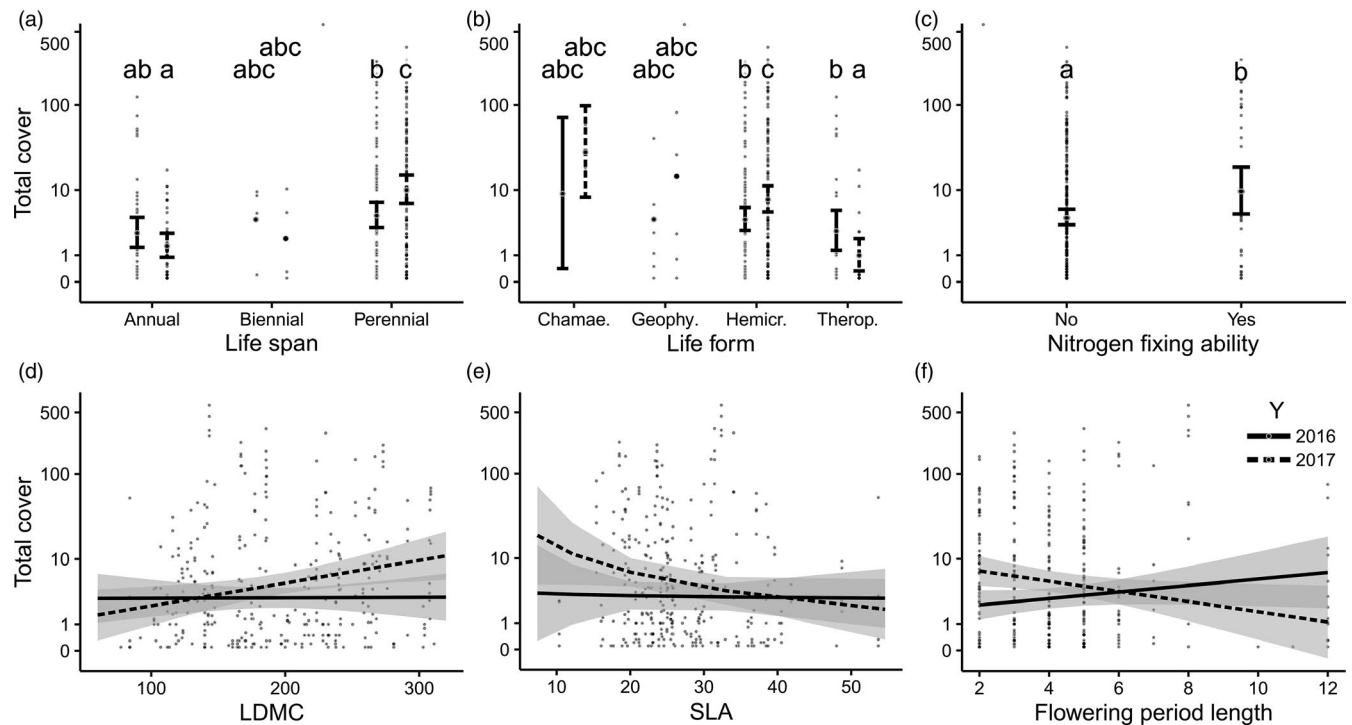
FIGURE 1 Species' colonization success as a function of species' traits and sampling year. Each panel presents the relationship between species success (i.e. the sum of cover a species yielded over all the plots on each sampling session) and the species' functional traits in interaction with sampling year. In this figure, we present only the traits that were significant predictors of species colonizing success. The interaction between year and functional traits was significant for all but nitrogen fixing ability. The small dots represent partial residual of each data points. Panels a to c, the larger dots with error bars represent the 95% confidence interval (CI) around the mean of each group (except for panel a and b, where the oversized CI due to low number of representing species were not drawn for biennials and geophytes, respectively). The letters represent statistical group differences ($p < .05$) according to the Tukey HSD test, taking into account the random variable, i.e. species identity. The solid line in panels d, e and f represents the slope estimate surrounded by 95% CI in coloured area [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Functional traits affecting species colonization success. The model presents the functional traits that have been selected to predict the colonization success of unsown species, (i.e. using the sum of species cover over all the plots on each sampling session). We present the ANOVA (type II) table of the most parsimonious model based on forward selection of predictors (including all species functional traits as well as their interaction with year) by AIC. Species identity was included as a random variable to take into account the non-independence of points (i.e. same species at different sampling sessions). The model used 327 observations from 110 groups (species). The variation explained by fixed and random factors was $R^2_C = .69$ and the variation explained by fixed factors only was $R^2_M = .16$

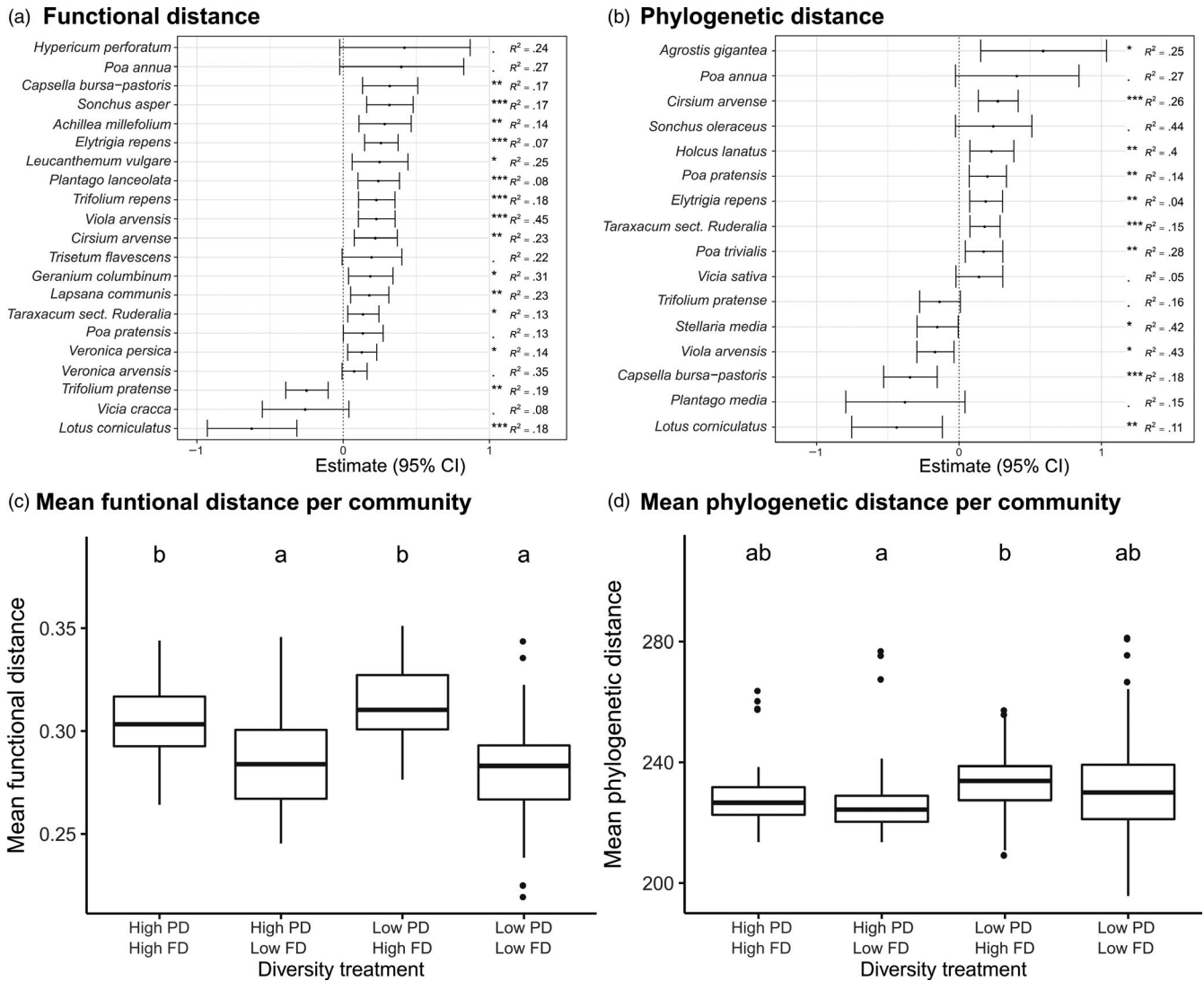| Variable	F value	p(>F)
Intercept	24.08	<0.001
Year	11.65	<0.001
Lifespan	6.66	0.002
Nitrogen fix	4.10	0.045
Year: Lifespan	15.52	<0.001

plots where they were functionally more different from the resident community. The variance explained by fixed factors (R^2_M) ranged from .07 to .45. When we considered phylogenetic distances, the

number of species with a significant relationship was reduced to 11 with 7 positives. R^2_M ranged from .04 to .43 (Figure 2b).

When considering the average distance of all colonizers to the residents per plot, communities with high sown FD were on average colonized by species more functionally distant from the residents than communities with low FD (Figure 2c). Communities with high sown PD tended to be colonized by species on average more phylogenetically similar to the residents than communities with low PD (Figure 2d). However, the differences in colonizers' phylogenetic distance among diversity treatments were relatively low, and significant only between high PD – low FD and low PD – high FD treatments (Figure 2d).

3.3 | Functional and phylogenetic structure of the resident community and its resistance to colonization

An important part of the variation in colonization level per plot, i.e. the sum of colonizing species cover within each plot per sampling session, was explained by year alone ($R^2_M = .20$, Table S4 model 2). However, adding the diversity treatment in the model substantially improved its fit ($R^2_M = .31$, Table 2a). The results show that resident communities with higher FD had a greater cover of colonizing species, particularly when PD was low (Figure 3a). With

(a) Functional distance

(b) Phylogenetic distance

(c) Mean funtional distance per community

(d) Mean phylogenetic distance per community

FIGURE 2 Colonizers' functional (a, c) and phylogenetic (b, d) average distances from the resident species. Panels a and b present the relationships between species cover and their functional (a) or phylogenetic (b) distance from the resident community. For each unsown species with more than 10 occurrences, a linear mixed effect model was fitted to predict the cover of the species by its mean functional (a) or phylogenetic (b) distance from the sown species of the resident community. The distances were scaled, centred around the mean and divided by SD, to standardize the coefficients and allow direct comparisons between species. The estimates of the slopes along with their 95% confidence interval are presented only for the models with $p < .1$. p-values are represented by symbols on the right: '.' for $p < .1$, '*' for $p < .05$, '**' for $p < .01$, '***' for $p < .001$). R^2 is the marginal coefficient of determination of the models representing the variation explained by the fixed factor only (i.e. phylogenetic or functional distance from the resident sown community). Panels c and d present the average of colonizers' functional (c) and phylogenetic (d) distances from the resident species in each community across the four diversity treatments. The letters above each box represent statistical groups differences ($p < .05$) according to Tukey HSD test, taking into account the random variable, i.e. plot identity

high PD, the colonization level in high FD communities was not significantly higher than in low FD communities. The interaction between the effect of year and diversity treatment was not significant ($F_{3,236} = 1.40$, $p = .245$; Table 2a), neither was the interaction between the effect of year and any individual traits, FD or CWM tested in the rest of the analysis (Table S4). Fertilization had no significant effect ($F_{1,72} = .59$, ns), nor its interaction with diversity treatment ($F_{3,72} = .80$, ns, Table S4).

When considering FD of each individual traits, only functional diversity based on seed mass (FD_{SEED_MASS}) and nitrogen fixing ability ($FD_{NITROGEN\_FIX}$) were significant (Table S4, model 5 to 11), rising the R^2_M to .29 and .26, respectively. When added in a single additive model, functional diversity based on species SLA (FD_{SLA}) was selected on top of FD_{SEED_MASS} and $FD_{NITROGEN\_FIX}$, and the model's R^2_M reached .33 (Table S4, model 12). FD_{SLA} reduced colonization while FD_{SEED_MASS} and $FD_{NITROGEN\_FIX}$ increased it. Models using individual CWM traits as predictors yielded comparable performance, with the exception of erosulate growth form and flowering period length, which were also significant predictors of plot colonization (Table S4 models 13 to 19). However, after forward

TABLE 2 Effect of the functional and phylogenetic structure of the resident community on resistance to colonization. For each model, we present the ANOVA (type II) table of the most parsimonious model based on forward selection of predictors by AIC. In model (a), diversity treatment, i.e. 4 combinations of high and low FD and PD, is used to predict the amount of cover colonized by unsown species in each plot. In model (b), sown community functional attributes have been selected to predict the amount of cover colonized by unsown species in each plot. Forward selection of predictors, including all community functional attributes as well as their interactions with year, was based on AIC. In both models, plot identity was included as a random variable to account for the non-independence of data points (i.e. same plot at different sampling sessions). R^2_M represent the variation explained by the fixed factors only and the conditional R^2 (R^2_C) represent the variation explained by both the fixed and random factors. Both models used 320 observations from 80 groups (plots)
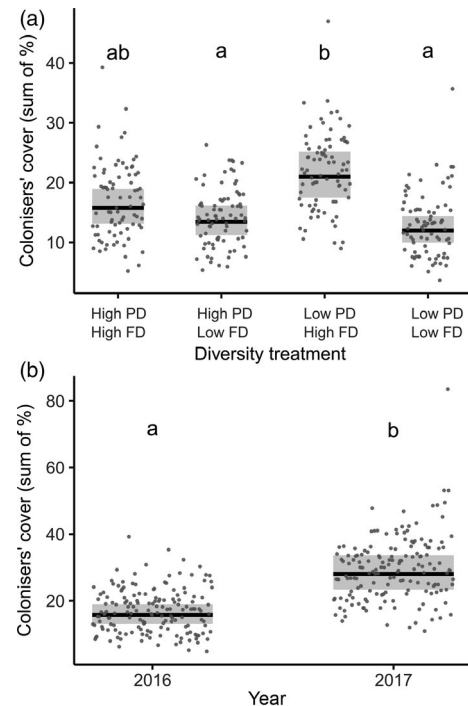
| Variable	F value	p(>F)
(a) Diversity treatments explain the level of colonization (R^2_M = .31, R^2_C = .60)		
Intercept	4,316.14	<0.001
Year	157.33	<0.001
Diversity treatment	7.02	<0.001
Year: diversity treatment	1.40	0.245
(b) Community functional attributes explain the level of colonization (R^2_M = .42, R^2_C = .60)		
Intercept	6,340.61	<0.001
Year	154.56	<0.001
$CWM_{NITROGEN\_FIX}$	27.71	<0.001
FD_{SEED_MASS}	9.14	<0.01
FD_{SLA}	11.53	0.001
$CWM_{FLOWERING\_PERIOD}$	5.59	0.020
CWM_{HEIGHT}	8.57	0.005
PD_{SOWN}	5.01	0.028

FIGURE 3 Conditional plots of sown functional (FD) and phylogenetic diversity (PD) treatment (a) and sampling year (b) on the level of colonization by unsown species (colonizers' cover). Each panel represents the partial effect of a single factor on the response when other variables are held constant, i.e. to their reference level: year 2016 for panel a and high PD high FD for panel b. Although the statistical inferences were made on ln-transformed cover values, the response variable is plotted on the original scale for graphical purposes. The black horizontal lines represent the mean value predicted by the models and the grey area their 95% confidence interval. The lower case letters represent statistical groups differences (p < .05) according to Tukey HSD test, taking into account the random variable, i.e. plot identity

selection on individual CWM traits, only $CWM_{NITROGEN\_FIX}$ and $CWM_{EROSULATE}$ were added to the best performing model, and the model's R^2_M reached .31 (Table S4, model 20).

Finally, the best predictive model of community colonization contained both CWM ($CWM_{NITROGEN\_FIX}$, $CWM_{FLOWERING\_PERIOD}$ and CWM_{HEIGHT}), FD (FD_{SEED_MASS} and FD_{SLA}) and sown PD as predictors, and it explained 42% of the variability (Table 2b). The partial effect of $CWM_{NITROGEN\_FIX}$ and FD_{SEED_MASS} were positive, i.e. increased colonization, while the partial effect of $CWM_{FLOWERING\_PERIOD}$, CWM_{HEIGHT} and FD_{SLA} were negative, i.e. decreased colonization (Figure 4).

4 | DISCUSSION

Our analyses, based on experimental plant communities with contrasting functional and phylogenetic levels, address the complexity of the colonization process via complementary approaches considering both the colonizers and the resident community perspective.

We found support that functional traits help in predicting species colonization success, but this effect also depended on time and on the dissimilarity between the colonizers and the resident community. The functional and phylogenetic diversity of resident species also presented an interactive effect on the resistance to colonization, underlying the effect of saturation in functional and phylogenetic space of the resident species.

4.1 | Functional traits promoting colonization success

Our analyses based on colonizing species' functional traits support observations made by previous studies, i.e. a shift in traits characterizing successful colonizers along successional phases of the colonization process: initial colonizers are replaced by species with different traits (Catford et al., 2019; Roscher et al., 2015; Thompson et al., 2001). In the first year after establishment, annual colonizers with therophytic life form, high SLA and low LDMC were relatively abundant, although no significant difference in abundance was detected
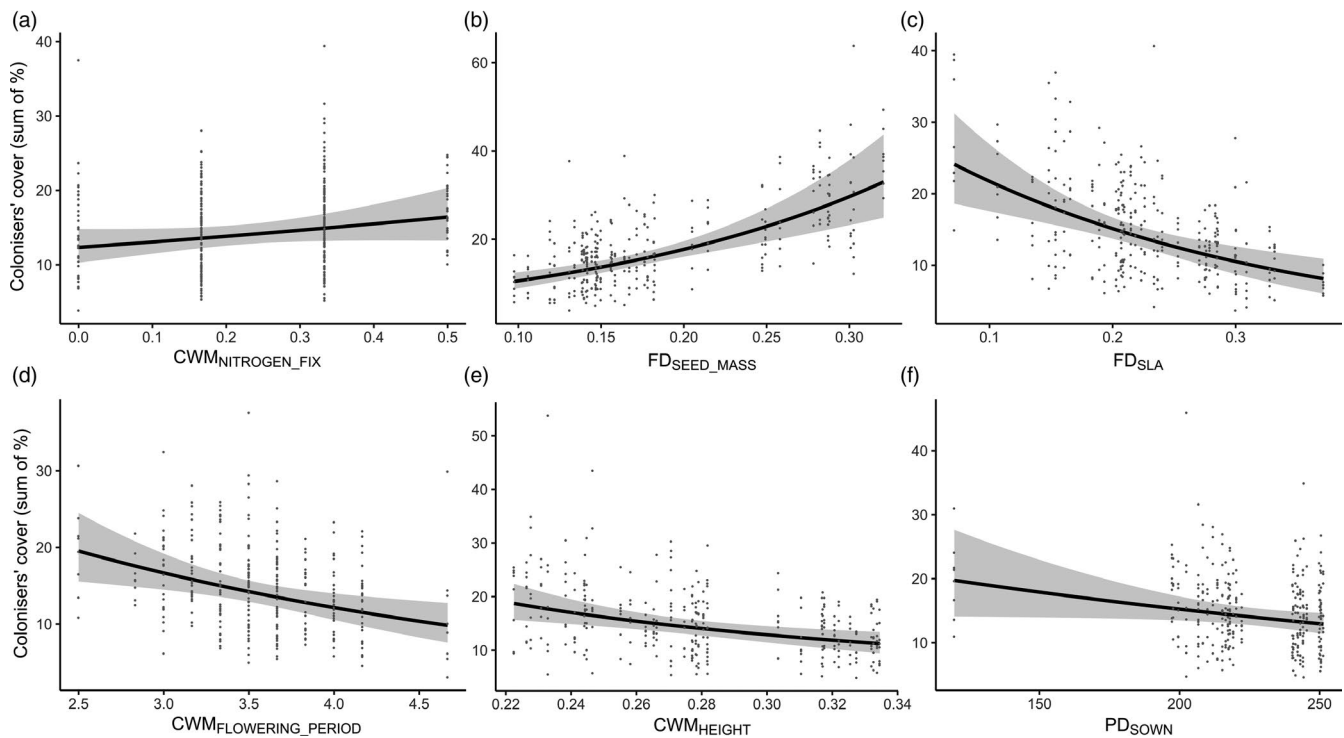
FIGURE 4 Conditional plots highlighting the effect of each predictor selected in the most parsimonious model (obtained by forward selection on the sown communities' functional attributes) on the level of colonization. Each plot represents the partial effect of a single component of community functional trait structure on the response when all other variables are held constant, i.e. to their median. Although the statistical inferences were made on ln transformed cover and standardized predictor (centred around the mean and standardized by *SD*), the response and predictive variable are plotted on their original scale for better interpretability. The black lines represent the mean value predicted by the models and the grey area their 95% confidence interval

compared to species with contrasting traits (Figure 1). However, only one year later, species with a perennial life cycle, hemicryptophytic life form, low SLA and high LDMC were significantly more successful. This pattern reflects the advantage of fast resource acquisition at the beginning of the colonization and growing importance of more conservative strategies as succession advances, when interspecific relationships become a stronger driver of the community composition (Catford et al., 2019; Crawley et al., 1996; Garnier, Cortez, Billès, Navas, & Roumet, 2004; Pyšek & Richardson, 2007).

Furthermore, shorter flowering period was one of the advantageous traits during the second year of sampling. This can be explained by the negative correlation between flowering period length and trait values associated with the afore-mentioned conservative strategy (Figure S5), which requires more investment in vegetative organs. Such a trade-off between investment in sexually reproductive versus vegetative functions is indicated by several studies associating a long flowering period with traits typical for an annual life cycle (Cadotte & Lovett-Doust, 2001; Crawley et al., 1996; Lake & Leishman, 2004; Roscher et al., 2015).

The last trait promoting successful colonization of the experimental communities was nitrogen fixing ability. In a 20-year-long field experiment where colonizers were sown into mature resident communities, Catford et al. (2019) also showed that the establishment success of colonizers was higher for legumes compared to non-legume species. However, unlike in our study, their result was significant only in terms of occupancy (presence/absence) of colonizers in seeded plots, not in

abundance neither in dispersion to the neighbouring unseeded subplots. The importance of nitrogen fixing ability on colonization success in our results could have been overvalued by the fast vegetative spread and competitive strength of some of the legume colonizers present in our experiment (e.g. *Trifolium repens*, *Lotus corniculatus*).

4.2 | Functional and phylogenetic distances between the colonizers and the resident community

Besides identifying the particular functional trait values upholding colonizers, another aspect of colonization success lies in the theories of niche complementarity (Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994) and limiting similarity (Macarthur & Levins, 1967). According to these theories, species should be more successful colonizers when their functional traits allow them to occupy an empty niche in the community, i.e. when they are more functionally different from the resident species (Thuiller et al., 2010).

Our analysis of colonizing species covers in relation to the functional and phylogenetic distances to the resident community revealed a significant advantage of being functionally more different for 16% of the species and phylogenetically more different for 9% of the species, indicating that these species occupied functional and phylogenetic 'gaps' unoccupied by the resident species. Using the measure of mean distance between colonizers and resident species, following the approach proposed by Ricotta et al. (2016), allows

to evaluate the presence of gaps in functional and phylogenetic space. Similarly, Fargione et al. (2003) found that established species suppressed colonizing species from the same functional group more strongly than functionally dissimilar ones. Recently, Feng et al. (2018) showed that functional distance between the native community and invasive species had a stronger positive effect on the performance of invasive species than phylogenetic distance. On the contrary, Breitschwerdt, Jandt, and Bruelheide (2015) found that colonizers experimentally introduced in semi-natural grassland communities had higher survival rate when they were more similar to the resident community. However, in several other cases, experiments failed to provide evidence for the limiting similarity hypothesis on the effect of phylogenetic and functional distances on the establishment of colonizing species (Bennett et al., 2014; Funk & Wolf, 2016). One source of discrepancy in those results, both within and between observational and experimental approaches, could be attributed to different methodological aspects. For instance, different sets of traits, distance metrics or scales at which vegetation is surveyed could affect the results from different studies.

In our study, negative relationships between the colonizer's functional or phylogenetic distance to the resident community and its cover were found in only 2% and 5% of the species, respectively. Similar results were found in a pot experiment on non-native invaders by Conti et al. (2018), showing that invaders' growth was less suppressed in functionally similar native communities. Those results are in line with the idea of weaker competitor exclusion (Mayfield & Levine, 2010), postulating that competition can sometimes favour species that are similar in their competitive behaviour, leading to trait and phylogenetic similarity between co-existing species. However, with less than 5% of such cases among our species, we cannot conclude that colonizers in our experiment generally follow a pattern that would present strong evidence for weaker competitor exclusion.

Recently, Roscher et al. (2018) showed that absolute trait distance between focal species and co-occurring species explained a very limited part of the variation in the productivity of the focal species. In line with our results, most of the variation in species productivity was explained by the actual trait values of the species, rather than their trait distance to the residents. Moreover, in a meta-analysis of experimental studies, Price and Pärtel (2013) suggest that functional group similarity has relatively small impact on biotic resistance.

Only four species showed significant relationships with both functional and phylogenetic distance analysis (*Cirsium arvense*, *Elytrigia repens*, *Taraxacum* sect. *Ruderalia* and *Lotus corniculatus*) and only one species showed significant but contradictory slopes in functional and phylogenetic distance analysis (*Viola arvensis*). The restricted overlap in colonizers' responses to functional or phylogenetic distance from the resident communities supports the idea that phylogenetic and functional distances are complementary rather than redundant in the information they carry.

It is important to stress that for the majority of species there was no significant relationship between colonizer success and its

functional or phylogenetic distance to resident species. The signature of limiting similarity in traits and phylogeny was evident only for a subset of the colonizers when considered individually (see above). Catford et al. (2019) found effects of absolute trait difference between colonizer and community on individual colonizers' success only for plant height. For other traits (i.e. SLA, seed mass, LDMC) only the trait hierarchical difference were significant predictors. It is possible that our sown communities with six species might not sufficiently saturate the functional space to trigger niche complementarity consistently. However, during the experiment, we observed 18.5 ± 3.5 species per plot (mean ± *SD*). A nearby experiment with identical habitat condition shows that after 20 years, species richness stabilized around 20 species/m², with about 12 species per plot yielding cover higher than 1% (Lepš personal communication).

Despite the signal of limiting similarity being weak when considering individual species, it was consistently stronger when considering the whole set of colonizers in a given plot (average of colonizers distances). This probably because of the limited 'power' of tests on individual species, often based on slightly more than 10 plots colonized per species, while with the averaging approach we maximized the number of observations. The sown communities with high FD were the ones where colonizers yielded the highest cumulated cover percentage (Figure 3a) and where those colonizers were on average more functionally distant from the residents (Figure 2c). In other words, in low FD plots the overall colonization success was restricted by the saturation of the trait space in the resident community.

4.3 | Functional and phylogenetic structure of the resident communities and their resistance to colonization

The analysis between sown FD and PD and resistance to colonization suggests a non-trivial interaction between the effects of PD and FD. In contradiction with the idea that functional diversity promotes resistance to colonization through a more complete use of available resources, communities with higher FD were generally more colonized (except in the case of FD$_{SLA}$, see below). However, this effect was significant only at low levels of PD, suggesting that high PD inhibits colonization in high FD communities. Our results are in opposition with those obtained by Feng et al. (2018), who show that the performance of alien plants decreased with increasing diversity of the native community (for both FD and PD). On the other hand, they are partially in line with the analysis of a large vegetation database by Loiola et al. (2018), which revealed that native communities invaded by aliens had both higher FD and PD. These slight differences could be explained by the fact that Loiola et al. (2018) used natural communities from different regions of the Czech Republic covering large environmental gradients, but also gradients of FD and PD which were not entirely independent, whereas our localized and experimentally designed communities allowed functional and phylogenetic orthogonal contrasts.

Although the effect of PD was weak, it appeared as an important factor in modulating the expression of FD. Moreover, PD was selected as a significant predictor in the best model along with

CWM and FD of individual traits (Table 2b). This could suggest that some important traits were not considered but are nonetheless reflected in the phylogeny of the species. Among potential candidates of unmeasured traits accounted for by phylogeny are clonal traits. There is growing evidence for the importance of clonal traits in interspecific plant competition (Benot, Bittebiere, Ernoult, Clément, & Mony, 2013; Saiz, Bittebiere, Benot, Jung, & Mony, 2016), as well as their phylogenetically conserved character, i.e. related species show similar clonal attributes. For example, Herben, Tackenberg, and Klimešová (2016) found relatively high values of Pagel's lambda (a measure of phylogenetic signal) between 0.8 and 0.95 for clonal traits, where a value of 1 indicates high phylogenetic conservatism.

Statistical models of colonization level per plot yielded similar performance whether they were based on forward selection of FD or CWM indices per trait (Table S4 models 12 and 20). Both models retained indices of nitrogen fixing ability, which reflects the high correlation between CWM and FD values for traits with only two levels ($r = .95$, Figure S4). However, the best model (Table 2b) issued from forward selection on all potential predictor variables integrated both FD and CWM indices, highlighting how the complementarity between the two types can provide a better representation of the community functional structure, as shown in Ricotta and Moretti (2011).

Colonizers were more abundant in communities that presented a higher proportion of legumes ($CWM_{NITROGEN\_FIX}$) or greater variation of seed mass (FD_{SEED_MASS}). A high percentage of legumes in the community might have made it more receptive to colonization because nitrogen fixation requires energy (Gutschick, 1981), at the expense of competitiveness, and releases nitrogen in the soil, increasing resource availability for competing species (Vitousek & Howarth, 1991). However, seed mass is usually associated with high competitive ability at the seedling stage (Bitomský, Mládek, & Cimalová, 2018). This unexpected positive relation might result from a confounding effect because, in this experiment, legume species had higher seed mass and the correlation between CWM_{N_FIX} and FD_{SEED_MASS} was significant ($r = .48$, p-value $< .05$ Figure S4).

Furthermore, colonization was negatively associated to CWM_{HEIGHT}, $CWM_{FLOWERING\_PERIOD}$ and FD_{SLA}. These results are expected as plant height is strongly related to competitive ability of plants, especially in terms of light pre-emption (Hautier, Niklaus, & Hector, 2009). The effect of $CWM_{FLOWERING\_PERIOD}$ on colonization can be interpreted as a reflection of other correlated traits that are indicative of a conservative strategy, rather than an effect of flowering period itself. Among sown species, long flowering period was strongly associated with low SLA and rosette growth form, with the latter two traits potentially leading to a large occupation of the surface of the plot, thus reducing the available space for colonizers. Finally, higher FD_{SLA} values should reflect complementarity between acquisitive and conservative strategies of the sown community, optimizing resource pre-emption, mostly regarding water and light (Wright et al., 2004). However, partial effects of FD_{SLA} and FD_{SEED_MASS} essentially compensated each other. The mean sum of colonizers' cover decreased from 24% to

8% along the FD_{SLA} gradient while it increased from 10% to 30% along the FD_{SEED_MASS} gradient (Figure 4, panels b and c). Such interplay between the effects of diversity in different traits can explain the a priori contradiction between the results in FD_{SLA} and multidimensional FD. It also emphasizes the complex interpretation of FD in multivariate trait space.

4.4 | Fertilization

Fertilization had no detectable effect, neither on the performance of colonizers nor on the resistance of the sown community to colonizers, a result also found in Lanta and Lepš (2008). One possibility could be that colonization processes and community dynamics are not affected by the level of nutrient availability, though this is in contradiction with studies showing strong competitive exclusion between species under fertilization treatments (Lepš, 2014). A second plausible explanation could be that both colonizers and resident species established on the plots at the same time and might have equally benefited from fertilization. Finally, the absence of an effect of fertilization could result from the already high plot coverage. Burke and Grime (1996) showed that the effect of fertilization was strengthened by disturbance, which created gaps in the vegetation cover.

Alternatively, we can hypothesize that the effect of fertilization was down-weighted because nutrient availability was not a strong limiting factor in our site, or because the difference in nutrient availability between fertilized and unfertilized plots was insufficient, due to an already high fertility level of the entire field. This could be the consequence of (a) the former exploitation of the site as crop field with a subsequent annual fertilization until 2001, and (b) the boosting effect of ploughing on mineralization processes by micro-organisms due to the increased oxygen availability in the soil (Grace, MacRae, & Myers, 1933). If these two factors are important, then their impacts should decrease in time and we can expect that in the future, the fertilization treatment will play a more important role in the communities' dynamics. Our results indicate that the effects of abiotic conditions such as increased nutrient availability strongly depend on specific site conditions and time.

5 | CONCLUSIONS

Our results reinforce the idea that beyond propagule availability, successful colonization relies on an interplay between the intrinsic characteristics of the potential colonizer and invasibility of the ecosystem. We brought evidence that successful colonizers were characterized by different combinations of traits along the successive steps of colonization, adding time as a key factor in characterization of colonization as in Thompson et al. (2001) and Catford et al. (2019). In our study, we found evidence for the limiting similarity theory, stating that colonizers should be more successful in communities from which they differ more, even though the effect was

weak, similarly to the conclusions of the meta-analysis conducted by Price and Pärtel (2013).

The interplay between FD and PD in their support of community resistance to colonizers is an important novel finding of this study. It supports the idea that, given the set of traits and the species pool considered in this study, FD and PD only partially overlap in their description of community structure. The widespread hypothesis that higher FD increases resistance by a more complete use of resources is challenged. Greater FD, especially at low species richness and low phylogenetic diversity, could rather provide an unsaturated functional trait space in which colonizers are on average more functionally dissimilar from the residents and yield higher cover.

AUTHORS' CONTRIBUTIONS

C.P.C., F.d.B., J.L. and L.G. conceived and designed the experiment; A.E.V., E.V., F.d.B., H.D., J.P., L.G., P.B., T.G and V.L. collected the data; G.A., J.P. and T.G. analysed the data; G.A., H.D, I.O., J.P., M.L. and T.G. drafted the manuscript. All authors contributed to the draft and gave final approval for submission.

DATA AVAILABILITY STATEMENT

Vegetation data have been archived on Dryad Digital Repository: https://doi.org/10.5061/dryad.5g6254c (Galland et al., 2019). Plant traits information can be retrieved from the LEDA database: http://www.uni-oldenburg.de/en/landeco/research/leda/data-files (Kleyer et al., 2008) and the BiolFlor database: http://www.biolflor.de (Kühn et al., 2004). Phylogeny data can be retrieved from the DAPHNE database: https://doi.org/10.6084/m9.figshare.3554421.v1 (Durka & Michalski, 2012).

ORCID

Thomas Galland https://orcid.org/0000-0003-0883-8871

Guillaume Adeux https://orcid.org/0000-0003-0903-391X

Anna E-Vojtkó https://orcid.org/0000-0001-6370-680X

Ildikó Orbán https://orcid.org/0000-0003-1547-675X

Michele Lussu https://orcid.org/0000-0002-1313-4732

Javier Puy https://orcid.org/0000-0002-6422-2791

Petr Blažek https://orcid.org/0000-0002-0901-4578

Vojtěch Lanta https://orcid.org/0000-0003-4484-3838

Jan Lepš https://orcid.org/0000-0002-4822-7429

Francesco Bello https://orcid.org/0000-0001-9202-8198

Carlos Pérez Carmona https://orcid.org/0000-0001-6935-4913

Enrique Valencia https://orcid.org/0000-0003-3359-0759

Lars Götzenberger https://orcid.org/0000-0003-3040-2900

REFERENCES

Barton, K. (2018). MuMIn: Multi-model inference. R Package Version 1.42.1.

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

Benot, M. L., Bittebiere, A. K., Ernoult, A., Clément, B., & Mony, C. (2013). Fine-scale spatial patterns in grassland communities depend on species clonal dispersal ability and interactions with neighbours. *Journal of Ecology*, 101, 626–636. https://doi.org/10.1111/1365-2745.12066

Bitomský, M., Mládek, J., & Cimalová, Š. (2018). Light limitation shapes the community seed mass of annual but not of perennial weeds. *Perspectives in Plant Ecology, Evolution and Systematics*, 31, 1–6. https://doi.org/10.1016/j.ppees.2017.11.005

Breitschwerdt, E., Jandt, U., & Bruelheide, H. (2015). Do newcomers stick to the rules of the residents? Designing trait-based community assembly tests. *Journal of Vegetation Science*, 26, 219–232. https://doi.org/10.1111/jvs.12235

Burke, M. J. W., & Grime, J. P. (1996). An experimental study of plant community invasibility. *Ecology*, 77, 776–790. https://doi.org/10.2307/2265501

Cadotte, M. W. (2013). Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences*, 110, 8996–9000. https://doi.org/10.1073/pnas.1301685110

Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, 4, 1–9. https://doi.org/10.1371/journal.pone.0005695

Cadotte, M. W., & Lovett-Doust, J. (2001). Ecological and taxonomic differences between native and introduced plants of Southwestern Ontario. *Ecoscience*, 8, 230–238. https://doi.org/10.1080/11956860.2001.11682649

Catford, J. A., Smith, A. L., Wragg, P. D., Clark, A. T., Kosmala, M., Cavender-Bares, J., … Tilman, D. (2019). Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. *Ecology Letters*, 22, 593–604. https://doi.org/10.1111/ele.13220

Conti, L., Block, S., Parepa, M., Münkemüller, T., Thuiller, W., Acosta, A. T. R., … Carboni, M. (2018). Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. *Journal of Ecology*, 106, 1607–1620. https://doi.org/10.1111/1365-2745.12928

Crawley, M. J., Harvey, P. H., & Purvis, A. (1996). Comparative Ecology of the Naive and Alien Floras of the British Isles. *Philosophical*

Transactions: Biological Sciences, 351, 1251–1259. https://doi.org/10.1098/rstb.1996.0108

de Bello, F., Carmona, C. P., Mason, N. W. H., Sebastia, M. T., & Lepš, J. (2013). Which trait dissimilarity for functional diversity: Trait means or trait overlap? *Journal of Vegetation Science*, 24, 807–819. https://doi.org/10.1111/jvs.12008

de Bello, F., Šmilauer, P., Diniz-Filho, J. A. F., Carmona, C. P., Lososová, Z., Herben, T., & Götzenberger, L. (2017). Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods in Ecology and Evolution*, 8, 1200–1211. https://doi.org/10.1111/2041-210X.12735

Dias, A. T. C., Berg, M. P., de Bello, F., Van Oosten, A. R., Bílá, K., & Moretti, M. (2013). An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology*, 101, 29–37. https://doi.org/10.1111/1365-2745.12024

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

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. Chicago, IL: University Chicago Press.

Faith, D. P. (1992). Conservation evaluation and phylogentic diversity. *Biological Conservation*, 61, 1–10. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

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

Fargione, J. E., & Tilman, D. (2005). Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, 8, 604–611. https://doi.org/10.1111/j.1461-0248.2005.00753.x

Feng, Y., Fouqueray, T. D., & van Kleunen, M. (2018). Linking Darwin's naturalisation hypothesis and Elton's diversity–invasibility hypothesis in experimental grassland communities. *Journal of Ecology*, 107, 794–805. https://doi.org/10.1111/1365-2745.13061

Finn, J. A., Kirwan, L., Connolly, J., Sebastià, M. T., Helgadottir, A., Baadshaug, O. H., … Lüscher, A. (2013). Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: A 3-year continental-scale field experiment. *Journal of Applied Ecology*, 50, 365–375. https://doi.org/10.1111/1365-2664.12041

Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology*, 92, 1573–1581. https://doi.org/10.1890/10-1245.1

Frankow-Lindberg, B. E. (2012). Grassland plant species diversity decreases invasion by increasing resource use. *Oecologia*, 169, 793–802. https://doi.org/10.1007/s00442-011-2230-7

Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., … Holle, B. V. (2007). The invasion paradox: Reconciling pattern and process in species invasions. *Ecology*, 88, 3–17. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

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

Funk, J. L., & Wolf, A. A. (2016). Testing the trait-based community framework: Do functional traits predict competitive outcomes? *Ecology*, 97, 2206–2211. https://doi.org/10.1002/ecy.1484

Galland, T., Adeux, G., Dvořáková, H., E-Vojtkó, A., Orbán, I., Lussu, M., … Götzenberger, L. (2019). Data from: Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5g6254c

Garnier, E., Cortez, J., Billès, G., Navas, M., & Roumet, C. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85, 2630–2637. https://doi.org/10.1890/03-0799

Gerhold, P., Pärtel, M., Tackenberg, O., Hennekens, S. M., Bartish, I., Schaminée, J. H. J., … Prinzing, A. (2011). Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *The American Naturalist*, 177, 668–680. https://doi.org/10.1086/659059

Grace, P. R., MacRae, I. C., & Myers, R. J. K. (1993). Temporal changes in microbial biomass and N mineralization under simulated field cultivation. *Soil Biology and Biochemistry*, 25(12), 1745–1753. https://doi.org/10.1016/0038-0717(93)90179-F

Gurvich, D. E., Tecco, P. A., & Díaz, S. (2009). Plant invasions in undisturbed ecosystems: The triggering attribute approach. *Journal of Vegetation Science*, 16, 723–728. https://doi.org/10.1111/j.1654-1103.2005.tb02415.x

Gutschick, V. P. (1981). Evolved strategies in nitrogen acquisition by plants. *The American Naturalist*, 118, 607–637. https://doi.org/10.1086/283858

Hautier, Y., Niklaus, A. P., & Hector, A. (2009). Competition for light causes plant. *Science*, 324, 636–638. https://doi.org/10.1016/j.matlet.2014.10.021

Herben, T., Tackenberg, O., & Klimešová, J. (2016). Reproduction by seed and clonality in plants: Correlated syndromes or independent strategies? *Journal of Ecology*, 104, 1696–1706. https://doi.org/10.1111/1365-2745.12646

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., … Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. https://doi.org/10.1890/04-0922

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363. https://doi.org/10.1007/11417170_5

Kempel, A., Chrobock, T., Fischer, M., Rohr, R. P., & van Kleunen, M. (2013). Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. *Proceedings of the National Academy of Sciences*, 110, 12727–12732. https://doi.org/10.1073/pnas.1300481110

Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M. H., Tilman, D., & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636–638. https://doi.org/10.1038/nature00776

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., … Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology*, 96, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Knops, J., Tilman, D., Haddad, N. M., Naeem, S., Mitchell, C. E., Haarstad, J., … Groth, J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, 2, 286–293. https://doi.org/10.1046/j.1461-0248.1999.00083.x

Kubát, K., Hrouda, L., Chrtek, J., Kaplan, Z., Kirschner, J., & Štěpánek, J. (2002). *Klíč ke květeně České republiky [key to the flora of the Czech Republic]*. Praha, CZ: Academia.

Kühn, I., Durka, W., & Klotz, S. (2004). BiolFlor – A new plant-trait database as a tool for plant invasion ecology. *Diversity and Distributions*, https://doi.org/10.1111/j.1366-9516.2004.00106.x

Küster, E. C., Kühn, I., Bruelheide, H., & Klotz, S. (2008). Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology*, 96, 860–868. https://doi.org/10.1111/j.1365-2745.2008.01406.x

Lake, J. C., & Leishman, M. R. (2004). Invasion success of exotic plants in natural ecosystems: The role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation*, 117, 215–226. https://doi.org/10.1016/S0006-3207(03)00294-5

Lanta, V., & Lepš, J. (2008). Effect of plant species richness on invasibility of experimental plant communities. *Plant Ecology*, *198*, 253–263. https://doi.org/10.1007/s11258-008-9401-6

Lepš, J. (2014). Scale- and time-dependent effects of fertilization, mowing and dominant removal on a grassland community during a 15-year experiment. *Journal of Applied Ecology*, *51*, 978–987. https://doi.org/10.1111/1365-2664.12255

Letten, A. D., Keith, D. A., & Tozer, M. G. (2014). Phylogenetic and functional dissimilarity does not increase during temporal heathland succession. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20142102–20142102. https://doi.org/10.1098/rspb.2014.2102

Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C. P., Pyšek, P., & Lososová, Z. (2018). Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. *Journal of Ecology*, https://doi.org/10.1111/1365-2745.12986

Macarthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, *101*, 377–385. https://doi.org/10.1086/282505

Mace, G. M., Gittleman, J. L., & Purvis, A. (2003). Preserving the tree of life. *Science*, *300*(5626), 1707–1709. https://doi.org/10.1126/science.1085510

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

Naeem, S., Knops, J. M. H., Tilman, D., Howe, K. M., Kennedy, T., & Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, *91*, 97–108. https://doi.org/10.1109/ICU.2005.1569975

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., & Woodfin, R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, *368*(6463), 734–737. https://doi.org/10.1038/368734a0

Palmer, M. W., Maurer, T. A. (1997). Does diversity beget diversity? A case study of crops and weeds. *Journal of Vegetation Science*, *8*, 235–240. https://doi.org/10.2307/3237352

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Pavoine, S., & Bonsall, M. B. (2011). Measuring biodiversity to explain community assembly: A unified approach. *Biological Reviews*, *86*, 792–812. https://doi.org/10.1111/j.1469-185X.2010.00171.x

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), https://doi.org/10.1126/science.aai9214

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2018). nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1.

Price, J. N., & Pärtel, M. (2013). Can limiting similarity increase invasion resistance? A meta-analysis of Experimental Studies. *Oikos*, *122*, 649–656. https://doi.org/10.1111/j.1600-0706.2012.00121.x

Prinzing, A., Reiffers, R., Braakhekke, W. G., Hennekens, S. M., Tackenberg, O., Ozinga, W. A., … van Groenendael, J. M. (2008). Less lineages – More trait variation: Phylogenetically clustered plant communities are functionally more diverse. *Ecology Letters*, *11*, 809–819. https://doi.org/10.1111/j.1461-0248.2008.01189.x

Pyšek, P., & Richardson, D. M. (2007). *Traits associated with invasiveness in alien plants: Where do we stand? In* Biological Invasions (pp. 97–125). Berlin, Heidelberg: Springer.

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rao, C. R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology*, *21*, 24–43. https://doi.org/10.1016/0040-5809(82)90004-1

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Ceranolini, B., & Pavoine, S. (2016). Measuring the functional redundancy of biological communities: A quantitative guide. *Methods in Ecology and Evolution*, *7*, 1386–1395. https://doi.org/10.1111/2041-210X.12604

Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*, *167*, 181–188. https://doi.org/10.1007/s00442-011-1965-5

Robinson, G. R., Quinn, J. F., & Stanton, M. L. (1995). Invasibility of experimental Habitat Islands in a California winter annual grassland. *Ecology*, *76*, 786–794. https://doi.org/10.2307/1939344

Roscher, C., Beßler, H., Oelmann, Y., Engels, C., Wilcke, W., & Schulze, E. D. (2009). Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. *Journal of Ecology*, *97*, 32–47. https://doi.org/10.1111/j.1365-2745.2008.01451.x

Roscher, C., Fergus, A. J. F., Petermann, J. S., Buchmann, N., Schmid, B., & Schulze, E. D. (2013). What happens to the sown species if a biodiversity experiment is not weeded? *Basic and Applied Ecology*, *14*, 187–198. https://doi.org/10.1016/j.baae.2013.01.003

Roscher, C., Gerighausen, U., Schmid, B., & Schulze, E. D. (2015). Plant diversity and community history shift colonization success from early- to mid-successional species. *Journal of Plant Ecology*, *8*, 231–241. https://doi.org/10.1093/jpe/rtu011

Roscher, C., Gubsch, M., Lipowsky, A., Schumacher, J., Weigelt, A., Buchmann, N., … Schmid, B. (2018). Trait means, trait plasticity and trait differences to other species jointly explain species performances in grasslands of varying diversity. *Oikos*, *127*, 865. https://doi.org/10.1111/oik.04815

Saiz, H., Bittebiere, A. K., Benot, M. L., Jung, V., & Mony, C. (2016). Understanding clonal plant competition for space over time: A fine-scale spatial approach based on experimental communities. *Journal of Vegetation Science*, *27*, 759–770. https://doi.org/10.1111/jvs.12392

Schittko, C., Hawa, M., & Wurst, S. (2014). Using a multi-trait approach to manipulate plant functional diversity in a biodiversity-ecosystem function experiment. *PLoS ONE*, *9*, e99065. https://doi.org/10.1371/journal.pone.0099065

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

Smith, M. D., Wilcox, J. C., Kelly, T., & Knapp, A. K. (2004). Dominance not richness determines invasibility of tallgrass prairie. *Oikos*, *106*, 253–262. https://doi.org/10.1111/j.0030-1299.2004.13057.x

Stohlgren, T. J., Binkley, D., Chong, G. W., Kalkhan, M. A., Schell, L. D., Bull, K. A., … Yowhan, S. (1999). Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, *69*, 25–46. https://doi.org/10.1890/0012-9615(1999)069[0025:EPSIHS]2.0.CO;2

Suter, M., Hofer, D., & Lüscher, A. (2017). Weed suppression enhanced by increasing functional trait dispersion and resource capture in forage ley mixtures. *Agriculture, Ecosystems and Environment*, *240*, 329–339. https://doi.org/10.1016/j.agee.2017.01.007

Tan, J., Pu, Z., Ryberg, W. A., & Jiang, L. (2015). Resident-invader phylogenetic relatedness, not resident phylogenetic diversity, controls community invasibility. *The American Naturalist*, *186*, 59–71. https://doi.org/10.1086/681584

Thompson, K., Hodgson, J. G., Grime, J. P., & Burke, M. J. W. (2001). Plant traits and temporal scale: Evidence from a 5-year invasion experiment using native species. *Journal of Ecology*, *89*, 1054–1060. https://doi.org/10.1046/j.0022-0477.2001.00627.x

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

Van Kleunen, M., Dawson, W., & Maurel, N. (2015). Characteristics of successful alien plants. *Molecular Ecology*, *24*, 1954–1968. https://doi.org/10.1111/mec.13013

Van Ruijven, J., De Deyn, G. B., & Berendse, F. (2003). Diversity reduces invasibility in experimental plant communities: The role of plant species. *Ecology Letters*, *6*, 910–918. https://doi.org/10.1046/j.1461-0248.2003.00516.x

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Vitousek, P. M., & Howarth, R. –W. (1991). Nitrogen limitation on land and in the sea: How can it occur ? *Biogeochemistry*, *13*, 87–115. https://doi.org/10.1007/BF00002772

Vítová, A., & Lepš, J. (2011). Experimental assessment of dispersal and habitat limitation in an oligotrophic wet meadow. *Plant Ecology*, *212*, 1231–1242. https://doi.org/10.1007/s11258-011-9900-8

Webb, C. O., Ackerly, D. D., Mcpeek, M. A., Donoghue, M. J., Ackerly, D. D., Mcpeek, M. A., … Donoghue, M. J. (2002). Phylogenetics and community ecology. *Annual Review of Ecology and Systematics*, *33*, 475–505.

Whitfeld, T. J. S., Lodge, A. G., Roth, A. M., & Reich, P. B. (2014). Community phylogenetic diversity and abiotic site characteristics influence abundance of the invasive plant *Rhamnus cathartica* L. *Journal of Plant Ecology*, *7*, 202–209. https://doi.org/10.1093/jpe/rtt020

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. https://doi.org/10.1038/nature02403

SUPPORTING INFORMATION

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

How to cite this article: Galland T, Adeux G, Dvořáková H, et al. Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *J Ecol*. 2019;107:2090–2104. https://doi.org/10.1111/1365-2745.13246