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Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members

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Abstract

1. Plant invasions can drastically change the structure of native communities, but it is not fully understood whether alien species occupy phylogenetic and functional space within the range occupied by natives, or provide a novel set of evolutionary origins and traits to the invaded communities.
2. Here, we evaluated this open question with data on a large number of plant communities from different terrestrial habitats. We used ~27,000 vegetation plots from 26 terrestrial habitats in the Czech Republic and compared phylogenetic and functional diversity (PD and FD, respectively) and community trait means in invaded and non-invaded plots. We tested for differences (1) between invaded vs. non-invaded plots, (2) among natives in invaded vs. non-invaded plots, and (3) in invaded plots only, with and without aliens. To minimize habitat filtering effects on PD and FD, we ran these tests within the habitat-specific species pools of the 26 vegetation types.
3. In general, PD, FD and trait mean values changed with invasion, with changes being rather consistent across the habitats considered. Invaded plots were less phylogenetically, but more functionally diverse than non-invaded plots. The greater FD in invaded plots, compared to non-invaded ones, was due to greater dissimilarity between natives. In fact, native species in invaded plots showed higher PD and FD than native species in non-invaded plots, while alien species reduced PD and FD in invaded plots. Changes in the trait means with invasion were due to differences in native species in invaded and non-invaded plots, rather than to an effect of alien species. Within most habitats, the trait means and variance of all aliens were similar to those of all natives, while in some habitats, the variability in traits was greater between aliens that belonged to phylogenetically closer clades.
4. *Synthesis*. Our results suggest that alien species more often occupy a phylogenetic and functional space within the range formed by the native species in a community. They do so either by filling empty gaps or by excluding natives from the

existing phylogenetic and functional space, rather than occupying or creating a phylogenetic and trait space outside of it.

KEYWORDS
community trait means, Darwin's naturalization hypothesis, environmental filtering, functional diversity, functional traits, invasion ecology, niche differentiation, phylogenetic diversity

1 | INTRODUCTION

Biological invasions are increasingly impacting biodiversity, communities and ecosystem functioning (Pyšek et al., 2012; Vilà et al., 2011). There has been a renewed interest in assessing mechanisms and consequences of plant invasion, focusing on the ecological similarity between potential invaders and resident species, either expressed as phylogenetic or functional similarity (Bezeng, Davies, Yessoufou, Maurin, & Bank, 2015; Carboni et al., 2016; Li et al., 2015; Ordonez, 2014). Such a comparison is often analysed at the regional scale, or by considering a given species pool (Leishman, Thomson, & Cooke, 2010; Lososová et al., 2015; van Kleunen, Weber, & Fischer, 2010), although the impact on biodiversity and ecosystem functioning takes place at the scale of local communities. Thus, assessing to which extent alien plants occupy a portion of the phylogenetic and functional space of natives in communities, or provide a novel subset of traits and evolutionary origins to the communities, is essential to understand mechanisms of invasion (Thuiller et al., 2010). Particularly, an expansion or contraction of the existing phylogenetic and functional space could have repercussions on ecosystem functioning and biodiversity maintenance (Finerty et al., 2016; Funk, Cleland, Suding, & Zavaleta, 2008; Gerhold et al., 2011).

Two long-standing and seemingly contradictory hypotheses have been proposed to predict the impact of invasion based on ecological differences between alien and native species within communities. On one hand, alien species must survive in the same conditions as native species and, therefore, aliens with high similarity to resident species might have a better chance to establish and spread. Such environmental filtering (Kembel & Hubbell, 2006) would cause alien species to occupy a portion of the phylogenetic and functional space originally occupied by native species in communities, leading to an increased similarity between species in invaded communities. On the other hand, "Darwin's naturalization hypothesis" (Rejmánek, 1996) states that immigrant species might be more likely to naturalize if they are phylogenetically and/or functionally different from native species, because they can exploit unfilled ecological niches (Thuiller et al., 2010). This hypothesis assumes that niche differentiation, related to "limiting similarity" between species and niche gap-filling by aliens, is the main driver of invasion success. As such, aliens might expand the space of invaded communities and provide a novel subset of traits and evolutionary origins to the invaded communities. Under this scenario, invasion would result in increased phylogenetic and functional diversity (PD and FD, respectively), when compared to non-invaded communities (Funk et al., 2008). Finally, competitive exclusion between species within a habitat can also cause the dominance of certain clades and of species bearing traits related to greater competitive abilities (de Bello et al., 2012; Mayfield & Levine, 2010), possibly leading to decreased PD and FD.

The ecological dissimilarity between natives alone also exerts a key role in invasion. Under the assumption of similar supply of resources, communities of native species with large PD and FD should use available niches more completely (Gerhold et al., 2011; Hejda & de Bello, 2013) and be more resistant to invasion (Levine, Adler, & Yelenik, 2004) than communities with low PD and FD. It is also possible that communities of native species with large PD and FD would be more susceptible to invasion (Gurvich, Tecco, & Díaz, 2005), since high dissimilarity between species could lead to empty gaps within the phylogenetic and functional space of a community (Blonder, 2016). These niches could be used by aliens to establish in the plant community and foster invasion. It is important to realize that the different effects of ecological dissimilarity between natives and aliens within communities, or only between natives, have been generally considered separately (Thuiller et al., 2010). There is, thus, evidence both supporting Darwin's naturalization hypothesis (e.g. Bezeng et al., 2015; Park & Potter, 2013; Strauss, Webb, & Salamin, 2006) and refuting it (e.g. Daehler, 2003; Duncan & Williams, 2002; Lososová et al., 2015), and also evidence supporting that the similarity between natives and between aliens and natives can affect resistance to invasion (Carboni et al., 2016; van Kleunen et al., 2010).

Two main issues seem to be responsible for these discrepancies in the literature. First, the effects of environmental filtering and limiting similarity are scale-dependent (Götzenberger et al., 2012). While environmental filtering is expected to be the most important driver of assembly *across* habitats, niche-sharing and gap-filling are expected to be more important at local scales *within* habitats that is between species that coexist within a given habitat. Testing for environmental filtering requires the comparison of PD and FD *across* habitat-specific species pools that is the set of species typical of a given habitat. In such studies, we expect to find clustered patterns of phylogenetic and functional diversity. In this direction, Lososová et al. (2015) showed the effect of alien species on the phylogenetic diversity of species pools from different habitat types, finding that

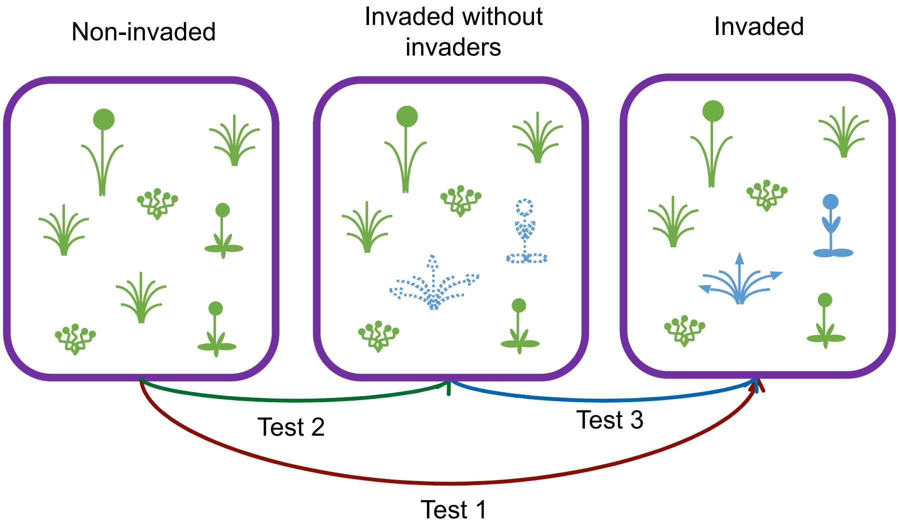

FIGURE 1 Scheme of the three tests comparing phylogenetic and functional diversity indices of non-invaded vs. invaded plots (Test 1); non-invaded plots against the set of native species in the invaded plots (Test 2); and exclusively invaded plots without aliens against the invaded plots with aliens (Test 3). Green and blue plants represent native and alien species, respectively

alien species occupy habitats with species phylogenetically closely related. Alien species seem to occupy a portion of the phylogenetic space in the habitats they invade. At local scales, on the contrary, it is less clear which portion of the phylogenetic and functional space the alien species might occupy. It is expected that niche-sharing and gap-filling become more central processes of community assembly, requiring tests *within* habitat-specific species pools to minimize habitat filtering effects on PD and FD. To do so, observed PD and FD in local communities should be compared with their expected values based on the same habitat-specific species pool (i.e. excluding species not found in a given habitat), since it is likely that environmental filtering could override the signal of patterns related to limiting similarity (de Bello et al., 2012). Studies using this approach are still rare (Bennett et al., 2016).

Second, because these hypotheses are usually examined by observational studies, comparing invaded and non-invaded communities might require an integrated set of tests (e.g. Thuiller et al., 2010; Figure 1). Changes in PD and FD due to invasion could be reflected in (1) a change of the whole community, (2) a change among the native species present in invaded vs. non-invaded communities, or (3) solely a change due to the addition of alien species. As such, PD and FD can be simply compared between invaded and non-invaded communities to detect the overall effect of invasion (Test 1, Figure 1). Differences between communities observed with this test could be caused by differences in PD and FD between native species, or by the contribution of the alien species. To clarify these two possible sources of variation, we propose two additional tests. One of them compares exclusively native species, in invaded to non-invaded communities (Test 2). Differences in PD and FD revealed by this test can suggest a predisposition of communities to invasion or that alien species have replaced some portion of the phylogenetic and functional space in the native communities. Even though the interpretation of this test cannot be conclusive, it is essential not to focus only on comparing invaded vs. non-invaded plots but to decompose its possible sources of variation and generate further testable hypotheses. Consequently, a third test compares PD and FD within a community, contrasting the whole community with the same invaded community, but omitting the aliens. This test allows us to assess how different is the phylogenetic and functional space occupied by aliens, considering the space occupied by native species (Test 3), which is informative about niche filling (Blonder, 2016). Assuming that the traits of dominant species in a community would not change, a decrease in FD revealed by this test might reflect gap-filling of the community by alien species, rather than enlarging the overall functional volume occupied by the community.

In this study, we combine these three tests for PD and FD. The inclusion of PD in this framework is important as (1) it might reveal patterns not observable only by the traits considered to compute FD, and (2) the complementary information of PD and FD can help us to better elucidate the process of biological invasions (Ordonez, 2014). Also, while it is becoming progressively clear that PD cannot be used as simple proxy of FD (Bernard-Verdier, Flores, Navas, & Garnier, 2013), it can allow broader comparisons and predictions to other regions, especially when trait information is missing (e.g. Li et al., 2015, Lososová et al., 2015). Also, we apply the three tests to trait mean values in a community (Garnier et al., 2004) to assess whether there is a differentiation in overall functional strategies among species (Kraft et al., 2015). A few key traits, such as specific leaf area (SLA), plant height or phenology, may differentiate between native and alien species (van Kleunen et al., 2010). Alien species tend to have higher efficiency in resource use than native species, which is reflected in relatively high SLA of aliens (Leishman et al., 2010). They also tend to be taller than native species, which accounts for advantage in competition for light. Aliens also have a longer flowering period (Pyšek & Richardson, 2007). While these tests are usually applied at the scale of a region or a given species pool, it is likely that the community means of key traits would also differ in the three tests delineated above. To run the tests in Figure 1, we assessed 26,559 vegetation plots of all major natural and semi-natural terrestrial habitats in the Czech Republic and compared values to the habitat-specific species pools taken as reference data.

2 | MATERIALS AND METHODS

2.1 | Dataset

The dataset used here was taken from the Czech National Phytosociological database, an electronic archive containing >110,000 vegetation plots (Chytrý & Rafajová, 2003) sampled following the Braun–Blanquet approach (Braun-Blanquet, 1964) or similar sampling protocols. We excluded the aquatic habitats, because they contained small numbers of species (1–2 in most plots). For the same reason, we excluded the terrestrial plots with less than three species. To minimize possible noise in the dataset, we used only a subsample of the available plots: those that had precise information on the location, a standard size and that were sampled after 1970. Only plots from a restricted size range within each vegetation type were selected. For example, most non-forest plots were of 16 or 25 m^2, and most forest plots were of 200 or 400 m^2. Based on their species composition, these plots were classified into 35 habitat types. In nine of the 35 habitats, the number of invaded plots was too low to allow for statistical analyses (<6), and therefore, results within habitats are reported for the remaining 26 habitats. To facilitate the interpretation of the results, we further aggregated the habitats into five broad habitat groups: forests, grasslands, man-made, wetlands and stony habitats.

We also assigned all the plots to cells of a geographical grid of 1.25 min of longitude × 0.75 min of latitude that is *c.* 1.5 × 1.4 km. To reduce the spatial non-independence of sampling of the same habitat type, we resampled the database by randomly taking one plot of the same phytosociological association from the same grid cell. No resampling was done for associations represented by less than eight plots in the country. The final dataset used in this study comprised 26,559 plots, with 1,839 vascular plant species from all terrestrial habitat types of the Czech Republic.

Each plot used here is considered a local plant community, as the species in a plot are presumably interacting with each other and their occurrence is determined by similar ecological conditions. This database represents a vast range of diversity of natural and semi-natural vegetation of inland Central Europe, including anthropogenic habitat types, such as spontaneous weed communities on arable land. To detect the effect of recent invasion, we divided species into native and archaeophytes vs. neophytes (alien species introduced to the study region in the last *c.* 500 years; sensu Pyšek et al., 2012). We considered a plot invaded when it contained at least one neophyte species—of the 1,839 species, 138 were neophytes (Pyšek et al., 2012). For each species in a plot, its cover was expressed in percentage.

2.2 | Data analysis

To account for species phylogenetic relatedness, we created a phylogenetic tree for the 1,839 species based on a dated ultrametric supertree for Central European vascular plant species (DaPhnE 1.0, Durka & Michalski, 2012). The few taxa not included in the supertree were supplemented manually to the existing nodes of the DaPhnE tree (Lososová et al., 2015). The species concept and nomenclature followed those used in the DaPhnE 1.0 supertree (Durka & Michalski, 2012). The topology of the phylogenetic tree is based on a backbone family phylogeny of the Angiosperm Phylogeny Group III. Subsequently, phylogenetic subtrees derived from 518 recent molecular studies were manually pruned onto the backbone tree, using multigene consensus topologies, when possible. Similarly, internal and root nodes were dated based on recent studies. The phylogenetic distances between species were square-rooted, following Letten and Cornwell (2015), to reflect that evolutionary relatedness is not linearly related to ecological distance between species.

To study the effect of functional dissimilarity on the invasion processes, we considered 16 functional traits from existing databases (Kleyer et al., 2008; Klimešová & de Bello, 2009) related to fitness, reproductive strategies and resistance to disturbance, besides being potential predictors of the species' effects on ecosystem functioning. The description of the importance and collection method of the data for each trait is given in the Supporting Information. The functional traits used were: SLA; leaf dry matter content (LDMC); canopy height; life-form; life span; vegetative propagation (including clonality); presence of rosette; root metamorphosis; type of reproduction; type of seed production; type of "seed" (germinule vs. dispersule); seed weight; average start of flowering; average flowering duration; and average number of flowering periods within a year. We used these functional traits for computing FD and community trait means.

To calculate FD in each plot, we computed all pairwise trait dissimilarities between species using the Gower distance, which can accommodate different types of traits and potential missing information for given traits (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009). Following Laliberté and Legendre (2010), we treated the dissimilarity between species with a principal coordinates analysis (PCoA) to account for potential trait correlations and extract main axes of trait variation. The species scores on the PCoA axes, which explained more than 80% of trait variation among species, were used to compute the dissimilarity between species and a multivariate FD measure, with axis contributions being weighted by their eigen values.

To compute PD and FD of plots, we considered two options. We considered mean pairwise dissimilarity (MPD), because it is unrelated to species richness, and the mean nearest taxon distance (MNTD), based on existing algorithms (de Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016; Swenson, 2014). These indices cover a wide variety of dimensions in ecological dissimilarities between species and are widely used. The MPD is the mean distance of all species pairs in a plot. This metric summarises the distance between all species combinations in a community, developed for functional analysis and adopted for phylogenetic studies (Swenson, 2014). MNTD averages the distances between the most similar species and focuses on possible interactions with the most ecologically close species. More sophisticated approaches, as the one proposed by Carmona, Bello, Mason, and Lepš (2016) based on trait probability distributions, could not be applied given the lack of data on intraspecific trait variability. We computed indices with and without the effect of species cover. However, (1) since we were mostly interested in the changes in overall phylogenetic and functional space in the communities, and not in the changes in abundance structure and (2) because species cover, over these large databases, can be estimated in different ways, we focused on indices not weighted by species cover. Regarding this point, we highlight that not taking cover into account allows for assessments of the whole phylogenetic and functional space, not only for that of the dominant species. Because the results were consistent among MPD and MNTD, we focused on MPD with presence/absence data and mention the specific cases showing different results in the text. Certainly, different indices of functional diversity, such as functional evenness or dispersion, could be used to assess other effects of alien species in community assembly patterns. Here, we consider that MPD and MNTD are suitable biological and mathematical tools which cover the main components of community structure enclosed by several related indices.

To account for community assembly patterns, we compared MPD and MNTD against randomizations of plots within a given habitat type. Randomizations were obtained in two ways. First, by shuffling species identity within a habitat-specific species pool that is in the plot x species matrix within each habitat type. This randomization maintains the species richness in a plot to account for differences in carrying capacity across plots within a habitat. This approach is better in detecting biotic assembly than randomizations that keep frequency within a habitat constant (Götzenberger et al., 2016). Thus, only species able to grow in the particular habitat type were included in the random communities to focus on niche partitioning patterns and excluding effects of environmental filtering (de Bello et al., 2012; Götzenberger et al., 2016). A second null model was applied, for Tests 1 and 3, by randomizing native species only within the pool of native species of the corresponding habitat, and aliens only within the pool of alien species (for those habitats with at least five alien species, Table S8). For both null models, an "effect size" of MPD, for example, was computed for each plot, as the observed MPD minus the average of 499 MPDs obtained from randomizations (de Bello et al., 2012). Positive values indicate that the MPD value is greater than the mean random expectations and vice versa. MPD values, both the observed values and the random expectations, are independent of species richness (de Bello et al., 2016). In our data, all correlations of PD and FD with species richness were generally very small and either negatively (mostly for PD) or positively (mostly for FD) related. Significant correlations occur mostly in habitats with a very high number of plots (Figure S1 and Table S7) suggesting liberal significance tests. These results suggest that MPD is not trivially related to species richness. The effect of different plot sizes in the dataset, with larger plots including more species, is considered by this index, which allows comparing plots of slightly different sizes within habitats.

For each functional trait, we calculated the mean of the trait values (Garnier et al., 2004). The community trait mean defines the most frequent trait values of a community, which can be interpreted in relation to the mass ratio hypothesis (Garnier et al., 2004), suggesting that frequent traits are determinants of ecosystem processes (Ricotta & Moretti, 2011). In this context, we use the trait means to assess changes between alien and native species.

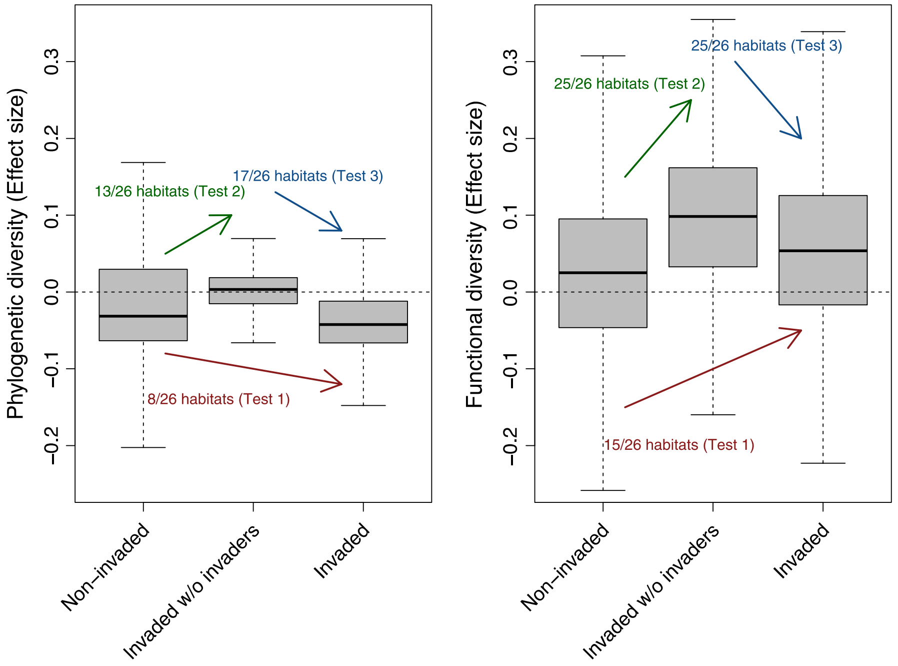

FIGURE 2 Phylogenetic and functional diversity indices, accounting for effect sizes of the plots in habitat groups of the Czech Republic. Differences were assessed through *t* tests between non-invaded and invaded plots within each habitat (red arrows, Test 1); among native species in non-invaded and invaded plots (green arrows, Test 2); and invaded plots only, without and with alien species (blue arrows, Test 3, paired *t* test in this case). The habitat types considered in the analysis are described in Table S1. The numbers of habitats for which results were found significant ($p < .05$) are shown

For PD, FD and trait means, we followed the three analyses delineated in Figure 1. Analyses were carried out within habitat types to compare similar plots and species that are under similar conditions, and global tests were also performed. First, we compared (1) non-invaded versus invaded plots within a given habitat (red-arrow test in Figure 2); then (2), we did the same comparison between native species in non-invaded plots versus invaded plots, (green-arrow test in Figure 2); and finally (3), only for invaded plots, we computed indices for all species with and without alien species (blue-arrow test in Figure 2). Comparisons of indices were done using *t* tests, paired in the case of Test 3, within habitat. To account for false discovery rates in the multiple comparisons, we applied Benjamini–Hochberg correction for each index.

In parallel, we performed a set of global tests on the whole dataset. We used linear mixed models for Test 1 (red-arrow test in Figure 2) with MPD or MNTD as the dependent variable, invaded vs. non-invaded status of each plot as the fixed factor and habitat type as the random factor. In a similar model, the fixed factor was the relative abundance of invasive species over the total plot cover, again with habitat type as the random factor. This last test assessed whether the effect of alien species was dependent on the presence and/or abundance of alien species. We apply global tests to give an overview of the whole dataset, although the *t* tests within each site seem more parsimonious in significance detection, because of the high number of plots in the dataset, which would result in a very liberal significance test. For this reason, the model assessing the effect of alien species abundance on FD and PD was also built for each habitat separately. All analyses were done in R (R Core Team, 2015), and mixed models were performed in package “nlme.”

We also tested whether the mean trait values and variance were different between natives and alien species within given habitats (Hulme & Bernard-Verdier, 2017), to include part of the tests usually found in the literature and assess changes at the level of a given species pool. As such, we ran *t* tests comparing quantitative traits in aliens vs. natives within each habitat type that had at least five alien species. Then, we tested whether the multivariate variance of traits and phylogeny were different between native and alien species. We measured the variance by comparing the multivariate homogeneity between aliens and natives, using the function “betadisper” in the “vegan” package in R (see also de Bello et al., 2011 on the relationship between this test and the variance with multitrait dissimilarity).

3 | RESULTS

The comparisons between non-invaded and invaded plots within each habitat (Test 1) revealed lower phylogenetic diversity in the invaded plots in 8 of the 26 habitats (31% of the habitats), and higher functional diversity in the invaded plots in 15 of the 26 habitats (58%, red arrows, Figure 2, Table S2). Similar results were obtained when using MNTD, with an increase of the number of habitats with lower phylogenetic diversity in invaded plots (13% or 50% of the habitats). When we used abundance, the most notable difference was a slight decrease of habitats with higher functional diversity in invaded plots (11% instead of 15%, or 42% of the habitats). Similarly, the effect of the abundance of alien species increased MPD and MNTD in 12 habitats (46% of the habitats). The global models confirmed these results, with a significant decrease in PD and increase in FD in invaded plots (according to the significant slope of the mixed models with invasive status of abundance on alien species on the indices; in all tests the high number of plots resulted in $p < .00001$).

When considering native species in non-invaded plots versus invaded plots (Test 2), we found that both PD and FD of natives were higher in invaded plots in 13 of the 26 and 25 of the 26 habitats, respectively (50% and 96% of the habitats, green arrows, Figure 2). With abundance, the number of plots decreased (PD 11% or 42% and FD 18% or 69% of the habitats). Considering only invaded plots, without and with alien species, the presence of alien species resulted in lower PD in 17 of the 26 habitats and lower FD in 25 of the 26 habitats (65% and 96% of the habitats, respectively, blue arrows, Figure 2, Test 3) mostly independently of the use of abundance weighted indices. The results of the Tests 1 and 3 were generally consistent when applying the second null model (randomizations within aliens and randomizations within native species only), with the number of significant tests being comparable or slightly inferior to the first null model (Table S8).

Results were generally consistent across habitat groups. In the first test, PD of invaded communities was lower than PD of non-invaded communities in most of the habitat groups (forests, grasslands, man-made and wetland), except stony habitats, which did not show difference in the first test (red arrows, Figure 3). FD of natives in invaded communities was higher than in non-invaded communities in all habitat groups, with noticeable difference for grasslands, where most invaded plots had lower FD (green arrows, Figure 3). For the second test, comparing native species in non-invaded vs. invaded plots, we observed higher PD in invaded plots in general, except for forests and stony habitats. The parallel increase in FD in invaded plots detected with this test was consistent throughout the habitat groups, in 25 of the 26 habitats (96% of the habitats, green arrows, Figure 3). Finally, the third test, comparing invaded plots without and with alien species showed PD lower in the latter, except in some forests and in one grassland habitat. FD was also lower in invaded plots across the five habitat groups in this test, except for one man-made habitat (Figure 3).

Analyses of traits indicate that differences in four traits were more consistent than in the others (Figure 4, Tables S3, and). Depending on the habitat, canopy height was different among habitats, but not consistently larger or smaller in the comparison of non-invaded to invaded plots, and stony habitats showed no significant difference (Test 1, red arrows, Figure 4). The same occurred for native species in invaded vs. non-invaded plots (Test 2, green arrows, Figure 4). Canopy height was higher in the comparison of invaded plots without and with alien species (Test 3, blue arrows). SLA was higher and LDMC was smaller in invaded than in non-invaded plots in most habitats (Test 1, red arrows) and in native communities

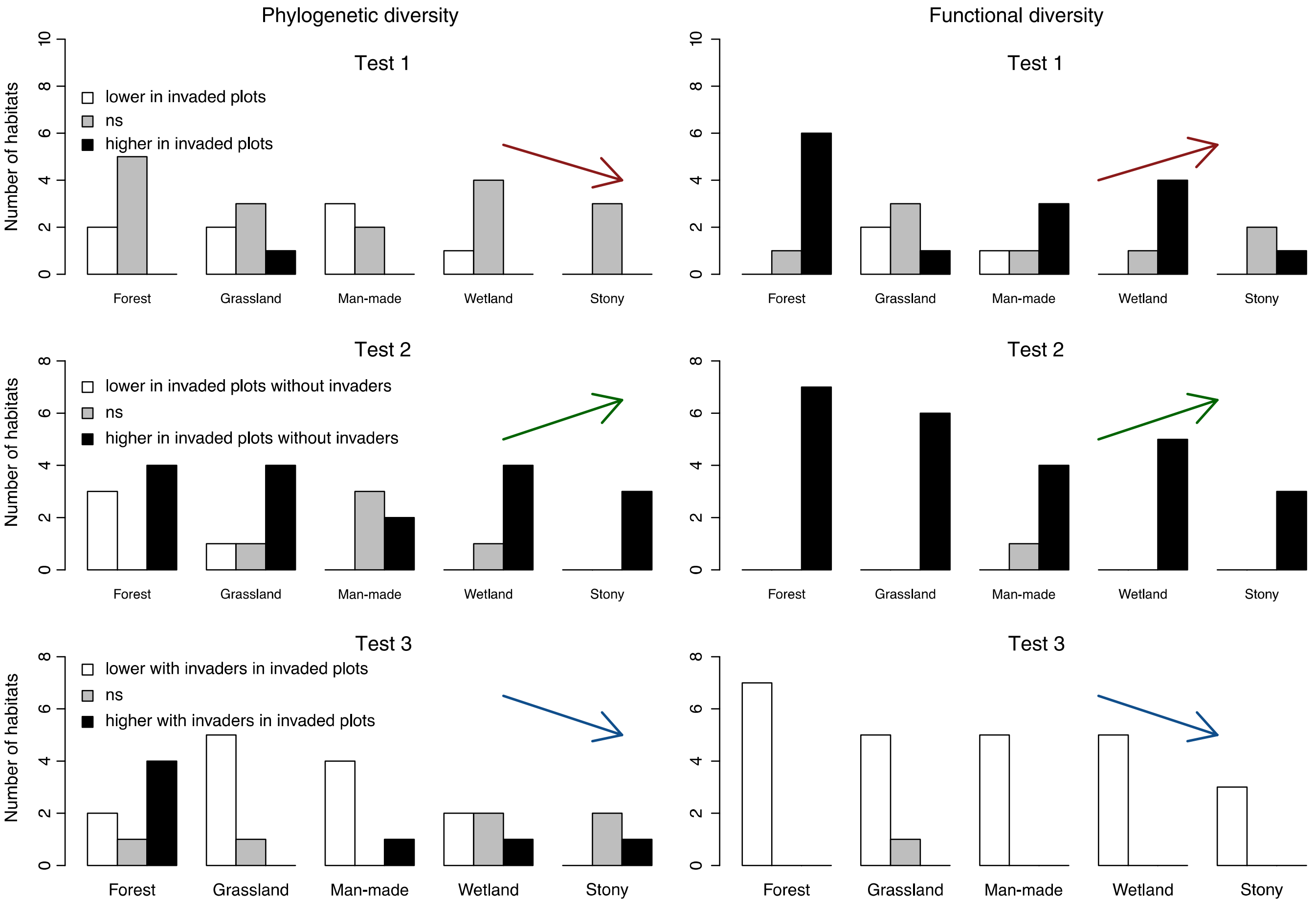

FIGURE 3 Effect of invasion on phylogenetic and functional diversity indices, analysed for five habitat groups: forests, grasslands, man-made, wetland and stony habitats (see Table S1 for further details on habitat types' grouping and on the specific habitats within each of these broad groups). Non-invaded compared to invaded plots (red arrows); native species of non-invaded plots compared to invaded ones (green arrows); and only invaded plots, excluding and including the alien species (blue arrows). Different colours of the bars (white, grey and black) indicate if the comparison indicated lower, equal or higher index value in the variant

of non-invaded compared to invaded plots (Test 2, green arrows, Figure 4). Flowering duration was extended in almost all habitats in invaded compared to non-invaded plots (Test 1, red arrows), among the native species of invaded plots, when compared to non-invaded plots (Test 2, green arrows). The third test did not show significant differences in most functional traits.

When checking for differences in the mean trait values between aliens and natives within each habitat type, the average trait values of aliens were very rarely different from those of native species (Table S6), except for traits related to flowering time (in up to 13 habitats out of 26, i.e. 50% of the habitats), but they represented only a portion of the traits used. The variance in traits of the alien species was, when the difference was significant (i.e. in only 6 of the 26 habitats, 23%), greater than the variance in traits of natives. This means that alien species have the same or more diverse traits than natives. For PD, we found that the variance in phylogenetic distance was either similar or greater in native than in alien species (in 8 of the 26 habitats, 31%) showing that in some cases aliens belonged to phylogenetically closer clades compare to natives.

4 | DISCUSSION

Our results, based on a large dataset of Central European terrestrial plant communities, show that invasion is related to the phylogenetic and functional structure of recipient communities and to the dissimilarity of both alien and native species there. We found that invaded communities are phylogenetically less, but functionally more diverse than non-invaded communities within a given habitat group. Further tests (green and blue arrows in figures) clarify this discrepancy between PD and FD, as Test 1 (red arrows) mixes different effects in invasion processes. While it is unrealistic to reach an unequivocal conclusion about invasion mechanisms using space-for-time substitution methods, the results suggest that aliens occupy a portion of the phylogenetic and trait spaces within the space used by native species in these communities. They either fill empty gaps or exclude natives in the existing niche space, rather than occupy or create novel parts of the phylogenetic and trait spaces (Gerhold et al., 2011; Ordonez, 2014).

The test comparing native species in invaded and non-invaded communities (Test 2) indicates that invaded communities are phylogenetically and functionally more diverse than non-invaded

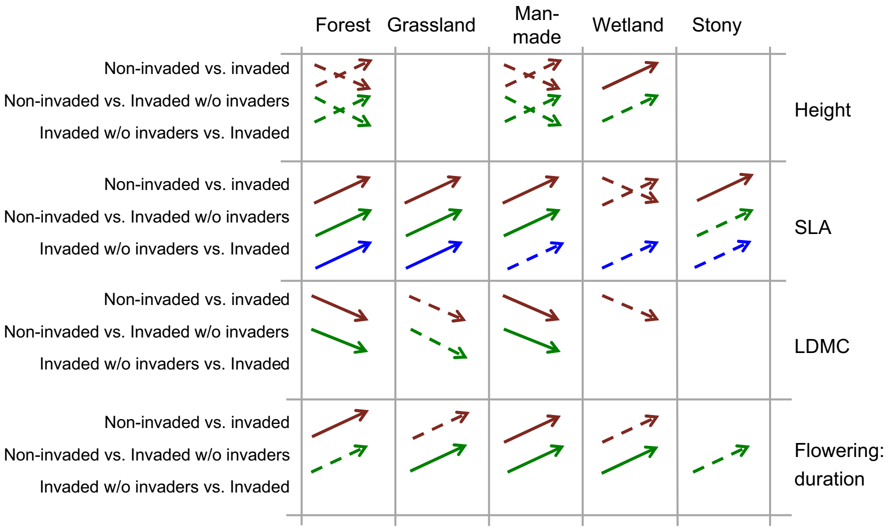

FIGURE 4 Effect of invasion on community trait means for four functional traits that showed most significant results in comparisons: Height for canopy height, SLA for specific leaf area, LDMC for leaf dry matter content and flowering duration. Each trait was analysed for five habitat groups (columns) and in three situations: not invaded compared to invaded plots (red arrows); native species in non-invaded compared to invaded plots (green arrows); and only invaded plots, disregarding and including the alien species (blue arrows). Solid lines indicate significant differences ($p < .05$) obtained with *t* tests for most habitats within that group, whilst dashed lines indicate significant results obtained for less than half of the habitats within that group. Arrows pointing up or down mean there were lower or higher values in the second group. For all results for individual habitats see the Supporting Information

communities in terms of the native species only. Based on our tests, we cannot conclude whether such increase in dissimilarity between native species is the cause or consequence of invasion. Nevertheless, these results seem to contradict the biotic resistance hypothesis formulated for species richness, by which an increased diversity of native species should foster resistance to invasion (Funk et al., 2008; Ordonez, 2014; Ordonez, Wright & Olff, 2010). Our results rather support the hypothesis of niche-filling (Thuiller et al., 2010), in which native species in non-invaded communities can be phylogenetically and functionally closer to each other than in invaded communities. According to this hypothesis, it is likely that in non-invaded communities, the niches available in an assemblage of species are more completely filled by native species, while in invaded communities available niches are left open by distant native species, providing a gap for invasion (Blonder, 2016; Thuiller et al., 2010). The idea that niche availability can foster invasion due to the presence of more ecologically different species, as also summarized by Funk et al. (2008), can be reflected in the patterns we detected with Test 2. Earlier predictions that greater PD and FD should confer greater resistance to invasion due to more complete niche occupation (Fridley & Sax, 2014; Gerhold et al., 2011; Hejda & de Bello, 2013) are thus not confirmed in this study, possibly because most of the existing studies did not assess filtering within given habitat-specific species pools, such as the tests presented in this study, to minimize potential confounding habitat filtering effects on PD and FD. It is also possible that alien species contribute to create such a gap in the invaded communities, increasing phylogenetic and functional dissimilarity of native plant communities by replacing some specific native species.

The absence of alien species was related to increases in PD and FD (Test 3 comparing indices with and without aliens). The higher phylogenetic and functional similarity in communities with alien species might be, as in the case of Test 2, due to aliens occupying available niches by filling a phylogenetic and functional “gap” in the community (Blonder, 2016), or alternatively, by aliens excluding natives from the existing niche space. Most of the alien species in our dataset originated from habitats similar to those invaded in the Czech Republic (Kalusová, Chytrý, Peet, & Wentworth, 2014) and have similar adaptations as native species (Pyšek et al., 2012). Additional analyses in our study, by comparing trait means and variance in alien vs. natives (Hulme & Bernard-Verdier, 2017, Table S6), confirmed this idea. Further results showing that aliens had similar or lower phylogenetic distance among them than natives, also support earlier observation based on habitat-specific species pools, that aliens belong to rather restricted phylogenetic groups (Lososová et al., 2015). Contrary to Hejda and de Bello (2013), higher FD values in the present analysis, considering all habitat types of the Czech Republic, were not related to the absence of alien species. It is possible that alien species profit from unoccupied ecological gaps, which may be more frequent in highly phylogenetically and functionally diverse native communities. The colonization of those communities by alien species fills such gaps and makes the phylogenetic and functional space more saturated. Our results suggest that the overall effect of invasion is to make all communities more redundant in terms of phylogeny and traits. In fact, a decrease in MPD has been linked to an increase in redundancy between species (Ricotta et al., 2016), hence suggesting that the lower availability of phylogenetic and functional space between species is associated with the presence of alien species in our dataset. Such effect is pronounced in the phylogenetic distance between species, bringing the PD value of invaded communities often below that of non-invaded communities, while FD remains higher in invaded than in non-invaded communities. This pattern is quite consistent across the habitat groups and it is in accordance with differences in PD and FD reported by previous studies (Ordonez, 2014). This study suggested that the inconsistency between PD and FD in invaded vs. non-invaded communities was caused by the low phylogenetic signal of the traits or by the lack of important phylogenetically conserved traits in their dataset. While we generally support the view that phylogeny is not a surrogate of functional diversity (Hulme & Bernard-Verdier, 2017) our tests provide a complementary explanation, based on a combination of characteristics of communities predisposed to invasion of the effects of alien species on communities.

Both this study, based on the assembly of local communities within habitat species pools, and a previous one, based on the comparison of habitat-specific species pools (Lososová et al., 2015), found that the presence of alien species is related to lower PD. The higher occurrence of invasion found in phylogenetically more diverse communities shown here is, however, in contrast with the results of this previous study at broader scale (Lososová et al., 2015). Opposing results at the two scales possibly highlight the different roles of abiotic and biotic effects on community assembly at different spatial scales. At the species-pool level, the invaded communities were those with native species phylogenetically clustered (Lososová et al., 2015). In the present study, in which species of local communities were filtered from the species pools, plots with less clustered native species were those with higher invasion. As species pools are generally the result of environmental filtering (de Bello et al., 2012; Swenson, Enquist, Thompson, & Zimmerman, 2007), alien species sharing ecological adaptations with natives tend to be successful invaders at a broad spatial scale. In contrast, results obtained for local communities within habitats tend to minimize the effect of environmental filtering due to the scale studied. This suggests that, at fine scale, invaded communities show higher phylogenetic and functional diversity due to different coexistence mechanisms, with aliens filling niche gaps or excluding native species. Environmental filtering is a leading factor in community assembly at coarse spatial scales, while its effect is counterbalanced by interspecific interactions on fine scale (Thuiller et al., 2010), whereas niche filling can play an important role at the community scale (Li et al., 2015). In this sense, competitive exclusion possibly caused by alien species, leading to a decrease in PD and FD, can also cause the dominance of certain clades and of species bearing traits that confer greater competitive abilities (de Bello et al., 2012; Mayfield & Levine, 2010).

Since we did not compare how dissimilar successful and unsuccessful invaders were from the native species, we cannot directly refute the Darwin's naturalization hypothesis. However, if alien species were different from the natives, the community's PD and FD would increase with the contribution of the alien species (Test 3, blue arrows), but the pattern tended to be the opposite. Test 3 (blue arrows) showed weaker patterns of change in community trait means (Figure 4), thus the relative change in the mean traits of the communities due to the aliens was small. This suggests again that aliens occupy available niche gaps or exclude the native species in the communities, rather than expanding the portion of the ecological space occupied by resident species. Indeed, if MPD changed markedly in Test 3, a change of community trait means would have been also possible.

Invasion was related not only to changes in phylogenetic and functional dissimilarity (Figures 2 and 3), but it was also related to changes in dominant trait values in communities, consistent with the results of previous studies (e.g. Carboni et al., 2016; Ordonez, 2014; Pyšek & Richardson, 2007; van Kleunen et al., 2010). Focusing on trait means highlights changes in the structure of functionally more "typical" species. Most changes in community trait means, though, were observed with Test 2, indicating changes in trait means across natives in invaded vs. non-invaded communities, and some changes were also observed with Test 3, showing an effect of the alien species. Results generally seem to support the view that a strong native competitor will share similar traits with a strong alien competitor (Leishman et al., 2010), but the functional spectra of native species include both strong and poor competitors, whereas successful aliens tend to be, on average, stronger competitors than natives (but see Daehler, 2003). Aliens tended to be taller than natives; therefore, the community mean plant height increases with invasion in most herbaceous community types. In some deciduous forests, however, the community mean of plant height decreased, probably because of the predominance of herb invaders, such as *Impatiens parviflora*, over tree or shrub invaders. Most community types are invaded by species with larger SLA and smaller LDMC, providing a more dynamic resource use strategy, associated with faster growth and higher photosynthetic rates compared to co-occurring native species (Wright et al., 2004), a pattern that we observed with SLA in Test 3, but not in LDMC. Finally, most community types showed longer flowering duration in invaded communities compared to non-invaded ones. A similar observation was made for invasions of Central European species in other parts of the world (Küster, Kühn, Bruelheide, & Klotz, 2008; Pyšek & Richardson, 2007) and its detection here for another group of alien species suggests a general pattern.

Altogether, the findings of this study indicate that invasion processes are linked to changes in the phylogenetic and functional structure of communities, both in terms of differences between natives, and between natives and aliens. Such changes in the phylogenetic and functional structure of communities can have remarkable consequences for the functioning of ecosystems (Cadotte, Albert, & Walker, 2013; Finerty et al., 2016). Results suggest that aliens more often occupy a phylogenetic and functional space within the range of native species within a community. They do so by either filling empty functional and phylogenetic gaps within communities, or excluding natives from their original space, leading to a loss of function provided by a native species. Changes in community trait means, often linked to changes in ecosystem functions (Finerty et al., 2016), were observed more strongly in terms of changes within natives than in terms of the impact of aliens, which generally had similar trait means of natives. The presence of alien species caused increased similarity between species in terms of phylogenetic and functional diversity, thus increasing the redundancy of invaded communities, likely affecting the relationship between diversity and ecosystem functioning (Ricotta et al., 2016).

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AUTHORS' CONTRIBUTIONS

F.d.B. and Z.L. conceived and designed the research; M.C. and Z.L. compiled the data; L.G., P.P. and C.P.C. helped to delineate the analysis; P.P.L., F.d.B. and Z.L. performed the analyses and wrote the first draft of the manuscript; all authors contributed substantially to revisions.

DATA ACCESSIBILITY

Plant traits data can be retrieved from the LEDA database: https://www.uni-oldenburg.de/en/landeco/research/leda/data-files (Kleyer et al., 2008) and the CLO-PLA database: http://clopla.butbn.cas.cz/ (Klimešová & de Bello, 2009). Phylogeny data can be retrieved from the DAPHNE database which is archived on Figshare: https://doi.org/10.6084/m9.figshare.3554421.v1 (Durka & Michalski, 2012). Vegetation plots are extracted from the Czech National Phytosociological Database: http://www.sci.muni.cz/botany/vegsci/dbase.php?lang=en (Chytrý & Rafajová, 2003).

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SUPPORTING INFORMATION

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

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