Global Ecology and Biogeography A Journal of Macroecology

Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2015) **24**, 786–794

RESEARCH PAPER

Alien plants invade more phylogenetically clustered community types and cause even stronger clustering

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ABSTRACT

Aim Several hypotheses postulate that species invasion is affected by an interplay between the phylogenetic position of the invading species and the phylogenetic structure of the invaded community type. Some of them suggest that phylogenetic relatedness of invaders to native species promotes naturalization, because phylogenetically related alien species tend to have similar environmental adaptations as native species. Others predict that phylogenetic relatedness hampers naturalization because of stronger competition of aliens with native species and shared enemies. Here we ask how phylogenetic diversity of native species affects invasion across community types.

Location Czech Republic.

Methods All major plant community types at a national scale ($n = 88$) were characterized by their species pools, i.e. lists of species that can potentially occur there. Of the total number of 2306 species, 1785 were native, 246 were archaeophytes and 275 were neophytes. For each species pool, we related the number of alien species to the phylogenetic diversity of the native species pool, calculated as mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD), including null models.

Results The number of alien species was related both to the phylogenetic structure of community types and to the phylogenetic position of alien species. Frequently disturbed herbaceous community types with strong phylogenetic clustering were more invaded than others, possibly due to disturbance acting as an environmental filter. Here, alien species increased the degree of phylogenetic clustering as they tended to be from the same lineages as native species. Such trends were not detected for phylogenetically more diverse community types such as forests.

Main conclusions Our findings support the hypothesis that relatedness of invaders to native species promotes invasion because of their shared adaptations to the same environments. Alien species more strongly invade community types that are phylogenetically clustered, and because they tend to be related to native species, invaded community types become even more clustered.

Keywords
Archaeophyte, biological invasions, neophyte, phylogenetic diversity, species pool, vegetation type.

DOI: 10.1111/geb.12317

INTRODUCTION

Knowledge about the relationship between the phylogenetic structure of plant community types and their level of invasion (i.e. the actual number or proportion of alien species; Chytrý *et al.*, 2008) may provide new insights for understanding and predicting biological invasions (e.g. Lambdon & Hulme, 2006; Strauss *et al.*, 2006; Diez *et al.*, 2008, 2009; Cadotte *et al.*, 2010; Gerhold *et al.*, 2011). Several hypotheses converge in suggesting that invasion is driven by an interplay between the phylogenetic position of the alien species and the phylogenetic structure of the invaded communities, with phylogeny often being considered as an indirect proxy for missing functional trait information. Empirical studies, however, have found rather inconsistent, and in some cases probably idiosyncratic, patterns, possibly because of inconsistencies in the scale of observations (Thuiller *et al.*, 2010).

There are several important mechanisms that affect the phylogenetic structure of native plant communities as well as relatedness between native and alien species. A key mechanism, referred to as environmental filtering, assumes that phylogenetically related species share similar traits and environmental requirements and therefore tend to occur in the same community types (Prinzing *et al.*, 2001; Wiens & Graham, 2005). Co-occurrence of closely related species in communities on the local scale is usually interpreted as environmental filtering on phylogenetically conserved traits (Webb, 2000; Kembel & Hubbell, 2006; Gerhold *et al.*, 2008; Bartish *et al.*, 2010). Under these assumptions, alien species invading native communities in which environmental filtering is more important than interspecific competition would profit from sharing the same ecological adaptations as the resident native species. Assuming phylogenetic conservatism of ecological adaptations (but see Cadotte *et al.*, 2013), aliens would most likely gain this advantage if they are phylogenetically related to the resident native species. In such a case, invasion would increase phylogenetic clustering. At the same time it has been noticed that phylogenetic clustering can also be caused by the combined effect of environmental filtering and species interactions, especially in more productive conditions where strong competitors from few lineages may exclude weaker competitors, thus decreasing phylogenetic diversity (Mayfield & Levine, 2010). However, this second mechanism should operate at a finer spatial scale, i.e. species communities, while environmental filtering can be assessed across different community types. For this reason assessing patterns at specific spatial scales should allow these two effects to be teased apart (Swenson *et al.*, 2006; de Bello *et al.*, 2013).

Empirical studies provide contradictory evidence of phylogenetic clustering due to species invasion. Data supporting phylogenetic clustering come, for example, from the floras of New Zealand and Australia (Duncan & Williams, 2002; Diez *et al.*, 2009) or Hawaii (Daehler, 2001). Other studies either found no relationship between natives and aliens with respect to their phylogenetic status (Lambdon & Hulme, 2006; Ricciardi & Mottiar, 2006) or reported increasing phylogenetic overdispersion due to invasion, for both plant and fish communities (Ricciardi & Atkinson, 2004; Strauss *et al.*, 2006; Schaefer *et al.*, 2011; Bezeng *et al.*, 2013). Overdispersion has been interpreted to be a result of stronger competition between closely related species than between distantly related species, because of the dependence of the former on the same resources due to their shared ancestry. This interpretation implies that alien species that have close relatives in invaded communities would be less successful due to stronger competition for resources. This hypothesis has sometimes been referred to in the invasion literature as Darwin's naturalization hypothesis (Daehler, 2001), although Darwin (1859) also stated the opposing hypothesis, that aliens can be successful in places with close relatives due to pre-adaptation (Elton, 1958; Fridley, 2007). Since this pattern should be observed at fine spatial scales, i.e. where competition can take place, working at broader spatial scales such as regions or community types (rather than at the local scale of plant communities) could better allow us to tease it apart from the effect of environmental filtering (Strauss *et al.*, 2006; Thuiller *et al.*, 2010). The pattern of introduction of alien species and their effect on the phylogenetic structure of communities depends, therefore, not only on the studied taxa but also on the scale of the study (Lambdon & Hulme, 2006; Diez *et al.*, 2008; Procheş *et al.*, 2008; Lim *et al.*, 2014). It has been shown that while at fine spatial scales plant species exclude similar ones because of their dependence on the same resources, at larger scales they co-occur, relying on similar environments (Procheş *et al.*, 2008; de Bello *et al.*, 2013), i.e. environmental filtering is the key mechanism acting at larger scales.

Current knowledge of mechanisms that drive invasion of alien species and their effects on community assembly is focused on either the very fine scale of vegetation plots (see, e.g., Bezeng *et al.*, 2013) or on the complete floras of large regions (Strauss *et al.*, 2006; Diez *et al.*, 2008, 2009). Gerhold *et al.* (2011), working with vegetation plots from many plant community types at a national scale (the Netherlands), showed that phylogenetically overdispersed plant community types are less invaded than clustered community types. In contrast to studies based on vegetation plots or floras of large regions, there is a lack of studies at regional and landscape scales working with species pools of particular types of plant communities (Zobel, 1997). Species pools reflect the potential of species to co-occur in a given plant community. Analyses based on species pools tend to produce robust results because they are free of errors and noise caused by different probabilities of species being recorded at particular sites. For this reason comparing different community types also allows a more direct focus on the effect of environmental filtering, while minimizing the effect of biotic interactions (de Bello, 2012). Alien plant species in central Europe represent quite a heterogeneous group in terms of their traits, origin, time of introduction and invasion status (Pyšek *et al.*, 2012a,b). European studies on different spatial scales have indicated that in comparisons across many habitats, two groups of alien plant species, archaeophytes (introduced before AD 1500) and neophytes (introduced after AD 1500), generally tend to invade the same communities (Chytrý *et al.*, 2005):

communities rich in archaeophytes tend to host many neophytes, and vice versa, although there are some differences between these two groups at a finer scale. Strongly invaded communities are often those experiencing frequent or strong disturbances, for example communities of arable fields or of other human-made habitats (Chytrý *et al.*, 2005).

Here we use a unique data set of regional species pools for 88 plant community types of the Czech Republic (Sádlo *et al.*, 2007) to answer the following questions: (1) does variation in phylogenetic structure of native species pools affect the number of alien species that invade different plant community types, and (2) do aliens decrease or increase the phylogenetic diversity of invaded community types as a consequence of their relatedness to native species? Residence time can further influence the time during which environmental filtering can take place. We therefore explored the questions of this study separately for archaeophytes and neophytes to assess whether the phylogenetic aspects of invasions differ between these two groups with different residence times in the invaded region.

MATERIALS AND METHODS

Plant community types

Lists of alien and native species were derived from a database of regional species pools for 88 plant community types occurring across the whole of the Czech Republic (Sádlo *et al.*, 2007). This database describes species affinities to particular community types as recorded or observed in the Czech Republic between 1990 and 2007. It comprises all major plant community types of that country, and is thus representative of the diversity of vegetation of inland temperate Europe at the transition between suboceanic and subcontinental climate with the exception of some alpine habitats. The database comprises 2306 species of vascular plants (1785 native species, 246 archaeophytes and 275 neophytes, following the classification by Pyšek *et al.*, 2012b) occurring in an area of *c.* 78,000 km^2. Some of these species are included in species pools for more than one community type. All subspecies contained in the original database were aggregated to the species level.

Phylogenetic tree

We prepared a phylogenetic tree for the 2306 species in the data set based on a dated, ultrametric supertree for central European vascular plant species (DaPhnE 1.0; Durka & Michalski, 2012). We took 2086 species from the DaPhnE supertree and the remaining 220 taxa that were absent in DaPhnE were supplemented manually to the existing nodes of the DaPhnE supertree. Each new species was attached to the root node of the most inclusive clade. These nodes represented the latest common ancestor of the added taxon with any taxon already included in the tree, always creating a polytomy at this node. The decision on the common ancestry was made based on the taxonomic information published in the 'Checklist of vascular plants of the Czech Republic' (Danihelka *et al.*, 2012). The species concept and nomenclature follow those used in the original DaPhnE 1.0 supertree (Durka & Michalski, 2012). Nomenclature of newly added species follows Danihelka *et al.* (2012).

Data analyses

We quantified phylogenetic diversity of each plant community type separately for the native species only and for all species, i.e. including both native and alien species (as in Winter *et al.*, 2009; Hejda & de Bello, 2013). First, we measured phylogenetic diversity using the MPD index (Webb *et al.*, 2002), which calculates mean phylogenetic distance between all species pairs within the species pool measured in millions of years. We then did the same using the MNTD index (Webb *et al.*, 2002), which measures the mean nearest taxon distance between all species pairs in the species pool. The MPD index was shown to be independent of species richness (Schweiger *et al.*, 2008), although MNTD can be negatively correlated with the number of species. The results were not weighted by species abundances, as such information was not available for our data set.

We tested the relationship between phylogenetic diversity of native species pools and the number of alien species invading respective community types using sets of linear regressions computed for alien species, archaeophytes and neophytes, respectively. We related the phylogenetic diversity (MPD) of native and alien species to detect their relationship. These relations were only calculated for species pools with more than five alien species. Since MNTD can be negatively correlated with the number of species we verified that the results also held true after doing randomizations to reduce such an effect (see the following paragraphs).

To express possible changes in phylogenetic diversity due to invasion of alien species, and to account for potential effects of different sizes of species pool, we considered null models with carefully chosen randomizations (see below). We assessed phylogenetic patterns using standardized effect sizes (SES) obtained by the null models. In this way we obtained MPD SES and MNTD SES values (Webb *et al.*, 2002) for each species pool. We calculated MPD SES (analogously MNTD SES) as:

$$\mathrm{MPD\ SES} = (\mathrm{MPD}_{\mathrm{obs}} - \mathrm{meanMPD}_{\mathrm{rand}})/\mathrm{sdMPD}_{\mathrm{rand}},$$

where $\mathrm{MPD}_{\mathrm{obs}}$ is the observed MPD, $\mathrm{meanMPD}_{\mathrm{rand}}$ is the mean of the MPD values obtained for the null species pools and $\mathrm{sdMPD}_{\mathrm{rand}}$ is the standard deviation of the MPD values of the null species pools. Near-zero values indicate species pools with random phylogenetic diversity, and deviations indicate overdispersion (phylogenetic divergence between species; MPD SES > 0) or clustering (convergence; MPD SES < 0) due to invasion of alien species. We obtained two-tailed *P*-values by comparing the observed MPD or MNTD values with those from the distributions of random matrices (significance of a two-tailed test occurs when SES values are above 1.96, i.e. overdispersion, and below −1.96, i.e. clustering).

We computed null models by creating random species pools where the identity of alien species was changed across the whole list of aliens. This was done by shuffling alien species names 999 times for each index, across all 88 species pools, first for all alien species together and then separately for archaeophytes and neophytes. For archaeophytes we tested their effect on phylogenetic diversity after invading communities of native species, and for neophytes the same effect after invading communities of native species and archaeophytes, as the latter would have been established in the study area long before. Such a null model, which maintains the phylogenetic diversity of the existing species pools and the number of invading species, was chosen because it assesses the change in phylogenetic diversity in species pools due to invasion of alien species. In this way the randomizations are done across different community types, which implies that species are randomized across habitats, allowing environmental filtering effects to be detected. It should be noted that the results of the null models (MPD SES and MNTD SES indices) calculated in this way do not depend on the number of species, because only a part of each species pool is randomized. In our case only alien species were randomized over the phylogenetic tree with all species. The SES values obtained were then related to the observed MPD and MNTD values of native species only.

Using both indices (MPD and MNTD) enabled us to assess the effect of phylogenetic relatedness on two phylogenetic scales, because MPD generally reflects overall relatedness of alien species to multiple native species while MNTD reflects the relatedness of alien species to a single (most related) native species (Strauss *et al.*, 2006). All phylogenetic indices were calculated in R (R Development Core Team, 2010) using functions *mpd* and *mntd* from package *picante* (Kembel *et al.*, 2010).

RESULTS

Phylogenetic diversity of species pools and the number of alien species

Species pools with a low phylogenetic diversity of native species contained more alien species (Fig. 1) than those with a high phylogenetic diversity. The same trend was detected for the proportion of alien species (Fig. 1). To check for bias due to a possible negative relationship between MNTD and species richness we ran randomization tests that detected a similar pattern for the relationship between the number of alien species and MNTD SES of native species (not shown). There was a significant positive relationship between the phylogenetic diversity (MPD) of native and alien species ($R^2 = 0.37$; calculated only for species pools with more than five alien species). This suggests that although the community types with phylogenetically diverse native species pools were invaded by fewer alien species, these aliens formed a phylogenetically diverse group; this trend was even stronger if we considered only neophytes (i.e. excluding archaeophytes) ($R^2 = 0.40$; calculated only for species pools with more than five neophytes). No significant relationships between the phylogenetic diversity of native species and archaeophytes, or between that of archaeophytes and neophytes invading the same community type, were detected.

Effect of invasion on phylogenetic relatedness within species pools

Based on the null models obtained for MPD and MNTD indices we detected that invasions by alien species increased phylogenetic similarity (indicating phylogenetic clustering) among plant species in 13 and 56 species pools, respectively, and resulted in no significant change in 52 and 21 species pools, respectively. The remaining 11 species pools contained fewer than five alien species, therefore they were not analysed. Only null models for the MPD index indicated 12 species pools where the addition of alien species decreased phylogenetic similarity and caused phylogenetic overdispersion. The most pronounced clustering effect of alien species was detected for species pools of annual and perennial ruderal vegetation, vegetation of wet disturbed soils and annual vegetation of arable land. The smallest numbers of alien species combined with almost no effect of alien species on the phylogenetic structure of species pools were found in spring and mire vegetation, mesic nutrient-poor grasslands and vegetation of saline soils (Appendix S1 in Supporting Information).

When assessing the effect of either archaeophytes or neophytes the general picture remained the same, although some results were modified. The addition of archaeophytes significantly increased phylogenetic similarity within the species pools of wetland and riverine vegetation, mesic and wet nutrient-rich grasslands, some types of sand, dry grasslands and steppes, and in ruderal and weed vegetation (Appendix S1). For other species pools the addition of archaeophytes had no significant effect on phylogenetic diversity. Null models obtained for MPD and MNTD indices calculated for neophytes only detected different patterns. MPD models indicated six species pools where invasion of neophytes led to increasing similarity; these species pools were those of nitrophilous herbaceous riverine vegetation and ruderal and weed vegetation. For 13 species pools, the addition of neophytes resulted in phylogenetic overdispersion. These species pools were those of some types of wetlands, dry grasslands and forests. The MNTD index for neophytes indicated only a clustering effect for 46 species pools or no significant effect (Appendix S1).

The effects of the addition of alien species on the phylogenetic diversity of the species pools depended on the phylogenetic diversity of native species (Fig. 2). The species pools whose native species were phylogenetically related to each other tended to receive alien species that were also phylogenetically related to those native species ($R^2 = 0.13$). Additions of both archaeophytes and neophytes increased the phylogenetic clustering of species in particular species pools (Fig. 2). Phylogenetically diverse species pools tended to receive neophytes that were phylogenetically distant from the species of the native species pool, and the phylogenetic overdispersion of these species pools was consequently increased. No such trend was detected for archaeophytes (MPD SES was negative or close to zero; Fig. 2).

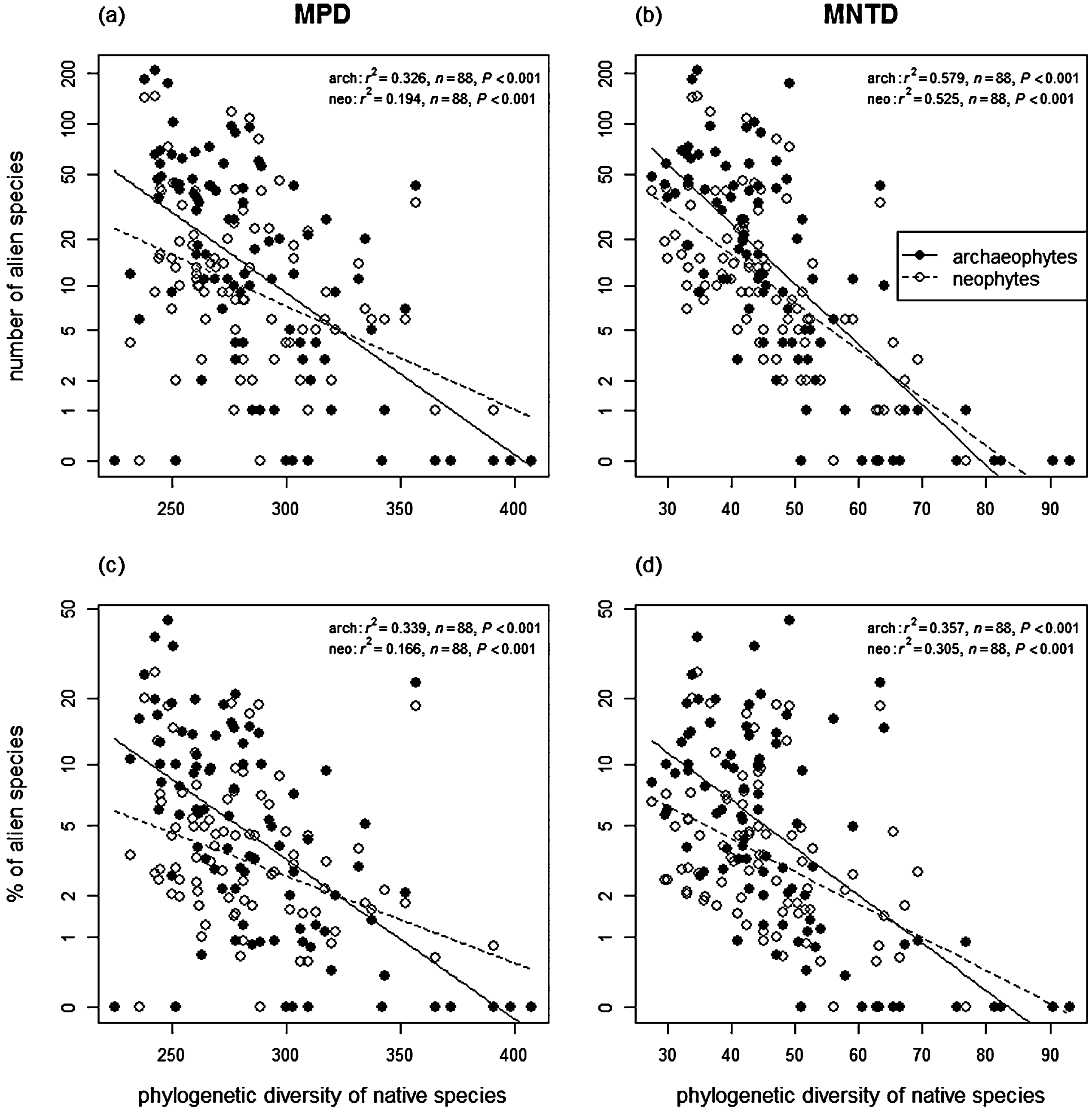

Figure 1 The relationship between the number of alien species in the species pools (upper panels) or the proportion of alien species in species pools (lower panels) and phylogenetic diversity of the native part of the species pools expressed by either mean phylogenetic distance (MPD, left) or mean nearest taxa distance (MNTD, right) indices for 88 plant community types. Alien species are divided into archaeophytes and neophytes according to their residence time. Note that vertical axes are log scaled [$\log_{10}(x+1)$].

DISCUSSION

Phylogenetic diversity of species pools and the number of alien species

We showed that the phylogenetic diversity of species pools of particular plant community types influences the number of alien plants species invading these community types. The number of alien species increases with decreasing phylogenetic diversity of the native species pools from overdispersed to clustered (see also Gerhold *et al.*, 2011). Community types with phylogenetically clustered native species pools are the most invaded. In the Czech Republic these community types comprise mainly weed and ruderal vegetation, as well as some types of grasslands and scrub (Chytrý *et al.*, 2005; Sádlo *et al.*, 2007). Our results indicate that the strong environmental filtering that

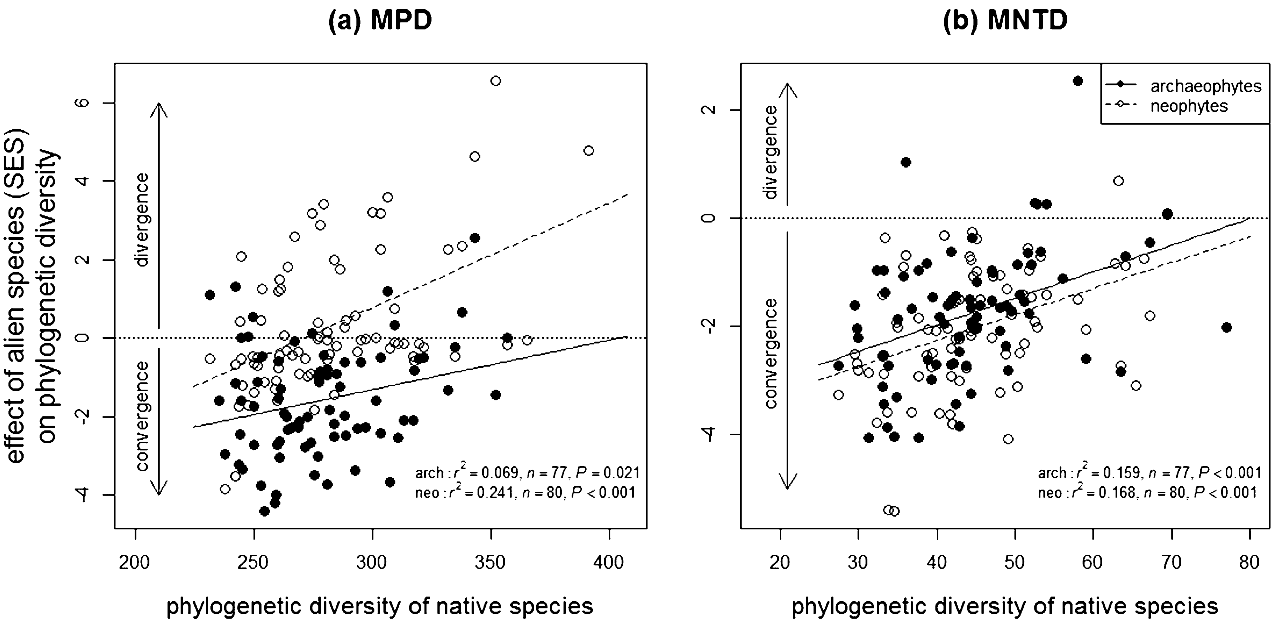

Figure 2 Relationship between the changes in phylogenetic diversity of species pools due to addition of alien species (SES, standardized effect sizes) and the phylogenetic diversity of the native parts of the species pools. Eleven species pools with fewer than five archaeophytes and eight species pools with fewer than five neophytes were not analysed. Negative values of SES indices indicate that alien species decrease phylogenetic distance among all species present in a species pool following the addition of alien species (invasion increases phylogenetic clustering). Positive values of SES indicate that alien species increase phylogenetic distance. Alien species are divided into archaeophytes and neophytes according to their residence time (see text).

shapes the phylogenetic diversity of native species pools is also the key factor behind the number of alien species invading particular community types. Frequent disturbances and fluctuating resources typical of ruderal habitats (Davis *et al.*, 2000) are strong filters which probably select lineages that evolved in these habitats, thus creating low phylogenetic diversity. We suggest that the high numbers of alien species occurring in community types with phylogenetically clustered native species pools are mainly due to large groups of closely related alien plants with pre-adaptations to disturbed environments that evolved in the habitats of their native range. Both native and alien species in these species pools profit from similar life strategies, being mostly annual, with rapid growth and producing many seeds with good dispersal ability (Lososová *et al.*, 2006). Gerhold *et al.* (2011) suggested that coexistence of numerous native and alien species in phylogenetically clustered community types is possible because of the lack of direct competition between species in frequently disturbed habitats. However, a high number of alien species in these community types could be also due to high propagule pressure, as these community types are often situated in or near human settlements.

Effect of invasion on phylogenetic relatedness within species pools

One of our key findings is that alien species influence the phylogenetic diversity of species pools of individual plant community types. Alien species not only invade community types with phylogenetically clustered species pool at disproportionally high numbers, but also increase the degree of clustering of these species pools because they are mostly from the same lineages as native species. Working at the scale of species pools therefore seems to downplay the importance of mechanisms which predict that coexistence of native and alien species is affected by the avoidance of negative interactions within lineages ('Darwin's naturalization hypothesis' *sensu* Daehler, 2001). Whether phylogenetic relatedness is often (or not) connected with functional similarity (Webb *et al.*, 2002) remains an open question (Cadotte *et al.*, 2013), which will be clarified when trait values become available for many species. However, the clustering that was detected should indeed provide a first robust indication that alien species which share ecological adaptations with native species are mainly successful invaders in phylogenetically clustered plant community types. The phylogenetically conserved adaptations that underlie the observed patterns are probably those that are important for niche preferences of species, for example moisture requirements or tolerance to soil salinity (Prinzing *et al.*, 2001).

A high number of alien species and their effect on phylogenetic diversity were detected for species pools of several community types with different evolutionary histories, including weed and ruderal vegetation, and different types of grasslands and thermophilous forests (see Appendix S1). Weed and ruderal community types occupy the youngest habitats in central Europe (Pinhasi *et al.*, 2005). These community types were mostly assembled through habitat filtering by drawing from already existing pools of pre-adapted species. Various disturbances favour lineages that possess annual species, selfers and species reproducing by seeds and forming persistent seed banks (Lososová *et al.*, 2006). However, these traits are related to each other: some of them (life strategy, leaf persistence) correspond to habitat properties rather than phylogeny, whereas others (e.g. pollination mode or dispersal) are strongly affected by phylogeny (Lososová *et al.*, 2006). The majority of alien species invading the above-mentioned community types arrived from the Middle East, the Mediterranean and other parts of Europe (Pinhasi *et al.*, 2005; Pyšek *et al.*, 2012a). Most of them originated in similar habitats and have similar pre-adaptations, and many of them belong to the same lineages as native plants (Pyšek *et al.*, 2012b), causing even stronger phylogenetic clustering.

Introduction of alien species increases the degree of phylogenetic clustering in many types of central European grasslands, including wetland and riverine vegetation and mesic and wet nutrient-rich grasslands. These community types are invaded mostly by annual and perennial, tall, fast-growing, nutrient-demanding herbs. The majority of these alien species belong to the family Asteraceae (e.g. the genera *Erigeron*, *Helianthus* and *Solidago*) and originate from eastern North America, where they grow in open, nutrient-rich habitats (Fridley, 2013). In contrast to community types with phylogenetically clustered species pools, the smallest numbers of alien species were detected for community types with phylogenetically diverse species pools, which are composed of species belonging to isolated old lineages together with those of more recent lineages (e.g. steppes, dry grasslands, beech forests). We suggest that community types with phylogenetically diverse species pools are more resistant to invasions because they are usually less disturbed, and hence experience less fluctuation of available resources (Davis *et al.*, 2000). Another explanation is that native species are functionally diverse. They utilize resources more efficiently and hence leave less for invaders.

The community types with phylogenetically diverse species pools (typically forests or aquatic vegetation) are invaded by pre-adapted species sharing the same strategies as resident native species, but our results based on the MPD values (Appendix S1) suggest that the few species invading these community types often belong to ancient lineages such as conifers (e.g. *Pinus nigra*, *Pinus strobus* and *Pseudotsuga menziesii*), or to phylogenetically isolated aquatic taxa such as *Azolla filiculoides* and *Elodea canadensis.* In such cases the addition of alien species of ancient lineages to the native species pool increases the mean phylogenetic distance among all species in the given species pool (Fig. 2). In contrast, the analyses based on MNTD detected only phylogenetic convergence or no effect on phylogenetic diversity due to invasion of alien species, suggesting that invasion of species from these ancient lineages is particularly successful if these species have native relatives in the target species pool.

Our study is based on regional species pools, i.e. assemblages of species that can occur in the same community types but do not necessarily grow all together at the same site. On such a scale the effect of interspecific interactions is less important for the resulting phylogenetic diversity and biological invasion than environmental filtering (Duncan & Williams, 2002; Diez *et al.*, 2009; Willis *et al.*, 2010). It is likely that on a finer spatial scale, such as that of vegetation plots, interspecific interactions would be more important (Thuiller *et al.*, 2010; Carboni *et al.*, 2013; Lim *et al.*, 2014). We are also aware that the test of the relationship between the phylogenetic structure of species pools and species richness could be theoretically biased due to compositional similarity between pairs of samples, because two compositionally similar samples do not bring two full degrees of freedom to the analysis. However, working with species pools of broadly defined community types minimized this problem, because individual samples were compositionally rather different.

Effect of residence time

Although the general pattern of incidence of alien species across species pools is similar between archaeophytes and neophytes, there are some notable differences. The addition of archaeophytes causes only increasing phylogenetic clustering or has no significant effect on the phylogenetic diversity of species pools. Archaeophytes that are phylogenetically more closely related to native species are more successful invaders, which supports the environmental filtering hypothesis and contradicts Darwin's naturalization hypothesis (*sensu* Daehler, 2001) for this group of species and at the scale of species pools. There are two plausible explanations of this pattern. Archaeophytes form a relatively phylogenetically and ecologically homogeneous group of species with a common origin in Europe or the Mediterranean region (Pyšek *et al.*, 2012a). Most of them belong to the commonest families of the Czech native flora, e.g. Apiaceae, Asteraceae, Lamiaceae or Poaceae (Pyšek *et al.*, 2012b). These species possess specific sets of traits that make them adapted to disturbed habitats such as arable fields or human settlements (Pyšek *et al.*, 2005; Sádlo *et al.*, 2007). Archaeophytes are represented by fewer species than native species or neophytes in central Europe (Pyšek *et al.*, 2012b), but since their introduction they have had enough time to spread to most of the suitable habitats (Pyšek *et al.*, 2005). Their presence in species pools leads to increasing taxonomic and functional clustering in numerous plant community types (Hejda *et al.*, 2009; Winter *et al.*, 2009; Hejda & de Bello, 2013), but our data show that this pattern is much more complex. More recently introduced neophytes also have a clustering effect on the phylogenetic diversity of species pools, especially those that are already clustered. However, a divergent effect also occurs during invasion by neophytes, particularly on a broad phylogenetic scale and for phylogenetically diverse species pools.

ACKNOWLEDGEMENTS

This study was funded by the Czech Science Foundation (Centre of Excellence PLADIAS, 14-36079G). F.d.B. was supported by the Czech Science Foundation (grant no. P505/12/1296). P.P.

was also supported by long-term research development project RVO 67985939 (Czech Academy of Sciences), and acknowledges support by Praemium Academiae award from the Czech Academy of Sciences. M.W. acknowledges funding by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig via the German Science Foundation (FZT 118). We thank Christina Alba for improving the English.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Effect of alien species on the phylogenetic diversity of species pools of 88 plant community types in the Czech Republic.

BIOSKETCH

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Editor: Arndt Hampe