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Phylogenetically Poor Plant Communities Receive More Alien Species, Which More Easily Coexist with Natives

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ABSTRACT: Alien species can be a major threat to ecological communities, but we do not know why some community types allow the entry of many more alien species than do others. Here, for the first time, we suggest that evolutionary diversity inherent to the constituent species of a community may determine its present receptiveness to alien species. Using recent large databases from observational studies, we find robust evidence that assemblage of plant community types from few phylogenetic lineages (in plots without aliens) corresponds to higher receptiveness to aliens. Establishment of aliens in phylogenetically poor communities corresponds to increased phylogenetic dispersion of recipient communities and to coexistence with rather than replacement of natives. This coexistence between natives and distantly related aliens in recipient communities of low phylogenetic dispersion may reflect patterns of trait assembly. In communities without aliens, low phylogenetic dispersion corresponds to increased dispersion of most traits, and establishment of aliens corresponds to increased trait concentration. We conclude that if quantified across the tree of life, high biodiversity correlates with decreasing receptiveness to aliens. Low phylogenetic biodiversity, in contrast, facilitates coexistence between natives and aliens even if they share similar trait states.

Keywords: alien species, community assembly, functional traits, invasions, phylogenetic diversity, species richness.

Introduction

Alien species establish unequally across a given region; some ecological communities harbor many more alien species than do others (Chytrý et al. 2009). Moreover, aliens, once established in a community, can potentially cause

extinctions of native species, alter relationships between species, and disturb nutrient cycling in food chains, in turn adversely impacting natural ecosystems worldwide (Vitousek et al. 1997; Blumenthal 2005; Chytrý et al. 2009). Understanding the reasons why some communities are more receptive to aliens and why aliens may cause extinctions in some communities and not in others would improve our ability to control future invasions and at the same time permit testing of major ecological theories (Blumenthal 2005; Callaway and Maron 2006). Community receptiveness to aliens has been associated with multiple biotic and abiotic factors (Maron and Connors 1996; Marler et al. 1999; Davis et al. 2000; Parker et al. 2006). Arguably the most persistent debate in invasion ecology is the role that species richness plays in determining the receptiveness of a community to aliens. It has been suggested since Elton (1958) that communities rich in native species are less receptive to aliens because of increased competition and a lack of empty niches (Kennedy et al. 2002). However, the opposite has also been found (Stohlgren 1999; Levine 2000; Gilbert and Lechowicz 2005).

Studies that relate biodiversity to community receptiveness to aliens may have come to different conclusions because all species have been treated as evolutionary equals, but they are not. Some species are more closely related to each other, while others are more distantly related. Likewise, some communities are characterized by closely related incumbent native species, and others are characterized by distantly related incumbent species. This point has never been taken into account, despite the fact that Darwin (1859; Ludsins and Wolfe 2001) discerned an evolutionary dimension to patterns of receptiveness to aliens at a biogeographical scale. Darwin (1859, p. 106) found

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that the endemic biotas of oceanic islands were more vulnerable to aliens and explained this as a result of the evolutionary history of the island floras and faunas: “On a small island, the race for life will have been less severe.” Despite recent studies addressing whether the phylogenetic relationships among alien species (Cadotte et al. 2009) or among alien and native species (Ricciardi and Mottiar 2006; Proches et al. 2008) predict invasion success, phylogenetic relationships in the recipient community as a predictor of community receptiveness to aliens are unstudied.

The establishment of aliens in a community might be favored in either of two ways: aliens might easily replace natives, or aliens might easily coexist with natives. Both of these mechanisms might be related to the phylogenetic relatedness of the natives in the recipient community. First, replacement of natives by aliens might be favored if the recipient community is composed of closely related species, that is, if it has a low phylogenetic dispersion. Natives in such communities have generally been exposed only to closely related species and might therefore be naive to alien species from distantly related lineages, that is, to their specific competition pressures and their associated pests and pathogens. Natives might thus be inferior to and consequently replaced by distantly related aliens (replacement hypothesis; fig. 1A). For instance, island biotas have been considered naive to the numerous distantly related continental lineages and therefore more vulnerable to replacement by aliens arriving from the continent (Darwin 1859). As in the island case, the species pools of particular types of environments were relatively closed to immigration from most lineages during the evolutionary past, despite dramatic transformations and redistributions, particularly during the past few thousand years (for remarkable examples, see Ortega et al. 1997; Prinzing et al. 2001; Crisp et al. 2009). Species from these isolated pools might have had no contact with and in turn lacked adaptation to antagonist species from a wide range of lineages. The local communities sampled today from these presumably naive species pools are phylogenetically underdispersed. Present-day processes such as dispersal limitation might further reduce phylogenetic dispersion of particular local communities. Incumbent populations are thus naive to competition with and the pathogens of distant lineages. Second, it might also be coexistence of aliens with natives that is favored in phylogenetically underdispersed recipient communities. In these communities, many phylogenetically distant lineages are absent, and aliens have a higher chance of belonging to such distant lineages. Distantly related species might then coexist more easily than closely related species (coexistence hypothesis; see below for mechanisms; fig. 1B; Webb et al. 2002; Prinzing et al. 2008). Both the replacement hypothesis and the coexis-

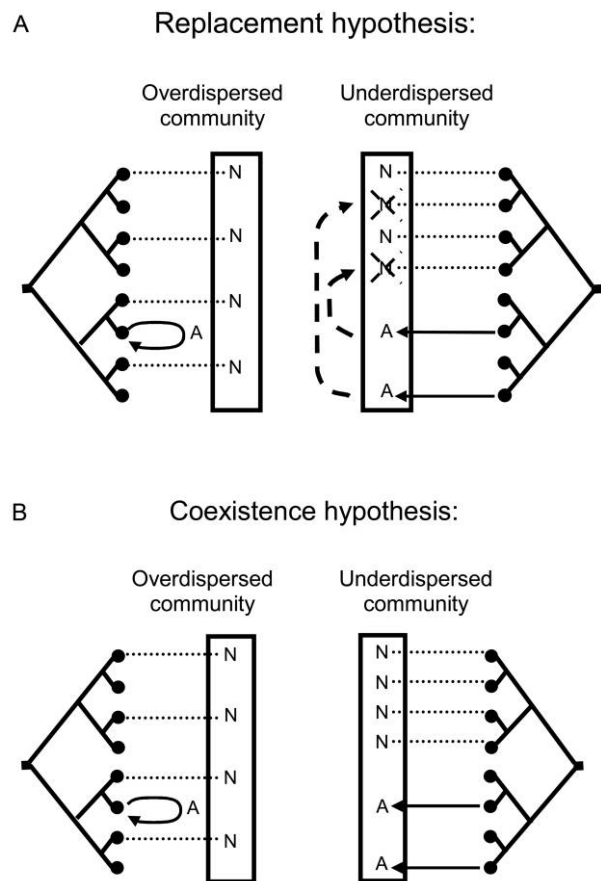


Figure 1: Hypotheses on the relationship between phylogenetic dispersion of local communities and how receptive they are to alien species. Dotted lines indicate the position of native species (*N*) in the phylogeny. Solid arrows indicate establishment (or not) of alien species (*A*) in a local community. Dashed arrows and crosses indicate replacement of native species by alien species. Hypothesis *A*, replacement of native species by aliens in phylogenetically underdispersed recipient communities. Hypothesis *B*, coexistence of native species and aliens in phylogenetically underdispersed recipient communities.

tence hypothesis hence predict more aliens to establish in phylogenetically underdispersed communities than in overdispersed communities. Both hypotheses also predict the aliens in phylogenetically underdispersed communities to come from more distantly related lineages. These aliens will increase the phylogenetic dispersion of underdispersed recipient communities more than in overdispersed communities, where many lineages are already represented and thus an increase of dispersion is inevitably more difficult to achieve. However, the replacement hypothesis predicts that aliens entering phylogenetically underdispersed communities reduce native species richness, whereas the coexistence hypothesis predicts no such reduction.

Coexistence between aliens and natives might be favored

in the following two ways: (i) aliens could occupy different ecological niches or functional trait states than could natives or (ii) aliens and natives could better partition similar ecological niches or functional trait states than could natives among each other. Both coexistence mechanisms might prevail in communities of low phylogenetic dispersion. First, if fewer lineages represent fewer niche/trait states (as suggested in Webb et al. 2002), alien species from distant lineages would likely represent trait states different from those of established natives and could thus coexist with natives. Second, in contrast, if coexisting species from the same lineage are under pressure to be particularly different in traits and niches (e.g., because they are particularly similar in the fundamental physiological strategies and the natural enemies they share; Gilbert and Webb 2007; Cavender-Bares et al. 2009), then communities assembled from fewer native lineages should represent highly divergent niche/trait states (for a review of mechanisms and confirmation of the pattern for most traits, see Prinzing et al. 2008). Alien species, being from distant lineages and thus unlikely to be similar to natives in ecological dimensions such as natural enemies, would not be under pressure to be different from the nonrelated natives. They could coexist with natives even if particular ecological or functional traits are similar to those of natives. Moreover, given the already high trait-state dispersion in the absence of aliens, aliens are likely to have traits similar to those of natives already present. The first hypothesis would thus predict that in communities without aliens, low phylogenetic dispersion correlates with low trait dispersion (e.g., low trait-state standard deviation for a continuous trait). The first hypothesis would also predict aliens to increase the dispersion of trait/niche states in phylogenetically underdispersed communities compared to overdispersed communities (fig. 2*a*). The second hypothesis, on the contrary, predicts that in communities without aliens, low phylogenetic dispersion correlates with high trait dispersion. Aliens would then add new species but not new trait states, the concentration of trait states would go up, and trait-state dispersion would decline (fig. 2*b*). We define these two hypotheses as coexistence with increasing trait-state dispersion and coexistence with increasing trait-state concentration. Note that different hypotheses might be true for different traits (Prinzing et al. 2008).

Here we combine recent, large, and unique databases on plant communities, proportions of alien species, functional traits, and phylogenetic positions of plant species. From these data sets we test our central hypothesis that phylogenetically poor communities harbor a higher proportion of alien species. We test this prediction by correlating the average local proportion of aliens across all sites per community type with the corresponding average local phylogenetic dispersion of sites without aliens. In our

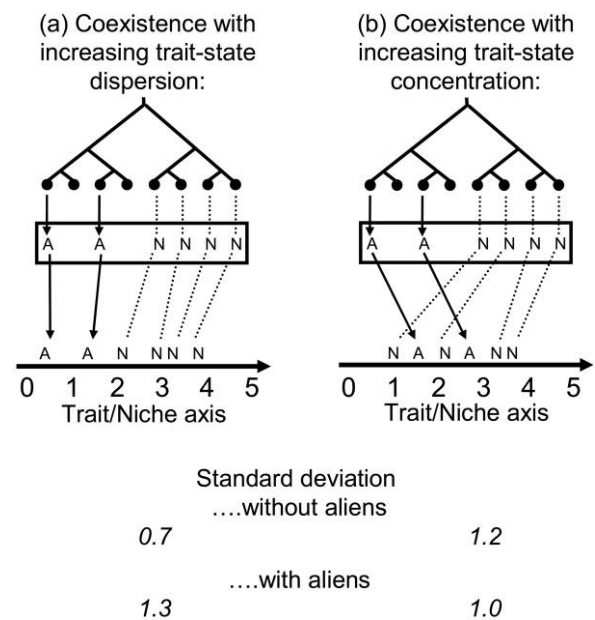


Figure 2: Hypotheses on the relationship between phylogenetic dispersion of local communities and coexistence between natives (*N*) and aliens (*A*). Thin vertical arrows indicate the establishment of alien species in a community. The position of a species along the bold horizontal arrow indicates niche position/trait state. Hypothesis *a*, coexistence of native and alien species with increasing trait-state dispersion; phylogenetically underdispersed communities are underdispersed in niche positions/trait states (“Introduction”). Alien species belonging to distant lineages bring in new niche positions/trait states, thus increasing the standard deviation of niches/trait states. Hypothesis *b*, coexistence of native and alien species with increasing trait-state concentration; phylogenetically underdispersed communities are overdispersed in niche positions/trait states (“Introduction”). Alien species belonging to distant lineages bring in niche positions/trait states similar to those already established, thus decreasing the standard deviation of niches/trait states.

study of averages within community types, our spatial scale is the local vegetation sample plot, which is the scale relevant to plant interactions and where the presence of alien species might most negatively influence native species (Stohlgren et al. 1999). We also test the respective predictions of the replacement hypothesis versus the coexistence hypothesis and the predictions of the coexistence with increasing trait-state dispersion hypothesis versus the coexistence with increasing trait-state concentration hypothesis, as outlined above. We account for the covarying factors species richness and environmental conditions.

Material and Methods

Characterizing Community Types

We used the Dutch Vegetation Database to describe community composition (Schaminée et al. 1995–1999). We

analyzed data of species presence/absence in 7,152 sample plots (for details on selection of plots, see Prinzing et al. 2008) divided into 201 community types, with 1,329 plant species including 116 aliens. Community types were defined as phytosociological associations (Schaminée et al. 1995–1999; for a list of community types and the ranges of proportions of aliens observed, see app. A in the online edition of the *American Naturalist*). We note that some community types are highly anthropogenic, that is, young, which seemingly excludes evolutionary mechanisms suggested by the replacement hypothesis. But even these community types reflect environmental conditions that may have existed for many millions of years, such as trampling. Also, we do not imply that community types are closed units, but categorization is needed as a tool to sufficiently portray the existing diversity and complexity of different environments and their incumbent communities.

Aliens were defined as those that arrived in the Netherlands after 1500 AD (i.e., neophytes; Statistics Netherlands, <http://www.milieunatuurcompendium.nl/tabellen/nl139802a.html>) and that have established beyond their specific site of introduction (Ozinga et al. 2005); that is, they have established at various localities within the Netherlands. This corresponds to the definition of “invasives” by Richardson et al. (2000) but is contrary to that of *Federal Register* (1999). The latter stresses the replacement of natives by invaders, which in this study is one of the hypotheses to be tested and can thus not be assumed from the outset. Most of these aliens originate from outside central or western Europe (see above Web site). Trees (only 33 species) were excluded, as they are planted mostly in the Netherlands.

For each community type, we quantified the phylogenetic dispersion in plots without aliens (1,284 plots without alien species in total and at least 11 per community type) to reflect the phylogenetic dispersion of the community type before the establishment of aliens. We defined the receptiveness of a community type to aliens as the average proportion of aliens across all plots of that community type and alien establishment as the average proportion of aliens in plots with aliens (i.e., no 0 values). Note that lower richness may increase the variance of proportion estimates (presence or absence of a single alien may strongly increase or decrease the proportion score) but will not affect the mean tendency.

We note that for a given community type, the phylogenetic dispersion of plots without aliens does not necessarily equal phylogenetic dispersion of plots with aliens before the arrival of the aliens. Abiotic conditions may vary to a minor degree even within community types. This variation might cause variation in both the receptiveness to aliens and phylogenetic dispersion. In that case, past alien-free phylogenetic dispersion of plots that received

many aliens would be different from present phylogenetic dispersion of plots that received no aliens. We cannot exclude the possibility that this difference varies systematically between community types of high mean phylogenetic dispersion and those of low mean phylogenetic dispersion. The tested correlations between mean present phylogenetic dispersions of plots that received no aliens and mean receptiveness to aliens thus need to be interpreted with some caution; we stress that our study tests whether correlative patterns are consistent with our hypotheses but it is not a strict test of the hypotheses themselves.

We measured phylogenetic dispersion as the dispersion of the species represented in a local community across lineages, that is, phylogenetic nodes, represented in a species-level phylogeny of the regional species pool (see Prinzing et al. 2008, which also compares this approach to alternative methodologies). The phylogeny of the species pool was based on the phylogenetic topology for higher plants of central Europe taken from Klotz et al. (2002; checked against Bremer et al. 2003 and Davies et al. 2004). This topology covers 97% of the species in the above phytosociological database. The degree of dichotomous resolution is high (70%), which is essential to resolve phylogenetic patterns of coexistence within a given regional species pool and even within a given habitat type (Cavender-Bares et al. 2006). In fact, in >99.5% of the local communities, >95% of the nodes between the root and the species represented in a community were dichotomies. We calculated phylogenetic dispersion as the standard deviation (SD; i.e., we measured dispersion by using the same units as the data) of the number of species per phylogenetic node multiplied by -1 (Prinzing et al. 2008). In communities of closely related species, few phylogenetic nodes subtend many species, while multiple other nodes subtend no species. This gives a high SD of species numbers per nodes and, multiplied by -1 , a low score of phylogenetic dispersion. Alternatively, if species are equally dispersed across the phylogeny, most nodes subtend an intermediate number of species, resulting in a low SD and high phylogenetic dispersion. Phylogenetic dispersion might change as a function of species richness; thus, we standardized the observed dispersions for a null expectation for a given level of species richness (as in Prinzing et al. 2008: (observation – mean null expectation)/(SD of null expectation)). We consider our parameter particularly useful when analyzing topologies (Prinzing et al. 2008) but acknowledge that analyses based on average pairwise phylogenetic distances between species within communities (Warwick and Clarke’s [1998] taxonomic distinctness applied to a phylogenetic topology; Webb 2000) led to the same conclusions. Both parameters characterize the dispersion of species across a phylogeny (Hardy and Senterre 2007).

We estimated the abiotic conditions in the plots without

aliens on the basis of habitat requirements of the constituent species for light, temperature, soil moisture, soil pH, soil nutrients (from Ellenberg et al. 1991; these Ellenberg values have been extensively confirmed by direct measurements [for a review, see, e.g., Hill and Carey 1997; Diekmann 2003]), and soil salinity (from Schaminée et al. 2007). For each community type, we quantified both the mean and the variation, that is, the SD. We standardized the SDs for a null expectation of random communities of the same species richness (as in Prinzing et al. 2008; $(\text{observed} - \text{mean} - \text{expected}) / (\text{SD} - \text{expected})$). Finally, we characterized the disturbance regime on the basis of mean disturbance strategies of species (from Klotz et al. 2002). We note that such indirect estimations of environment based on species' requirements should be used as relative rather than absolute estimates and should be applied with caution if the main focus is a species-environment relationship (which was not the case in this study).

We analyzed 16 traits considered related to the type of resources used, either directly or indirectly, or to other axes of niche differentiation (table 4), during either the established phase or the dispersal phase. Trait data were taken from the databases BIOPOP (Poschlod et al. 2003) and LEDA (Kleyer et al. 2008). Detailed explanations of the trait data and databases are given in appendix B in the online edition of the *American Naturalist*; we note that all of these traits are phylogenetically conserved (Prinzing et al. 2008). We did not pursue multivariate measures of trait-state dispersion across species because different traits may show distinctly different patterns (Prinzing et al. 2008). Because seed weight varied for six orders of magnitude, we \ln transformed it. Plant height varied much less (10%–90% percentiles within one order of magnitude), and other traits were ordinal or categorical. Dispersion of the trait states of a given trait was analyzed as the SD for continuous or ordinal traits and as Simpson's diversity index in its natural logarithm (Rosenzweig 1995) for categorical traits. We standardized observed values for a null expectation on the basis of random communities of identical species richness: $(\text{observed} - \text{mean} - \text{expected}) / (\text{SD} - \text{expected})$ (Prinzing et al. 2008).

Statistical Analyses

To test predictions of our core hypothesis, we related phylogenetic dispersion of community types to their receptiveness to aliens by using linear regression analysis (supplemented by nonparametric analysis in the case of nonnormal or heterogeneous distribution of residuals). We note that the results of this analysis did not depend on the invasive or noninvasive status of the aliens. Only 5% of the 116 alien species are classified as invasive aliens according to the DAISIE Web site ([\[aliens.org/\]\(http://aliens.org/\)\), and these six species characterize \(i.e., are found in \$\geq 20\%\$ of the plots\) only 4% of the 201 community types. Excluding this 4% of communities did not influence the results \(\$r = -0.382\$ vs. initially \$r = -0.380\$ \) nor did restriction to only these communities \(\$r = -0.67\$ \).](http://www.europe-</p>
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We then tested, using multiple regression with stepwise backward exclusion (threshold $P = .05$), whether the relationship between phylogenetic dispersion and receptiveness to aliens persists after including the above-mentioned covariates (species richness, means, and variation of environmental conditions). As phylogenetic dispersion may be related to the presence or absence of particular dominant lineages, we also included the proportion of species belonging to Poaceae and the proportion of species belonging to Fabaceae as covariates. Poaceae is the most species-rich family and is thus numerically dominant. Fabaceae are considered by some authors to dominate plant community assembly by fixing nitrogen (Maron and Connors 1996). The model did not take into account the degree to which communities are influenced by human impacts, in particular by anthropogenically induced seed rain of aliens. Therefore, we completed a separate analysis with an additional covariate that ranked the anthropogenic impact versus the naturalness of the community types; this covariate was available for 125 of the 201 community types (Schaminée and Hennekens 2003).

The replacement hypothesis and the coexistence hypothesis both predict aliens to increase phylogenetic dispersion in underdispersed communities in comparison to communities that are already phylogenetically overdispersed in the absence of aliens. To test this prediction, we quantified for each community type the inferred change in phylogenetic dispersion corresponding to the establishment of aliens as the difference between average phylogenetic dispersion in plots containing aliens and in plots without aliens. We then tested whether in phylogenetically poor community types, as compared to phylogenetically rich community types, plots of high alien establishment showed increased phylogenetic dispersion. We accounted for the fact that the alien establishment (i.e., considering only plots with aliens) can vary drastically. We hence used multiple regression analysis with difference in phylogenetic dispersion as the dependent variable and alien establishment, phylogenetic dispersion, and the alien establishment \times phylogenetic dispersion interaction term as independent variables. To account for possible statistical effects of species richness before the arrival of aliens, we also included richness in plots without aliens in the model (which did not affect the conclusions).

The replacement hypothesis and the coexistence hypothesis make opposite predictions on the effect of aliens on native species richness. To test consistency with these

predictions, we quantified for each community type the proportional difference of native species richness between plots with and without aliens: (average native species richness in plots containing aliens – average native richness in plots without aliens)/(average native richness in plots without aliens) (alternative definitions lead to the same conclusions). We then analyzed how phylogenetic dispersion in plots without aliens modifies the statistical effect of alien establishment on the proportional difference of native species richness due to aliens. In other words, we tested whether invaded plots have larger or smaller native species richness than uninvaded plots. We used multiple regression analysis with proportional difference in native species richness as the dependent variable and alien establishment, phylogenetic dispersion, and the alien establishment \times phylogenetic dispersion interaction term as independent variables. To account for possible covariation between native richness and alien establishment, we also included native richness without aliens in the model (which did not affect the conclusions).

To test the predictions of the coexistence with increasing trait-state dispersion hypothesis and the coexistence with increasing trait-state concentration hypothesis, we first tested whether in the absence of aliens phylogenetically poor community types have a lower or higher dispersion of trait states. We conducted correlations between phylogenetic and trait dispersion across all 16 traits considered. As these were multiple tests across multiple, partly intercorrelated variables, we additionally (a) applied a sequential Bonferroni correction (Holm 1979) of the P values and (b) conducted a principal component analysis (based on a correlation matrix; StatSoft 2009) across the 16 variables, and we retained the first axis and correlated this with phylogenetic dispersion. This principal component axis explained 23% of the total variance and was positively correlated with dispersions of 14 of 16 traits; the two remaining negative correlations were very weak (ranked as eleventh and sixteenth, respectively, in strength of the relationship). It could hence be used as a single derived variable in place of the multiple intercorrelated original variables.

Second, we tested whether in phylogenetically poor community types compared to phylogenetically rich community types, alien establishment within plots correlates with a decreased or increased dispersion of trait states. We used multiple regression analysis with difference in trait-state dispersion (plots with aliens – plots without aliens of a given community type) as the dependent variable. As independent variables we included the phylogenetic dispersion, trait-state dispersion, and species richness in plots without aliens, the alien establishment, and the alien establishment \times phylogenetic dispersion interaction term. Again we tested trait-state dispersions of each of the 16

traits individually (with and without sequential Bonferroni correction) and then tested the first axis of the above principal component analysis across trait-state dispersions of all 16 traits.

Results

We found that average phylogenetic dispersion (in the absence of aliens) and receptiveness to aliens (average proportion of alien species across all plots) varied considerably among community types (fig. 3). Apparently ecologically similar community types could be ranked from very low to very high in phylogenetic dispersion (e.g., the wetland communities *Ericetum tetralicis* and *Ranunculo–Senecionetum juncetosum articulati* yield phylogenetic dispersions of -3.4 and 7.2 , respectively). This indicates that phylogenetic dispersion was not an abstract measure of an obvious pattern in variation across communities.

Low phylogenetic dispersion correlates with increased receptiveness to aliens. We found that community types with a low phylogenetic dispersion (in the absence of aliens) harbor a higher proportion of alien species ($t_{1,199} = -5.8$, $P < .0001$; fig. 4A). A multiple regression

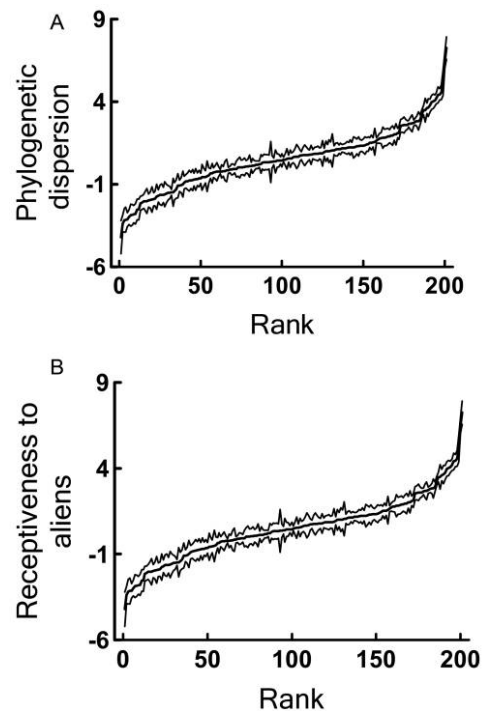


Figure 3: A, Average (\pm SE) phylogenetic dispersion of 201 community types in plots without aliens. B, Average (\pm SE) receptiveness to aliens of different community types (i.e., proportion of aliens across all plots). Community types are ranked from smallest to largest.

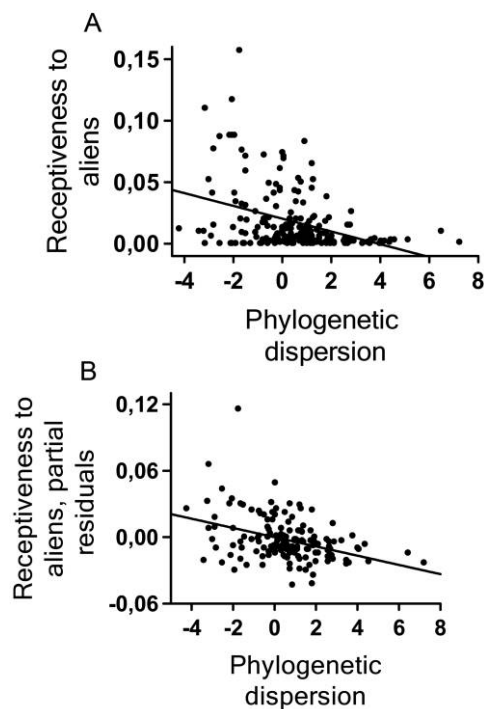


Figure 4: Relationship between average phylogenetic dispersion of community types and average receptiveness to aliens (terms defined in fig. 3; $n = 201$). A, Simple regression ($r_p = -0.38$, $P < .0001$; note that nonparametric analysis leads to the same result: $r_s = -0.34$, $P < .0001$). B, Partial residuals from multiple regression accounting for the influence of species richness, means and variation of abiotic conditions (light, temperature, soil moisture, soil pH, soil nutrients, and soil salinity), disturbance level, and the presence of Poaceae and Fabaceae (partial correlation: $r = -0.23$, $t = -3.14$, $P = .002$).

accounting for the influence of species richness, the means and variation of abiotic conditions (light, temperature, soil moisture, soil pH, soil nutrients, and soil salinity), the disturbance level, and the presence of Poaceae or Fabaceae confirmed these results ($t_{1,192} = -3.14$, $P = .002$; fig. 4B; table 1). The stepwise backward regression excluded species richness (which in itself is a good predictor of receptiveness to aliens; $r = -0.41$) and retained variables strongly correlated with richness such as pH or the variability of light, moisture, soil nutrients ($r > -0.40$ to -0.75), or temperature ($r = 0.24$). These may thus be the environmental factors that ultimately contribute to the univariate relationship between richness and receptiveness to aliens. Note also that inclusion of anthropogenic impact into the model did not change the effect of phylogenetic dispersion ($t_{1,116} = -2.43$, $P = .016$).

Low phylogenetic dispersion in plots without aliens correlates with an increased phylogenetic dispersion in plots with high alien establishment. Overall we found that higher

alien establishment (i.e., average proportion of aliens across plots with aliens) correlated with a decrease in community phylogenetic dispersion. This trend, however, was greatly reduced in community types that were phylogenetically underdispersed in the absence of aliens (negative interaction term in table 2). This pattern is consistent with the following scenario: everything else being equal, phylogenetically underdispersed communities gain more lineages or lose fewer lineages as a result of the establishment of aliens than do phylogenetically overdispersed communities. This confirms the assumption of both the coexistence with increasing trait-state dispersion hypothesis (fig. 2a) and the coexistence with increasing trait-state concentration hypothesis (fig. 2b).

Low phylogenetic dispersion in plots without aliens correlates with coexistence between aliens and natives in plots with high alien establishment. We found that the statistical effect of alien establishment on the gain or loss of native species across community types strongly depended on the community types' phylogenetic dispersion in the absence of aliens. The general relationship between alien establishment and the corresponding proportional change of native species richness was negative (table 3), but with declining phylogenetic dispersion, this negative relationship became increasingly positive (negative interaction between phylogenetic dispersion \times alien establishment; table 2). This relationship is clarified in figure 5: in phylogenetically rich community types, the establishment of only a few aliens correlates with a reduced native species richness, whereas in phylogenetically poor communities, such reduced native species richness is observed only where large proportions of aliens establish. In general, in the phylogenetically poor community types, alien establish-

Table 1: Stepwise backward regression analysis explaining variation in receptiveness to aliens of community types by phylogenetic dispersion and multiple ecological characteristics of plots without aliens

	β	$t_{1,192}$	P
Phylogenetic dispersion	.23	-3.14	.0019
Mean light	-.62	-6.34	<.0001
Variation in light	-.34	-3.52	.0005
Mean temperature	.18	2.14	.0335
Variation in soil moisture	.22	2.82	.0053
Mean soil pH	-.40	-4.72	<.0001
Variation in soil pH	-.21	-2.53	.0122
Variation in soil nutrients	.31	4.02	<.0001

Note: Variables excluded from the model were variation in mean temperature, mean soil moisture, mean soil nutrients, mean soil salinity, variation in soil salinity, species richness, proportion of Poaceae, and proportion of Fabaceae. (Note that species richness was included as a covariable and deleted by the model.) $N = 201$ community types, $r^2 = 0.46$, $F = 20.74$, $P < .0001$. See also figure 4B.

Table 2: Regression analysis explaining differences in the mean phylogenetic dispersion of community types between plots with aliens and plots without aliens

	β	$t_{1,166}$	P
Phylogenetic dispersion	.44	2.38	.0182
Species richness	-.58	-4.12	<.0001
Alien establishment	-.89	-8.80	<.0001
Phylogenetic dispersion \times alien establishment	-.81	-6.15	<.0001

Note: Independent variables are alien establishment (average proportion of aliens across plots with aliens), average phylogenetic dispersion and average species richness in plots without aliens, and the interaction between phylogenetic dispersion and alien establishment. Phylogenetically underdispersed community types tend to gain proportionally more (or lose less) native species due to alien establishment than do phylogenetically overdispersed communities. $N = 171$ community types with aliens, $r^2 = 0.35$, $F = 22.7$, $P < .0001$.

ment even corresponds to the establishment of additional native species (note that differences in initial native species richness of the community types are taken into account in the analysis in table 2). This result confirms the prediction of the coexistence hypothesis (fig. 1B) and contradicts the replacement hypothesis (fig. 1A).

Low phylogenetic dispersion in plots without aliens correlates mostly with high trait-state dispersion. Testing 16 different traits (including niche positions), we found that most traits tended to be overdispersed in phylogenetically underdispersed community types; that is, trait-state dispersion was correlated negatively with phylogenetic dispersion (significantly so for 12 traits, compared to three significantly positive correlations; $N = 201$ community types; app. C in the online edition of the *American Naturalist*). Almost all of these relationships persisted after sequential Bonferroni correction. Also, the first principal component, reflecting overdispersion of most trait variables (see “Material and Methods”), was strongly correlated with phylogenetic clustering ($r = -0.66$, $P < .0001$). This confirms for most traits the assumption of the coexistence with increasing trait-state concentration hypothesis (fig. 2b) and not that of the coexistence with increasing trait-state dispersion hypothesis (fig. 2a).

Low phylogenetic dispersion in plots without aliens tends to correlate with a decrease in trait-state dispersion in plots with high alien establishment. We found significant effects of phylogenetic dispersion on the change of trait-state dispersion with increasing alien establishment (i.e., significant interaction terms; table 4) in six traits and a marginally significant effect ($P = .065$) in one further trait. In five of these traits (light and soil fertility niche, life form, life strategy, and height), phylogenetically underdispersed communities were increasingly underdispersed in trait states where aliens established relative to phylogenetically

overdispersed communities; that is, the interaction term in table 4 was positive. In two traits (vegetative reproductive structures and growth form), the trend was the opposite. Sequential Bonferroni correction confirmed one of the positive and none of the negative interaction terms. The first principal component, reflecting overdispersion of most trait variables (“Material and Methods”), showed a distinctly positive interaction term ($\beta = 0.39$, $P = .0091$). Positive interaction terms confirm predictions from the coexistence with increasing trait-state concentration hypothesis (fig. 2b); negative interaction terms confirm predictions from the coexistence with increasing trait-state dispersion hypothesis (fig. 2a). The strongest relationship found is illustrated in figure 6.

Traits that are particularly overdispersed in phylogenetically underdispersed community types (highly negative correlations between trait-state and phylogenetic dispersion in plots without aliens; app. C) become increasingly underdispersed with the establishment of aliens in such communities (interaction terms listed in table 4): $N = 16$ traits, $r = -0.54$, $P = .03$ (correlations and interaction terms transformed into effect sizes [Fisher’s Z ; Rosenthal 1984] before correlation with each other).

Discussion

Our results show that community types composed of species from phylogenetically distinct lineages (i.e., phylogenetically rich or overdispersed communities) are less receptive to alien establishment. In contrast, community types consisting of closely related species (i.e., phylogenetically poor or underdispersed) are more receptive to aliens. Our results are in accord with patterns previously observed at a biogeographical scale (Darwin 1859). In a manner similar to that of many oceanic islands, particular

Table 3: Regression analysis explaining variation in the proportional difference of species richness between plots without aliens and plots with aliens across community types

	β	$t_{1,166}$	P
Phylogenetic dispersion	.35	2.10	.038
Species richness	-.58	-5.94	<.0001
Alien establishment	-1.09	-14.65	<.0001
Phylogenetic dispersion \times alien establishment	-.78	-9.58	<.0001

Note: Independent variables are alien establishment (average proportion of aliens across plots with aliens), average phylogenetic dispersion and species richness in plots without aliens, and the interaction between phylogenetic dispersion and alien establishment. Phylogenetically underdispersed community types tend to gain proportionally more (or lose less) native species due to alien establishment than do phylogenetically overdispersed communities. $N = 171$ community types with aliens, $r^2 = 0.47$, $F = 36.5$, $P < .0001$. See also figure 5 for an illustration of the interaction term.

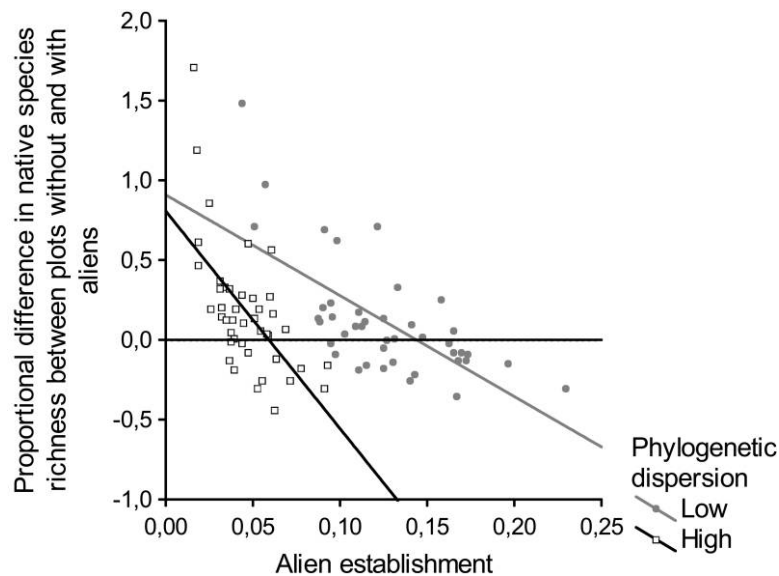


Figure 5: Relationship between alien establishment (average proportion of aliens across plots with aliens) and the proportional change of native species richness corresponding to the establishment of aliens (“Material and Methods”). The relationship is a lot less negative for community types with a low phylogenetic dispersion than for community types with a high phylogenetic dispersion (lower and higher quartile of phylogenetic dispersions, respectively). Only in the latter does alien establishment often correspond to a loss of native species. One outlier was omitted (proportional difference in species richness = -1.2 , high phylogenetic dispersion community type). For statistical analysis see table 3.

mainland plant communities across a landscape tend to be phylogenetically poor and more receptive to aliens. However, contrary to the suggestions of Darwin and others for islands, native species in phylogenetically poor mainland communities do not appear to be particularly naive to and easily replaced by alien species. The results indicate that aliens likely displaced distinctly fewer native species in phylogenetically poor community types than in phylogenetically overdispersed communities. This confirms the hypothesis of coexistence of native and alien species in phylogenetically poor communities (fig. 1*B*). While we cannot exclude future extinctions of natives from some of the plots over a longer timescale, we note that we are studying regionally well-established alien species. The impact of these species on the native flora hence persists already for decades.

Coexistence of native and alien species in phylogenetically poor communities could occur in trait space. The trait space of phylogenetically poor community types was more dispersed for most traits than was that of phylogenetically rich communities. While this confirms the findings of Prinzing et al. (2008), the precise mechanisms explaining this pattern remain unknown and need to be studied. Possible candidate mechanisms are, among others, shared natural enemies or shared metabolic strategies in phylogenetically poor communities (see “Introduction”).

In a phylogenetically poor community, alien species that belong to distant lineages would therefore introduce only trait states already present and thus increase the concentration of trait space. Given the differences in physiological strategies and in the associated natural enemies, the aliens are unlikely to have a strong negative impact on the distantly related native species and are therefore unlikely to replace them (for a detailed review of mechanisms, see below and Prinzing et al. 2008). We found correlative evidence that establishment of alien species in phylogenetically poor community types increased phylogenetic dispersion compared to phylogenetically rich community types; that is, aliens belonged to lineages not yet represented in these community types (see also Strauss et al. 2006). We also found correlative evidence that after establishment of aliens, initially phylogenetically underdispersed communities have a more concentrated trait space; that is, additional species brought in trait states already established (fig. 2*b*). The opposite scenario of increasing dispersion of trait-state space due to aliens (fig. 2*a*) was consistent with patterns found in only two traits; these were the traits that were underdispersed in phylogenetically underdispersed communities. These are thus the traits of very high phylogenetic conservatism (Prinzing et al. 2008). Overall, the phylogenetic conservatism of traits may ultimately determine whether aliens in phylogenetically

Table 4: Regression analyses explaining differences in trait-state dispersion of community types between plots without aliens and plots with aliens

	Trait-state dispersion (β , P)	Species richness (β , P)	Phylogenetic dispersion (β , P)	Alien establishment (β , P)	Phylogenetic dispersion \times alien establishment (β , P)
Persistence traits:					
Light niche	-.18, .002	.09, .571	-.66, .002	.17, .175	<u>.58, <.001</u>
Soil nitrogen niche	.09, .255	.61, <.001	-.44, .051	.35, .004	<u>.36, .022</u>
Soil moisture niche	-.42, <.001	-.28, .129	.33, .125	.63, <.001	.23, .147
Life span	-.02, .782	.72, <.001	-.59, .011	.05, .654	.18, .242
Height	-.20, .009	-.15, .360	-.25, .227	.08, .491	<u>.28, .065</u>
Life form	-.22, .027	.40, .018	-.54, .016	.43, <.001	<u>.43, .008</u>
Life strategy	.03, .737	.34, .061	-.30, .175	.33, .009	<u>.33, .042</u>
Growth form	.06, .44	-.39, .027	.56, .014	-.17, .182	<u>-.39, .018</u>
Dispersal traits:					
Extent of sexual reproduction	-.41, <.001	.12, .504	-.30, .203	.16, .167	.21, .160
Clonal extension	.16, .051	.06, .751	.11, .623	-.02, .877	-.20, .223
Vegetative reproduction structures	.12, .09	-.61, <.001	.85, .001	-.09, .433	<u>-.433, .006</u>
Seed weight	.69, <.001	.27, .006	-.12, .345	.43, <.001	.08, .403
Diaspore size	-.03, .678	.05, .777	.08, .724	.48, <.001	-.04, .775
Diaspore form	-.08, .357	.12, .480	-.10, .645	.51, <.001	.02, .870
Abiotic dispersal vector	.06, .619	-.14, .469	.21, .351	.21, .095	.08, .642
Biotic dispersal vector	-.05, .635	-.06, .760	-.09, .687	.06, .636	.18, .259
Principal component 1	-.14, .163	.24, .131	-.25, .227	.71, <.001	<u>.39, .009</u>

Note: Independent variables are alien establishment (average proportion of aliens across plots with aliens), phylogenetic dispersion, species richness and trait-state dispersion in plots without aliens, and the interaction between phylogenetic dispersion and alien establishment. Our hypotheses refer to the interaction terms, and those with P values $<.1$ are underlined (after sequential Bonferroni correction, the interaction term for light niche remains at $P < .05$, and that for vegetative reproductive structure is at $P < .1$). The last line gives the corresponding regression model for the first component of a principal component analysis correlated positively with overdispersion of most traits ("Material and Methods"). $N = 171$ community types with aliens. See also figure 6 for an illustration of the interaction term for the light niche trait.

poor communities establish by filling up or expanding the trait-state space occupied by natives.

Coexistence of native and alien species in phylogenetically poor communities may occur because of a lack of negative indirect interactions. Most alien species belong to alien lineages (see above). Species from an alien lineage are less likely to share, and hence acquire, the pests, pathogens, and herbivores of incumbent native species (Goßner et al. 2009). Conversely, incumbent native species are less likely to acquire the pests, pathogens, and herbivores of alien species. This paucity of shared negative biotic mediators can reduce apparent competitive interactions between aliens and natives (Holt and Lawton 1994).

Finally, coexistence of native and alien species in phylogenetically poor communities may occur within the species pool; phylogenetically poor local communities recruit from a smaller regional native species pool than do phylogenetically rich, overdispersed communities (Gerhold et al. 2008). Such small species pools could impede the establishment and turnover of native species across local communities within a region and thus facilitate the establishment of alien species introduced from foreign species pools.

We stress that further direct tests of our hypotheses

would require experimental control, which was not feasible with our macroecological approach covering all environments in a given region. However, finding consistency of such large-scale patterns with particular hypotheses will increase the focus on these hypotheses and justify future direct tests by small-scale experiments, and it will guide these experiments. For instance, our results may guide the choice of appropriate community types on which alien treatments can be applied, and they would advocate performing experiments with established community types in nature rather than with artificially assembled ones, as in the latter, assembly processes are to a large degree replaced by seeding and weeding.

The hypothesis of coexistence of native and alien species in phylogenetically poor communities might open a new avenue for the enduring debate about community saturation—the idea that biotic interactions limit the number of species within a community and more species-rich communities therefore better resist the establishment of aliens (going back to Elton 1958). Community saturation in terms of species richness has found little empirical support (Kennedy et al. 2002), and recently the whole concept has been suggested to be rather a myth (Stohlgren et al. 2008).

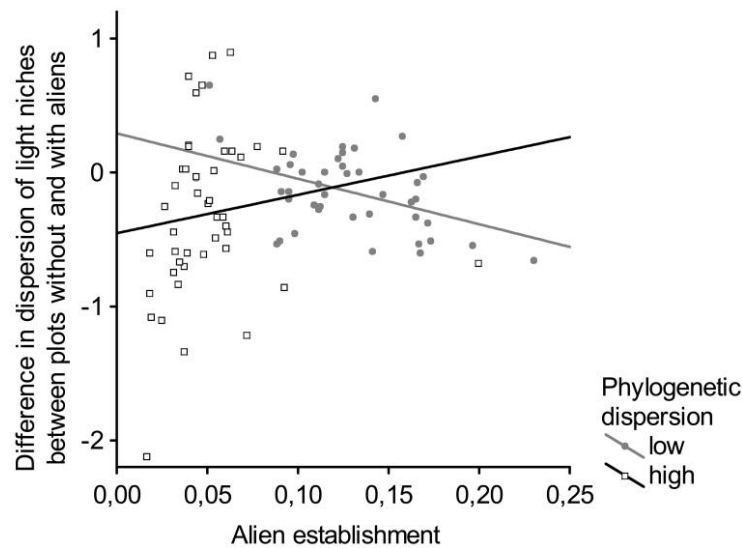


Figure 6: Relationship between alien establishment (see fig. 5) and the change of dispersion of the light niche within communities (“Material and Methods”) corresponding to the establishment of aliens. The relationship is positive for community types of high phylogenetic dispersion but negative for community types of low phylogenetic dispersion (lower and higher quartile of phylogenetic dispersions, respectively). For statistical analysis of this and 15 other traits see table 4.

Similarly, there is no good evidence for saturation at the individual level, as species abundances in ecological communities rather covary positively in time, not negatively as expected by competition theory (Houlahan et al. 2007). Our findings support the idea that phylogenetic proximity and the trait states of both present and potential new species are more important in determining the success and outcome of establishment of aliens than just numbers of species per se (see also Starzomski et al. 2008). Thus, it is time to move beyond the saturation concept of species numbers and explore the evolutionary history behind species richness numbers (e.g. Bartish et al. 2010).

Our results have clear implications for the protection of biodiversity and for advancing the field of conservation biogeography (Richardson and Whittaker 2010). The results suggest that consequences of aliens on native richness may vary not only between the local scale and the landscape scale (Knight and Reich 2005) but also at the local scale between communities differing in phylogenetic dispersion. Phylogenetically less diverse communities are more receptive to alien species. Even though these aliens do not reduce native species richness in these phylogenetically underdispersed communities, they represent a door through which alien species can enter into a region. Such communities should thus warrant increased protection from alien species. This knowledge could be used in conservation planning, for example, in the selection of protection areas and in regional conservation programs. Predicting receptiveness to aliens from the phylogenetic

dispersion of a community can now be effectively applied, as phylogenies are readily available for many groups of species worldwide (Judd et al. 2002; Klotz et al. 2002; Bremer et al. 2003). Our study has shown that the merging of traditional phytosociological databases with modern phylogenies can be a powerful tool to approach these conservation goals.

Overall, our results help to resolve the long-standing debate on the role biodiversity plays in determining how receptive a community is to aliens. If biodiversity is quantified across the entire tree of life and not just by counting the tips of a tree (i.e., species), increased biodiversity indeed correlates with decreasing receptiveness to aliens. Strong negative interactions between aliens and incumbent natives, leading to the observed replacement of natives by aliens, may explain why phylogenetically rich communities are less receptive to aliens. Inversely, phylogenetically poor communities might be receptive to aliens because aliens can coexist with natives even if they share similar trait states, leading to an increase of species richness and of trait-state concentration with the establishment of aliens. Such coexistence between functionally similar aliens and natives in phylogenetically poor communities might be favored by their phylogenetic dissimilarity.

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Present-day vegetation carries signals of past evolutionary diversification, driving present-day assembly of aliens and natives. Photograph by Marcel Horsthuis.