Functional and phylogenetic similarity of alien plants to co-occurring natives

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Abstract. Over the years, several arguments have been proposed to explain the invasibility
of a given community based on the properties of the recipient community. Here, I assessed
whether the balance between native species' phylogenetic and functional variability determines
vulnerability to invasion. I explored this hypothesis using a consensus phylogenetic tree and a
database of leaf, height, and seed traits of alien and native species co-occurring over 83 sites
worldwide. An analysis of contrasts between aliens and natives indicates that aliens are as
phylogenetically close to the incumbent native community as natives are among themselves
(aliens are nested within the native community phylogeny), but functionally distinct to the
native community (aliens are more functionally distant to the community of native taxa than
natives are among themselves). These contrasting trends are consistent for different
comparison criteria (comparisons to all natives or to the nearest native) and comparisons
both within and across communities, habitats, and continents. Furthermore, aliens are more
functionally divergent than the native community and the closest native relative in both
phylogenetically poor and rich communities. The phylogenetic similarity and functional
distinctiveness of aliens with respect to the incumbent native community may explain why
certain species succeed in some communities and not others. This is a step forward in resolving
the long-standing debate on the role diversity—both phylogenetic and functional—plays in
determining the success of introduced plants.

Key words: *alien species; biological invasions; context dependence; environmental filtering; functional
diversity; functional–phylogenetic differentiation; functional traits; invasion ecology; phylogenetic community
structure.*

INTRODUCTION

One of the central questions driving invasion ecology
research is what makes a given community susceptible to
invasion (Drake et al. 1989, Mack et al. 2000). The
ability to answer this question is paramount to predict
potential invaders and prevent the ecological and
economic losses associated with them (Mack et al.
2000). Recent efforts addressing this question have
focused on the role of functional (trait composition; e.g.,
Ordonez et al. 2010, van Kleunen et al. 2010, Hulme and
Barrett 2013) and evolutionary (phylogenetic position;
e.g., Strauss et al. 2006, Jiang et al. 2010, Ricotta et al.
2010, Davies et al. 2011) overlap between natives and
aliens (either noninvasive or invasive), as a way to
determine the likelihood of a species being successful
once introduced into a new area. Based on these efforts,

aliens might be able to establish in a community by
either matching natives' niches (i.e., matching hypothesis Fig. 1A), filling up the phylogenetic and functional
space unused by natives (i.e., filling hypothesis Fig. 1B),
or being completely different from the native community
(i.e., aliens with no close relatives in the introduced area
will be more successful due to reduced competition with
natives, as described by Daehler [2001] as "Darwin's
naturalization hypothesis"). The underlying assumption,
irrespective of the mechanism, is that the position of the
alien relative to the functional and phylogenetic
composition of the native community could be used to
predict invasion success.

When determining alien success based on the degree
of functional similarity, the principal assumption is that
the interaction between phenotypic realizations (i.e., a
specific trait, or trait combination) is what drives the
community assembly process (Kraft et al. 2008).
Consequently, alien success driven by functional similarity would imply that an introduced species could be
successful by being competitively superior to natives
(functional match with natives; Fig. 1A), or by having
viable functional trait combinations not present in the
native community (filling up natives' unused space; Fig.

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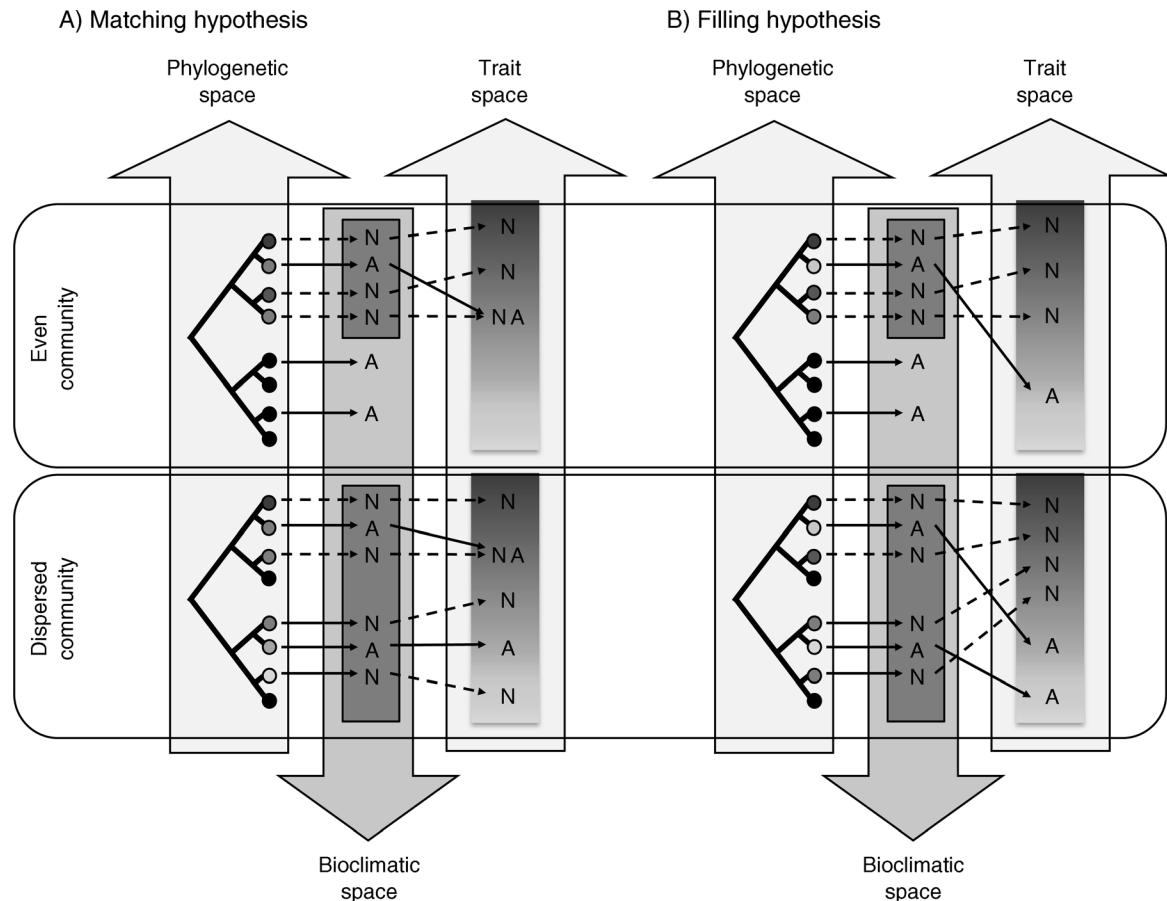E-mail: alejandro.ordonez@biology.au.dk

Fig. 1.   Hypotheses on the association between phylogenetic dispersion of the incumbent native community, the coexistence between natives (N) and aliens (A), and the position of these taxa along the community trait space. Lines indicate the position of viable alien (solid) and native (dashed) taxa given the bioclimatic conditions (dark gray arrows) in the phylogeny/trait space (light gray arrows). Color ramp in the trait space region indicates the range of viable traits given the environmental conditions. The figure represents two alternative hypotheses of alien success based on the phylogenetic and functional similarity of natives and aliens: (A) matching hypothesis and (B) filling hypothesis (see *Introduction*).

1B). Either of these situations can occur in both clustered (i.e., underdispersed) and even (i.e., over-dispersed) native community scenarios (Fig. 1). None-theless, determining which species are replaced by invaders as assumed by the functional match between aliens and natives, is very difficult at broad spatial scales due to lack of sufficient data. Therefore, evaluating the realized community patterns to assess these mechanisms (which only represent outcomes, not interactions in processes) serves as the best proxy for the role of a functional similarity in the invasion process.

Another limitation when assessing the functional similarity between natives and introduced aliens is defining and obtaining information on all relevant functional dimensions. Relatedness serves as a proxy for the integrated phenotype, and thus, for unmeasured phenotypic traits, providing an overview of community functional composition. This phylogenetic similarity assumption implies that introduced aliens might be able to replace, or coexist with, natives depending on the

native community's phylogenetic composition (clustered [even community] Fig. 1) and the spatial scale of the comparison (Proches et al. 2008, Davies et al. 2011, Gerhold et al. 2011). In the case of clustered commu-nities, space filling by aliens might be possible due to the absence of phylogenetically distant lineages (Strauss et al. 2006), as natives in such communities have mostly been exposed only to closely related species. In the case of even communities, space filling by aliens might be possible due to the existence of functional gaps in the trait spectrum (Thuiller et al. 2010, Gerhold et al. 2011), or natives being naïve to alien species from closely related lineages (favoring matching; Rejmanek 1996). Reality is a bit more complex, as the assembly process is determined by the perceived phenotype, not relatedness per se, making relatedness only useful when it captures the community composition of assembly-related traits because it serves as a proxy for the integrated phenotype and, thus, for unmeasured phenotypic traits.

The recent increase in the amount, coverage, and availability of large and detailed phylogenies has allowed the evaluation of phylogenetic similarity between alien and natives using empirical data. While several studies indicate that there is an association between the relatedness of invasive aliens to the native biota and invasion success (e.g., Strauss et al. 2006, Jiang et al. 2010, Ricotta et al. 2010, Davies et al. 2011, Gerhold et al. 2011), evidence of the opposite has also been recorded (as revised by Diez et al. 2008, and Thuiller et al. 2010), and shown to depend on the comparison scale (Proches et al. 2008, Thuiller et al. 2010, Davies et al. 2011). This conflicting evidence, encapsulated under the term Darwin's naturalization conundrum (Diez et al. 2008), would seem to support two seemingly contradictory hypotheses: that introduced aliens are more likely to be successful when they are either phylogenetically similar (phenotypic similarity) or dissimilar (Darwin's naturalization hypothesis) to the native community. Likewise, studies focusing directly on functional similarity have also shown a mixture of patterns depending of the comparison scale and the phylogenetic structure of the incumbent community. For example, while some global studies (Ordonez et al. 2010, van Kleunen et al. 2010, Ordonez and Olff 2013) found support for the functional distinctiveness of invasive aliens when compared to natives, country-level comparisons in New Zealand (Diez et al. 2008, Diez et al. 2009) have provided support for the functional similarity between aliens and natives. Meanwhile, regional-level comparisons indicate no trend in the functional relatedness of aliens and natives (Lambdon and Hulme 2006, Lambdon et al. 2008), or whether traits of successful aliens are dependent on the phylogenetic structure of the recipient native community (across plots in the Netherlands; Gerhold et al. 2011).

These conflicting results are clear indicators of the need for studies with a regional to global coverage as the way to determine the importance of phylogenetic and functional similarity of the incumbent community on the success of alien species. By using a broad geographic coverage and evaluating phylogenetic and functional distance at different scales, one could generate statistical generalizations as to (1) how the phylogenetic and functional positioning of aliens in relation to the native community relates to alien success, (2) how the native community structure determines these patterns, and (3) the role of scale (sites–habitats–continents) on alien–native similarity. This study builds from this premise and evaluates patterns of phylogenetic and functional relatedness between aliens and natives (hereafter alien-to-natives) and natives among themselves (hereafter native-to-natives) across multiple communities, habitats, and continents.

The goal of this study was to establish a link between the phylogenetic–functional composition of the incumbent community (that is, the native assemblage) and the phylogenetic–functional similarity of aliens to the native community. I hypothesized that successful aliens colonize the phylogenetic space defined by the native community in three ways: (1) filling up the functional gaps between incumbent natives (indicating phenotypic similarity; Proches et al. 2008); (2) placing themselves at the edges of the functional and phylogenetic spectrum (as suggested by Darwin's naturalization hypothesis; Daehler 2001), particularly if the recipient native community is clustered; or (3) sharing broad environmental preferences, particularly if the recipient native community is phylogenetically even (Proches et al. 2008, Gerhold et al. 2011). For this, three types of data (phylogenetic, phenotypic, and spatial) were used to establish the phylogenetic and functional association of co-occurring species in communities where alien species have been successfully introduced. These factors are often confounding, but in this study, they were disentangled using a unique global database of co-occurring native and alien plants paired according to their phylogenetic relatedness and spatial co-occurrence patterns.

MATERIALS AND METHODS

Community database compilation and selection of traits

This study focuses on three traits: specific leaf area (SLA in cm^2/g, a proxy of a species position along the "leaf economics spectrum"), individual seed mass (SWT in mg; a proxy of the investment by a plant on seed production, propagule pressure, and establishment success), and typical maximum plant height (H_{max} in cm; a proxy for species position along the "height spectrum"). The focus on these attributes is due to their association to fundamental axes of functional differentiation (Westoby et al. 2002, Wright et al. 2004, Moles and Westoby 2006), their relation to community assembly processes (Kraft et al. 2008), and the strong linkages between these traits and the phylogenetic relatedness of species in a site (Moles et al. 2005, Cavender-Bares et al. 2006, Kraft et al. 2007). Furthermore, these traits are proxies for a species' dispersal capabilities, establishment success, and acquisition of water, nutrients, and energy (Westoby et al. 2002). As a consequence, they are some of the most frequently quantified attributes, making them more readily available in the literature than other plant traits (e.g., photosynthetic rate, nutrient stoichiometry, hydraulic conductance, relative growth rates) related to the same ecological strategies. Thus, the traits used in this analysis are not necessarily the best for measuring functional similarity (they do not capture vulnerability to pathogens or factors related to density dependence biotic interference, among other significant dimensions of functional differentiation), but represent a portion of the best candidates for this purpose that also happen to be widely available in the literature.

A database of native and alien species traits was compiled from both published and unpublished sources,

focusing on studies measuring aliens or natives under natural conditions (greenhouse studies were discarded). The database was built by searching the ISI Web of Science (1945–2010) using individual and combinations of relevant keywords (plant traits, SLA, leaf mass per area [LMA], leaf size, leaf nutrients, plant height, seed size, seed mass, seed production, plant attributes, leaf–height–seed spectrum [LHS], plant physiology, weed, weeds, naturalized, invasive, exotic, noxious, introduced, alien, foreign, nonnative), examining the references on these publications, and direct communication with the managers of large databases. A data set was considered suitable if it included trait information (or could be completed using traits databases) for over 80% of all coexisting species included in the study. For each entry, a location (e.g., latitude and longitude), habitat type (as defined by the WWF Biomes of the World; Olson et al. 2001), continent, and environmental conditions were assigned based on published information or a reasonable geographical approximation.

Information was summarized by study area, so that each evaluated community referred to species that co-occur in a defined, local-scale geographic area (ranging from 5 to 100 km^2) under similar environmental conditions (as defined in the source publication). In this way, species within each community are more likely to interact with each other than with species that do not locally co-occur, but are the same time are strongly affected by environmental conditions (McGill 2010). The database was based on 83 communities and contains 4705 species (3664 with measures in the native range, 919 in the introduced, and 122 on both ranges) from 191 plant families and a wide range of growth forms (herbs, graminoids, forbs, shrubs, sub-shrubs, and trees). A summary of the database is provided in Supplement 1.

Species were classified as native or alien based on definitions outlined by Richardson et al. (2000). Consequently, the term "alien" throughout this paper refers to those species whose presence in a community is due to human introduction (intentional or accidental) and that have self-sustaining populations. This includes both naturalized aliens, (also called noninvasive aliens) that reproduce consistently, and sustain populations over many life cycles without direct intervention by humans; as well as invasive species, defined as naturalized species that produce reproductive offspring often in large numbers, at considerable distances from parent plants.

A phylogeny for all species in the database was built using the stand-alone version of PHYLOMATIC (Webb and Donoghue 2005) using the APG3 mega-tree (maximally resolved seed plant phylogeny; Angiosperm Phylogeny Website, *available online*)[2] as a backbone. Unresolved branches were fully resolved to genus level

[2] http://www.mobot.org/MOBOT/research/APweb/

using recently published molecular phylogenies (over 80% of splits are dichotomous for the master phylogeny, and all nodes between the root and phylogeny tips were dichotomies in 90% of the communities), an essential factor in analyzing phylogenetic patterns of coexistence within a given regional species pool and even within a given habitat type (Cavender-Bares et al. 2006, Swenson 2009). Branch lengths of the database mega-tree were estimated using the BLADJ (branch length adjustment) procedure in PHYLOCOM (Webb et al. 2008), where node ages were established using Wikstrom et al. (2001) estimations of divergence times. The phylogeny and a list of the studies used to resolve it are presented in Supplement 2.

Statistical analysis

To determine how novel an alien (A) species is relative to the invaded native (N) community, the mean phylogenetic (MPD$_{A-N}$) and functional (MFD$_{A-N}$) distance between each alien taxon and all native species it co-occurs with were calculated. Additionally, the mean phylogenetic (MPD$_{N-N}$) and functional (MFD$_{N-N}$) distance from each native to the entire co-occurring native species were also determined for comparison purposes. Phylogenetic and functional distances of each alien to all natives, and of each native to all other natives were calculated for all species in all communities. These metrics summarize the degree of "uniqueness" of a taxon with respect to the overall community and provide a community-wide perspective on the role of similarity in introduction success. Given that these distances are standardized metrics of differentiation (scaled by the maximum distance for all compared taxa), comparing alien and native distances within and between communities is possible. Alien and native distances were compared for each of the 83 evaluated sites, using a Bonferroni-corrected unequal sample sizes t test (i.e., MPD$_{A-N}$ vs. MPD$_{N-N}$ and MFD$_{A-N}$ vs. MFD$_{N-N}$). A significant difference between distances from aliens-to-natives and native-to-natives would suggest that successful aliens are dissimilar to the recipient native community (phylogenetically and/or functionally) and would indicate the importance for alien success of an evolutionary and functional differentiation between native and alien taxa.

Mean phylogenetic (MNNPD) and functional (MNNFD) distance to the nearest native relative for all alien (MNNPD$_{A-N}$ and MNNFD$_{A-N}$) and native (MNNPD$_{N-N}$ and MNNFD$_{N-N}$) taxa, in each of the 83 evaluated sites, were also compared using Bonferroni-corrected unequal sample sizes t test. These distances are also standardized metrics of differentiation (standardized by the maximum distance for all compared taxa) so that alien and native values within and between communities are comparable. Comparing alien and native species distances (phylogenetic and functional) to the closest native determined if the alien phylogenetic and functional characteristics are novel in the native

community, or if these are contained within the native community's phylogenetic and functional differentiation ranges. Moreover, this second set of contrasts allowed the assessment of whether limiting similarity to a single taxon is important in determining invasiveness.

Phylogenetic distance between two species was measured as the total branch length separating those species. In the case of the database super-tree (as it is an aged tree), this will be twice the time since divergence (in millions of years [Myr]) from the most recent common ancestor (branch length from species 1 to the most recent common ancestor plus branch length from the most recent common ancestor to species 2). Functional distance was determined as the difference between the target alien or native species, and the traits of the native species in the evaluated community.

Given that compiled studies vary in the number of compared species and in spatial coverage, contrasts of mean and nearest native distances were calculated for three categories: (1) globally, (2) within continents, and (3) within habitat types. To do this, I used log-ratios of the phylogenetic and functional distances of co-occurring taxa, calculated following the formulations of Hedges et al. (1999). Effect sizes (i.e., mean log-ratios) were calculated using a flexible meta-analytic procedure, as this method allows the comparison of the non-independent log-ratios without merging them within categories prior to a meta-analysis, hence avoiding the loss of statistical power (Nakagawa et al. 2007). This method is based on a linear mixed model (LMM) approach with a restricted maximum likelihood method optimization (REML, nlme package in R; Pinheiro et al. 2009), using species as a grouping random factor and weighing individual observations by the inverse variance of the corresponding log-ratio. This metric was used to describe the proportional change in alien-to-natives distances relative to the native-to-natives differentiation (using alien-to-natives as the treatment and native-to-natives as the control). Furthermore, it provides a standardized measurement of phylogenetic and functional similarity, while controlling for those differences introduced by other covariates (e.g., scale of the study, sample size, or metric). The sign of the effect size shows the directional pattern of differentiation (positive indicates alien differences are larger than native differences, while negative indicates the opposite). In the case of similarity (effect sizes indistinguishable from zero), a series of power tests were done to determine if the observed alien-to-natives similarity is an artifact of the number of observations (by determining the sample size required to obtain a effect size different from zero) or of the sampled communities (by bootstrapping the sampled community and estimating the probability of detecting differences between groups).

To test the predictions from the matching, filling, and distinctiveness hypotheses, MFD and MNNFD effect sizes were determined within communities showing phylogenetic evenness (i.e., communities composed of

taxa from phylogenetically distinct lineages) and those showing phylogenetic clustering (i.e., communities composed of taxa from phylogenetically close lineages). The working hypothesis is that aliens' functional differentiation patterns depend on the phylogenetic structure of the incumbent community; so that effect sizes of functional differences are closer to zero in even communities (aliens are nested within the native functional phylogenetic range), while effect sizes in clustered communities will tend to be positive and higher that those of even communities (alien-to-natives > native-to-natives differences).

Phylogenetic structure of the evaluated communities was measured using two alternative indices: net relatedness index (NRI) and nearest taxon index (NTI). Both indices are standardized measures of phylogenetic similarity (difference between the observed and expected MPD, in the case of NRI, and MMPD, in the case of NTI, is standardized by the standard deviation of the distribution of null assemblages to represent the standardized effect size of each metric), allowing the comparison among communities (Webb et al. 2002). Following Webb (2000), positive values of NRI and NTI indicate phylogenetic clustering (underdispersion), and negative values indicate phylogenetic evenness (overdispersion). The statistical significance of the phylogenetic structure of a group of assemblages was calculated using one-sample t tests where the null expectation is zero (i.e., a random sample of species with respect to phylogeny). As the results obtained with NRI were qualitatively the same as those obtained with NTI, functional similarity contrast for phylogenetically clustered and even communities are based on the latter.

RESULTS

Phylogenetic similarity patterns

Within each of the evaluated communities, MPD and MNNPD distances showed a large variability in magnitude for both alien and native contrasts. Nonetheless, there was a consistent phylogenetic similarity between the native and alien community components as indicated by overlapping MPD values (effect sizes overlap zero; Fig. 2A) and significant Bonferroni-corrected t tests in only 13% of the evaluated communities (significant MPD in 11 out of 83 communities). Furthermore, alien taxa were less or as distantly related to the native community than natives are among themselves (MPD$_{A-N}$ ≤ MPD$_{N-N}$ for 41 out of 83 communities, 14 out of 15 habitat types and for all of the continental comparisons). Analysis of MNNPDs showed overlapping distances across all communities and for most of the evaluated communities, as indicated by significant Bonferroni-corrected t tests in 17% of within community contrasts (significant MNNPD in 14 out of 83 communities) and effect sizes overlapping zero (Fig. 2B). Additionally, MNNPD$_{A-N}$ were lower that (or equal to) MNNPD$_{N-N}$ in 37% of the evaluated communities, but these differences consistently varied

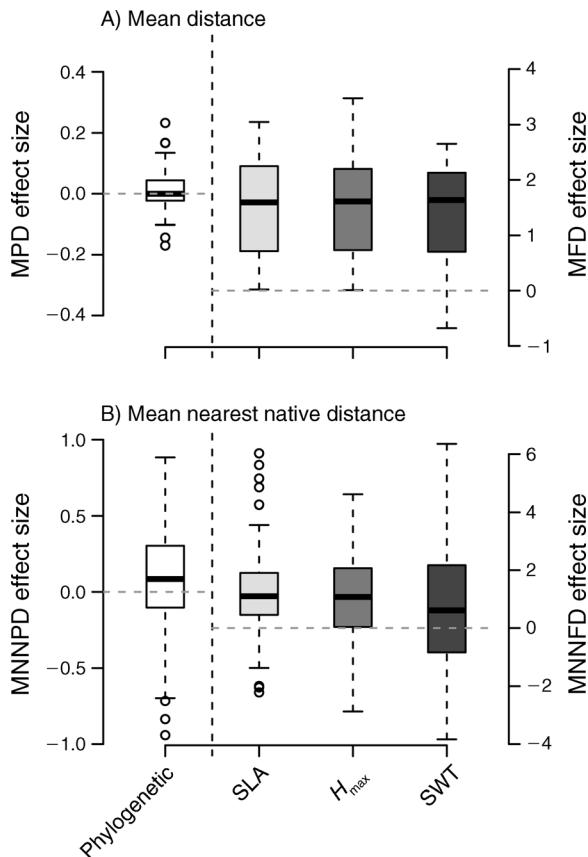## A) Mean distance

B) Mean nearest native distance

FIG. 2. Boxplots of phylogenetic (white box) and trait (gray boxes) effect sizes (*y*-axis) across all 83 sampled sites. Two contrast criteria are plotted: (A) mean phylogenetic (MPD) and functional (MFD) distance, and (B) distance to the phylogenetically nearest native (phylogenetic [MNNPD] and functional [MNNFD]). Effect sizes represent the phylogenetic and functional association between alien [alien-to-natives distances] and native [native-to-natives] taxa, and the incumbent native community (see *Materials and methods* for details). The line in the box represents the median effect size, box limits indicate the effect size in the 25–75th percentile range, and whiskers indicate the 95% confidence interval. Outliers (points) determined as observations 1.5 times the interquartile range. The effect size is considered significant if the 95% confidence interval (whiskers) does not overlap 0 (dashed gray line). Functional differences based on three eco-morphological traits: specific leaf area (SLA, in cm^2/g), typical maximum plant height (H_{max}, in cm), and individual seed mass (SWT, in mg).

across habitat types and continents (Fig. 3B, D). Overall, aliens were more distant to natives than natives were among themselves in North America and Indo-Malaysia ($MNNPD_{A-N} > MNNPD_{N-N}$); but the same in Australasia, the neotropics, and the Palearctic regions. These results suggest how in a phylogenetic space, introduced aliens are as equally related to the native community as native taxa are to one another, and that aliens are as related to the nearest native in the evaluated community as natives are.

Differences in MPD aliens and natives distances showed no significant differences across all sites

(MPD, $t_{68} = -1.49$, $P = 0.14$; Fig. 2A), a pattern also observed for MNNPD distances (MNNPD, $t_{68} = 1.62$, $P = 0.11$; Fig. 2B). For both MPD and MNNPD, effect sizes show a consistent community similarity for alien and native plants across communities, most habitat types, and continents, as these were indistinguishable from zero (MPD and MNNPD in Figs. 2 and 3A, B, E, F). A post hoc power analysis (test sets to a with power $(1 - \beta)$ set at 0.80 and $\alpha = 0.05$, two tailed) indicated that given the number of communities sampled and the variability in MPD and MNNPD, the database had enough power to detect a difference between alien-to-natives and native-to-natives contrasts (in order for an effect of this size to be detected [80% chance] as significant at the 5% level, a sample of 20 and 37 sites, respectively, would be required). Thus, it is unlikely that these negative findings can be attributed to a limited sample size. Furthermore, observed similarity patterns for both MPD and MNNPD contrasts are not an artifact of the compared communities as indicated by Bootstrap simulations (*P* was higher than 0.05 in 90% of the MPD and 60% of the MNNPD contrast across 1000 simulations). These results support the idea that phylogenetic similarity is associated with the success of introduced aliens. In other words, within a given community, aliens tend to be as related to the native community as natives are among themselves.

Functional distance patterns

Estimates of mean functional differentiation (MFD) for alien-to-natives and native-to-natives showed a prevalence of significant differences for within-community comparisons (significant Bonferroni-corrected *t* tests for MFD in 84% for SLA, 70% for H_{max}, and in 61% of the communities for SWT) and positive effect sizes (Fig. 2A). A pattern indicating that aliens are more functionally distant to the community of native taxa than natives are among themselves. Moreover, the functional distance between each alien taxa and its nearest native in the community was significantly different to that of natives in 83% to 94% of the evaluated communities (significant Bonferroni-corrected *t* tests for MNNFD in 83% for SLA, 88% for H_{max}, and in 94% of the communities for SWT), indicating a consistent functional differentiation of aliens with respect to closely related natives (Fig. 2B).

Contrasts across communities, habitat types, and continents showed that alien taxa are more functionally distinct to the native community than natives are among themselves in almost all of the 83 evaluated communities (mean $MFD_{A-N} > MFD_{N-N}$ in 100% for SLA, 100% for H_{max}, and in 97% for SWT of the evaluated communities). Moreover, MFD effect sizes were significantly different from zero (for SLA, $t_{58} = 11.03$, $P < 0.001$; for H_{max}, $t_{58} = 9.92$, $P < 0.001$; for SWT, $t_{56} = 10.95$, $P < 0.001$) and positive across all communities (Fig. 2A), habitat types (Fig. 3E), and continents (Fig. 3G). This shows how aliens are functionally dissimilar to the

recipient native community and that this pattern is somehow persistent across habitats and continents. This differentiation pattern was also observed for MNNFD distances, as effect sizes for SLA, H_{max}, and SWT comparisons were significantly different from zero across communities (for SLA, $t_{57} = 9.38$, $P < 0.001$; H_{max}, $t_{57} = 4.8$, $P < 0.001$; SWT, $t_{57} = 2.37$, $P = 0.021$; Fig. 2B), showing how aliens are functionally different to the closest native and supporting the idea that limiting similarity to a single taxon is important in determining invasiveness. When evaluated within each habitat type (Fig. 3F) and continents (Fig. 3H), a consistent functional differentiation to the native community and the nearest native was observed, as effect sizes did not overlap zero in almost all the evaluated habitats and continents.

Balance between phylogenetic community structure and functional differentiation

Across the evaluated communities, 69% showed a phylogenetically clustered composition, while the remaining 31% showed a phylogenetic evenness signal. This pattern was consistent when phylogenetic structure was determined based on either NRI or NTI. In accordance with the proposed hypotheses, alien species in phylogenetically clustered communities were both functionally different from the native community and the phylogenetically closest native, as shown by MFD and MNNFD effect sizes being significantly higher than zero (Table 1). Although aliens tend to be functionally closer to the native community in even communities for all three traits, as indicated by smaller MFD and MNNFD effect sizes than those of clustered communities, there were only significant differences between aliens and natives MFD for SLA ($t_{57} = 2.72$, $P = 0.009$), and marginally significant differences for SWT ($t_{55} = 1.94$, $P = 0.05$). The generalized functional dissimilarity (large distances) in both even and clustered communities indicate the prevalence of functional distinctiveness, at the scale of this study, as one of the main mechanisms behind aliens' success.

DISCUSSION

The results presented here show that aliens are phylogenetically similar, but functionally distinct to the native community at community, habitat, and continental scales. This indicates that successful introduced alien species can be considered phylogenetically nested yet functionally divergent (at both the community scale and to the closest native) to the native members of the evaluated community. These results support the idea of phylogenetic similarity (consistent with Duncan and Williams 2002, Diez et al. 2008, Diez et al. 2009, Ricotta et al. 2010) and functional dissimilarity (consistent with Pyšek and Richardson 2007, Ordonez et al. 2010, van Kleunen et al. 2010) of aliens to co-occurring natives. It is important to highlight that the phylogenetic similarity pattern was

neither an artifact of sample size or compared communities as shown by the post hoc power analyses.

The two types of phylogenetic and functional relatedness metrics used in this study (distance to nearest relative and distance to the native community) reflect two different kinds of ecological mechanisms underlying the success of introduced aliens. Distance to the nearest taxon reflects the effects of biotic interactions between an alien and a given native, which might be the most phenotypically similar species (Webb et al. 2002, Strauss et al. 2006). If limiting similarity is indeed the mechanism preventing establishment, distance to the nearest taxon will reflect the interactions between functionally related species and the post-establishment success of aliens (Scheffer and van Nes 2006). Alternately, distance to the native community is a metric that more accurately reflects the diverse dynamics and interactions among multiple species in a community, as it represents the overall positioning of an introduced alien with respect to any and all natives with which it might interact (Strauss et al. 2006). Distance to the native community would be the most important mechanism if multiple resources limit the lifetime success of introduced taxa (e.g., natives of disturbed, fertile habitats are indistinguishable from aliens of similar habitats; Leishman et al. 2010) if natural enemies are polyphagous (Prieur-Richard et al. 2002, Pyšek and Richardson 2007), and/or if community-scale evolutionary naïveté to a particular interaction is an important mechanism (Strauss et al. 2006, Verhoeven et al. 2009, Davies et al. 2011).

The described phylogenetic similarity of aliens to the native community indicates how, at the scale of this study, there is a higher likelihood that aliens respond to the same group of environmental conditions as natives (e.g., climatic and edaphic conditions) and that the responses to these conditions are similar to those observed in the native community. This is as closely related species are most likely to share similar responses to environmental conditions, due to a shared evolutionary history (Peterson et al. 1999, Webb et al. 2002). Therefore, a close relation to the native community would increase the likelihood of an alien succeeding in the new range, as it will be similarly adapted to the local conditions (Duncan and Williams 2002, Diez et al. 2008, Diez et al. 2009, Ricotta et al. 2010). This similarity would be limited by the accumulation, duration, and the scale of negative indirect interactions (e.g., pests, pathogens, and herbivores), given that a taxon from an introduced lineage is most likely to share or develop the same negative interactions as closely rated natives in the recipient community (Holt and Lawton 1994).

The observed functional differentiation of aliens to the native community implies that, at the scales of this study, species that are more functionally distant to the incumbent community are also more likely to succeed when introduced to a new region. This indicates the importance of functional distinctiveness of aliens with
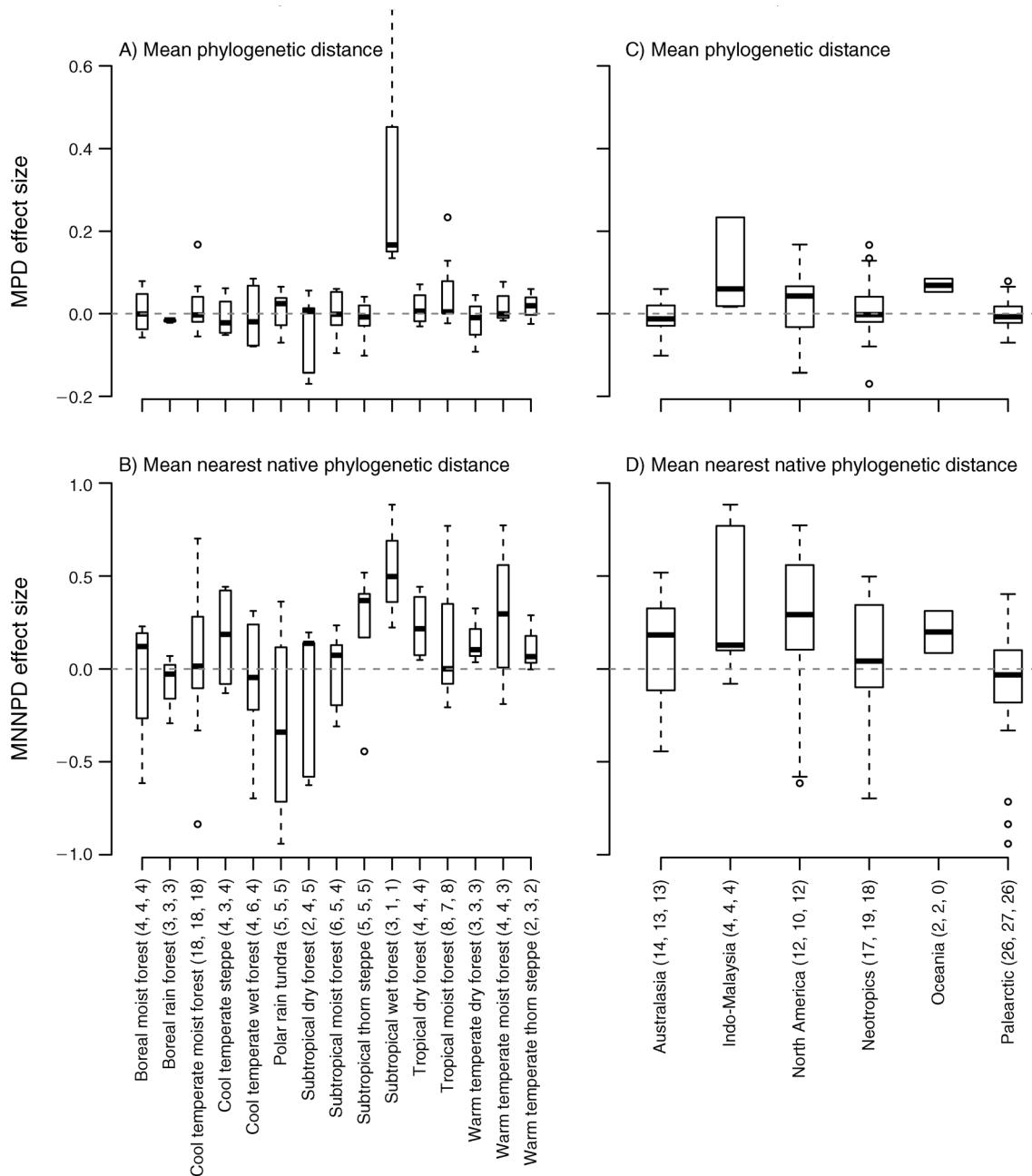
Fig. 3. Boxplots of (A, B, C, D) phylogenetic and (E, F, G, H) functional distances effect sizes (*y*-axis) segregated across 14 habitat types and six ecological realms (*x*-axis). Line in box, limits of box, whiskers, and outliers as in Fig. 2. The same constant criteria as in Fig. 2 are presented here. Functional differences are based on the same eco-morphological traits as those in Fig. 2. See Fig. 2 for clarification of abbreviations. Values in parentheses are the number of communities per category in the following order: SLA, H_{max}, and SWT.

respect to natives in the introduced community in determining the likelihood of an alien succeeding in the new range. Based on this, it is logical to assume that successful aliens should possess distinctive traits relative to the native taxa that would reflect a distinct use of resources (Prieur-Richard et al. 2002, Daehler 2003, Rejmanek et al. 2005, Pyšek and Richardson 2007,

Ordonez and Olff 2013). This idea of functional divergence is based on the effects of competition, dispersal, and stress tolerance, which can be thought of as a mechanism pushing the traits of co-occurring species towards divergence (Jiang et al. 2010, Thuiller et al. 2010, van Kleunen et al. 2010). Nevertheless, is also possible that aliens and natives display functional
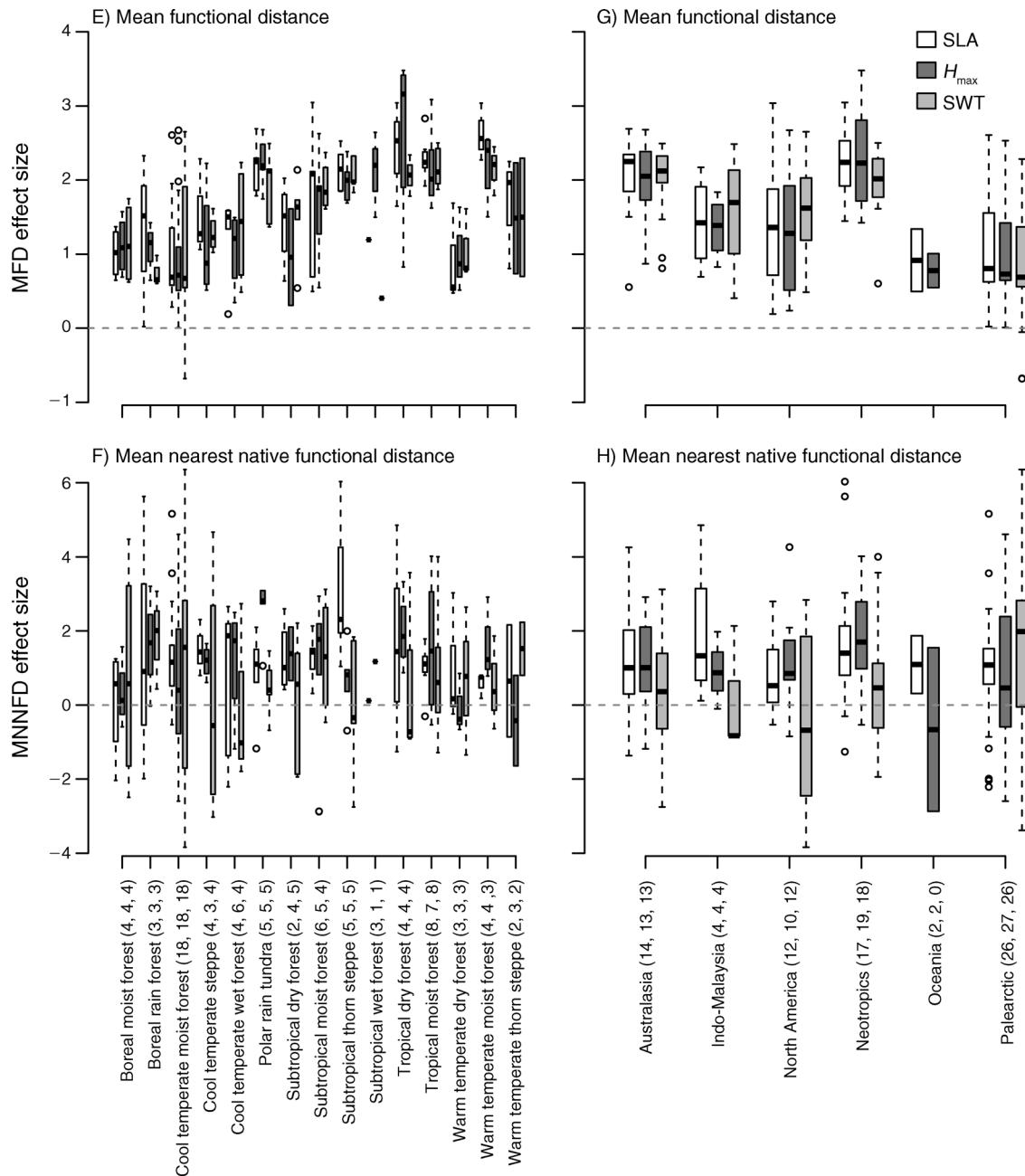
Fig. 3. Continued.

similarity in other traits than those analyzed here. This pattern could potentially emerge from both successful aliens and invasive natives exhibiting the same set of traits due to human selection (Keddy 1992, Weiher et al. 1998), or environmental restrictions to the range of viable strategies to use the resources (Thompson et al. 1995, Alpert 2006).

As pointed out by Proches et al. (2008), Thuiller et al. (2010), and Davies et al. (2011), the spatial scale and level of phylogenetic resolution (in the case of MPD and MNNPD) should be important considerations when testing both the similarity of co-occurring species and differences among groups (e.g., aliens vs. natives). By doing standardized cross-scale contrasts using log-ratios within communities and effect sizes within and across habitats, continents, and globally, it is possible to determine how patterns of phylogenetic and functional distance vary as the comparison scale increases. Nonetheless, the spatial scale of the smallest unit of evaluation (communities) is at the intersection of ecological and environment constraints to species occurrences (McGill 2010). This may, in turn, drive

TABLE 1. Results of meta-analyses for alien-native functional differentiation (measured as effect sizes; mean ± SE) across communities, where the native community shows either low (clustered or poor) or high (even or rich) phylogenetic dispersion.

Distance and trait	Phylogenetically even				Phylogenetically clustered			
	Effect size	t	P	df	Effect size	t	P	df
MFD								
SLA	1.36 ± 0.18	7.43	<0.001	57	1.79 ± 0.16	11.29	<0.001	57
H_{max}	1.46 ± 0.2	7.38	<0.001	57	1.66 ± 0.17	9.91	<0.001	57
SWT	1.3 ± 0.17	7.61	<0.001	55	1.61 ± 0.14	11.15	<0.001	55
MNNFD								
SLA	1.02 ± 0.36	2.8	0.007	56	1.43 ± 0.16	8.86	<0.001	56
H_{max}	1.53 ± 0.52	2.96	0.004	56	1.01 ± 0.23	4.41	<0.001	56
SWT	0.18 ± 0.63	0.29	0.776	56	0.61 ± 0.27	2.24	0.029	56

Notes: Significance of effect sizes was evaluated using a flexible meta-analytic procedure (Nakagawa et al. 2007) using a linear mixed model (LMM) approach with a restricted maximum likelihood method optimization (REML, nlme package in R; Pinheiro et al. 2009). The approach uses species as a grouping random factor and weighs individual log-ratios by the inverse of its variance (see *Materials and methods*). Abbreviations are: mean functional distance, MFD; mean functional distance to the nearest native relative, MNNFD; specific leaf area, SLA; typical maximum plant height, H_{max}; and individual seed mass, SWT. Uneven sample t test between even vs. clustered MFD distances: SLA, $t_{57} = 2.72$, $P = 0.009$; H_{max}, $t_{57} = 1.1$, $P = 0.247$; and SWT, $t_{55} = 1.94$; $P = 0.05$. Uneven sample t test between even vs. clustered MNNFD distances: SLA, $t_{57} = 1.03$, $P = 0.309$; H_{max}, $t_{57} = 0.94$, $P = 0.353$; SWT, $t_{55} = 0.63$; $P = 0.533$.

the distinct phylogenetic and functional patterns, if the scale is large enough for regional patterns to emerge (e.g., similarity of environmental requirements; and hence, phylogenetic similarity) or small enough to detect the signal generated by competitive interactions (divergence in attributes related to important ecological strategies; and hence, functional distinctiveness). Furthermore, phylogenetic and functional distances have the potential of being important aspects in determining alien success over time. This would especially be the case if bioclimatic-niche overlap and competitive exclusion (or its avoidance in the case of aliens) were indeed two of the main mechanisms limiting the post-introduction success of introduced taxa. However, the importance of these factors in predicting invasiveness can only be fully assessed after considering those species that, after being introduced, have failed to invade (information that is unavailable at the scales evaluated in this study).

The results presented here also show that aliens in native communities composed by phylogenetically distinct lineages (i.e., phylogenetically rich or even) are functionally different from the closest native, but distinct from the overall community, perhaps located at the edge of the native community functional spectrum. Similarly, aliens who are functionally different from both the incumbent native community and the closest native can more easily colonize communities composed of closely related taxa (i.e., phylogenetically clustered), making these communities more receptive to alien introductions from large geographic distances. Thus, the results of this study are in accordance with patterns previously observed by meta-analyses (Ordonez et al. 2010, van Kleunen et al. 2010) as they consistently show that successful aliens are functionally dissimilar to the native community. Furthermore, aliens appear to be nested within the native community's phylogenetic spectrum, whether as large as in even communities or as small as in clustered communities. Aliens are also most likely to occupy the empty phylogenetic space between native species, resulting in a phylogenetic clustering of aliens within the native community.

An important shortcoming of this and similar studies is the unknown phylogenetic and functional position of natives that might have been replaced by the aliens. Because the information used in this work considered only post-establishment alien populations, the results presented here do not inform the importance of nearest native taxon or native community relatedness at the establishment phase (for which knowledge of failure to establish by introduced species would be key), but only in the survival and spread phases. In fact, both the degree of establishment success and replacement of natives by aliens might vary as a function of the phylogenetic structure of the community (Rejmanek et al. 2005, Pyšek and Richardson 2007). Additionally, the observed alien-to-natives similarity would indicate increased success of aliens resembling natives only if there would also be aliens in the region that do not resemble the local natives, and hence, failed locally. Unfortunately, limited information on native replacement and unsuccessful introductions limits the ability to test these hypotheses. Nonetheless, the coverage of species, functional forms, habitats, and continents in this study provides solid generalizations as to the mechanisms determining the invasibility of particular communities and the role of phylogenetic and functional similarity in this process.

Conclusion

Overall, the results of this work point to the direction of phylogenetic similarity and functional distinctiveness of alien taxa with respect to the incumbent community as the key mechanisms determining alien success and shaping the phylogenetic and functional patterns of successfully introduced taxa. This is consistent with previous work showing that introduced aliens need to be able to cope with the same environmental conditions as native species (bioclimatic niche overlap as represented by phylogenetic similarity; e.g., Peterson et al. 1999, Graham et al. 2004) and that successful invaders are primarily those that are most functionally distinct from the native species and can therefore avoid direct competition (as discussed in Pyšek and Richardson 2007, Ordonez et al. 2010, and van Kleunen et al. 2010).

In summary, this study has shown how factors determining the success of alien species drive successful aliens to be both phylogenetically similar and functionally dissimilar to natives in the evaluated community. Phenotypic and phylogenetic patterns provide useful and complementary information for the development of methods to screen the risk of novel species becoming invasive. For example, given the potential interaction between climate change and biological invasions (Walther et al. 2009), it would be possible to determine which plant species are likely to be successful (phylogenetically close, but functionally distinct) under current and future climatic conditions using easily obtainable data on evolutionary and life history attributes. Furthermore, the results presented here are a step forward in resolving the long-standing debate on the role that diversity—both phylogenetic and functional—plays in determining the success of an introduced plant. The phylogenetic clustering and functional divergence of aliens within respect to the incumbent native community may explain why certain species succeed in some communities and not others.

Literature Cited

Alpert, P. 2006. The advantages and disadvantages of being introduced. Biological Invasions 8:1523–1534.

Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87(Supplement):S109–S122.

Daehler, C. C. 2001. Darwin's naturalization hypothesis revisited. American Naturalist 158:324–330.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. Annual Review of Ecology, Evolution, and Systematics 34:183–211.

Davies, K. F., J. Cavender-Bares, and N. Deacon. 2011. Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated. Diversity and Distributions 17:35–42.

Diez, J. M., J. J. Sullivan, P. E. Hulme, G. Edwards, and R. P. Duncan. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecology Letters 11:674–681.

Diez, J. M., P. A. Williams, R. P. Randall, J. J. Sullivan, P. E. Hulme, and R. P. Duncan. 2009. Learning from failures: testing broad taxonomic hypotheses about plant naturalization. Ecology Letters 12:1174–1183.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson. 1989. Biological invasions: a global perspective SCOPE (Scientific Committee on Problems of the Environment) 37. John Wiley, Chichester, UK.

Duncan, R. P., and P. A. Williams. 2002. Ecology: Darwin's naturalization hypothesis challenged. Nature 417:608–609.

Gerhold, P., M. Partel, O. Tackenberg, S. M. Hennekens, I. Bartish, J. H. J. Schaminee, A. J. F. Fergus, W. A. Ozinga, and A. Prinzing. 2011. Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. American Naturalist 177:668–680.

Graham, C. H., S. R. Ron, J. C. Santos, C. J. Schneider, and C. Moritz. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58:1781–1793.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25:495–520.

Hulme, P. E., and S. C. H. Barrett. 2013. Integrating trait- and niche-based approaches to assess contemporary evolution in alien plant species. Journal of Ecology 101:68–77.

Jiang, L., J. Q. Tan, and Z. C. Pu. 2010. An experimental test of Darwin's naturalization hypothesis. American Naturalist 175:415–423.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. American Naturalist 170:271–283.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322:580–582.

Lambdon, P. W., and P. E. Hulme. 2006. How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. Journal of Biogeography 33:1116–1125.

Lambdon, P. W., F. Lloret, and P. E. Hulme. 2008. Do alien plants on Mediterranean islands tend to invade different niches from native species? Biological Invasions 10:703–716.

Leishman, M. R., V. P. Thomson, and J. Cooke. 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. Journal of Ecology 98:28–42.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.

McGill, B. J. 2010. Matters of scale. Science 328:575–576.

Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005. A brief history of seed size. Science 307:576–580.

Moles, A. T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. Oikos 113:91–105.

Nakagawa, S., N. Ockendon, D. O. S. Gillespie, B. J. Hatchwell, and T. Burke. 2007. Assessing the function of house sparrows' bib size using a flexible meta-analysis method. Behavioral Ecology 18:831–840.

Olson, D. M., et al. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. Bioscience 51:933–938.

Ordonez, A., and H. Olff. 2013. Do alien plant species profit more from high resource supply than natives? A trait-based analysis. Global Ecology and Biogeography 22:648–658.

Ordonez, A., I. J. Wright, and H. Olff. 2010. Functional differences between native and alien species: a global-scale comparison. Functional Ecology 24:1353–1361.

Peterson, A. T., J. Soberon, and V. Sanchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2009. nlme: linear and nonlinear mixed effects models. R package version 3.1-96. R Foundation for Statistical Computing, Vienna, Austria.

Prieur-Richard, A. H., S. Lavorel, Y. B. Linhart, and A. Dos Santos. 2002. Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. Oecologia 130:96–104.

Proches, S., J. R. U. Wilson, D. M. Richardson, and M. Rejmanek. 2008. Searching for phylogenetic pattern in biological invasions. Global Ecology and Biogeography 15: 5–10.

Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: Where do we stand? Pages 97–125 in W. Nentwig, editor. Biological invasions. Ecological studies 193. Springer-Verlag, Berlin, Germany.

Rejmanek, M. 1996. A theory of seed plant invasiveness: The first sketch. Biological Conservation 78:171–181.

Rejmanek, M., D. M. Richardson, S. I. Higgins, M. J. Pitcairn, and E. Grotkopp. 2005. Ecology of invasive plants: state of the art. Pages 104–161 in H. Mooney, R. Mack, J. McNeely, L. Neville, P. J. Schei, and J. Waage, editors. Invasive alien species: A new synthesis. Island Press, Washington, D.C., USA.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Ricotta, C., S. Godefroid, and D. Rocchini. 2010. Invasiveness of alien plants in Brussels is related to their phylogenetic similarity to native species. Diversity and Distributions 16: 655–662.

Scheffer, M., and E. H. van Nes. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. Proceedings of the National Academy of Sciences USA 103:6230–6235.

Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. Proceedings of the National Academy of Sciences USA 103:5841–5845.

Swenson, N. G. 2009. Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. PLoS ONE 4:e4390.

Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: More of the same? Ecography 18: 390–402.

Thuiller, W., L. Gallien, I. Boulangeat, F. de Bello, T. Munkemuller, C. Roquet, and S. Lavergne. 2010. Resolving Darwin's naturalization conundrum: a quest for evidence. Diversity and Distributions 16:461–475.

van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13:235–245.

Verhoeven, K. J. F., A. Biere, J. A. Harvey, and W. H. van der Putten. 2009. Plant invaders and their novel natural enemies: who is naive? Ecology Letters 12:107–117.

Walther, G.-R., et al. 2009. Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution 24: 686–693.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. American Naturalist 156:145–155.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100.

Webb, C., D. Ackerly, M. McPeek, and M. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. Molecular Ecology Notes 5:181–183.

Weiher, E., G. D. P. Clarke, and P. A. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos 81:309–322.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33:125–159.

Wikstrom, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings of the Royal Society B 268:2211–2220.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

SUPPLEMENTAL MATERIAL

Supplement 1

Summary of the trait values used in this study and data use policy (*Ecological Archives* E095-102-S1).

Supplement 2

Community super-tree and polytomies resolution references (*Ecological Archives* E095-102-S2).