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BIODIVERSITY RESEARCH

Phylogenetic patterns differ for native and exotic plant communities across a richness gradient in Northern California

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ABSTRACT

Aim Increasingly, ecologists are using evolutionary relationships to infer the mechanisms of community assembly. However, modern communities are being invaded by non-indigenous species. Since natives have been associated with one another through evolutionary time, the forces promoting character and niche divergence should be high. On the other hand, exotics have evolved elsewhere, meaning that conserved traits may be more important in their new ranges. Thus, co-occurrence over sufficient time-scales for reciprocal evolution may alter how phylogenetic relationships influence assembly. Here, we examined the phylogenetic structure of native and exotic plant communities across a large-scale gradient in species richness and asked whether local assemblages are composed of more or less closely related natives and exotics and whether phylogenetic turnover among plots and among sites across this gradient is driven by turnover in close or distant relatives differentially for natives and exotics.

Location Central and northern California, USA.

Methods We used data from 30 to 50 replicate plots at four sites and constructed a maximum likelihood molecular phylogeny using the genes: *matK*, *rbcl*, *ITS1* and *5.8s*. We compared community-level measures of native and exotic phylogenetic diversity and among-plot phylobetadiversity.

Results There were few exotic clades, but they tended to be widespread. Exotic species were phylogenetically clustered within communities and showed low phylogenetic turnover among communities. In contrast, the more species-rich native communities showed higher phylogenetic dispersion and turnover among sites.

Main conclusions The assembly of native and exotic subcommunities appears to reflect the evolutionary histories of these species and suggests that shared traits drive exotic patterns while evolutionary differentiation drives native assembly. Current invasions appear to be causing phylogenetic homogenization at regional scales.

Keywords
Biodiversity, biological invasions, community assembly, ecophylogenetic diversity, invasion, phylobetadiversity, species turnover.

INTRODUCTION

The assembly of local communities is the result of the tension between local, often negative, and possibly deterministic interactions, and larger-scale environmental or dispersal constraints or stochastic events (Berlow, 1997; Levine, 2000; Lovette & Hochachka, 2006). Larger-scale environmental conditions and dispersal limitation filter a larger pool of potential colonists into one that includes species with the appropriate suite of traits for arrival and persistence (Keddy,

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1992; Weiher & Keddy, 1995). As non-indigenous species are added to regional species pools, their ability to invade local communities is the result of successfully passing through each of these filters controlling arrival, establishment and spread.

To test hypotheses about the assembly mechanisms generating diversity patterns, ecologists increasingly are employing phylogenies to quantify the potential evolutionary divergences among species that might be relevant to community assembly (Webb, 2000; Webb *et al.*, 2002; Cavender-Bares & Wilczek, 2003; Cavender-Bares *et al.*, 2006, 2009; Lovette & Hochachka, 2006; Helmus *et al.*, 2007; Cadotte *et al.*, 2009). The underlying premise of using a phylogenetic tree to represent phenotypic dissimilarity is that ecological divergence is correlated with the time since two species shared a common ancestor (Darwin, 1859; Felsenstein, 1985; Harvey & Pagel, 1991; Prinzing *et al.*, 2001; but see: Dormann *et al.*, 2010). Thus, to the degree that phylogeny correlates with phenotypic or niche variability, phylogenetic community patterns can provide important insights into the assembly and maintenance of ecological communities and the relative roles of differentiating and similarity-promoting community-assembly mechanisms (Cavender-Bares *et al.*, 2009). Specifically, analysis of phylogenetic community structure has been used to test whether local communities are composed of species that are more closely related (i.e. phylogenetically clustered) or more distantly related (i.e. phylogenetically over- or evenly dispersed) than expected at random (Webb, 2000; Webb *et al.*, 2002; Cavender-Bares & Wilczek, 2003; Cavender-Bares *et al.*, 2006; Helmus *et al.*, 2007). It is typically thought that phylogenetic clustering (or lack thereof) in co-occurring species may provide evidence about the relative strengths of environmental filtering (or trait convergence) compared to niche differentiation (trait divergence) (Webb *et al.*, 2002).

The ability to detect phylogenetic assembly patterns depends on both the structure of the source phylogeny and strength and depth of the phylogenetic signal in functional traits that drive community structure (Kembel, 2009; Swenson, 2009). However, plant communities contain species associations that have developed over long evolutionary time-scales (i.e. natives), while some members of regional floras are relatively recent additions (i.e. exotics). It remains untested whether these evolutionary associations are reflected in phylogenetic community patterns. Species assemblages that have co-occurred over sufficiently long time-scales are likely to have reciprocal evolutionary influences on resource use and interactions. For such assemblages, niche divergence should be stronger than, e.g., random Brownian motion evolution (Prinzing *et al.*, 2008). Species evolving elsewhere are not likely to have responded to the same pressures along the same axes of differentiation nor stumbled across the same partitioning strategies, and the net effect of combining such disparate taxa should be that, on average, niche differences conform more to random or Brownian niche evolution. Here, conserved traits should influence community patterns among exotics more than for native species.

Therefore, examining the composition of plant communities across a large spatial gradient in species richness in central/northern California (see Fig. S1), we hypothesize that native species, with higher pressure for character divergence, should show less of a phylogenetic signal in community patterns; whereas conserved traits should be more important for limiting the distribution of exotics species. Further, if conserved traits are more important for exotics, we hypothesize that successful exotic lineages should be distributed more broadly across the gradient and phylogenetic turnover (e.g. phylobetadiversity: Graham & Fine, 2008) should be low compared to the levels of phylobetadiversity for natives. It has been shown recently that successful exotics are phylogenetically distinct within their invaded communities (Mitchell *et al.*, 2006; Strauss *et al.*, 2006; Diez *et al.*, 2008), and closely related exotics tend to be similarly successful in new regions (Cadotte *et al.*, 2009). Here, we ask whether these underlying phylogenetic patterns matter for our interpretation of the processes driving community assembly across spatial scales.

METHODS

Locations and sampling

Percent plant cover was estimated for species present in four herbaceous-dominated sites in central California, USA: Jasper Ridge Biological Preserve, Mclaughlin Natural Reserve, Sierra Foothills Research and Extension Center and Hopland Research and Extension Center. Jasper Ridge Biological Preserve is located in central coastal California (37.4° N, 122.2° W), a 481- ha preserve, and research is at 120 m in elevation and receives 65 cm of precipitation. McLaughlin Natural Reserve (38°52′26″ N, 122°25′54″ W), a >2800- ha research site at around 400- m elevation, receives approximately 65 cm of annual precipitation. Sierra Foothills Research and Extension Center (39.285, −121.289), located in the western foothills of the Sierra-Nevada range, is at around 300- m elevation and receives approximately 65 cm of annual precipitation. Finally, Hopland Research and Extension Center (39.000, −123.090) is located at around 500- m elevation in the eastern foothills of the California Coastal range and receives approximately 94 cm annual precipitation (see Fig. S1 for location map and Table S1 for environmental summary).

At each site, three closely associated blocks with 10 permanently marked 1-m^2 plots were sampled for plant cover in 2007, except for Sierra, which had five more distantly distributed blocks (these plots are part of the Nutrient Network experiments, and general methodological descriptions are available as Appendix S1). At peak biomass (April–May 2007), areal cover was estimated in each of the plots for each plant species separately using a modified Daubenmire method (Daubenmire, 1959), in which cover is estimated to the nearest 1% for each species overhanging the plot. All taxa were identified to the species level, unless there was insufficient plant material present; in these cases, identifications were made to the genus or family level.

Phylogenetic construction

We constructed a phylogeny for all 98 species recorded at the four sites (see Appendix S2 for a list of all species). In August 2008, we searched Genbank (Benson *et al.*, 2005) for four sequences commonly used in published angiosperm phylogenies: *matK*, *rbcl*, *ITS1* and *5.8s*. Of the 98 species, 72 had at least one sequence represented in Genbank. Nine species were not included in Genbank, and we used sequences from a congeneric relative; 17 species were not identified to species level (see Appendix S2). Of these 17, three were identified only to family: Apiaceae, Iridaceae and Asteraceae, and as placeholders we used *Apium graveolens*, *Iris forrestii* and *Helianthus annuus*, respectively. For the other 14 species identified to genus, we used species known to occur in western North America (Niehaus, 1976; Spellenberg, 2001). Additionally, we included two representatives of early diverging lineages as outgroup species, including *Amborella trichopoda* and *Magnolia grandiflora*. For these 100 species, we aligned sequences using MUSCLE (Edgar, 2004). We then selected best-fit models of nucleotide substitution for each gene using the Akaike Information Criterion, as implemented in Modeltest and MrModeltest (Posada & Crandall, 1998, 2001).

Using the aligned sequences and the estimated models of nucleotide substitution, we estimated a maximum likelihood phylogeny using the PHYML algorithm with a BIONJ starting tree (Guindon & Gascuel, 2003; Anisimova & Gascuel, 2006). To assess nodal support on maximum likelihood phylogenies, we report approximate likelihood ratio test (aLRT) scores that have been shown to correlate with ML bootstrap scores but require much less computational time (Guindon & Gascuel, 2003). The maximum likelihood tree with nodal support values is shown in Fig. S2.

Statistical analysis

Phylogenetic diversity across the richness gradient

We used several approaches to assess compositional and phylogenetic differences between plots and sites along the gradient in species richness. The phylogenetic tree file was read into R 2.7.1 (http://www.r-project.org) using the ape 2.0-1 library (Paradis *et al.*, 2004), and all analyses were performed in R (functions created for our analyses are available in Appendix S3). It was necessary to ask whether there were compositional differences between sites and plots within sites, because we are testing phylogenetic patterns across a large richness gradient. We used detrended correspondence analysis (Hill & Gauch, 1980; Oksanen & Minchin, 1997) using the vegan 1.13-1 package in R (Oksanen *et al.*, 2008).

To assess phylogenetic patterns across the gradient for both natives and exotics, we used four complimentary metrics. First, we calculated community phylogenetic diversity (PD) as the total phylogenetic branch lengths connecting all species in a plot and not retaining the tree root (Faith, 1992, 1994; Cadotte *et al.*, 2008). PD represents the total evolutionary history and thus total opportunity for trait divergence, contained within a plot, and we used it to examine broad patterns among plots.

The second measure we use is the mean minimum phylogenetic distance, or mean nearest neighbour distance (MNND), which is the minimum phylogenetic distance to the closest relative averaged over all taxa (Webb *et al.*, 2002). Next the mean pairwise distance (MPD) (Webb *et al.*, 2002) is the average distance between each species and all others. Basically, MNND is used to ask how closely related co-occurring species can be and MPD is an average of overall patterns of relatedness. Both of these metrics were calculated using the R package picante 0.1-2 (Kembel *et al.*, 2010). These measures reveal average patterns of relatedness among species.

To make inferences about how all three of these metrics varied across a richness gradient, we compared observed PD, MNND and MPD. For PD, we randomized community composition 999 times from either exotic or native species pools, at each richness level and calculated PD. For MNND and MPD, we used the randomized values from the ses.mnnd and ses.mpd in picante, which swaps species names along the phylogeny for a given community and was repeated 999 times. For this, we excluded the outgroup species from the phylogeny since the addition of their long branch lengths would bias the null expectations. For these and all subsequent analyses, we removed all plots with a single species.

We also examined the phylogenetic distances of exotic species relative to natives with the deviation of observed MNND and MPD values from null expectations (Webb *et al.*, 2002). For both measures, a negative value indicates that the observed community is phylogenetically under-dispersed relative to the community phylogeny containing natives.

Phylobetadiversity

We examined how PD was partitioned into three additive scale components (Lande, 1996; Graham & Fine, 2008): mean within-plot or local PD ($\overline{\mathrm{PD}}_\alpha$), total across or within-site PD (PD_γ) and average among site or plot phylogenetic turnover (PD_β). PD_γ was simply calculated as the sum of the phylogenetic branch lengths connecting all the species at a site or across sites (depending on whether the comparison was among site or within sites). Mean local PD was calculated as:

$$\overline{\mathrm{PD}}_\alpha = \sum_{i=1}^{C} q_i \cdot \mathrm{PD}_i$$

where

$$q_i = \frac{S_i}{\sum_{i=1}^{C} S_i}$$

and S_i is the number of phylogenetic tips in plot *i*. Thus, q_i weights PD_i by the proportion of the tips in a plot relative to other plots and reduces the influence of species-poor plots. Finally, the among-plot phylobetadiversity is:

$$PD_\beta = PD_\gamma - \overline{PD}_\alpha.$$

We compared $\overline{PD}_\alpha$ and PD_β values to those from 999 randomizations where species names were shuffled across the entire phylogeny. Site and community phylogenies were then extracted from the randomized tree and used to calculate null $\overline{PD}_\alpha$ and PD_β. R scripts to calculate phylobetadiversity are available in Appendix S3.

Abundance and occupancy patterns across the richness gradient

To test for a phylogenetic signal of occupancy measures, we calculated Blomberg's *K* (Blomberg *et al.*, 2003), using code from the R package picante (Kembel *et al.*, 2008). Blomberg's *K* is a measure that explicitly quantifies trait variation given the phylogeny variance–covariance matrix, against trait values expected from Brownian evolution (Blomberg *et al.*, 2003). Values near 0 indicate a lack of a phylogenetic signal and approximately 1 typifies Brownian character evolution (i.e. a tendency for close relatives to be very similar). We calculated *K* to assess whether close relatives had similar occupancy patterns for both natives and exotics. We assessed the significance of the *K*-values by randomly shuffling occupancy values among species 999 times and calculated 95% confidence intervals (see Cadotte *et al.*, 2009 for R script). Thus, *K*-values greater than predicted by a null distribution represent close relatives having more similar occupancies than expected by chance.

RESULTS

The four sites contained a total of 133 sampled plots. Of the four sites, Hopland contained the greatest number of species ($n = 42$), followed by Sierra (41), Jasper Ridge (34) and McLaughlin (16). Hopland also had the greatest average plot richness ($\bar{x} = 18.92$, SD = 4.87), followed by Jasper Ridge ($\bar{x} = 14.37$, SD = 2.77), Sierra ($\bar{x} = 6.78$, SD = 2.29) and McLaughlin ($\bar{x} = 3.44$, SD = 1.34). Furthermore, plots within sites were generally much more compositionally similar to one another than to plots from other sites (Fig. S3). Plots from McLaughlin had the highest among-plot similarity, while plots within Sierra tended to show the greatest compositional differences (Fig. S3). These compositional differences appeared to have a minimal relationship with precipitation or elevation, although with four sites statistical testing is not informative.

Relatedness of exotic to native communities

The biomass of the communities sampled in this study tended to be dominated by exotic species, especially annual grasses. Individual plots ranged from 33.3% to 92.8% ($\bar{x} = 66.8\%$) exotic species, with Jasper Ridge having the greatest number of exotics relative to natives ($\bar{x}_{exotic} = 12.07$, $SD_{exotic} = 2.39$; $\bar{x}_{native} = 2.47$, $SD_{native} = 0.81$). Hopland was the next most invaded ($\bar{x}_{exotic} = 10.12$, $SD_{exotic} = 3.06$; $\bar{x}_{native} = 8.81$, $SD_{native} = 2.64$), followed by Sierra ($\bar{x}_{exotic} = 4.90$, $SD_{exotic} = 1.25$; $\bar{x}_{native} = 3.11$, $SD_{native} = 1.15$) and McLaughlin ($\bar{x}_{exotic} = 2.56$, $SD_{exotic} = 0.73$; $\bar{x}_{native} = 2.22$, $SD_{native} = 0.67$). There was generally a positive relationship between native and exotic species richness especially across sites excluding Jasper Ridge (Fig. S4). Within sites, there was generally little correlation, and only Hopland showed a significant positive relationship ($P < 0.05$). Within plots, the phylogenetic distribution of exotic species relative to all species showed under-dispersion or clumping, as indicated by negative MNND and MPD values for the exotics. Exotic species, in general, tended to be clumped in the phylogeny, falling within several major clades (e.g. Asteraceae, Caryophyllaceae and Poaceae, Fig. 1). Conversely, the natives in these communities tended to have positive MNND and MPD values and were thus over-dispersed.

Phylogenetic diversity across the richness gradient

We examined how patterns of phylogenetic distances varied across a gradient in species richness. For both exotics and natives, community PD increased with increasing community richness (Fig. 2) as phylogenetic branches were added with new taxa. However, the exotic subcommunities contained lower PD than expected from randomized communities of equal size (Fig. 2a). Species-poor communities contained especially low PD, relative to the null models. However, native species subcommunities generally follow the null distribution and tend to have greater PD than the null distribution (Fig. 2b). Further, for the exotic subcommunities, low richness plots had low MNND (Fig. 3a), and MPD (Fig. 3b) compared to null communities. Again, deviation from the null is greatest for species-poor communities, and native assemblages were much less likely to be under-dispersed (Fig. 3).

When we examined sites individually (Fig. S5), some of the patterns apparent in Fig. 3 are weakened. Within-site MPD for species-poor communities (<8 spp m^2) is below the null communities in McLaughlin and Sierra but not in Hopland and Jasper (Fig. S5). This is likely due to the fact that minimum community richness for plots within Hopland and Jasper are generally high and even more species-rich than the most species-rich communities within McLaughlin or Sierra. For all sites, MNND is generally lower than the null expectation.

Phylobetadiversity

When we partitioned PD into the additive components (α, β and γ), the exotic subcommunities generally had lower PD_β, relative to PD_α (Fig. 4), indicating larger ranges for individual exotic species across the spatial gradient. Further, exotic PD_α was higher than PD_β for Hopland and Jasper Ridge (Fig. 4a). Native species in communities had much higher PD_β among sites than exotics (Fig. 4b). Further, within sites, the native subcommunities had equal proportions of PD_α and PD_β for all sites but Sierra, which had a high PD_β (Fig. 4b).

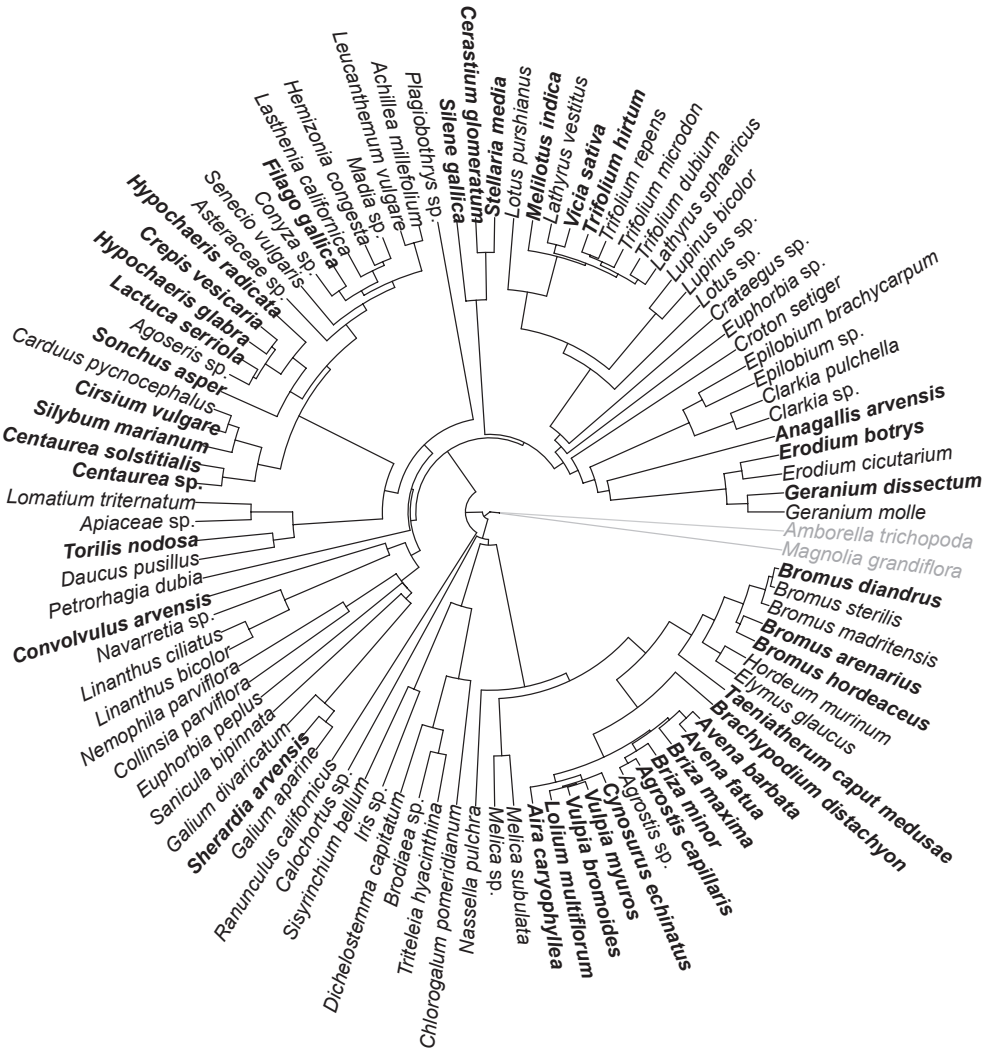

Figure 1 The maximum likelihood molecular phylogeny for the species (or congeners) observed in this study. Species in bold are exotic, and the two grey species represent anciently diverging lineages used as outgroups.

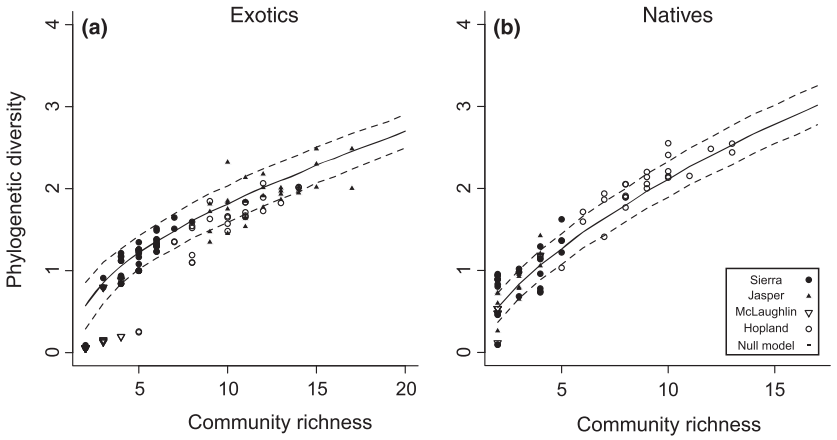

Figure 2 The relationship between plot phylogenetic diversity (PD) and species richness for the exotics (a) and natives (b). Sites where plots are located are indicated. The solid lines show mean PD from 999 randomizations at each species richness level, and dashed lines show the 95% confidence interval.

The high PD_β among sites appears to be driven by the turnover of some deeper clades (Fig. 5). Specifically, Hopland contained many Fabaceae, Caryophyllaceae and members of the Asparagales relative to other sites, while McLaughlin plots were missing key clades (Fabaceae, Asteraceae and Apiaceae). However, some grasses were extremely widespread, leading to

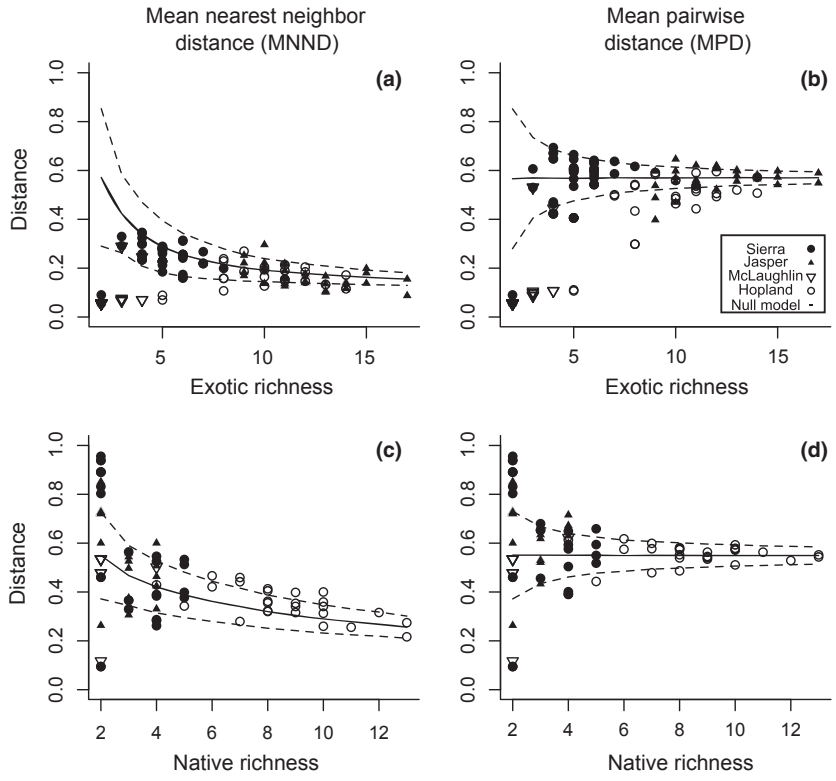

Figure 3 The relationship between two plot-level distance-based metrics [a, c – mean minimum phylogenetic distance (MNND) and b, d – mean pairwise distance (MPD)] and species richness for exotics (top row) and natives (bottom row). Sites in which plots are located are indicated. The solid lines show mean values from 999 randomizations at each species richness level, and dashed lines show the 95% confidence interval.

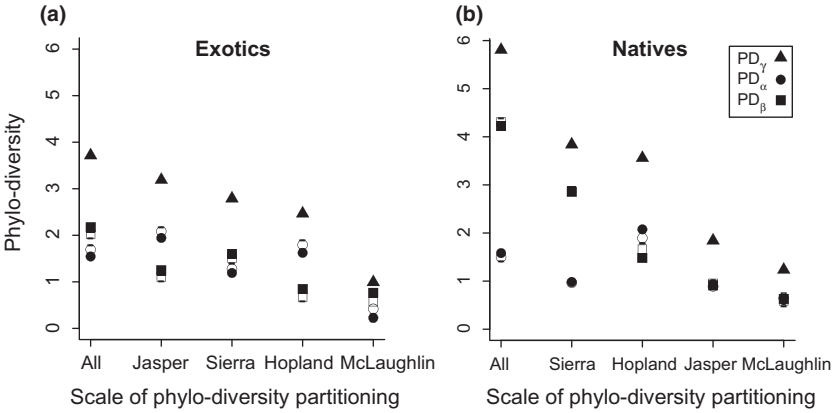

Figure 4 Patterns of phylogenetic diversity at alpha (plot), beta (among plot) and gamma (site) scales for the exotics (a) and natives (b). Open symbols indicate mean diversity values from 999 randomized communities.

little turnover among the grasses and providing a likely explanation for the lack of a pattern in the nearest neighbour distance among plots within and between sites.

Abundance and occupancy patterns across the richness gradient

There was a strong correlation between the number of sites occupied by individual exotic species and their abundance (mean percent cover, Fig. 6a) across all sites ($r = 0.589$, $P < 0.001$) and among plots at Hopland ($r = 0.671$, $P = 0.0012$), Jasper Ridge ($r = 0.457$, $P = 0.019$) and Sierra ($r = 0.671$, $P = 0.0034$), but not at McLaughlin ($r = 0.595$, $P = 0.159$). The native subcommunities did not show any significant relationship between abundance and occupancy either within or across sites ($P > 0.05$, Fig. 6b).

The number of sites occupied by exotic species did not show a significant phylogenetic signal either across all sites ($P > 0.05$) or within sites ($P > 0.05$ for every site). Thus, close relatives of successful exotics were not more likely to be successful themselves. The native communities also lacked significant phylogenetic signal in occupancy ($P > 0.05$ with and across all sites). Thus, close relatives do not have occupancy patterns any more similar than randomly chosen species.

DISCUSSION

Here, we developed an evolutionary phylogeny of plant species to examine native and exotic co-occurrence and turnover across a species richness gradient in central and northern California. Our phylogenetically informed community analyses

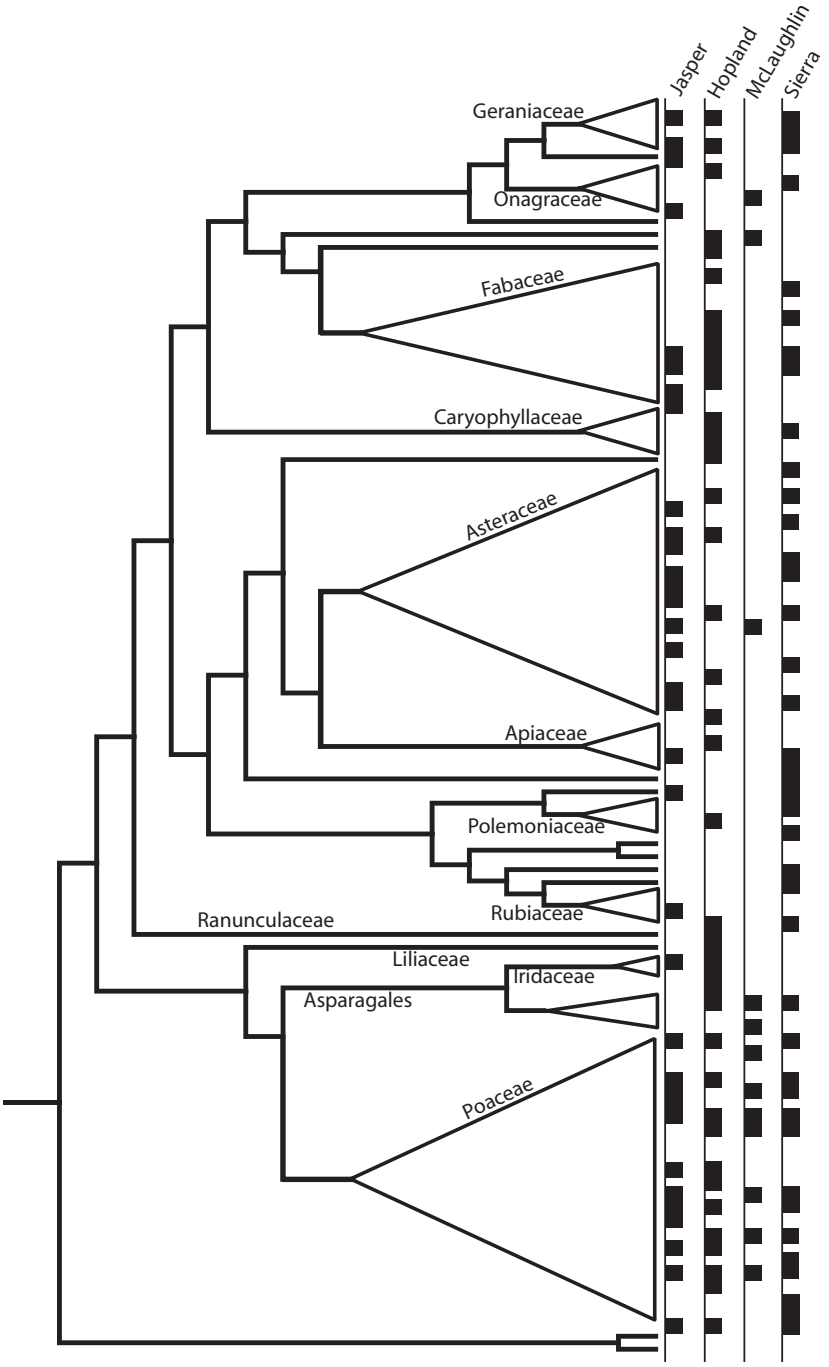

Figure 5 Clade occupancy in the four sites. Individual taxa are collapsed into higher clades to aid in visualizing higher-level occupancy.

provide new insights into how patterns of species relatedness are influenced by the processes driving community assembly. Within plots, natives and exotics differ in their dispersion across the phylogeny; natives are generally less related than expected by chance, and exotics are generally more related than expected by chance. Exotics have much lower phylobetadiversity than natives, suggesting that clades of successful invasive species tend to be more widespread than those within the native flora. This homogenization of PD represents a change in how diversity is spatially distributed (Mckinney & Lockwood, 1999; Mckinney, 2004; Winter *et al.*, 2009). Central California grasslands have gone from communities with high evolutionary specialization and diversity to invaded communities containing species from a few successful clades.

There are two key differences between native and exotic subcommunities that seem to drive these results. First, exotic subcommunities are phylogenetically clustered, while native subcommunities tend to be phylogenetically diverse ($MNND_{exotics}$ (SD) = 0.184 (0.08); $MNND_{native}$ (SD) = 0.485 (0.21)). The second key difference is the spatial phylogenetic turnover. Across the four sites, exotics tended to have lower phylogenetic turnover compared to within-plot PD, whereas

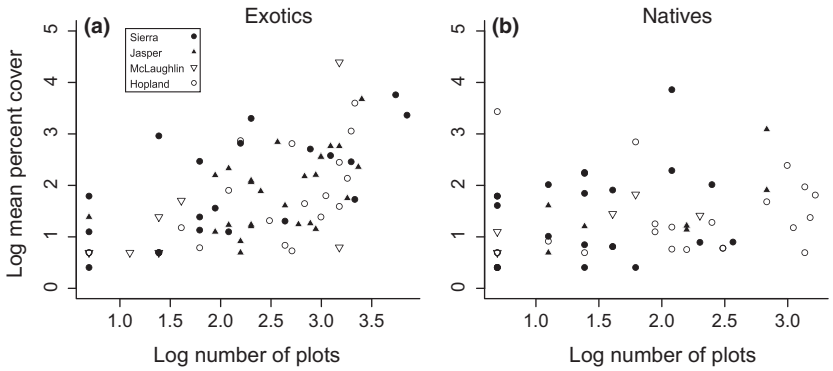

Figure 6 Correlation between the number of plots a species inhabits within each of the four sites and its mean abundance (percent cover) for the exotics (a) and natives (b).

average native phylogenetic turnover among plots was equal to mean native within-plot PD (except for Sierra). Sierra, where $PD_{\beta} >> PD_{\alpha}$, is likely an exception because blocks are scattered widely across the landscape and likely span more environmental variability than plots within the other sites and thus showed greater composition variation among plots (Fig. S2).

Exotic species are more consistently represented across all study sites than natives. These exotics tend to be closely related (see Fig. 1) and have spread across large spatial extents without much apparent influence from local environments, whereas the majority of native lineages are spatially restricted, perhaps to particular environments (Strauss *et al.*, 2006). The smaller native range arises from the high diversity of endemism and relict species isolated in glacial refuges (Stebbins & Major, 1965; Raven & Axelrod, 1978; Calsbeek *et al.*, 2003). This suggests that the longer evolutionary history of natives in this environment has led to stronger matches between traits and local conditions compared to the exotics (Questad & Foster, 2008).

Supporting this, exotics found in many plots had, on average, higher local abundances than exotics with more restricted ranges, consistent with classic spread models where local dynamics influence propagule availability and therefore range sizes (Skellam, 1951; Holt *et al.*, 1997). In contrast, the number of sites and mean abundances were decoupled for native species, indicating a stronger role of environmental heterogeneity. Alternatively, the breakdown of an occupancy–abundance relationship in the natives could result from native abundance declining in response to the spread of exotics.

An important future direction to extend this work will be to explicitly consider the critical functional traits that influence community assembly and underlie the emergent phylogenetic community patterns (Cavender-Bares *et al.*, 2009). Species traits simultaneously influence where species occur across gradients (i.e. beta niche) and how they partition niches within habitats (i.e. alpha niche); this habitat/trait knowledge can help delineate the phylogenetic scales driving patterns (Silvertown *et al.*, 2006; Cavender-Bares *et al.*, 2009). For example, while convergent traits may be critical for determining the pool of potential community members (e.g. herbaceous annuals in disturbed systems), other conserved traits may be critical for understanding which species are likely to coexist at local scales. Further, by knowing the phylogenetic scale at which various traits are conserved, we can develop more well-informed null expectations about phylogenetic clustering or over-dispersion (Kraft *et al.*, 2007).

CONCLUSIONS

Overall, we found that exotic lineages are phylogenetically clustered and have large ranges, suggesting that range size is determined by dispersal and not by environmental filtering. In contrast, native species are phylogenetically diverse within local communities, suggesting local niche partitioning, but have high phylogenetic turnover among sites, suggesting a relatively strong importance of habitat filtering at larger spatial scales for this subcommunity. In addition, species-poor communities tend to be composed of closely related species because of the increasing dominance of the phylogenetically clustered exotic species across a gradient of declining species richness.

These results show that native–exotic status can alter how evolutionary information relates to patterns of within- and among-community diversity and can lead ecologists to differing conclusions of the relative importance of habitat filtering and niche partitioning for influencing patterns of diversity. Given modern global change, there is a critical role for understanding these controls and influences on community assembly.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 The locations of the four sampling sites in central and northern California.

Figure S2 The maximum likelihood phylogeny showing nodal bootstrap support values.

Figure S3 The first two axes from a detrended correspondence analysis on community composition within plots.

Figure S4 The relationship between the number of exotics and natives within each plot, identified by site.

Figure S5 The distance-based metrics from Fig. 3 and plot richness within sites.

Table S1 Site characteristics.

Appendix S1 Experimental Protocol for Nutnet experiments.

Appendix S2 Genbank accession numbers for the species and gene sequences used in the phylogenetic analysis.

Appendix S3 Ecophylogenetic R scripts.

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BIOSKETCH

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