



# Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated

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## ABSTRACT

**Aim** To determine why some communities are more invisable than others and how this depends on spatial scale. Our previous work in serpentine ecosystems showed that native and exotic diversity are negatively correlated at small scales, but became positively correlated at larger scales. We hypothesized that this pattern was the result of classic niche partitioning at small scales where the environment is homogeneous, and a shift to the dominance of coexistence mechanisms that depend on spatial heterogeneity in the environment at large scales.

**Location** Serpentine ecosystem, Northern California.

**Methods** We test the above hypotheses using the phylogenetic relatedness of natives and exotics. We hypothesized that (1) at small scales, native and exotic species should be more distantly related than expected from a random assemblage model because with biotic resistance, successful invaders should have niches that are different from those of the natives present and (2) at large scales, native and exotic species should not be more distantly related than expected.

**Result** We find strong support for the first hypothesis providing further evidence of biotic resistance at small scales. However, at large scales, native and exotic species were also more distantly related than expected. Importantly, however, natives and exotics were more distantly related at small scales than they were at large scales, suggesting that in the transition from small to large scales, biotic resistance is relaxed but still present. Communities at large scales were not saturated in the sense that more species could enter the community, increasing species richness. However, species did not invade indiscriminately. Exotic species closely related to species already established the community were excluded.

**Main conclusions** Native communities determine the identity of exotic invaders even at large spatial scales where communities are unsaturated. These results hold promise for predicting which species will invade a community given the species present.

## Keywords

Biological invasions, biotic resistance, community invasibility, diversity–invasibility paradox, phylogenetic diversity, spatial scale.

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## INTRODUCTION

Biological invasions are one of the largest ecological and economic problems we face. Invasive species represent one of the most significant threats to biological diversity, along with habitat loss and fragmentation (Wilcove *et al.*, 1998; Pimentel *et al.*, 2000). Thus, any knowledge we can contribute to understanding the process of invasion will have huge benefits

for humanity. In particular, identifying the factors that make communities more or less invisable is critical.

Why some communities are more invisable than others and how this can depend on the spatial scale at which we observe them are questions that have long intrigued ecologists (Levine *et al.*, 2004; Davies *et al.*, 2005; Fridley *et al.*, 2007; Diez *et al.*, 2008; Stohlgren *et al.*, 2008; Cadotte *et al.*, 2009). These questions underlie fundamental concepts in community

ecology: species coexistence and assembly (Chesson, 2000a,b; Tilman, 2004). Therefore, their exploration continues to offer insights into why communities are structured the way they are. Further, questions about the invasibility of communities are of both great conservation and economic importance.

When communities are observed and manipulated at small spatial scales, we tend to detect negative relationships between native and exotic diversity (Elton, 1958; Turelli, 1981; Case, 1990; Tilman, 1997; Knops *et al.*, 1999; Stachowicz *et al.*, 1999; Levine, 2000; Naeem *et al.*, 2000; Lyons & Schwartz, 2001; Brown & Peet, 2003; Davies *et al.*, 2005), suggesting that native diversity armours a community against invasion. In contrast, when communities are observed at large spatial scales, we tend to detect positive relationships between native and exotic diversity, suggesting that diverse communities are more invulnerable (Lonsdale, 1999; Stohlgren *et al.*, 1999, 2008; Davies *et al.*, 2005, 2007a; Richardson *et al.*, 2005). This has been referred to as the diversity–invasibility paradox. Previously, Davies *et al.* (2005) suggested that negative relationships tend to be detected at scales at which the environment and resources are relatively homogenous and classic niche partitioning (and competitive exclusion) dominate (Grime, 1973; Tilman, 1999). We suggested that the relationship between native and exotic diversity becomes positive at scales at which spatial heterogeneity in the environment is such that coexistence mechanisms that depend on heterogeneity become dominant, resulting in communities that could be considered ‘unsaturated’. A comprehensive review of the paradox (Fridley *et al.*, 2007) came up with a similar framework built on the shift from biotic to abiotic drivers as scale increases. Eight processes that could generate either negative or positive relationships were identified, but all could be fitted within their framework.

The new field of community phylogenetics has allowed ecologists to use information about evolutionary relatedness of species within communities to understand invasibility (Strauss *et al.*, 2006; Proches *et al.*, 2008; Cadotte *et al.*, 2009). Ideas from this field have strong analogues with ideas about diversity, invasibility and scale (Davies *et al.*, 2005; Fridley *et al.*, 2007; Melbourne *et al.*, 2007). At small spatial scales, native species are likely to resist invasion of closely related invaders because they are likely to occupy similar niches. Density dependent factors associated with limiting similarly are hypothesized mechanisms, including effects of competition, and predator, pathogen and disease resistance (Webb *et al.*, 2002, 2006; Cavender-Bares *et al.*, 2004, 2009; Strauss *et al.*, 2006; Davies *et al.*, 2007a,b; Gilbert & Webb, 2007). Thus, coexisting species should be phylogenetically more distantly related than a random assemblage model. In contrast, at large scales, coexisting species should be more closely related than expected because of the effect of environmental filtering on membership of regional communities (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2006, 2007; Willis *et al.*, 2010). Considering relationships between native and exotic species, Darwin’s naturalization hypothesis is an analogue of the small scale hypothesis but considers genera rather than species. It suggests that exotic genera with no close relatives in a new area are

more likely to colonize than exotic genera with close relatives, because of the lack of competitive exclusion (Darwin, 1859). An important issue is the extent to which phylogenetic relatedness provides information about ecological similarity and niche overlap. While there is evidence for trait similarity and niche conservatism in plants (Ackerly & Reich, 1999; Prinzing *et al.*, 2001; Kerkhoff *et al.*, 2006; McCarthy *et al.*, 2007), it is often the case that within groups of close relatives (e.g. oak species or anolis lizards), species are labile in functionally important ways, and phylogenetic relatedness does not predict ecological similarity (e.g. Cavender-Bares *et al.*, 2004; Losos, 2008). At increasing phylogenetic scales, such as those encompassed in diverse plant communities that include many distinct lineages, phylogenetic relatedness of species is likely to be more predictive of ecological similarity (Cavender-Bares *et al.*, 2006, 2009; Swenson *et al.*, 2006, 2007). Disease resistance, for example, is well predicted in experimental studies by phylogenetic distance between hosts (Gilbert & Webb, 2007). In general, if traits evolve according to a Brownian motion model of evolution, greater divergence in trait values between species is expected with a longer time since divergence (e.g. Butler & King, 2004; Losos, 2008; Ackerly, 2009). To the extent that phylogenetic relationships provide reasonable information about the evolutionary relationships among species and their divergence times, the phylogenetic distances between species provide an integrated estimate of the relative magnitude of the genetic and phenotypic differences between species.

Phylogenetic distances between species may thus provide an estimate of the ecological similarity and niche overlap of species and therefore help us to predict which species are more or less likely to invade a community given which species are present and their phylogenetic relationships to potential invaders. Several invasion studies have found the phylogenetic relatedness of native species to exotics to be an important predictor of invasion success. In California, successful exotic grass invaders were significantly less phylogenetically related to native species in new geographic areas compared with non-invasive exotic species (Strauss *et al.*, 2006). In New Zealand, the proportion of introduced species that become naturalized is higher for plants that have native congeners than for those that do not (Duncan & Williams, 2002). A species-addition experiment in prairie grasslands showed that established species most strongly inhibited introduced species from their own functional group so that there was greater competitive inhibition of invaders that were similar to established abundant species (Fargione *et al.*, 2003). None of these studies considers the effects of scale. However, Cadotte *et al.* (2009) examined the occupancy of exotic plant species in Royal National Park, Australia and then also examined the occupancy of those exotic species at a continental scale using herbarium records. Natives and exotics were more closely related than expected at large scales, suggesting that invaders and natives share ecological traits that make them successful. At small scales, exotics were neither more nor less closely related.

In Californian serpentine plant ecosystems, we found negative relationships between native and exotic diversity at small scales, and positive relationships at large scales (Davies *et al.*, 2005). We defined diversity as species richness. We demonstrated that the observed relationship between native and exotic diversity flipped from negative to positive at scales at which spatial heterogeneity in the environment came into play (was correlated with native and exotic diversity and beta diversity). We hypothesized that this is because at small scales, the environment is homogeneous and biotic interactions dominate, whereas at large scales, spatial heterogeneity in the environment increases and coexistence mechanisms that depend on spatial heterogeneity in the environment dominate. Recent experiments showed that phylogenetic clustering increases with spatial scale but also with experimental increases in the heterogeneity in the environment within the same spatial scale (Willis *et al.*, 2010). We expect that the predicted effects are not dependent on spatial scale *per se*, but rather on the fact that heterogeneity in the environment almost always increases with increasing scale (Davies *et al.*, 2005). Here, we test these hypotheses using the phylogenetic relatedness of natives and exotics in the same system. Given our findings for diversity, we hypothesized that (1) at small scales, native and exotic species should be more distantly related than expected from a random assemblage model if there is biotic resistance as successful invaders should have niches that are different from those of the natives present. The idea of biotic resistance is that direct and indirect interactions between resident species and an invader can make it difficult for an invader to invade. (2) At large scales, native and exotic species should not be more distantly related than expected, or may even be more closely related than expected if the environment filters membership of communities.

## METHODS

### Data collection

Our survey site was located in patchy serpentine and non-serpentine grassland in the McLaughlin University of California Reserve (38°51'N, 123°30'W), 120 km north of San Francisco, California. We collected data at 96 sites that comprised a 550 × 350-m grid, in the spring of 2001 and 2002. Sites were located 50 m apart in 12 rows and eight columns. At each site, we collected plant composition data in four 1-m square quadrats, located around a central marker. We detected 156 grass and forb species, of which 112 species were native and 44 species were exotic.

For this work, we considered two spatial scales: (1) nine sites within each block (site: 16 m<sup>2</sup>) and (2) 12 blocks within the grid (block: 10,816 m<sup>2</sup>). Ideally, the local scale is the scale at which individuals interact with individuals of their own and other species. Operationally, we defined this as the smallest spatial unit, although the scale of interactions may have been smaller than this. In a previous paper from which this work originated (Davies *et al.*, 2005), we considered an additional two spatial scales. For simplicity, we consider only two scales

here, but these encompass the relationships presented in Davies *et al.* (2005).

### Creating the phylogenies

A literature-based phylogeny was constructed using the Davies *et al.* (2004) angiosperm supertree from the total species using PhyloMatic (Webb *et al.*, 2004) (Fig. 1). Taxon names were initially checked for synonyms to match standardized names from the integrated taxonomic information system (ITIS) using Nix (Kembel, 2007). In groups where intra-generic resolution from the backbone phylogeny was low, polytomies were resolved with branching arrangements from recently published literature. Branching patterns were manipulated in MESQUITE version 2.6 (Maddison & Maddison, 2006) based on the phylogenetic hypotheses presented by Panero & Funk (2008) for Asteraceae, Downie *et al.* (2000) for Apioideae, McMahon & Sanderson (2006) for Papilionoid Legumes and Bouchenak-Khelladi *et al.* (2008) for Poaceae. Inclusion of these published relationships within clades increased resolution of the tips of the phylogeny to 56% from 62% based on the Davies *et al.* (2004) tree alone. Branch lengths were estimated using the branch length adjustment algorithm (BLADJ) in PHYLACOM version 4.0.1 (Webb *et al.*, 2008) using minimum ages from the fossil record from Wikstrom *et al.* (2001). While there are known limitations to the reliability of branch lengths estimated using this approach (Webb *et al.*, 2008), it represents an important advance over methods that use nodal distances as proxies for branch lengths. This literature-based phylogeny takes advantage of existing phylogenetic data, synthesizing published expert knowledge, without the considerable expense and time involved in developing molecular phylogenies.

### Data analysis

We used R (R Development Core Team, 2007) for all analyses. We used the sum of phylogenetic diversity (Faith, 1992; Webb, 2000; Webb *et al.*, 2002; Cadotte *et al.*, 2008, 2009) calculated as:

$$d_k^* = \sum_i \sum_j d_{ij}$$

where  $d_{ij}$  is the phylogenetic distance between native species  $i$  and exotic species  $j$ . Our metric was  $d^*$  the mean summed distance across sites or blocks, where  $n$  is the number of sites or blocks:

$$d^* = \frac{1}{n} \sum_k d_k^*$$

### Phylogenetic distance between natives and exotics

*Native versus exotic phylogenetic distance at two spatial scales (sites and blocks)*

We asked: is the phylogenetic distance between natives and exotics greater than expected (for both small and large scales)?



Figure 1 Phylogeny of serpentine plant ecosystem community ( $n = 152$ ). Filled circles at the tips of the phylogeny indicate native species, open circles indicate exotic species. Radially extending branch lengths are drawn proportional to distance.

We calculated the observed phylogenetic distance between natives and exotics by calculating the phylogenetic distance between every pair wise combination of natives and exotics in the site or block of interest and then calculating the sum. Across the entire grid, we then took the mean of this number to give one value that represented overall site or block phylogenetic distance between natives and exotics (observed phylogenetic distance). We then compared this observed phylogenetic distance between natives and exotics to those from 10,000 randomizations where we randomly shuffled the species occurrence matrix. We established that our null model had no inherent bias as outlined in Appendix S1.

## RESULTS

### A phylogenetic distance between natives and exotics

In communities at small scales, native and exotic species were significantly more distantly related than expected supporting hypothesis one (observed distance 31,693.06; 95% CI of the expected distances under the null model 27,411.28, 29,964.48). In contrast, we found no support for hypothesis two that at large scales, phylogenetic distance between natives and exotics should be equal to or greater than expected. Instead, at large scales, we found that native and exotic species were more

distantly related than expected (observed distance 30,6340.10; 95% CI of the expected distances under the null model 24,8407.25, 27,4654.47). We also tested whether the distance between natives and exotics was significantly greater at small than large spatial scales and determined that it was greater ( $P < 0.001$ ).

## DISCUSSION

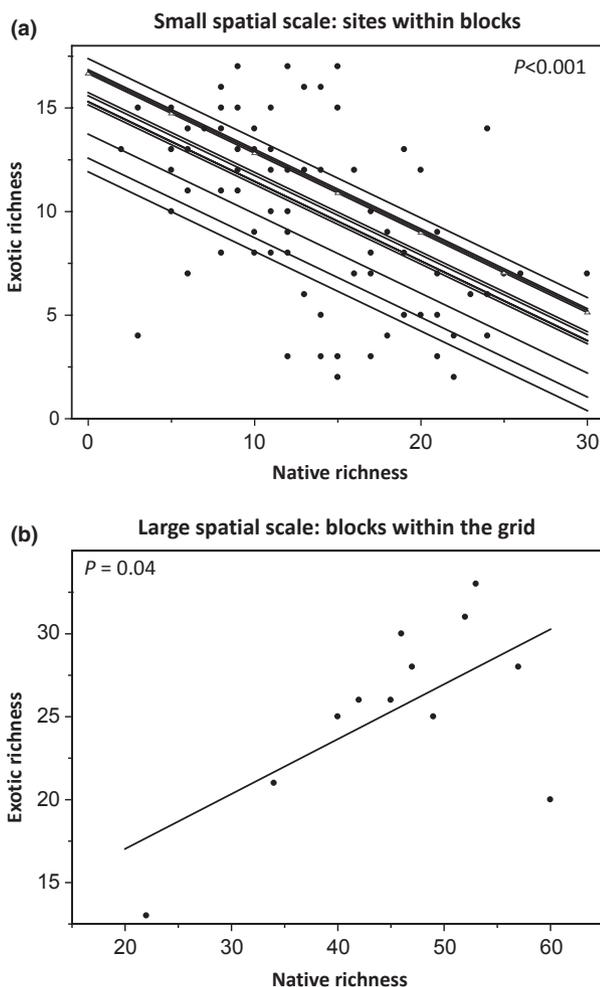
As predicted, at small scales, native and exotic species were more distantly related than expected, while in contrast to our predictions, at large scales, native and exotic species were also more distantly related than expected. The small scale result provides support for the hypothesis that native and exotic diversity are negatively correlated at small scales where biotic resistance is the dominant mechanism influencing community assembly (Davies *et al.*, 2005) (Fig. 2a). At large scales, we previously found that native and exotic diversity were positively correlated (Davies *et al.*, 2005) (Fig. 2b). We hypothesized that the relationship flips from negative to

positive at scales where spatial heterogeneity in the environment is large and where coexistence mechanisms that depend on spatial heterogeneity in the environment dominate. In our earlier study, this hypothesis was supported by a positive relationship of spatial environmental variance with native and exotic diversity and beta diversity. These earlier findings are consistent with theoretical perspectives about the invasibility of communities and scale (Fridley *et al.*, 2007; Melbourne *et al.*, 2007). Our contrasting results here using phylogenetic diversity suggest that there is more to the story at large scales. We elaborate on this in the following two paragraphs.

Native and exotic species were more distantly related than expected at both small and large scales. However, natives and exotics were more closely related at large than small scales, suggesting that community resistance to invasion was lower at large scales. Thus, as we move from small scales to large scales, biotic resistance is relaxed but is still operating at large scales. The richness results and phylogenetic distance results tell us about different things: richness about how many native and exotic species can coexist with each other and phylogenetic distance about how the extent of shared evolutionary history influences which species can coexist with each other. At large scales, heterogeneity allows species to coexist to the extent that locations that are good for natives also have more exotic species, and communities appear unsaturated. However, resistance to invasion is maintained so that certain species are excluded: those exotic species that are phylogenetically closely related to the species already established in the community.

Recently, Stohlgren *et al.* (2008) suggested that invasion, rather than diminishing the diversity of native species in a community, has the overall effect of increasing the diversity of communities by adding exotic species. They based their conclusion on evidence that communities are unsaturated at large spatial scales and, at least for plants, a lack of species extinctions driven by competitive interactions. Consequently, we should generally find positive relationships between native and exotic diversity at large scales. Stohlgren *et al.* (2008) suggest that ultimately competition appears to play no role in structuring communities at large scales, even if competition is important in structuring communities at small scales and thus is of little interest to invasion studies. However, our results directly contradict this finding by illustrating that even when native and exotic diversity are positively correlated, suggesting lack of saturation, biotic resistance to invasion still structures communities. Exotic species that are phylogenetically closely related to the species already established in the community are excluded (see also Harrison, 2008).

A recent study, similar to our study, examined the relationship between phylogenetic distance between native and exotics at multiple spatial scales and found no phylogenetic signal at small scales, but detected phylogenetic clustering at large scales, suggesting that invaders and natives share ecological traits that make them successful at large scales (Cadotte *et al.*, 2009). This pattern provides evidence for environmental filtering, as has been shown in other studies (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2006; Willis *et al.*,



**Figure 2** Relationships between native diversity and exotic diversity at two spatial scales: (a) sites within blocks and (b) blocks within the entire grid.

2010). The scales considered by Cadotte *et al.* (2009) were larger than those considered here (continent and regional scale versus regional and local scale in our study), and this likely explains the differences in our findings.

The observed phylogenetic distances between native and exotic species not only offer insights into the invasibility of communities but also offer insights into why communities are structured the way they are. Our results confirm that communities are structured not only by biotic resistance but also by environmental heterogeneity (Chesson, 2000a), and further, that while competition and heterogeneity interact, they also operate at different scales (local versus regional), at least in plant communities (Chesson, 2000a; Chesson *et al.*, 2005). Finally, we find that communities can appear unsaturated but still be structured by biotic resistance.

In summary, ultimately, the phylogenetic identity of species predicted which species were able to invade communities, even at large spatial scales, offering an important illustration of the predictive power of phylogeny in ecological studies (Cavender-Bares *et al.*, 2009). With knowledge of which species are present in the community and phylogenetic relationships to potential invaders, there is potential to predict which species are more or less likely to invade a community in other systems. Intriguingly, we found that as we move from small scales to large scales, the effect of biotic resistance is relaxed but is still present at large scales. Environmental heterogeneity allows species to coexist to the extent that locations that have many niches for native species also have many niches for exotic species, but biotic resistance is still acting so that exotic species that are closely related to native species already established in the community are excluded. In other words, at large scales, even when native and exotic diversity are positively correlated, suggesting lack of saturation, biotic resistance to invasion still structures communities. Future research should determine at which spatial scales the effects of biotic resistance dissipate so that exotics closely related to the species in a given community are no longer excluded. What occurs at these scales that causes these effects to disappear? Further, how broadly do our results apply to other systems?

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## REFERENCES

- Ackerly, D. (2009) Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences USA*, **106**, 19699–19706.
- Ackerly, D.D. & Reich, P.B. (1999) Convergence and correlation among leaf size and function in seed plants: a comparative test using independent contrasts. *American Journal of Botany*, **86**, 1272–1281.
- Bouchenak-Khelladi, Y., Salamin, N., Savolainen, V., Forest, F., van der Bank, M., Chase, M.W. & Hodkinson, T.R. (2008) Large multi-gene phylogenetic trees of the grasses (Poaceae): progress towards complete tribal and generic level sampling. *Molecular Phylogenetics and Evolution*, **47**, 488–505.
- Brown, R.L. & Peet, R.K. (2003) Diversity and invasibility of southern Appalachian plant communities. *Ecology*, **84**, 32–39.
- Butler, M. & King, A.A. (2004) Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist*, **164**, 683–695.
- Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008) Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences USA*, **105**, 17012–17017.
- Cadotte, M.W., Hamilton, M.A. & Murray, B.R. (2009) Phylogenetic relatedness and plant invader success across two spatial scales. *Diversity and Distributions*, **15**, 481–488.
- Case, T.J. (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences USA*, **87**, 9610–9614.
- Cavender-Bares, J., Ackerly, D.D., Baum, D.A. & Bazzaz, F.A. (2004) Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist*, **163**, 823–843.
- Cavender-Bares, J., Keen, A. & Miles, B. (2006) Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology*, **87**, S109–S122.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Chesson, P. (2000a) General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, **58**, 211–237.
- Chesson, P. (2000b) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.
- Chesson, P., Donahue, M.J., Melbourne, B.A. & Sears, A.L. (2005) Scale transition theory for understanding mechanisms in metacommunities. *Metacommunities: spatial dynamics and ecological communities* (ed. by M. Holyoak, M.A. Leibold and R.D. Holt), pp. 279–306. University of Chicago Press, Chicago.
- Darwin, C. (1859) *The origin of species*. J. Murray, London.
- Davies, T.J., Barraclough, T.G., Chase, M.W., Soltis, P.S., Soltis, D.E. & Savolainen, V. (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences USA*, **101**, 1904–1909.
- Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A. & Rice, K.J. (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology*, **86**, 1602–1610.

- Davies, K.F., Harrison, S., Safford, H.D. & Viers, J.H. (2007a) Productivity alters the scale dependence of the diversity–invasibility relationship. *Ecology*, **88**, 1940–1947.
- Davies, T.J., Meiri, S., Barraclough, T.G. & Gittleman, J.L. (2007b) Species co-existence and character divergence across carnivores. *Ecology Letters*, **10**, 146–152.
- Diez, J.M., Sullivan, J.J., Hulme, P.E., Edwards, G. & Duncan, R.P. (2008) Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. *Ecology Letters*, **11**, 674–681.
- Downie, S.R., Katz-Downie, D.S. & Watson, M.F. (2000) A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA *rpl16* and *rpoC1* intron sequences: towards a suprageneric classification of subfamily apioidae. *American Journal of Botany*, **87**, 273–292.
- Duncan, R.P. & Williams, P.A. (2002) Ecology – Darwin's naturalization hypothesis challenged. *Nature*, **417**, 608–609.
- Elton, C.S. (1958) *The ecology of invasions*. Methuen, London, UK.
- Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.
- Fargione, J., Brown, C.S. & Tilman, D. (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences USA*, **100**, 8916–8920.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Holle, B. (2007) The invasion paradox: reconciling pattern and process in species invasion. *Ecology*, **88**, 3–17.
- Gilbert, G.S. & Webb, C.O. (2007) Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences USA*, **104**, 4979–4983.
- Grime, J.P. (1973) Control of species density in herbaceous vegetation. *Journal of Environmental Management*, **1**, 151–167.
- Harrison, S. (2008) Commentary on Stohlgren *et al.* (2008): the myth of plant species saturation. *Ecology Letters*, **11**, 322–324.
- Kembel, S.W. (2007) Nix: software for taxonomic informatics. Available at: <http://phylodiversity.net/nix/>.
- Kerkhoff, A.J., Fagan, W.F., Elser, J.J. & Enquist, B.J. (2006) Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *The American Naturalist*, **168**, E103–E122.
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Groth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances, and diversity. *Ecology Letters*, **2**, 286–293.
- Levine, J.M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science*, **288**, 852–854.
- Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1007.
- Lyons, K.G. & Schwartz, M.W. (2001) Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters*, **4**, 358–365.
- Maddison, W.P. & Maddison, D.R. (2006) Mesquite: a modular system for evolutionary analysis. Version 1.11.
- McCarthy, M.C., Enquist, B.J. & Kerkhoff, A.J. (2007) Organ partitioning and distribution across the seed plants: assessing the relative importance of phylogeny and function. *International Journal of Plant Sciences*, **168**, 751–761.
- McMahon, M.M. & Sanderson, M.J. (2006) Phylogenetic supermatrix analysis of GenBank sequences from 2228 papilionoid legumes. *Systematic Biology*, **55**, 818–836.
- Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K. & Yokomizo, H. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters*, **10**, 77–94.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, **91**, 97–108.
- Panero, J.L. & Funk, V.A. (2008) The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution*, **47**, 757–782.
- Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience*, **50**, 53–65.
- Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2383–2389.
- Proches, S., Wilson, J.R.U., Richardson, D.M. & Rejmanek, M. (2008) Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography*, **17**, 5–10.
- R Development Core Team (2007) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org>.
- Richardson, D.M., Rouget, M., Ralston, S.J., Cowling, R.M., van Rensburg, B.J. & Thuiller, W. (2005) Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience*, **12**, 391–402.
- Stachowicz, J.J., Whitlatch, R.B. & Osman, R.W. (1999) Species diversity and invasion resistance in a marine ecosystem. *Science*, **286**, 1577–1579.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.

- Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C. & Kartesz, C. (2008) The myth of plant species saturation. *Ecology letters*, **11**, 315–326.
- Strauss, S.Y., Webb, C.O. & Salamin, N. (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., Enquist, B.J., Pither, J., Thompson, J. & Zimmerman, J.K. (2006) The problem and promise of scale dependency in community phylogenetics. *Ecology*, **87**, 2418–2424.
- Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770–1780.
- Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81–92.
- Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455–1474.
- Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences USA*, **101**, 10854–10861.
- Turelli, M. (1981) Niche overlap and invasion of competitors in random environments. 1. Models without demographic stochasticity. *Theoretical Population Biology*, **20**, 1–56.
- Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist*, **156**, 145–155.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2004) *Phylocom: phylogenetic analysis of communities and characters*. Available at: <http://www.phylodiversity.net/phylocom>.
- Webb, C.O., Gilbert, G.S. & Donoghue, M.J. (2006) Phylodiversity-dependent seedling mortality, size structure, and disease in a bornean rain forest. *Ecology*, **87**, S123–S131.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.
- Wikstrom, N., Savolainen, V. & Chase, M.W. (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2211–2220.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *BioScience*, **48**, 607–615.
- Willis, C.G., Halina, M., Lehman, C., Reich, P.B., Keen, A., McCarthy, S. & Cavender-Bares, J. (2010) Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography*, **33**, 565–577.

## SUPPORTING INFORMATION

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

### Appendix S1 Test for null model bias.

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Author contributions: K.F.D. and J.C.-B. conceived the ideas; K.F.D. collected the data (with Brian Inouye); N.D. and J.C.-B. created the phylogeny; K.F.D. analysed the data; and K.F.D. led the writing with assistance from J.C.B.

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