

Phylogenetic relatedness and plant invader success across two spatial scales

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ABSTRACT

Aim Successful invaders often possess similar ecological traits that contribute to success in new regions, and thus under niche conservatism, invader success should be phylogenetically clustered. We asked if the degree to which non-native plant species are phylogenetically related is a predictor of invasion success at two spatial scales.

Location Australia – the whole continent and Royal National Park (south-eastern Australia).

Methods We used non-native plant species occupancy in Royal National Park, as well as estimated continental occupancy of these species from herbarium records. We then estimated phylogenetic relationships using molecular data from three gene sequences available on GenBank (*matK*, *rbcL* and *ITS1*). We tested for phylogenetic signals in occupancy using Blomberg's *K*.

Results Whereas most non-native plants were relatively scarce, there was a strong phylogenetic signal for continental occupancy, driven by the clustering of successful species in Asteraceae, Caryophyllaceae, Poaceae and Solanaceae. However, we failed to detect a phylogenetic signal at the park scale.

Main Conclusions Our results reveal that at a large spatial scale, invader success is phylogenetically clustered where ecological traits promoting success appear to be shared among close relatives, indicating that phylogenetic relationships can be useful predictors of invasion success at large spatial scales. At a smaller, landscape scale, there was no evidence of phylogenetic clustering of invasion success, and thus, relatedness plays a much reduced role in determining the relative success of invaders.

Keywords

Angiosperm phylogeny, Australia, biological invasions, community assembly, niche conservatism.

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INTRODUCTION

Predicting how species respond to new environments, especially in the absence of prior information, is critically important when species potentially have large economic, health and conservation repercussions. One particularly useful tool that has emerged is the use of evolutionary relatedness to understand and predict species responses across environmental gradients (Ackerly, 2003; Cavender-Bares *et al.*, 2006). The application of this idea to the study of biological invasions offers similar reward for our ability to understand the drivers of success among invasive species (Strauss *et al.*, 2006; Proches *et al.*, 2008).

Considering the global flora as a pool of potential plant invaders, only a particular subset of this pool can pass through environmental filters and become successful invaders in a new geographical region (Fig. 1). At large spatial scales (e.g. continental

scales), successful invaders often possess similar ecological traits that contribute to success in the new region (e.g. Hamilton *et al.*, 2005). From this we can predict that invasive species will be phylogenetically clustered under phylogenetic niche conservatism (Ackerly, 2003, 2004; Wiens & Donoghue, 2004; Wiens, 2004; Wiens & Graham, 2005; Silvertown *et al.*, 2006a,b). Indeed, there is some evidence that species' ecological traits are phylogenetically conserved at continental scales (e.g. maximum elevational range, Silvertown *et al.*, 2006a). At smaller spatial scales, however, we do not necessarily expect phylogenetic clustering because there is a wide range of ecological factors, including local interactions and habitat disturbance, that will influence invasion success, ultimately leading to decreasing phylogenetic signal among successful invaders (Bohning-Gaese & Oberrath, 1999; Webb *et al.*, 2002; Cavender-Bares *et al.*, 2006; Horner-Devine & Bohannan, 2006; Webb *et al.*, 2006). Indeed,

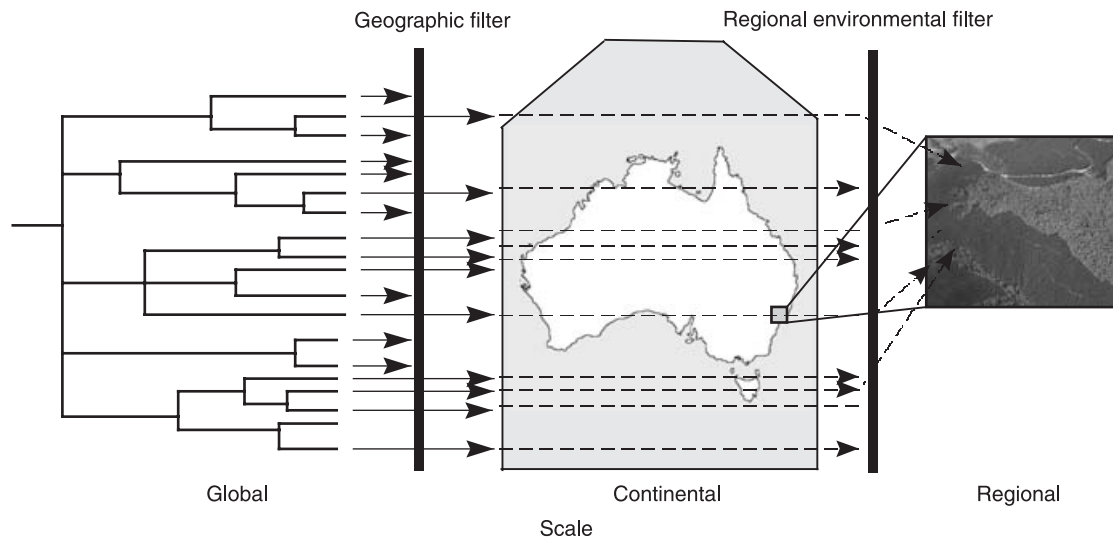


Figure 1 Non-native plant species from a global species pool have to be pre-adapted to environmental conditions in the novel geographical entity. This geographical filter should select for phylogenetic clustering, as related species should be adapted to similar broad environments, but also includes species undergoing human-mediated dispersal. However, regional scale assembly is dependent on numerous processes such as local environmental filters, resource competition, disturbance and dispersal dynamics. Here we expect phylogenetic signals to break down.

earlier work at extremely small spatial scales has found either phylogenetic overdispersion, where closely related species are unlikely to co-occur together (Webb, 2000; Cavender-Bares *et al.*, 2006), or little evidence for relationships between phylogenetic distance between species and their ecological trait similarities (Silvertown *et al.*, 2006b).

Furthermore, there is evidence that successful non-native plant invaders may be significantly less related phylogenetically (compared with non-invasive exotic plant species) to native species in new geographical regions (Strauss *et al.*, 2006 – but see Duncan & Williams, 2002; Lambdon & Hulme, 2006). Given that phylogenetic uniqueness relative to native communities may be a predictor of invasion success, the resulting question is whether closely related non-native plant species are similarly successful invaders in new regions. This is predicated on the idea that if phylogenetic uniqueness corresponds to novel traits or niche requirements (Strauss *et al.*, 2006; Cadotte *et al.*, 2008), then a non-native species that is closely related to a successful phylogenetically unique species might also be likely to invade successfully under niche conservatism (Pheloung *et al.*, 1999; Reichard & Hamilton, 1997).

In the present study, we examine patterns of phylogenetic clustering in relation to invasion success among non-native plants introduced to Australia in the last 220 years since the European settlement. At a large spatial scale (e.g. the Australian continent, see Fig. 1) we predict that large-scale occupancy measures that represent invasion success will be phylogenetically clustered. Given shifts in the relative importance of phylogenetic niche conservatism at contrasting spatial scales, we further predict that patterns of phylogenetic clustering will disappear at a landscape scale (Royal National Park).

METHODS

Framework for comparisons

Phylogenetic patterns underpinning successful biological invasions can be investigated in a number of ways (Hayes & Barry, 2008). We use a target-area approach (*sensu* Pysek *et al.*, 2004) to explore variation in invasion success in relation to phylogenetic relationships among a pool of species introduced to a new region. This approach has been effectively used in previous work to relate variation in invasion success to a range of plant traits (Pysek *et al.*, 1995; Rejmanek & Richardson, 1996; Grotkopp *et al.*, 2002; Brandle *et al.*, 2003; Lloret *et al.*, 2004; Hamilton *et al.*, 2005; Cadotte *et al.*, 2006; Harris *et al.*, 2007).

Exotic plant taxa and invasion success

Data for continental and landscape scale occupancy were obtained from Hamilton (2004) and Hamilton *et al.* (2005). Data at both spatial scales were continuous, rather than categorical, which permitted detailed analyses of comparative levels of invasion success. Invasion success of each species at the landscape scale was estimated as the proportion of 200 sites occupied by each species across Royal National Park in south-eastern Australia after comprehensive vegetation surveys (see Hamilton *et al.*, 2005 for further details). This park spans 15,068 ha on the outskirts of Sydney. Continental invasion success of the same taxa was measured using herbarium records from herbaria located across Australia (e.g. Murray *et al.*, 2002). Residence time data, measures of how long each non-native species has been present in Australia, were obtained for each species from an

unpublished database of non-native plants in Australia (John Ingram, unpublished data). Ingram's database is the result of many years of effort and wide-ranging searches of source material such as Australian nursery lists and herbarium records for known dates of plant introduction. Altogether, 155 non-native plant species were observed in the 200 samples at the regional scale. These species were distributed across 50 angiosperm families, and continental occupancy was estimated for all 155 species. Residence time data were available for 146 of the 155 species.

Phylogenetic relationships among non-native plant taxa

We constructed two working phylogenies for the study taxa using two different methods. The first method was based on the publicly available 'supertree' from Phylomatic (<http://www.phylodiversity.net/phyloomatic/>), which compiles published angiosperm phylogenies (Davies *et al.*, 2004) and represents a working hypothesis of phylogenetic relationships among angiosperms. We then used the BLADJ procedure in PHYLOCOM (Webb *et al.*, 2007) to scale branch lengths using known node ages. For angiosperms, we used the divergence times estimated by Wikstrom *et al.* (2001). Therefore, our estimates of phylogenetic distance are in millions of years. We refer to our phylogeny constructed using this method as the supertree phylogeny.

We then constructed a second phylogeny using maximum likelihood molecular techniques. For each of the 155 species, we searched GenBank (Benson *et al.*, 2005) for three gene sequences commonly used in published angiosperm phylogenies: *matK*, *rbcl* and *ITS1*. Of the 155 species, 95 had at least one gene represented in GenBank. For a further 46 species, we used gene sequences for a congeneric relative. We also included two distantly related angiosperm species as out-group species, *Amborella trichopoda* and *Magnolia grandiflora*. Several preliminary phylogenetic analyses revealed poorly resolved clades, which in most cases were the result of closely related species being represented by sequences from different genes. To overcome these resolution problems, we added 10 highly sequenced species to serve as 'sequence bridges' for related taxa. All species and genes (and the GenBank accession numbers) are listed in Appendix S1 in the Supporting Information section. For this total of 153 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 (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, which have been shown to correlate with ML bootstrap scores, but require much less computational time (Guindon & Gascuel, 2003). We refer to our phylogeny constructed using this method as the molecular tree phylogeny (see Fig. 2 and the Newick file is available in Appendix S2 in Supporting Information).

In order to increase species membership in this phylogeny, we added eight species as polytomies with congeneric relatives in the molecular phylogeny. For species included in genera with two or more representatives in the molecular phylogeny, we calculated the new species' branch length as the average of the other congenics. For those being paired with a single generic representative we used the average branch length for all congeneric pairs in the phylogeny (see Appendix S1 for list of these species).

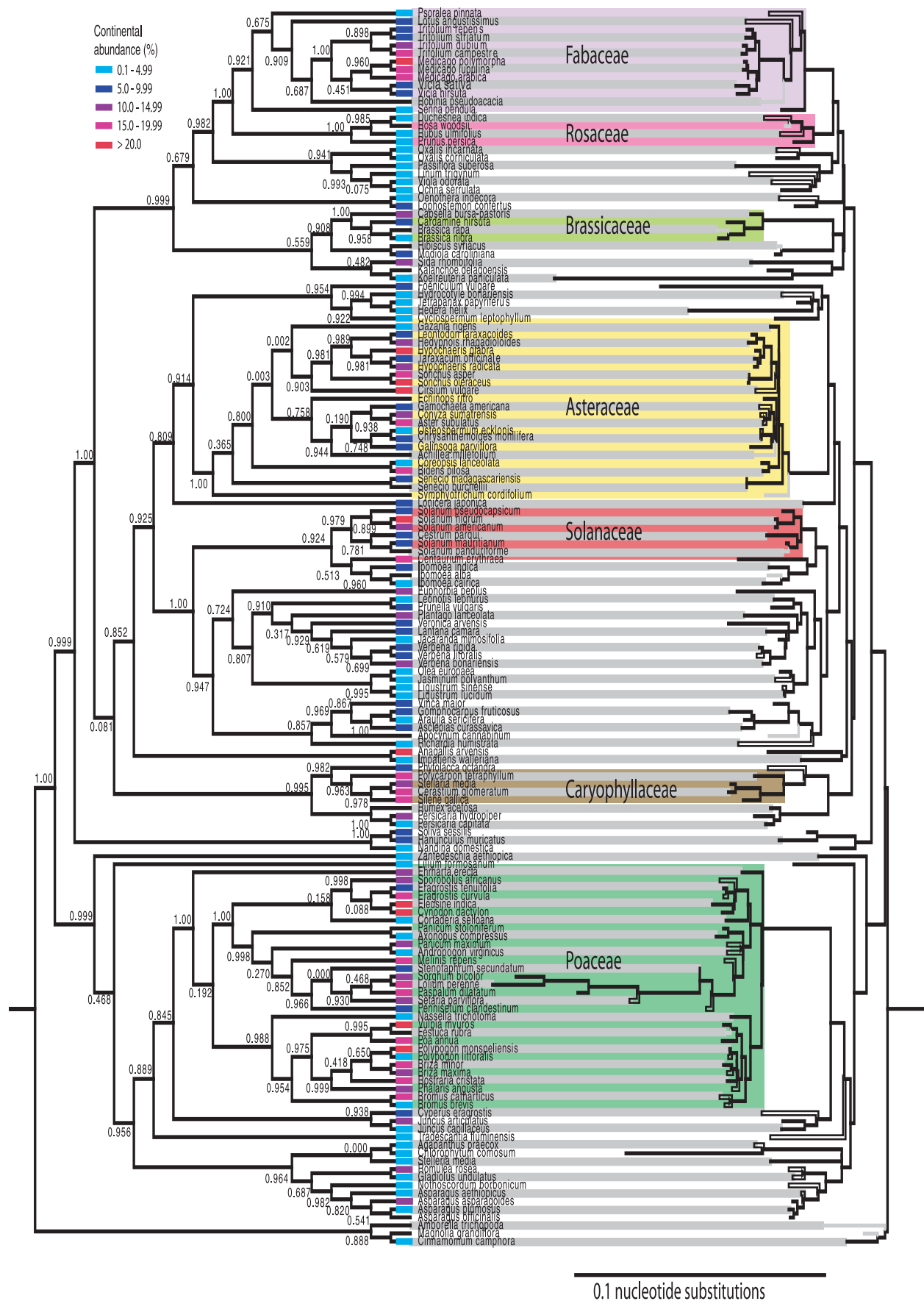
Data analyses

Both phylogeny (Newick) files were read into R 2.7.1 (<http://www.r-project.org>) using the ape 2.0–1 library (Paradis *et al.*, 2004). To test for a phylogenetic signal of occupancy measures we calculated Blomberg's *K* (Blomberg *et al.*, 2003), using code from the forthcoming R package 'Picante'. Blomberg's *K* is the ratio of the mean squared error of the occupancy data divided by the mean squared error of the data calculated from the phylogeny variance–covariance matrix, and this observed ratio is standardized by the ratio expected from Brownian evolution (Blomberg *et al.*, 2003). The mean squared error of the occupancy data is measured from a phylogenetically corrected mean, which is an estimated trait value at the root node of the tree (Garland *et al.*, 1999). The reason for standardizing the observed ratio by the expected ratio under Brownian evolution is that the observed ratio is affected by tree topology, and the standardization removes this confounding effect. Values near 0 indicate a lack of a phylogenetic signal, and values around 1 typify Brownian character evolution (i.e. a tendency for close relatives to be very similar). We calculated *K* for the continental and park occupancy. We assessed the significance of the *K*-values by randomly shuffling occupancy values among species 1000 times and calculated 95% confidence intervals (see Appendix S3 in Supporting Information for the R code).

For our dataset, arcsine-square root transformed continental occupancy was significantly affected by residence time ($F_{1,144} = 21.01$, $P < 0.0001$, $R^2 = 0.14$), whereas transformed regional occupancy was not ($F_{1,144} = 0.111$, $P = 0.7390$, $R^2 = 0.001$). Therefore we also examined the phylogenetic signal of continental occupancy standardized by residence time. In the previous paper (Hamilton *et al.*, 2005), we found that at the scale of the park, non-native occupancy was significantly related to residence time, but with much poorer explanatory power ($R^2 = 0.06$) than for continental occupancy ($R^2 = 0.33$). We did not have data on how long individual species have been in the park (i.e. residence time at the park scale), and although it may be unsurprising then that non-native plant occupancy in the park is poorly correlated with residence time at the continental scale, that does not mean that park occupancy patterns are not influenced by residence time (Mack *et al.*, 2000).

RESULTS

At both the continental and landscape scales, the most widespread species were found at about 50% of locales (Fig. 3). At the same time, the majority of species was quite less abundant, being found at fewer than 10% of locales. Furthermore, landscape and



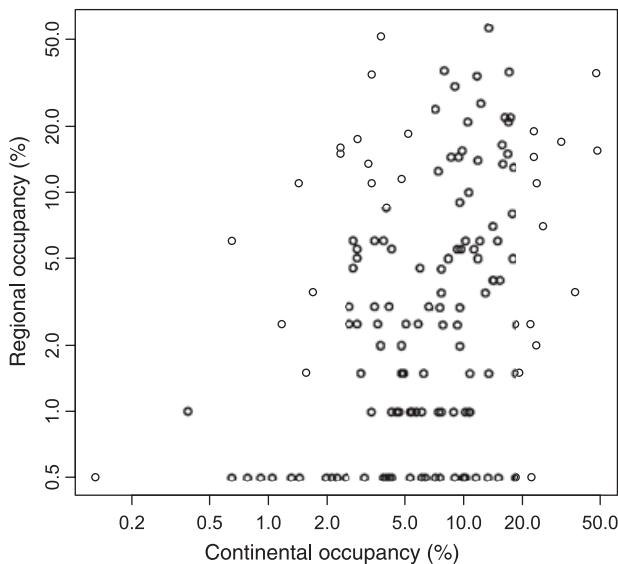


Figure 3 The relationship between regional and continental occupancy patterns. Regional occupancy is the proportion of 100 m² plots occupied and continental occupancy is the proportion of 100 km² grid cells occupied. Occupancy at these two scales is significantly positively correlated ($r = 0.381$, $P < 0.0001$).

continental occupancy patterns were significantly correlated, but much variation remained (Fig. 3). For example, the 39 most restricted species in the park (i.e. those found at just a single site, or in 0.5% of sites) had continental occupancies spanning the complete range of variation in continental occupancy. So although species widespread in the park tended to also be continentally widespread, species rare in the park were not necessarily continentally restricted.

We then asked if occupancy showed a phylogenetic signal at both the continental and Park scales using Blomberg's K and a randomization test. At the continental scale, occupancy showed a phylogenetic signal for both the supertree and molecular phylogenies ($K_{\text{super}} = 0.295$ and $K_{\text{mol}} = 0.004$) and were significantly greater than the random expectations ($\bar{K}_{\text{rand}} = 0.187$, 95% CI = 0.140–0.234, for the supertree and $\bar{K}_{\text{rand}} = 0.001$, 95% CI = 0.0007–0.002 for the molecular phylogeny) (see Fig. 4). Regardless of whether abundance at this scale was standardized by residence time or not, the results did not change.

At the Park scale, abundance had lower phylogenetic signals for both the supertree and molecular phylogenies ($K_{\text{super}} = 0.178$ and $K_{\text{mol}} = 0.001$) and were indistinguishable from randomized K -values ($\bar{K}_{\text{rand}} = 0.183$, 95% CI = 0.154–0.216, for the supertree and $\bar{K}_{\text{rand}} = 0.001$, 95% CI = 0.0008–0.002, for the molecular tree) (see Fig. 4).

The most continentally abundant invaders are not randomly distributed through the phylogeny, but rather strong phylogenetic

clustering (Fig. 2). The phylogenetically informed mean abundance (i.e. the ancestral node from parsimony trait reconstruction) is 5.176% of locales occupied. This mean was greatly exceeded in several clades including: the *Medicago* clade within the Fabaceae; the Asteraceae clade containing *Hypochoeris*, *Sonchus* and *Cirsium*; the Solanaceae; the Caryophyllaceae; and several clades within the Poaceae (Fig. 2).

DISCUSSION

Our findings show that at the scale of the Australian continent, the patterns of occupancy of non-native plant species have a strong phylogenetic signal. Phylogenetic clustering was found regardless of whether or not occupancy was corrected for residence time. Our results indicate that successful non-native plant invaders tend to be phylogenetically related to other successful invasive species. At the other end of the spectrum, non-invasive species also tend to be clustered within certain evolutionary clades. At the large spatial scale of the Australian continent, occupancy differences are most likely a reflection of differences in the pervasiveness of individual species niche or environmental requirements. Thus, our findings reveal that niche conservatism may explain correlated occupancy patterns among related exotic species. However, an alternative hypothesis for the phylogenetic patterns of non-native success is that human introduction effort reflects phylogenetically non-random preference patterns. That is, human valuation is likely to show phylogenetic patterning because society selects for certain traits that are likely to be shared among close relatives such as large flowers or forage value. Thus, human transport and rearing may supplement the establishment and spread of these valued species and their close relatives. Regardless of the habitats that filter species success, our results concord other studies that search for patterns at extremely large spatial and phylogenetic scales (e.g. Daehler, 1998; Pysek, 1998). Furthermore, these results give merit to the use of phylogenetic information for understanding modern ecological patterns of invasions (Wiens & Donoghue, 2004; Proches *et al.*, 2008).

It has been shown that at extremely small scales, communities tend to be phylogenetically overdispersed, likely because close relatives compete most intensely for shared resources (Webb, 2000; Webb *et al.*, 2002; Cavender-Bares *et al.*, 2006). Our results reinforce the emerging view that different and potentially opposing patterns of biological invasions can be observed at different spatial scales (Hamilton *et al.*, 2005; Cadotte, 2006, 2007). Although we may predict opposing phylogenetic co-occurrence patterns at two scale extremes, what happens at intermediate scales is an important question. Our results for the Australian dataset, at the scale of Royal National Park, show very little indication of clustering. This supports the view that at intermediate spatial scales, historical, dispersal and interaction

Figure 2 The molecular phylogeny for species (or their congeners) for which gene sequences were available. The tree on the left shows the topology with nodal support values (tip branch values have been removed for clarity). White branches outlined in black indicate species where congeneric sequences were used. Grey branches represent the 12 species added to provide gene coverage (see methods). The tree on the right shows branch length information. Tinting indicates major family-level clades. Coloured tips correspond to the percentage of locales occupied.

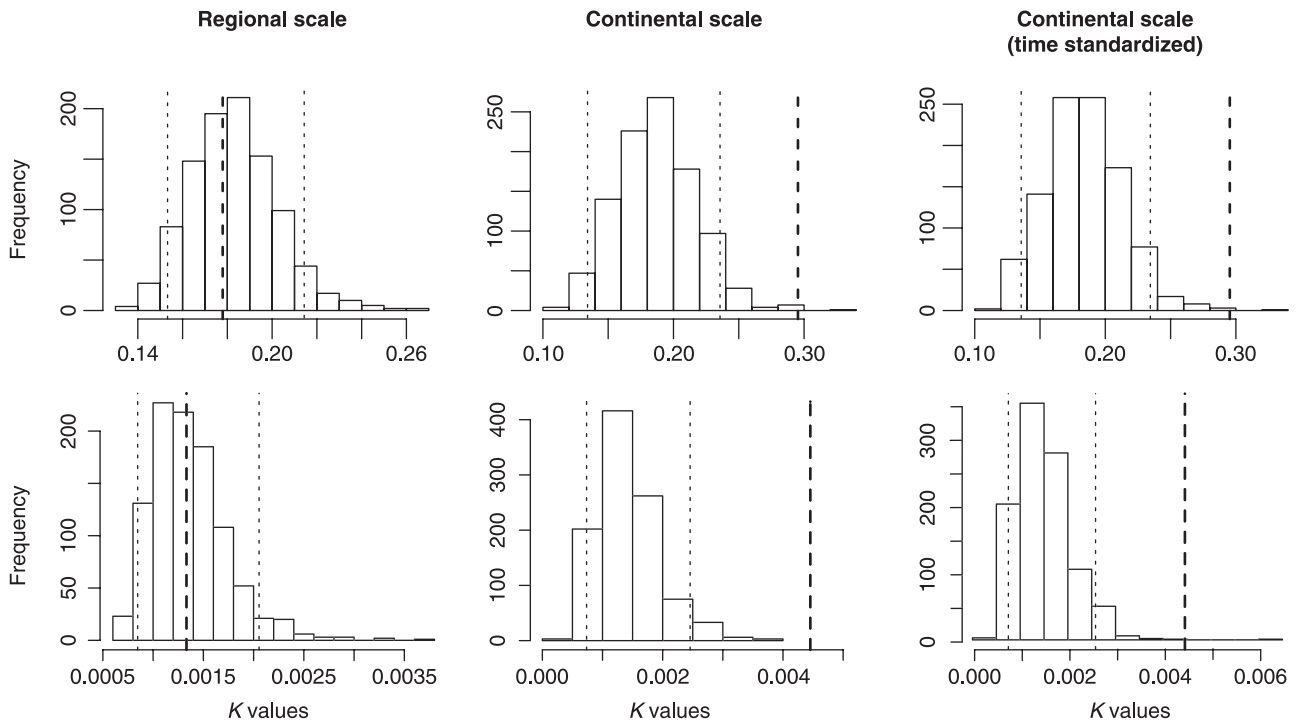


Figure 4 Values of Blomberg's K (dashed line) for regional abundance, continental abundance and time-standardized continental abundance. Histogram bars represent K -values based on 1000 randomizations. Continental abundances show significantly more phylogenetic signal than by random chance. The top row represents results from the supertree phylogeny, whereas the bottom row represents the molecular phylogeny. Dotted lines give the 95% confidence interval.

contingencies influence current species prevalence (Silvertown *et al.*, 2006a). Alternatively, the discrepancy in results between scales could be because at the scale of the park, which represents a natural ecosystem, successful species are those that do well in naturally assemble communities. Whereas at the scale of the continent, successful non-natives are those that have been selected by humans or pre-selected for success in human dominated landscapes.

Although our study did not compare the non-native clustering relative to native phylogenies, our results have some implications and suggest avenues for future research. We observed phylogenetically correlated large-scale non-native occupancy patterns, which could mean one of three things. First is that these non-natives are on average less related to natives than less successful non-natives (e.g. Strauss *et al.*, 2006), meaning they likely fill some unique niche. Second, they could be behaving phylogenetically idiosyncratically meaning that there are no consistent phylogenetic patterns (e.g. Lambdon & Hulme, 2006). Or finally, that successful non-native species are actually closely related to natives (e.g. Duncan & Williams, 2002) meaning that they fill similar successful niches and potentially have greater impacts on the native flora, than if they were phylogenetically unique.

Although our results potentially confirm recent thinking on niche conservatism, these results also inform our understanding and decision making concerning the potential threat from non-native plants. Authors have shown that phylogeny should matter for invasions (Mack, 2003; Strauss *et al.*, 2006). More importantly, however, evolutionary relatedness is important for management decisions. Being closely related to a known successful invader is

sometimes used in determining the potential risk represented by a species (Reichard & Hamilton, 1997; Pheloung *et al.*, 1999; Caley & Kuhnert, 2006). Such risk analyses evaluate risk through association via a congeneric 'weedy' species. Our analyses show that invasive species occupancy patterns are correlated with phylogenetic relatedness and some taxonomic patterns have emerged at the level of family. However, more research is needed to find out more accurately the actual levels of this phylogenetic correlation.

A crucial limitation for most phylogenetic analyses of ecological data is the availability of adequate phylogenies. Although the readily available angiosperm consensus tree (Davies *et al.*, 2004) is a terrific resource for analysing ecological patterns in large datasets, it does contain pervasive polytomies below the family level. A polytomy is the incomplete resolution of the phylogeny, resulting in the hypothesis that there were multiple simultaneous radiations from a single ancestral node. The presence of polytomies can limit inference and affect statistical tests (Purvis & Garland, 1993). We analysed phylogenetic signals from this supertree and a molecular phylogeny, which largely resolves these polytomies. Both phylogenies gave very similar results, indicating a strong phylogenetic signal at the continental scale and no detectable signal at the scale of the Park. Similarly, for other ecological patterns, recent analyses have revealed only minor explanatory differences between the supertree and fully resolved molecular phylogenies (Cadotte *et al.*, 2008).

Although it appears that for large-scale ecological patterns, the level of phylogenetic resolution may have a minor effect on our ability to detect phylogenetic signals, we recommend caution in

this interpretation. The polytomies in the supertree mean that we are limited in our ability to detect sub-familial phylogenetic patterns, which a molecular phylogeny resolves. However, the supertree does represent the best understanding of evolutionary patterns above the family level, whereas an ad hoc molecular phylogeny may not be as good a hypothesis at this level because of sensitivities to the taxa or genes sampled for analysis.

ACKNOWLEDGEMENTS

Steven Kembel kindly offered advice on using PHYLOCOM and provided us with the R script to calculate Bolmberg's K and MWC greatly benefited from discussions with Todd Oakley and T. Jonathan Davies. BRM warmly thanks John Ingram for his generosity in sharing his unpublished database of exotic plants in Australia and Megan Phillips for her assistance with data collection. BRM was supported by an ARC Discovery Grant (DP0879494). For MWC, this work was conducted while a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0553768), the University of California, Santa Barbara, and the State of California.

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Editor: John Wilson

SUPPORTING INFORMATION

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

Appendix S1 The species and genes used for the molecular phylogeny.

Appendix S2 The Newick phylogeny file.

Appendix S3 The R script for the analyses in this manuscript.

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