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LETTER

# Learning from failures: testing broad taxonomic hypotheses about plant naturalization

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## Abstract

Our understanding of broad taxonomic patterns of plant naturalizations is based entirely on observations of successful naturalizations. Omission of the failures, however, can introduce bias by conflating the probabilities of introduction and naturalization. Here, we use two comprehensive datasets of successful and failed plant naturalizations in New Zealand and Australia for a unique, flora-wide comparative test of several major invasion hypotheses. First, we show that some taxa are consistently more successful at naturalizing in these two countries, despite their environmental differences. Broad climatic origins helped to explain some of the differences in success rates in the two countries. We further show that species with native relatives were generally more successful in both countries, contrary to Darwin's naturalization hypothesis, but this effect was inconsistent among families across the two countries. Finally, we show that contrary to studies based on successful naturalizations only, islands need not be inherently more invasible than continents.

## Keywords

Darwin's naturalization hypothesis, island–continent invasion patterns, taxonomic patterns of naturalization.

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## INTRODUCTION

Only a fraction of species introduced to a new region become naturalized, establishing self-replacing populations (Williamson & Fitter 1996). Understanding the factors distinguishing the successes from the failures promises basic insights into how ecological communities are structured and guidance for predicting new invasions. For plants, most of this understanding is based on observations of the successful species because the failures – those species that are introduced but fail to naturalize – are typically unknown and often unknowable. Omission of the failures, however, risks biasing our understanding of the naturalization process by conflating the probabilities of introduction and naturalization (Simberloff 1986; Simberloff & Boecklen 1991; Simons 2003). Studies of vertebrates (Blackburn & Duncan 2001; Forsyth *et al.* 2004; Jeschke & Strayer 2005), invertebrates (Suarez *et al.* 2005) and small taxonomic subsets of plants (Mulvaney 2001; Gravuer *et al.* 2008; Dawson *et al.* 2009) have shown the importance of including naturalization failures.

General explanations for invasions are difficult to find, but broad taxonomic patterns have suggested several common hypotheses as useful starting points for understanding invasions. First, there appears to be a broad taxonomic bias to non-native floras, suggesting that some taxa are consistently more successful invaders (Daehler 1998; Pyšek 1998; Duncan & Williams 2002b). Taxa may be over-represented in non-native floras either due to phylogenetically correlated traits that aid naturalization, similarities in the invaded environments, or due to biased introduction effort. Although a number of traits have been associated with invasiveness in different contexts, such as plant height and vegetative growth capacity, universal patterns have been difficult to find (Pyšek & Richardson 2007). Because taxonomy, and more detailed phylogenies when available, may serve as integrative measures of ecological similarity, they may be more revealing of patterns across the whole flora than individual traits. Differences in introduction effort may also play an important role in shaping taxonomic patterns in invasion (Cassey *et al.* 2004; Lambdon *et al.* 2008). If some taxa are more frequently introduced (e.g. for agriculture or horticulture), this bias could be mistaken for greater invasiveness. Furthermore, similarities in invaded habitats across regions may contribute to a taxonomic bias towards taxa associated with those habitats.

Another common hypothesis about broad-scale taxonomic patterns of species naturalizations suggests that introduced species with relatives in the target region will be less successful due to increased competition and/or shared natural enemies. This hypothesis, now commonly referred to as Darwin's naturalization hypothesis, has enjoyed support from some observed patterns of successful naturalizations (reviewed by Proches *et al.* 2008), but a flora-wide test in New Zealand found the opposite relationship (Duncan & Williams 2002a). A positive correlation between relatedness and naturalization success could arise from shared adaptations among relatives to a region's climate, facilitative interspecific interactions and/or shared mutualists. One reason for conflicting results in different studies may be that the relationship depends on the spatial scale examined (Lambdon & Hulme 2006b; Diez *et al.* 2008). Nonetheless, the consistency of these relationships with related natives is unknown across broad geographic areas and taxonomic scope.

A third long-standing, broad-scale hypothesis is that island ecosystems are inherently more invasible than continents (Elton 1958). Islands tend to harbour more non-native species than continents both per unit area and as a proportion of total species richness (Lonsdale 1999). Hypotheses to explain this pattern tend to derive from the idea that islands offer reduced biotic resistance due to lower species richness or a more 'naive' native community (Denslow 2003; Daehler 2006; Pyšek & Richardson 2006). As with the other hypotheses, however, this tends to be supported by observations of successful naturalizations only (Lonsdale 1999) or limited taxonomic subsets (Gimeno *et al.* 2006). Tests that include failed naturalizations across a broad taxonomic range are lacking for plants.

In this study, we used uniquely comprehensive databases to evaluate these hypotheses about taxonomic patterns of plant naturalizations. Using flora-wide data on the successful and failed naturalizations on the microcontinental islands of New Zealand and the 29 times larger continental landmass of Australia, we asked: (i) whether some taxa (genera and families) are consistently more successful at naturalizing, despite the different range of environments found in these two countries; (ii) whether the positive relationship between naturalization and relatedness to natives, previously observed in New Zealand, holds for Australia as well, and if the strength and direction of the relationship are consistent for families in the two countries; and finally (iii) whether the islands of New Zealand are inherently more invasible than continental Australia. Together, these analyses offer the first flora-wide comparative test of these major hypotheses incorporating both failed and successful naturalizations.

## METHODS

### Databases

We were able to explore flora-wide patterns of introduction and naturalization in New Zealand and Australia due to the relatively recent European colonization of both countries, which coincided with a period in which botanists were actively accumulating introduction records. We compiled comparable databases for New Zealand and Australia that catalogue the introduced and naturalized plant species found in each country (Table 1). For New Zealand, we used a national database of 25 049 exotic plant species known to have been intentionally or accidentally introduced since 1840. This database, compiled from a variety of sources, has been updated from the 24 744 species used in Duncan & Williams (2002a), and used for a different analysis in Diez *et al.* (2008). Of the 25 049 species introduced, 2146 species have been recorded as successfully naturalizing. We use a comparable list of 28 866 species that have been introduced to Australia (Randall 2007), similarly compiled from a wide variety of historical records. For this study, we restricted analysis to species introduced from outside each country's borders, removing from the database native species

**Table 1** The numbers of native, introduced and naturalized plant species, genera and families in Australia and New Zealand

| | Australia | | | New Zealand | | | Shared (in both countries) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Species | Genera | Families | Species | Genera | Families | Species | | Genera | | Families | |
| Native | 15 822 | 2158 | 248 | 1915 | 369 | 111 | 247 | | 138* | | 65* | |
| Introduced | 28 866 | 4702 | 344 | 25049 | 3935 | 348 | 12927 | | 2663 | | 155 | |
| | | | | | | | Aus | NZ | Aus | NZ | Aus | NZ |
| Naturalized | 2741 | 1096 | 169 | 2136 | 894 | 174 | 1713 | 1617 | 807 | 746 | 152 | 155 |
| Naturalized/introduced | 0.09 | 0.23 | 0.49 | 0.09 | 0.23 | 0.50 | 0.13 | 0.13 | 0.30 | 0.28 | 0.98 | 1.00 |
| Naturalized/total richness | 0.15 | – | – | 0.53 | – | – | | | | | | |

Aus, Australia; NZ, New Zealand.

*The shared group contains only those species that were introduced to both countries. The number of genera and families are the number of genera and families of shared species, as opposed to the number of shared genera and families.

classified as naturalized outside their native range. Both the New Zealand and Australian databases continue to evolve as new species are discovered and deemed to have naturalized, but they represent our best current understanding. Nonetheless, they omit an unknown number of accidental introductions that were never detected. Lists of native species were obtained from the Allan Herbarium online Flora of New Zealand database (Moore & Edgar 1970; Allan 1982; Edgar & Connor 2000) and the Census of Australian Vascular Plants (Hnatiuk 1990). For each genus introduced to either New Zealand or Australia, its climatic origin was recorded from Mabberley (1997) as either: temperate, tropical or cosmopolitan (both temperate and tropical origins, but not necessarily more widespread). This coarse classification followed from what we believed was one of the major climatic differences between New Zealand and Australia, namely the presence of extensive (*c.* 42% of the landmass) tropical climates in Australia.

New Zealand and Australia offer a revealing island-continent case study because of a shared geological history and geographic proximity, but markedly different physical and biological environments. They also share a similar recent history of European colonization, which has meant that many of the same species have been introduced to both countries. Australia has roughly 29 times the landmass as New Zealand (7 741 220 and 268 680 km$^2$ respectively), and contains a larger diversity of habitats. Although they share similar temperate climate zones, Australia also has extensive areas of arid desert and moist tropical vegetation. New Zealand and Australia are separated by more than 1600 km of ocean. Current evidence suggests that much of New Zealand's landmass was submerged during the Oligocene (Landis *et al.* 2008), implying that New Zealand's native flora predominately arrived subsequently via long-distance dispersal (Pole 1994; Trewick *et al.* 2007). Thus, the New Zealand native flora was likely a product of a complex process of at least 25 million years of introductions, subsequent radiations, climatic shifts and extinctions. Although many New Zealand species may have originated in Australia, and some Australian species in New Zealand, vascular plant species endemism is high in both countries, suggesting differences in selection pressures and enough evolutionary time for divergence. At a generic level, the native New Zealand flora is now largely a cool temperate subset of the Australian flora (McGlone *et al.* 2001). The flora of Australia is broadly distributed according to moisture gradients (Burbidge 1960), whereas altitudinal temperature gradients are more dominant in New Zealand (Wardle 1991).

## Statistical methods

The probability of naturalization in each country was assessed in two ways: first, using all of the introduction data available for each country, and second, using only the shared species that were introduced to both countries (Table 1). In each case, a hierarchical Bayesian framework was used to account for non-independence of taxonomically grouped data at the genus and family levels (Harvey & Pagel 1991; Gelman & Hill 2007; McMahon & Diez 2007). The probability of naturalization was considered a *Bernoulli* process in which each introduced species $i$ had a probability of successful naturalization $p_i$. This probability was made conditional on the species' genus through a logit link function and genus level intercept logit($p_i$) = $\alpha_g$. These genus-level intercepts were nested within families using family-specific intercepts, $\alpha_f$, which were drawn from a normal distribution with overall mean, $\alpha_0$ and variance estimated from the data. A multilevel model was constructed for both New Zealand and Australia, allowing us to compare the probability of naturalization for each genus, family and overall. The relationships between the genus and family-level probabilities of naturalization in the two countries were estimated using reduced major axis regression to account for variability in both axes (Sokal & Rohlf 1981). We further asked whether broad climatic tolerances could help explain the relative performance of different taxa in Australia and New Zealand by including temperate/tropical/cosmopolitan origin as an explanatory variable at the genus level in the models.

The effect of native relatives on the probability of naturalization was tested by including the number of native congeners as a covariate in the models. The coefficient describing the effect of native congeners on the probability of naturalization was allowed to vary by family, thereby allowing for the possibility that those effects are family-specific. The family-level effects were modelled as random effects drawn from overall country-level coefficients.

The question of whether New Zealand is more invasible than Australia was assessed by recasting the question of invasibility as a series of more specific comparisons. First, using all species introduced to each country, we asked whether the overall probability of naturalization, $\alpha_0$, was higher in New Zealand than Australia. This is arguably the most direct and general test of whether naturalization success is different between countries. We then compared the probabilities of naturalizing across different families, $\alpha_f$, to determine whether more invasive families in one country tended also to be more invasive in the other. Third, we repeated the above analyses using only the subset of species introduced to both countries (Table 1). This should prevent any bias in naturalization rates among countries due simply to differences in which species were introduced.

Finally, we used these models to predict the probability that a new species will successfully naturalize within each family and overall (a species in a new family, treating family as a random effect). These probabilities were more conservative than estimates of observed rates, but predicting new events is the most direct approach to answering the question of interest: does the probability of naturalization for a new introduced species differ between countries? These predicted values were obtained by inserting a 'new' species with unknown genus and family into the model. The Markov chain Monte Carlo model fitting process then estimated the probability conditional on all parameter uncertainty in the model.

As Bayesian models, all parameters were given prior distributions, which in this case were noninformative to allow the data to drive estimation. The overall intercept $\alpha_0$ and regression coefficients were assigned *Normal* prior distributions with mean 0 and variance 1000, and variance terms at each level are given broad uniform priors on the standard deviation following Gelman (2006). Models were fitted using OpenBugs v2.10 (Thomas *et al.* 2006) called using the BRugs package from R 2.4.1 (R Development Core Team 2008) and run for between 70 000 and 100 000 iterations with burn-in periods of tens of thousands of iterations and thin rates of 10 to achieve convergence. Convergence was monitored using the Gelman–Rubin statistic and inspection of sample histories.

## RESULTS

The total numbers of plant species recorded as introduced and naturalized were comparable in New Zealand and Australia (Table 1). However, because there are over eight times more native species in Australia than New Zealand, naturalized species represented 53% of total plant species richness in New Zealand but only 15% in Australia. Slightly fewer than half of the species introduced to either country had been introduced to both countries. Although their ranking differed between the two countries, the 20 most successful families in each country also tended to be the most successful in the other country (Table 2), and occur on the list of most invasive families worldwide (Pyšek 1998). A few families ranking high on the global list but not ranking high in New Zealand or Australia include Papaveraceae, Oxalidaceae, Ranunculaceae and Convolvulaceae, despite being well-represented in the introduced flora (more

**Table 2** The 20 most successful plant families introduced to New Zealand, Australia and worldwide

| New Zealand | | | Australia | | | | | Worldwide (successes)* | |
|---|---|---|---|---|---|---|---|---|---|
| Family | No. species (nat/intro) | Proportion successful | Family | No. species (nat/intro) | Proportion successful | NZ | Aus | Family | Mean % |
| Juncaceae | 34/45 | 0.756 | Juncaceae | 25/41 | 0.61 | | | Papaveraceae | 1.2 |
| Poaceae | 256/562 | 0.456 | Amaranthaceae | 27/63 | 0.429 | ✔ | ✔ | Chenopodiaceae† | 0.67 |
| Cyperaceae | 44/105 | 0.419 | Cyperaceae | 57/146 | 0.39 | ✔ | ✔ | Amaranthaceae | 0.61 |
| Amaranthaceae | 22/62 | 0.355 | Poaceae | 355/1170 | 0.303 | ✔ | ✔ | Brassicaceae | 0.6 |
| **Solanaceae** | 59/188 | 0.314 | Brassicaceae | 88/292 | 0.301 | ✔ | ✔ | Polygonaceae | 0.59 |
| Polygonaceae | 35/122 | 0.287 | **Verbenaceae** | 25/87 | 0.287 | ✔ | ✔ | Gramineae | 0.58 |
| Onagraceae | 22/86 | 0.256 | **Solanaceae** | 65/255 | 0.255 | ✔ | ✔ | Juncaceae | 0.5 |
| Salicaceae | 25/106 | 0.236 | Caryophyllaceae | 63/269 | 0.234 | ✔ | ✔ | Geraniaceae | 0.49 |
| Malvaceae | 27/117 | 0.231 | Onagraceae | 27/118 | 0.229 | ✔ | ✔ | Caryophyllaceae | 0.48 |
| Apiaceae | 36/161 | 0.224 | Boraginaceae | 32/152 | 0.211 | ✔ | ✔ | Pinaceae | 0.39 |
| Brassicaceae | 75/386 | 0.194 | Salicaceae | 26/1 25 | 0.208 | ✔ | ✔ | Solanaceae | 0.38 |
| Caryophyllaceae | 52/293 | 0.177 | Polygonaceae | 28/136 | 0.206 | ✔ | ✔ | Onagraceae | 0.37 |
| Boraginaceae | 23/132 | 0.174 | Asteraceae | 265/1361 | 0.195 | | | Oxalidaceae | 0.36 |
| Asteraceae | 230/1334 | 0.172 | Malvaceae | 36/194 | 0.186 | ✔ | ✔ | Malvaceae | 0.35 |
| Rosaceae | 105/670 | 0.157 | Fabaceae | 289/1612 | 0.179 | | | Fumariaceae | 0.28 |
| **Lamiaceae** | 73/565 | 0.129 | Apiaceae | 31/203 | 0.153 | ✔ | ✔ | Rosaceae | 0.27 |
| Fabaceae | 138/1107 | 0.125 | **Euphorbiaceae** | 48/333 | 0.144 | | | Ranunculaceae | 0.24 |
| Scrophulariaceae | 57/466 | 0.122 | **Acanthaceae** | 29/218 | 0.133 | | | Convolvulaceae | 0.23 |
| **Pinaceae** | 22/201 | 0.109 | Rosaceae | 98/866 | 0.113 | ✔ | ✔ | Asteraceae | 0.22 |
| **Geraniaceae** | 22/252 | 0.0873 | Scrophulariaceae | 56/494 | 0.113 | ✔ | ✔ | Apiaceae | 0.21 |

In bold are those families not found in the top 20 list for the other country.

Nat, naturalized; intro, introduced; Aus, Australia; NZ, New Zealand.

✔ Check marks indicate whether the family is among the top 20 naturalized families in these two countries.

*Data from Pyšek 1998: 20 most invasive families measured as the average per cent of the total number of species in the family that is found invasive elsewhere.

†Chenopodiaceae placed in Amaranthaceae by Angiosperm Phylogeny Group (2003).

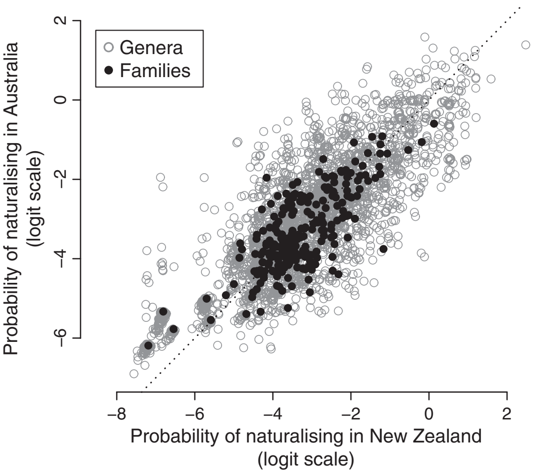

**Figure 1** Relationship between probabilities of naturalization at the family level (black dots) and genus level (grey circles) that have been introduced to both countries. The logit transformed probabilities of naturalization [$\ln(p/(1-p))$], where $p$ is the probability of naturalization, are shown to better visualize the low probabilities. Dashed 1 : 1 line shows the expectation if taxa had the same probability in each country. Those points where the logit probability in New Zealand is less than −6 belong to the families Orchidaceae, Bromeliaceae and Cactaceae.

than 59 species introduced of each family). The Juncaceae were the most successful in both countries by wide margins.

Genus and family-level probabilities of naturalization in the two countries were positively correlated (Fig. 1): the family-level relationship had a slope of 0.986 (and 95% CI 0.908, 1.06), and intercept of −0.0896 (−0.359, 0.179), whereas the genus level relationship had a slope of 0.884 (0.867, 0.900) and intercept of −0.226 (−0.290, −0.162). Removing the three families in Fig. 1 with logit probabilities less than −6.0 (Orchidaceae, Bromeliaceae and Cactaceae) yielded a slope for the generic relationship of 0.975 (0.952, 0.997). These relationships were similar for both the total species lists and the shared species pool. While these slope estimates are clearly positive and close to 1, their confidence intervals are likely to underestimate the variability in the data because each genus and family has associated uncertainty. The probability of naturalization also varied depending on the climatic origin of species (Table 3). In both countries, cosmopolitan genera were the most successful. Temperate genera naturalized more successfully than tropical genera in New Zealand, while there was no difference in Australia (Fig. 2).

Species from genera with native congeners generally had higher probabilities of naturalization in both countries (Fig. 3), although some families in each country had slightly negative relationships. The Asteraceae had the strongest negative effect of congeners in both countries, representing something of an outlier relative to other families (Fig. 3). The family-level estimates of the effect of relatedness were positively correlated between the two countries [Pearson's correlation = 0.51, RMA slope = 1.75 (1.41, 2.10)].

The overall probability of naturalization in New Zealand and Australia was not significantly different. Using all

**Table 3** Effects of climatic origin on species and genus level naturalization rates

| | Australia | | | New Zealand | | | Shared | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Temperate | Tropical | Both | Temperate | Tropical | Both | Temperate | | Tropical | | Both | |
| Introduced | 4841 | 4786 | 19012 | 4668 | 3156 | 17183 | 2609 | | 1545 | | 8772 | |
| | | | | | | | Aus | NZ | Aus | NZ | Aus | NZ |
| Naturalized | 443 | 265 | 2021 | 436 | 65 | 1634 | 291 | 370 | 128 | 47 | 1293 | 1200 |
| Proportion | 0.092 | **0.055** | ***0.106*** | 0.093 | **0.021** | ***0.095*** | 0.112 | 0.142 | **0.083** | **0.030** | 0.147 | 0.137 |
| | Australia | | | New Zealand | | | Shared | | | | | |
| *Genera* | Temperate | Tropical | Both | Temperate | Tropical | Both | Temperate | | Tropical | | Both | |
| Introduced | 1104 | 1179 | 2192 | 1032 | 741 | 2138 | 803 | | 590 | | 1670 | |
| | | | | | | | Aus | NZ | Aus | NZ | Aus | NZ |
| Naturalized | 248 | 154 | 686 | 253 | 52 | 588 | 188 | 245 | 118 | 46 | 617 | 539 |
| Proportion | 0.225 | **0.131** | ***0.313*** | 0.245 | **0.070** | ***0.275*** | 0.234 | 0.305 | **0.200** | **0.078** | 0.369 | 0.323 |

This is a summary of the raw data behind results in Fig. 2. In bold are the differences between the proportion of tropical taxa successfully naturalizing in the two countries. In bold italics are the highest rates of naturalization, for those taxa from both tropical and temperate origin (cosmopolitan).
Aus, Australia; NZ, New Zealand.

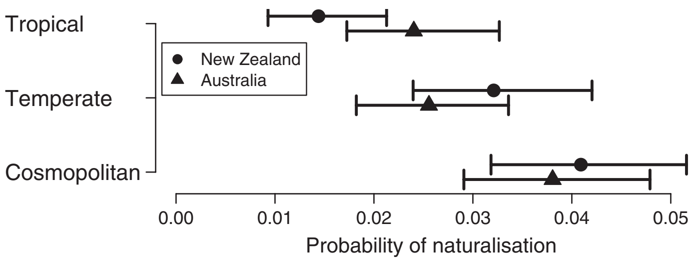

**Figure 2** Estimated probabilities of naturalization in New Zealand and Australia for plant species belonging to genera from different climatic regions. Points mark the mean probabilities in New Zealand (circles) and Australia (triangles), and the lines mark the 95% credible intervals.

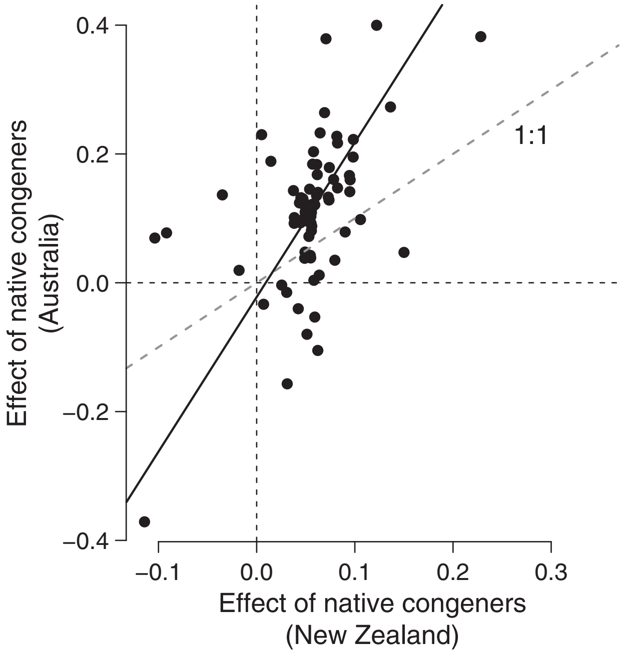

**Figure 3** Effects of native relatives on the probability of naturalization in Australia and New Zealand. Point represents the effects of native congeners on the probability of naturalizing for each family. Only those families in which at least one introduced species has native congeners in each country are included. The dashed 1 : 1 line shows the expectation if families showed the same response in each country, and the black solid line shows the RMA regression line (slope = 1.75). The one family with a negative value in both countries is the Asteraceae.

available data for each country, the overall probabilities of naturalization were 0.035 (with 95% credible interval 0.026, 0.044) and 0.032 (0.025, 0.040) for New Zealand and Australia respectively. Because means only differed by 0.003 and the credible intervals are widely overlapping, these probabilities cannot be considered different. Within only the shared species pool, we subtracted the probability of naturalization in Australia from that in New Zealand, and the difference was −0.0032 (−0.028, 0.019), again suggesting no difference between the countries.

The predicted probabilities of naturalization for a new species were also nearly identical in New Zealand and Australia. Using all available data for each country, the predicted probabilities for a new species in a new family were 0.099 (0.00086, 0.60) and 0.097 (0.00071, 0.59) for New Zealand and Australia respectively. The high variation compared to the estimated overall probabilities reported above reflects the variability among taxa. Within only the shared species pool, the difference between the overall predicted probability of naturalization in New Zealand and Australia was −0.013 (−0.68, 0.60), the broad overlap of zero again suggesting no difference between countries.

## DISCUSSION

Large-scale databases of non-native species distributions around the world play an increasingly important role in addressing questions in community ecology and invasion biology (Kolar & Lodge 2001; Cassey *et al.* 2005). Interpreting observed patterns of naturalized species can be difficult when introduction histories are unknown. Our findings in this study, using databases of introduced and naturalized plant species in New Zealand and Australia, support the hypotheses that some taxa are more likely to naturalize than others and that broad climatic tolerances help shape patterns of naturalization. However, the hypotheses that having native relatives may inhibit invasion and that islands are inherently more invasible than mainlands were not supported.

### Taxonomic patterns of invasion

The strong positive relationship between probability of naturalizing in New Zealand and Australia (Fig. 1) is striking, given the differences in bioclimatic conditions between the two countries. Some genera and families appear to be more successful than others once introduced. Although this is the first demonstration of such a widespread pattern that accounts for failed naturalizations, this result is consistent with studies based on successful naturalization events alone (Pyšek 1998). We suggest that this taxonomic pattern likely results from a combination of three interacting factors: shared traits among taxa that influence the probability of naturalization, habitat homogenization associated with human activity and greater introduction effort for some taxa.

For shared traits to be important in shaping taxonomic patterns, two conditions must be met: traits must be important in determining species' success and those traits must be taxonomically clustered. Limited progress has been made in identifying traits associated with plant invasion success (Kolar & Lodge 2001; Pyšek & Richardson 2007). Although case studies have highlighted the importance of certain traits (such as vegetative reproduction or height) in some regions, universal patterns have been difficult to discern (Hayes & Barry 2008). Nonetheless, the success of some weed risk assessment schemes suggests that combining trait information with knowledge of invasion success elsewhere can achieve substantial levels of predictability (Pheloung *et al.* 1999; Gordon *et al.* 2008). The second condition – that ecologically important traits are taxonomically or phylogenetically constrained – has garnered some support but remains an active area of research (Webb *et al.* 2002).

One way that traits can be important is by shaping climatic tolerance, which is often assumed to be a key filter determining whether species can naturalize (Rejmanek 2000). We found support for this in that introduced species from tropical genera were less likely to naturalize in New Zealand than those from temperate genera, matching New Zealand's temperate climate. There was no distinguishable difference between temperate and tropical genera in Australia, likely reflecting the wide climatic range across the continent. Cosmopolitan genera were the most successful in both countries suggesting that species from genera of broad climatic origin may be more successful than those from narrower origins. Our use of genus-level origins, categorized as temperate, tropical and cosmopolitan, is clearly a coarse measure of climatic tolerance. Although a more precise approach would be to determine more detailed climate matches at a species level, such data for the large number of species in this study are unavailable. It is possible, however, that climatic relationships are important only for some species (Maron 2006; Duncan *et al.* 2009; Hulme 2009a), such that general patterns emerge only at coarser scales (Pyšek 1998). Detailed climate matching is further complicated by the potential for significant niche shifts post-invasion (Broennimann *et al.* 2007).

Taxonomic patterns in naturalization success could also arise if similar habitats were invaded across regions and taxa tend to cluster within habitats. In both Australia and New Zealand, as in other parts of the world, humans have created many highly modified habitats, such as urban areas, parks and gardens, roadsides and wastelands, pastures, arable fields and numerous edge habitats, that share many attributes. These widespread, human-modified habitats can serve as invasion hotspots, often favouring introduced European species (e.g. Fridley 2008 in North America). Because related species tend to have similar biome associations (Crisp *et al.* 2009), it is possible that clustered relatedness in human-modified habitats may contribute to similar taxonomic patterns in the two countries.

Finally, taxonomic biases in naturalization success may result from variation in introduction effort (i.e. different propagule pressure among taxa). Particularly for regions such as New Zealand and Australia, which share a similar history of European colonization, culture and economic activity, the propagule pressures of taxa associated with agriculture, horticulture or trade are expected to be similar. Unfortunately, quantitative data on factors such as the number of introduction attempts or pathways available for spread are difficult to determine even for small taxonomic subgroups (Mulvaney 2001; Gravuer *et al.* 2008), and near impossible on a flora-wide basis. Another consequence of varying introduction effort among taxa is that the relative numbers of accidental versus intentional introductions will differ among taxa. Because records of failed accidental introductions are lacking, those taxa with relatively more accidental introductions will appear to be more successful at naturalizing. Together, these hidden influences of human activity caution against over-interpreting the biological significance of taxonomic correlations in naturalization success.

## Darwin's naturalization hypothesis

Opposing arguments have been made for why relatedness to the native community could either increase or decrease invasion success (Diez *et al.* 2008; Proches *et al.* 2008). Although species with native relatives may be pre-adapted to the new environment (Darwin 1859), novel species may be less subject to competition from similar species. We found that in both Australia and New Zealand, introduced species were more likely to naturalize when they had native congeners, consistent with previous results for New Zealand alone (Duncan & Williams 2002a). We further found that this relationship can vary among families in each country. For these two countries, therefore, it appears that the presence of native relatives may signal that an introduced species is pre-adapted to the region. This explanation is the most consistent with the large scale at which these database studies were conducted (Diez *et al.* 2008). It is possible that positive associations between native relatives and naturalization success could also arise out of facilitation between relatives or shared mutualists, but these mechanisms are better tested at small scales where interactions between species are more likely (Lambdon & Hulme 2006a).

Although the overall relationship is positive in both countries, and family-level relationships were positively correlated in the two countries, families showed quite different strengths of the relationship in New Zealand and Australia. We expected that the relationships would be consistent across regions because if the presence of native congeners signals a suitable environment for an introduced species, this should be the case in both countries. That this appears to be a weak relationship suggests either differences in the importance of species' adaptations in the different countries or different introduction processes in the two countries that decouple success from broad-scale suitability.

### Island–continental patterns of invasion

Per unit area and as a proportion of the total flora, New Zealand has more non-native, naturalized plant species than Australia, mirroring a broader island–continental pattern that forms the basis of the hypothesis that islands are inherently more invasible than continents (Elton 1958; Lonsdale 1999). This case study, however, supports the results from other studies that a greater level of invasion need not represent greater inherent 'invasibility' (Sol 2000; Blackburn & Duncan 2001; Jeschke & Strayer 2005; Chytry *et al.* 2008). Although different genera and families were better able to naturalize in either New Zealand or Australia, overall rates of naturalization and predicted probabilities for new species were not significantly different between the two countries. Thus, which place is more 'invasible' depends on the genus and family, but neither country appears inherently more susceptible to invasion. This conclusion is consistent with a synthetic concept of invasion that depends on characteristics of both the invader and invaded place (Richardson & Pyšek 2006).

The theoretical arguments and empirical evidence are in fact mixed about whether islands should be inherently more invasible. Most theoretical arguments are based on principles of biotic resistance – the lower species richness and higher endemicity on islands offer less resistance to invasion. The evidence for large-scale biotic resistance is lacking, however, with a generally positive relationship between native and exotic species richness at larger scales among islands (Sax & Gaines 2008). The hypotheses that higher endemicity or lack of functional groups on islands yields inherently less competitive island species (Simberloff 1995; Pyšek & Richardson 2006) also lack broad-scale evidence (but see Hulme 2004, for example, using observed successful naturalizations in Mediterranean islands). To the contrary, continents may be more invasible than islands if islands exhibit a reduced resource base, forcing native species to evolve greater competitive abilities (Grant 1968, Keast 1970), or if continents have a wider range of environments, providing more opportunities for naturalization. The often distinct abiotic environments of islands, owing to their isolation in space and time, may even confer advantages for well-adapted native species.

Of course, we cannot generalize from this example to all islands and continents, but one may also question whether such generalization will ever be fruitful if divorced from mechanisms. As Simberloff (1995) surmises, 'one must always speak of a specific island and mainland and also determine the relevant resource base empirically'. In addition to resources, it may be useful to account for differences in environmental heterogeneity. For example, the wide range of climatic conditions in Australia may increase the overall naturalization rate, offsetting other reasons for higher rates in New Zealand. The positive taxonomic correlation, however, suggests common mechanisms, whether human-driven or taxonomically correlated traits. Ultimately, differences in propagule pressure between islands and continents arising from differences in volume of external trade and connectedness through international transport networks (Hulme 2009b), or different land use patterns, may be more important than land form *per se*.

## SUMMARY

Overall, our results support an emerging picture of invasions driven by introduction processes, and modified by a suite of species traits that may interact with the invaded environment. Evaluating the relative importance of different mechanisms in shaping broad patterns of naturalization will continue to be difficult without knowledge of which species failed to naturalize. Detailed introduction histories have been accumulated for some plant taxa in some regions (e.g. Mulvaney 2001; Gravuer *et al.* 2008), but generally not a wide enough taxonomic range to allow broad-scale questions about naturalization success. Where widespread introduction data have been available, propagule pressure is a key determinant of plant invasion patterns (Krivánek *et al.* 2006; Dawson *et al.* 2009), but this remains the least understood determinant of plant invasion success (Pyšek & Richardson 2006; Gravuer *et al.* 2008). Once naturalized, species' spread and further invasion patterns can be investigated using comparative studies of species' performance (Lloret *et al.* 2005). Such studies should not be misinterpreted, however, as informing the probability that a newly introduced species will become invasive (Sol *et al.* 2008). For that, we must learn from failures.

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