



# Searching for phylogenetic pattern in biological invasions

Şerban Procheş<sup>1\*</sup>, John R. U. Wilson<sup>1</sup>, David M. Richardson<sup>1</sup> and Marcel Rejmánek<sup>2</sup>

<sup>1</sup>Centre for Invasion Biology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa, <sup>2</sup>Section of Ecology and Evolution, University of California, Davis, CA 95616, USA

## ABSTRACT

It has been suggested that alien species with close indigenous relatives in the introduced range may have reduced chances of successful establishment and invasion (Darwin's naturalization hypothesis). Studies trying to test this have in fact been addressing four different hypotheses, and the same data can support some while rejecting others. In this paper, we argue that the phylogenetic pattern will change depending on the spatial and phylogenetic scales considered. Expectations and observations from invasion biology and the study of natural communities are that at the spatial scale relevant to competitive interactions, closely related species will be spatially separated, whereas at the regional scale, species in the same genera or families will tend to co-occur more often than by chance. We also argue that patterns in the relatedness of indigenous and naturalized plants are dependent on the continental/island setting, spatial occupancy levels, and on the group of organisms under scrutiny. Understanding how these factors create a phylogenetic pattern in invasions will help us predict which groups are more likely to invade where, and should contribute to general ecological theory.

## Keywords

Biological invasions, competition, Darwin's naturalization hypothesis, invasibility, invasion biology, invasiveness, naturalization, niche, phylogenetic resolution, spatial scale.

\*Correspondence: Şerban Procheş, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa.  
E-mail: sproches@sun.ac.za

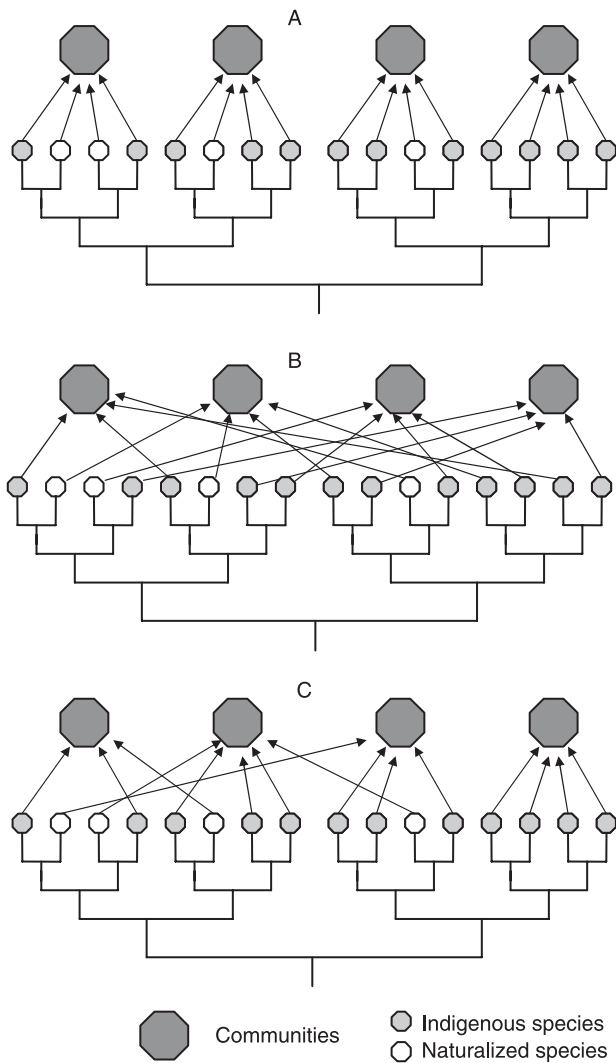
## DARWIN'S NATURALIZATION HYPOTHESIS

Biological invasions undoubtedly represent a major component of global change (D'Antonio & Vitousek, 1992; Vitousek *et al.*, 1997), and predicting which species can invade where would be essential in invasion management, and ultimately in limiting negative effects. One of the oldest ideas in ecology is that the composition of local assemblages can be used to predict which additional species can establish. Charles Darwin made some astute observations with regard to this. Based on the fact that indigenous species have traits making them compatible with local conditions, he posited that alien plant taxa were more likely to succeed where similar species were already present, since they would be more likely to share those same success-assuring traits. What he actually observed was the opposite: 'floras gain by naturalization, proportionally with the number of the native genera and species far more in new genera than in new species' (Darwin, 1859). More than half the genera containing plants naturalized in the US were genera new to this region, a fact already noted by Alphonse de Candolle a few years earlier (1855). Darwin placed these observations in the context of his discussion on the 'struggle

for existence' between similar organisms: 'As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera'. The notion that naturalization is more likely for aliens with no close relatives in the new land, due to lack of competitive exclusion, was given the name of 'Darwin's naturalization hypothesis' (Daehler, 2001) – although, strictly speaking, Darwin's original expectation was the opposite.

## RECENT ANALYSES

Recent work on the phylogenetic patterns in biological invasions has produced results that show phylogenetic clustering (non-native species are more closely related to native species than expected) as well as phylogenetic overdispersion (non-native species are less closely related to native species than expected) (cf. Cavender-Bares *et al.*, 2004; Fig. 1). But much of the discrepancy is attributable to the diversity of approaches adopted. Indeed, the precise predictions under scrutiny are not always comparable, as



**Figure 1** Phylogenetic patterns of species co-occurrence in natural communities range from clustering, through no obvious pattern, to overdispersion (Webb *et al.*, 2002). Naturalized species may show different patterns from those observed in the natural communities they colonize. Naturalized species may show clustering, overdispersion or no pattern with respect to other naturalized species, or may be more related to indigenous species, less related to indigenous species or as related to indigenous species as expected. Three of the possible combinations of patterns are presented here: A, phylogenetic clustering in both indigenous and naturalized species; B, overdispersion in both indigenous and naturalized species; C, phylogenetic clustering of indigenous species and possible overdispersion of naturalized species.

they depend on the method used to assess the connection between competition and taxonomic/phylogenetic patterns. While all of these predictions (summarized in Box 1) work together intuitively, they are distinct enough for some to be supported while others are rejected using the same data set (see the two hypotheses discussed by Duncan & Williams, 2002).

Data sets used in recent plant invasion studies have confirmed Darwin's observation that invasive species tend to increase the

number of genera in a flora relatively more than the number of species (Mack, 1996; Duncan & Williams, 2002; Lambdon & Hulme, 2006). However, such observations are not particularly meaningful, as they are relative to the invaded floras and not relative to the rest of the world (the species pool from which the species becoming naturalized actually come). More recent studies have therefore adjusted their expectations according to the total number of taxa worldwide, or in relevant regions of origin (Rejmánek, 1996, 1998; Daehler, 2001).

Duncan & Williams (2002) were able to go further. They had information on species introductions, and so could directly compare species that became naturalized with those that failed to naturalize. They showed that the proportion of introduced species that become naturalized is higher in New Zealand for plants that have indigenous congeners there than for those that don't. However, a similar study of fishes introduced to various parts of the world found no significant effects (Ricciardi & Mottiar, 2006).

It has to be noted, however, that genera (like all taxonomic levels) are artificial human-made categories, and their non-equivalence is bound to impact upon the results of all studies in which they are used as basic units. The latest step has been to replace taxa with a more objective continuous variable: phylogenetic relatedness. Strauss *et al.* (2006) examined the degree of relatedness between native and invasive grass species (Poaceae) in California, and showed that invasive grasses are more distantly related to indigenous ones than expected from random sampling of a familial super-tree. This confirmed previous observations, where Rejmánek (1996, 1998) found that European grasses from non-indigenous genera were over-represented in California's naturalized flora. The implication is that indigenous plants can indeed, at least in certain cases, prevent invasion by close relatives. However, there are reasons to believe that similar patterns may not be observed in other groups. Grass species are often dominant taxa, likely to compete against each other both above and below ground, and indeed exclude each other from entire regions. In other plant families, where most species are localized (e.g. rock-outcrop dwellers) with low dispersal abilities, the introduction of a few well-dispersed species may not meet with any resistance. Indeed, searching for patterns in such taxa at the spatial scale at which most data are available (i.e. landscape scale) is meaningless.


## LESSONS FROM NATURAL COMMUNITIES

Similar patterns are also evident in natural communities, but the processes producing such patterns may be significantly different. If, over evolutionary time, certain lineages have acquired key innovations that allow them to colonize specific environments, then we may expect closely related organisms to co-occur wherever the environment is suitable (Weiher & Keddy, 1995) (i.e. phylogenetic clustering). On the other hand, if closely related species are likely to compete against each other because of their shared features, then we would expect distantly related species to co-occur more often than expected by chance, since they can compartmentalize ecological space better into clear-cut niches (MacArthur & Levins, 1967) (i.e. phylogenetic overdispersion).


Box 1 Tests for phylogenetic patterns in invasions date back to the 1800s. However, different tests have been based on at least four different hypotheses. The observation that aliens are less likely to become naturalized where there are close indigenous relatives ('Darwin's naturalization hypothesis', suggesting phylogenetic overdispersion) was supported by some subsequent studies (+), but not by others, which found phylogenetic clustering (–), or no clear pattern (0). Non-indigenous species shown as white symbols, different shapes indicate distant taxa.

1. Compare the naturalised species with a random sample of the native species pool


de Candolle, 1855	+/-
Darwin, 1859	+
Mack, 1996	+/-
Duncan & Williams, 2002	+
Lambdon & Hulme, 2006	+



A. de Candolle

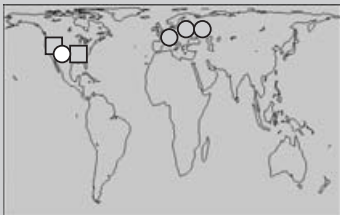


C. Darwin



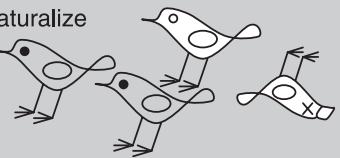
2. Compare the naturalized species with a random sample of the non-native species pool from anywhere in the world, or from the relevant area of origin

Rejmánek, 1996; 1998	+
Daehler, 2001	–



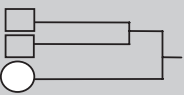
3. Compare introduced species that became naturalized with introduced species that failed to naturalize

Duncan & Williams, 2002	–
Lambdon & Hulme, 2006	0
Ricciardi & Mottiar, 2006	0



4. Compare the phylogenetic branch length added by the naturalized species to that added by a random sample

Strauss <i>et al.</i> , 2006	+
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It has been suggested that the two opposing hypotheses need not be mutually exclusive (Cavender-Bares *et al.*, 2006; Procheş *et al.*, 2006). Rather, they may be valid in the same system, but across different spatial scales and at different levels of phylogenetic resolution. At fine spatial scales (in relation to plant size), one can expect closely related organisms to occur in mutually exclusive patterns due to competitive interactions. At larger (regional) spatial scales, related species would be more likely to co-occur in the same biogeographical region as they tend to share broad environmental preferences, and are unlikely to be excluded by interspecific competition. For less closely related

species, the timing of their ancestral divergence may matter less. The separate lineages may have had enough chances to readjust their environmental preferences, but the shared evolutionary history could still dominate their broad-scale preferences. In this case they may show co-occurrence at both plot and regional spatial scales (see Prinzing *et al.*, 2001; Silvertown *et al.*, 2006).

Spatial scale and level of phylogenetic resolution should be important considerations when testing Darwin's naturalization hypothesis. Is it appropriate to look for competition effects in regional-scale data (Azovsky, 1996)? Newcomers can out-compete indigenous species, or may fail to establish because of the presence

of particular native taxa. In these cases, their establishment and failure will be noted in regional lists. Competition studies of recently introduced species show that aliens will indeed put severe competitive pressure on indigenous biota in some cases (Ricciardi *et al.*, 1998), whereas in other cases, long-term co-occurrence is likely at the regional scale, though not necessarily at the habitat scale (Livdahl & Willey, 1991). This would mean that although some patterns can be observed at the regional scale, analyses at finer scales may have more power. Recent studies looking for phylogenetic patterns at the plot scale (Procheş *et al.*, 2006), and alien–indigenous comparisons considering neighbouring plants (Vilà *et al.*, 2006) suggest that cross-scale approaches would be most useful.

## THE EMPTY NICHE

Many of the arguments surrounding phylogenetic patterns in both invasion biology and community ecology depend on the ideas of competition and niche. It is now widely agreed that species are far from interchangeable, and the recent popularity of neutralist theory (Hubbell, 2001) has been seriously questioned, both in natural communities (McGill *et al.*, 2006) and in biological invasions (Fargione *et al.*, 2003). The concept of ‘niche saturation’, although often criticized (e.g. Austin *et al.*, 1996), appears to be strongly supported by invasion biology on oceanic islands: there is little doubt that invasions are more likely to happen on islands where all indigenous biota come from a limited number of colonization events (Moulton & Pimm, 1986; Lonsdale, 1999; Mack, 2003). This may explain why one is likely to find clearer support for phylogenetic overdispersion on continents (Rejmánek, 1996, 1998; Strauss *et al.*, 2006), where resistance from indigenous species can be expected to be stronger than on islands (Daehler, 2001; Duncan & Williams, 2002). Even on continents, the regional absence of important lineages may facilitate invasion (Mack, 2003). For example, the lack of frost-resistant or fire-adapted indigenous trees has contributed to the rampant invasion of introduced pines in the warm temperate parts of southern Africa (Richardson & Cowling, 1992). Environments characterized by rapid extinction–recolonization dynamics (such as sand dunes and the open surface of water bodies) also function as temporary ‘vacant niches’, and are prone to invasion, particularly in the absence of natural enemies. If extinction episodes are related to herbivore action, then a newly introduced, enemy-free species may take advantage of the empty phase. In general, the traits allowing a species to fill in such an ‘empty niche’ are generally restricted to certain clades, and are therefore likely to be reflected in the phylogenetic pattern.

## THE WAY FORWARD

We have argued that phylogenetic patterns in biological invasions will change depending on the spatial and taxonomic scale as the different mechanistic processes operate at different scales (Swenson *et al.*, 2006). To gain further clarity on this we need analyses that cover multiple scales. In this section we set out a few recommendations for future work, with the provision that

meaningful results can only be obtained after testing against carefully considered null hypotheses.

Floras and lists of naturalized plants are now available for many regions. Comprehensive lists of all species introduced to a region are more difficult to compile (but see Imada *et al.* 2005). Where these are not available, lists of species commonly cultivated or kept can be used for the purposes discussed here. Lists at various spatial scales are also needed – from the complete regional list to local assemblages (e.g. phytosociological plots and pairs of closest neighbours for plants). At the fine scale, data sets exist that will provide a reasonable amount of replication for solid conclusions. However, the issue of spatial autocorrelation may become increasingly important in this context, and the mathematical background for dealing with both spatial and phylogenetic patterns is still a very active area of research (see Roxburgh & Chesson, 1998; Rangel *et al.*, 2006).

Another aspect that will need further attention is the precise nature of the competitive interactions between indigenous and alien plants. These need not represent direct competition for resources, but may be mediated by third parties, e.g. herbivores in the case of plants (Mack, 1996; Mitchell *et al.*, 2006). Understanding the relative importance of such complex and often case-specific interactions may be essential in assessing the generality of phylogenetic patterning in invasions.

It will also be interesting to explore what happens as invasions progress (as species move along the naturalization–invasion continuum *sensu* Richardson *et al.*, 2000). Species lists, at whatever scale, are snapshots whose accuracy, validity and usefulness change with climate, habitat modification, new introductions and with time. Key factors, such as the duration of time for which an alien species has been in the newly colonized region, the potential range it can reach and the pattern of introduction are likely to influence the probability that it will interact with indigenous relatives (Wilson *et al.*, 2007). In this same context, studies of changes in phylogenetic diversity during succession would be highly relevant.

The search for taxa that are particularly invasive worldwide has been under way for some time, in both plants and animals. Families with unusually high numbers of invasive species have been identified, but these are often families with higher introduction rates (e.g. bird families that include species popular as pets, and plant taxa from northern temperate regions moved by European settlers) (Daehler, 1998; Pyšek, 1998; Lockwood, 1999). While invasion success is largely idiosyncratic, certain traits have been associated with invasion success (e.g. reproductive traits in *Crotalaria*; Wu *et al.*, 2005). The phylogenetic position of present-day invaders offers little predictive power without understanding where and when in the phylogeny such key traits have appeared. Trait-minded phylogenetic analysis may become an important tool for predicting how fast and how far invasive species can spread. In this context, the search for phylogenetic pattern in invasion biology could find itself at the crossroads between bioclimatic modelling and trait mapping in phylogenies, both extremely dynamic fields with relevance to understanding past evolutionary history and predicting the effects of future global change.

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## BIOSKETCHES

**Şerban Procheş** is a post-doctoral researcher in the School of Biological and Conservation Sciences at the University of KwaZulu-Natal. He is interested in global and southern African biogeography, plant–insect interactions and community ecology.

**John Wilson** is a post-doctoral associate in the Centre for Invasion Biology at Stellenbosch University (<http://www.sun.ac.za/cib>). He focuses on ecological statistics, particularly as applied to plant invasions and biological control.

**Dave Richardson** is Professor of Ecology at the Centre for Invasion Biology, Stellenbosch University. He is interested in the determinants of diversity and distributions, particularly with reference to biological invasions.

**Marcel Rejmánek** is Professor of Ecology at the University of California Davis. His interests include succession, disturbance and the stability of biotic communities, with a special focus on biological invasions and the invasibility of ecosystems.

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