A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY REVIEW

Resolving Darwin's naturalization conundrum: a quest for evidence

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ABSTRACT

Aim The study of biological invasions has long considered species invasiveness and community invasibility as separate questions. Only recently, there is an increasing recognition that integrating these two questions offers new insights into the mechanisms of biological invasions. This recognition has renewed the interest in two long-standing and seemingly contradictory hypotheses proposed by Darwin: phylogenetic relatedness of invaders to native communities is predicted to promote naturalization because of appropriate niche-adaptation but is at the same time predicted to hamper naturalization because of niche overlap with native species. The latter is known as Darwin's naturalization hypothesis.

Location Global.

Methods and Results We review the studies that have tested these hypotheses and summarize their largely inconsistent outcomes. We argue that most of the inconsistency arises from discrepancies in the applied conceptual frameworks and analytical approaches and not from different model organisms and different ecological contexts. First, observed patterns and results can be seriously flawed by different spatial and phylogenetic scales, which do not equally reveal community assembly mechanisms. Second, different studies have used different metrics, which may test for different specific hypotheses. Thus, we propose a set of metrics derived from the alpha niche concept to measure invaders relatedness to native communities. Finally, approximating species niche differentiation from phylogenetic relatedness is not exempt of assumptions, and invasive species naturalization may result from various ecological mechanisms of biotic resistance that are not necessarily revealed by species phylogeny alone.

Main conclusions The quest for resolving the conundrum of Darwin's naturalization hypothesis will only be successful if appropriate scales, metrics and analytical tests are thoroughly considered. We give several recommendations and suggest, whenever possible, to use trait-based measurements of species dissimilarity as the most promising avenue to unravel the mechanisms driving alien species invasions.

Keywords

Alpha niche, biological invasions, community invasibility, community phylogenetics, ecological niche, environmental filtering, niche differentiation, null models, phylogenetic relatedness.

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INTRODUCTION

The rise in human transportation has lead to a substantial increase in species movements out of their native geographic ranges, ultimately resulting in biotic homogenization of ecosystems world-wide and dramatic changes in ecosystem functioning (Mooney & Hobbs, 2000; Thuiller, 2007). Understanding and predicting the spread and impact of invasive species thus have become central research objectives in fundamental and applied ecology (Nentwig, 2007; Walther

et al., 2009). In particular, invasion ecology has focussed on two questions: (1) which species traits make introduced species more likely to become invaders (Rejmánek, 1995; Thuiller *et al.*, 2006; Pyšek & Richardson, 2007)? and (2) why are some natural communities more prone to invasion than others (Davis *et al.*, 2000; Levine *et al.*, 2004; Tilman, 2004; Richardson *et al.*, 2005)?

Recently, there has been a renewed interest in long-standing hypotheses that merge the two questions by focusing on the phylogenetic relatedness between potential invaders and recipient communities (Fig. 1). Based on an original observation of De Candolle (1855), Darwin (Darwin, 1859), in *The origin of species*, hypothesized that immigrant species are more likely to naturalize when they belong to genera with no native species in the region. This hypothesis, termed 'Darwin's naturalization hypothesis' (Rejmánek, 1996), states that introduced species that are phylogenetically unrelated to local communities should be more successful because they can exploit unfilled ecological niches in native communities (Fig. 1). It implies niche differentiation and niche gap-filling from invaders to be the main drivers of invasion success. However, Darwin also recognized that immigrant species from native genera might have a better chance to naturalize because they share similar pre-adaptations to local environmental conditions with allied species. Following this line of argument, an increase in the phylogenetic relatedness between an introduced species and its recipient community increases its probability of invasion (Fig. 1). This implies that related species have similar environmental requirements and/or benefit from mutualistic or facilitative interspecific interactions because of their shared evolutionary history (Bruno *et al.*, 2003; Wiens & Graham, 2005). These two seemingly contra-

dicting hypotheses, i.e. that introduced species are more likely to naturalize when they are phylogenetically similar versus dissimilar to the native community, have both been originally proposed by Darwin (1859) and are therefore encapsulated under the term 'Darwin's naturalization conundrum' (Diez *et al.*, 2008). Both hypotheses make testable predictions: if species with non-overlapping niches in time or space are more likely to co-exist (Chase & Leibold, 2003), and if species niches have been conserved during evolutionary history, then successful invaders should exhibit a particular phylogenetic position relative to native communities.

A number of recent studies have tested these predictions with empirical data. They have in common that they have treated the two hypotheses as mutually exclusive (with the exception of Diez *et al.*, 2008 and Procheş *et al.*, 2008). However, few, if any, general patterns emerged (Table 1). Of course, the discrepancy between studies may partly be explained by different biological systems and environmental settings that may influence the relative importance of environmental filtering versus biotic interactions in driving community assembly. However, we argue that much of the inconsistency is ostensible and arises from discrepancies in the applied conceptual frameworks and analytical approaches. To our understanding, the main three points that have obscured a general understanding of community invasibility by the mean of species dissimilarity are a matter of spatial and phylogenetic scale, a matter of metric and null expectations and a matter of quantification of niche (dis)similarity. The application of a standard framework across different biological systems should ultimately allow us to assess whether Darwin's naturalization hypotheses can explain current patterns of biological invasions.
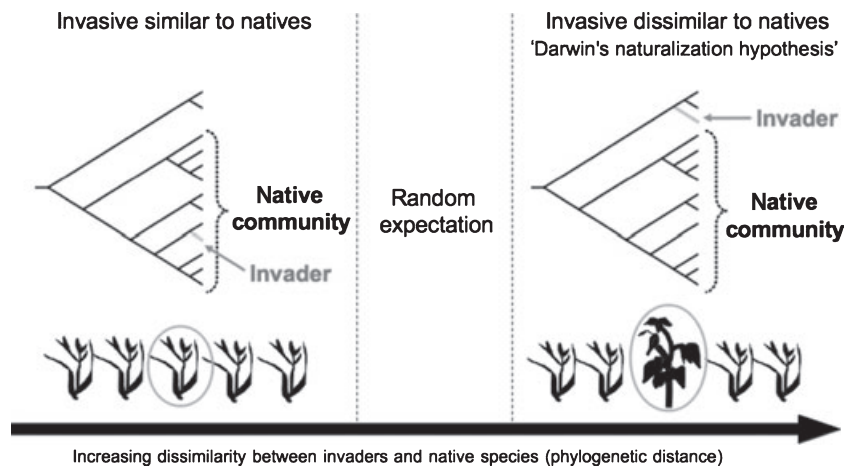

Figure 1 Conceptual diagram depicting classic hypotheses about species naturalizations and phylogenetic relatedness. Bold arrow at the bottom represents a gradient of species dissimilarity (phylogenetic distance) between invasive and native species. Left panel illustrates the hypothesis that invaders tend to be closely related to native than expected under random expectation. Right panel depicts the actual Darwin's naturalization hypothesis that immigrant species that phylogenetic unrelated to the native species will be more likely to naturalize because they may harbour different traits (invader represented with a different morphology) and possibly exploit distinct niches than native species. In both panel, the invasive species is represented in grey (grey branch in the phylogenetic tree or grey circle in the drawing of hypothetical community).

Table 1 Studies on phylogenetic patterns of invasions in a nutshell. Different studies build on different hypotheses (see Fig. 1) and therefore compare successful invaders with different potential species pools (cf. Box 1 in Procheş et al., 2008), use different spatial and phylogenetic scales, consider different additional information and utilize different statistical tests. The conclusions of the different studies vary greatly. Some promote the hypothesis that invaders are phylogenetic more dissimilar to natives than would be expected by chance (cf. 'Darwin's naturalization hypothesis', indicated by + in the conclusions' column), others contradicting this hypothesis (−), finding no clear pattern (0) or draw more detailed conclusions depending on different tested scales or species pools. [The following pseudo-code is used in the table to describe regression models: response variable ~ explanatory variable$_1$ + explanatory variable$_2$; GL(M)M: generalized linear (mixed) model].

Reference	Taxa	Spatial scale/spatial grain	Phylogenetic level	Statistic model (test)	Species pool	Additional information	Conclusion
Rejmánek (1996)	Plants (Gramineae, Compositae)	California/California	Genus	Number of naturalized species vs. species pool against number of species in European only vs. shared genera (contingency table, Chi-square test)	'Available' species from area of origin (Europe)		+
Daehler (2001)	Plants (Angiosperms)	Hawaii/Hawai	Family (pooling multiple genera)	Probability that naturalized species belongs to native genera (expectation under binomial distribution)	1. Global species of families with naturalized species 2. All naturalized (early vs. later naturalized) 3. All accidentally naturalized (early vs. later naturalized)		1., 2. and 3. −*
Duncan & Williams (2002)	Plants (Angiosperms, Gymnosperms)	New Zealand/ New Zealand	Genus	Naturalization rate (number of naturalized species as a proportion of pool) ~ 'genus having at least one native species (fixed effect) + family (random effect) (GLMM)	Genera containing introduced species		−
Ricciardi & Atkinson (2004)†	Aquatic systems (fishes, invertebrate, algae and vascular plants)	Global/sites	Genus	Number of high-impact invaders vs. number of low-impact invaders against number of invaders in genera shared vs. unshared with natives (meta-analysis of region-specific contingency tables, Fisher Exact tests)	All invaders		+
Lambdon & Hulme (2006)	Plants	Islands of the Mediterranean Basin/regional, local and habitat	Genus, family, order, subclass	Naturalization status (0/1) ~ presence of congeneric + species variables + island variables (GLM)	Common invaders	Species characteristics, island characteristics, habitat characteristics, introduction frequency	0‡

Table 1 (Continued)

Reference	Taxa	Spatial scale/spatial grain	Phylogenetic level	Statistic model (test)	Species pool	Additional information	Conclusion
Ricciardi & Mottiar (2006)	Fishes	Global/sites	Genus	Number of successful invaders vs. number of failed invaders against number of invaders in genera shared vs. unshared with natives (meta-analysis of region-specific contingency tables, Fisher Exact tests)	All introduced species		0
Strauss *et al.* (2006)†	Plants (Gramineae)	California/California	Phylogenetic supertree	Phylogenetic distance (mean distance to natives, distance to nearest native relative) ~ pest vs. non-pest invaders (*t*-test)	All naturalized	Area of origin	+
Diez *et al.* (2008)	Plants	Aukland region/ Aukland region, habitat	Genus	1. Probability of naturalization ~ number of native congenerics + abundance of native congenerics 2. Exotic abundance ~ number of native congenerics (region) + abundance of native congenerics (region) 3. Exotic abundance ~ number of native congenerics (habitat) + abundance of native congenerics (habitat) (hierarchical Bayesian framework)	All introduced species	Habitat characteristics, stages of invasion (naturalization and spread), naturalization period	1. – (numb.) + (abund.) 2. 0 (numb.) – (abund.) 3. 0 (numb.) + (abund.)
Diez *et al.* (2009)	Plants	Australia and New Zealand/ Australia and New Zealand, Australia vs. New Zealand	Family, genus	Probability of naturalization ~ presence of native congenerics + genus + climatic origin + family (random effect) (hierarchical Bayesian framework)	All introduced species	Climatic origin	–*

*The general patterns supported the hypothesis of phylogenetic similarity of invaders and natives (i.e. Darwin's naturalization hypothesis) but there were few families with no pattern or a pattern contradicting the hypothesis.

†These studies test whether the impact (and not the potential to invade) of an invader is driven by phylogenetic dissimilarity.

‡The authors concluded that identified patterns were marginal and prone to be generated through artefacts.

A MATTER OF SCALE

In our opinion, the apparent contradiction between the outcomes of different studies (Table 1) can be partly solved by a detailed examination of the conceptual framework. In particular, we suggest to explicitly consider different spatial and phylogenetic scales (Proches̗ et al., 2008) and to integrate theoretical understanding of neutral dynamics and niche-based dynamics (Chesson, 2000; Macdougall et al., 2009) when formulating predictions. We use the term spatial scale to refer to the spatial resolution at which invaders naturalization and spread is assessed (e.g. community plot, region, continent), and the term phylogenetic scale to refer to the aggregation level of a phylogenetic reconstruction or classification, that is whether species, genera or families form the leaves of the phylogenetic tree.

Spatial scale

Spatial scale and phylogenetic relatedness are the two key axes on which each working hypothesis makes unique testable predictions about ecological processes and resulting patterns. A point that has been little recognized, so far, is that these two axes should be considered together (Fig. 2). Under the
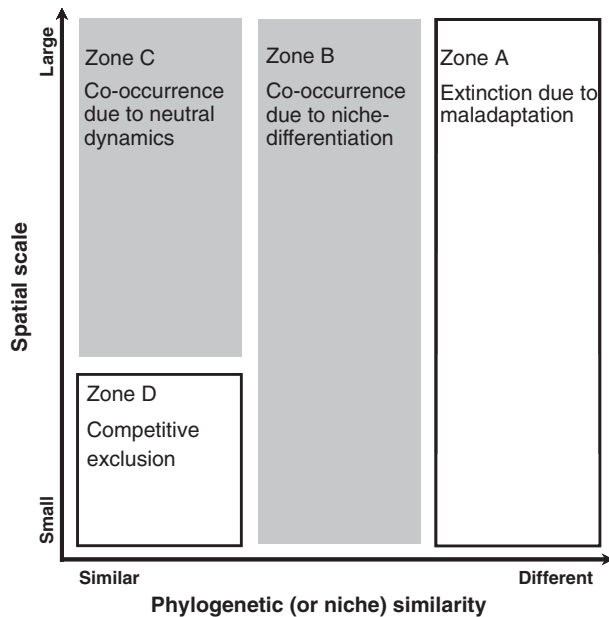

Figure 2 Different predictions for the outcome of species introduction or immigration according to the spatial scale of study and the phylogenetic (or functional) similarity between introduced species and the native species assemblage. Spatial scale corresponds to the spatial scale at which the process of naturalization is quantified, from 'small' (e.g. community or plot level) to 'large' (e.g. regional or continental level). Phylogenetic similarity is the phylogenetic 'distance' of the introduced species to the native species assemblage (see Table 2 for different metrics of phylogenetic relatedness). Each prediction refers to the ecological processes that are hypothesized to be important for one given combination of spatial scale and phylogenetic relatedness.

theoretical assumption of niche conservatism and no possible evolutionary convergence, invaders that are phylogenetically very dissimilar to native communities have an almost null probability of invasion success, no matter of the spatial scale (zone A, Fig. 2). In this case, invaders are assumed to occupy niches so dissimilar to natives that these niches will be virtually absent in the recipient region (e.g. phylogenetically conserved biome affinities (Crisp et al., 2009). In reality, niche conservatism may not be strict and trait or niche convergence may occur because of similar habitats in different regions and may lead to equally adapted but phylogenetically unrelated species. However, in average, phylogenetically very dissimilar invaders can be predicted to be maladapted and to have an increased chance to go extinct because of environmental filtering.

When invaders are phylogenetically moderately dissimilar to native communities, invasions have a much higher chance to be successful independently of the spatial scale (zone B, Fig. 2). In this case, invaders occupy slightly different niches than native species, and there is a good chance that the invader's niche exists in the recipient region. Phylogenetically distinct invaders are able to fill this niche and naturalize if either the niche is empty or the invader is able to outcompete native species occupying the niche (Proches̗ et al., 2008). This niche-filling process of moderately dissimilar invaders produces a phylogenetic pattern consistent with Darwin's naturalization hypothesis (Ricciardi & Atkinson, 2004; Strauss et al., 2006). When invaders are phylogenetically very similar to native communities, invasion success (comparable to processes of community assembly in general) should be highly dependent on spatial scale (Cavender-Bares et al., 2006; Swenson et al., 2006). At small spatial scales, invaders very similar to native species are less likely to coexist with native species because of competitive exclusion (Gause, 1934; Chesson, 2000) and/or clustering of common enemies such as herbivores and pathogens (Levine et al., 2004; Mitchell et al., 2006). At larger spatial scales, these invaders may be able to co-occur with phylogenetically related native species (at least over ecological time-spans) because of neutral processes and dispersal limitation (Chesson, 2000; Hubbell, 2001).

Thus, analyzing how phylogenetic relatedness between invaders and native species favours or hampers the process of invasion relates to the corpus of coexistence theory that has long explicitly considered the effects of spatial scale (Chesson, 2000). But this conceptual link with the field of biological invasions had been little emphasized so far (Macdougall et al., 2009). Spatial scale may vary from small scales at which species frequently interact and potentially compete (coexistence) to large spatial scales at which species only rarely interact because of dispersal limitations (co-occurrence). As originally pointed out by Lambdon & Hulme (2006) and Proches̗ et al. (2008), the quest for evidence for Darwin's naturalization hypothesis at very large scales is probably meaningless if it supposes to test the outcome of processes of local species interactions and niche gap-filling (Duncan & Williams, 2002; Ricciardi & Mottiar, 2006; Diez et al., 2008, 2009). We argue that, for the same reason, Darwin may have been wrong himself to suggest that

continental scale patterns of species naturalizations would be driven by biotic interactions between species. Patterns observable at large scales very unlikely reflect the outcome of species interactions but more likely reflect environmental filtering, regional heterogeneity and species dispersal abilities. Accordingly, studies performed at large spatial scales tend to confirm that introduced species naturalize when they have allied species in the native flora (Duncan & Williams, 2002; Diez *et al.*, 2009). Recent studies considering (even if only superficially) spatial scale showed that the scale alters the relationship between phylogenetic relatedness and invasion success (Lambdon & Hulme, 2006). In conclusion, when carefully considering the appropriate spatial scale, these two hypotheses are not conflicting but compatible in a common framework.

Phylogenetic scale

The outcome of tests for phylogenetic patterns of invasions also depends on the phylogenetic scale (Proches *et al.*, 2008). Species dissimilarities can be quantified from phylogenetic distances obtained from phylogenetic reconstructions or classifications, assuming that species relatedness captures (dis)similarity of ecological niches (discussed in the following text). Potential biases arising from the use of phylogenetic data to capture species ecological similarity are twofold.

First, as shown by studies of community assembly, phylogenetic scale can impact the observed signal of phylogenetic structure and therewith dissimilarity measures in natural communities (Hardy & Senterre, 2007). This can be illustrated by plotting – in an over-simplified example – a linear relationship between species niche similarity (represented across increasing aggregation levels) and the potential of species coexistence because of stabilizing mechanisms (Fig 3). If we measure differences between an invasive species and native species based on a small aggregation level (e.g. subspecies or species), we are in principal able to capture fine dissimilarities and therefore test for Darwin's naturalization hypothesis (Fig. 1). However, when measuring at higher aggregation levels (e.g. genera or family), we can only capture broad dissimilarities, which may preclude any accurate test of Darwin's naturalization hypothesis. For example, when niche differentiation is occurring only at lower aggregation levels (e.g. subspecies can invade, congeners not), an analysis conducted at higher levels (e.g. genus or family) will not detect any effect of phylogenetic relatedness although it is there. Instead, the effect of environmental filtering for broad adaptations would be prominent.

Different studies that have tested the effect of phylogenetic relatedness between introduced and native species on the outcome of invasions have used very different phylogenetic or taxonomic information (Table 1), ranging from very crude classification at the family level (e.g. Daehler, 2001) to more detailed classifications at the genus level (e.g. Diez *et al.*, 2008) and fully resolved phylogenies at the species level (e.g. Strauss *et al.*, 2006). As outlined earlier, this variation in the precision of phylogenetic information can strongly influence the
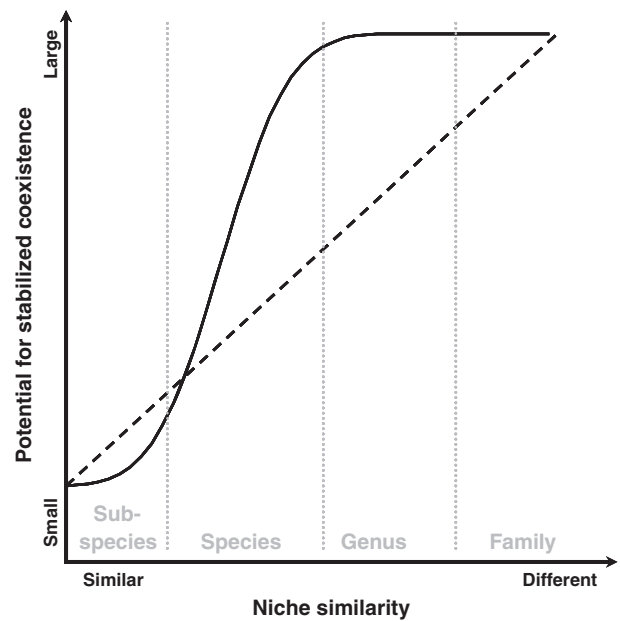

Figure 3 Diagram of possible relationship between species similarities, the phylogenetic scale similarities are measured at and the potential for stabilizing coexistence dynamics. Sketched are a linear (dashed line) and a step-wise relationship (continuous line) between similarity and coexistence. According to this diagram and the underlying assumptions, some tests for invasion patterns necessitate small phylogenetic scales (subspecies and species) because strong species similarity can only be observed at these scales and a positive relationship between similarity and coexistence potential may only occur at these scales (given a step-wise function).

observed patterns of phylogenetic relatedness and invasion success and precludes any generalization, a problem widely underestimated.

Second, the majority of studies so far implicitly assume a linear relationship between species similarity and the potential for stabilized coexistence, i.e. increasing dissimilarity at all phylogenetic scales is related to constantly increasing stabilized coexistence. Coexistence theory does not necessarily support this assumption. There may not be an advantage of further differentiation when species already occupy different niches. However, if we relax the over-simplified assumption of a linear relationship between similarity and coexistence, potential limitations related to the choice of a large phylogenetic scale become evident. For example, when assuming a more step-like relationship, studies measuring dissimilarities at higher phylogenetic scales (e.g. genus or family) will tend to find no relationship between similarity and invasion success (Fig. 3).

To conclude, Darwin's naturalization hypothesis explicitly refers to direct species interactions as driving mechanisms for coexistence patterns. With increasing spatial and phylogenetic scales, these direct interactions get less and less important, and it therefore is not relevant to test Darwin's naturalization hypothesis at large scales. If the chosen phylogenetic scale is too broad, we expect phylogenetic similarity to be unrelated to invasion success, i.e. patterns that do not differ from random null-models (Table 1).

A MATTER OF METRICS AND NULL MODELS

Darwin's naturalization conundrum is at least partly because of the diverse body of statistical metrics and models that have been utilized to test the specific predictions (Table 1), sometimes without clearly stating the underlying assumptions and limitations. We propose a set of metrics to quantify the similarity of introduced species to native communities that include both established and new approaches. We further propose a guideline for choosing the appropriate null model to test the 'significance' of the observed patterns and clarify the underlying theories of different commonly used null models.

Phylogeny versus taxonomy

With the exception of very few studies (e.g. Strauss *et al.*, 2006), the relatedness between introduced and native species has only been quantified on the basis of taxonomic classification (Table 1). Many studies have hypothesized that invasion was related to the number of congeneric species occurring in the same region or habitat (Daehler, 2001; Duncan & Williams, 2002; Lambdon & Hulme, 2006), or alternatively related to the mean abundance of congeneric species (Diez *et al.*, 2008). In theory, the number and abundance of species congeneric to the invader (Table 2) are poor predictors of introduced species relatedness to the native flora, as they both assume that all congeneric species are equally related and that this relatedness does not vary between genera (coarse phylogenetic scale). Not only some genera had such a history of diversification that even congeneric species can be very distantly related and exhibit very dissimilar traits or niches (e.g. Hughes & Eastwood, 2006). Also, different genera largely differ in their evolutionary age so that species relatedness cannot be considered constant between different genera. Although clearly practical, it is not a generally acceptable assumption to consider that all species of a given genus are equally similar (in terms of niches), especially when this genus is more than 50 million years old, has a world-wide distribution and counts several hundreds of species. Furthermore, such an approach makes the results highly sensitive to taxonomy biases that may exist between different clades or biogeographic regions.

For the above-mentioned shortcomings, we advocate that taxonomy-based metrics of species relatedness should be avoided. With the increasing availability of gene sequence data and computational methods for the reconstruction of phylogenies with several thousand of taxa (e.g. Smith *et al.*, 2009), it is now a very reasonable objective to obtain a molecular phylogenetic tree for any biogeographic study performed at large spatial scale. Supertrees can also be combined from several published phylogenies in order to produce the most up-to-date phylogenetic hypotheses (Bininda-Emonds *et al.*, 2002). However, current available sequences or phylogenetic data may not always allow obtaining a fully resolved phylogenetic tree, which may limit analytical power, as discussed earlier ('Phylogenetic scale' section). Alternatively, some studies have focused on specific taxa for which fully resolved phylogenies are available (e.g. Poaceae, Strauss *et al.*, 2006). Thus, independently of whether and how evolutionary relatedness captures niche similarity, we strongly recommend measuring invasive and native species relatedness from phylogenetic distances more than from taxonomic (mostly morphological) classifications.

The α niche conceptual framework

Surprisingly, previous tests of Darwin's naturalization hypothesis have failed to relate it to the concept of α niche. The α niche of a species is a community-scale measurement that quantifies the resources exploited by this species in comparison with the resources exploited by co-existing species (Pickett & Bazzaz, 1978). In other words, the α niche corresponds to a niche differentiation between a species and its community neighbours. It can thus be applied to functional and phylogenetic dissimilarities. For example, Ackerly & Cornwell (2007) define the α trait niche as the deviation for a given species trait from the community average trait value. Thus, if a species exhibits functional traits radically different from the rest of the community where it occurs, it is considered to occupy a different trait niche than co-occurring species, probably reflecting a different resource use (Stubbs & Wilson, 2004).

This α niche concept should be considered when testing whether naturalizations of introduced species are favoured or hampered by their dissimilarity to native communities, i.e. whether a species invasion success is driven by its potential α niche in recipient communities. Following the niche gap-filling, a potential invader with a high α niche has more chance to invade than an invader with a low α niche value. Indeed, because of expected lower niche overlap with high α niche, it is less likely to be under strong competitive pressure or to suffer from pathogens or herbivore attacks.

By analogy and in the absence of relevant functional traits, the α phylogenetic niche of a species could be estimated as the mean phylogenetic distance of the species to the rest of the community. The α phylogenetic niche can be estimated relative to the overall phylogenetic position in the community or just within a given family or guild depending on the objectives and hypotheses under investigations. The α phylogenetic niche is the optimal representation of phylogenetic similarity between an invasive species to the rest of the community allowing to properly test Darwin's hypotheses.

In conclusion, a species α niche can be computed from species dissimilarities matrices that are derived from a species phylogenetic tree or from a species classification based on functional traits. Testing Darwin's naturalization hypothesis implies testing how introduced species naturalizations are related to their α phylogenetic niche or their α trait niche.

Different metrics to describe invader relatedness to native communities

To measure an invader's relatedness to native communities, we propose to use the α niche concept together with a set of

Table 2 Overview of different metrics, which can be used to quantify the phylogenetic relatedness (or niche/functional similarity) between an immigrant species and the native species assemblage (community, regional species pool). Each metric is described, along with its assumptions. The word distance refers to a quantitative measurement of species similarity that can be equally obtained from a phylogenetic reconstruction or a multivariate analysis of functional traits or niche dimensions.

Measure	Description	Assumptions
NCS Number of congeneric species	Number of native species belonging to the same genus than the invader	All species within the same genus are equally related (and functionally similar), and this relatedness does not vary between genera. Each native species contribute equally to the overall biotic resistance (or facilitation) of the community
MACS Mean abundance of congeneric species	Mean abundance of native species belonging to the same genus than the invader	All species within the same genus are equally related (and functionally similar), and this relatedness does not vary between genera. The contribution of each species to the overall biotic resistance (or facilitation) of the community depends on its relative abundance
MDNS Mean distance to the native species	Mean distance between each native species and the invader	The similarity of species niches or traits is well captured by their phylogenetic distance Each native species contribute equally to the overall biotic resistance (or facilitation) of the community
WMDNS Weighted mean distance to the native species	Mean distance between each native species and the invader, weighted by the abundances of native species	The similarity of species niches or traits is well captured by their phylogenetic distance The contribution of each species to the overall biotic resistance (or facilitation) of the community depends on its relative abundance
DMANS Distance to the most abundant native species	Distance between the invader and the most abundant native species	The similarity of species niches or traits is well captured by their phylogenetic distance Community's biotic resistance (or facilitation) is driven by the most abundant native species
DNNS Distance to the nearest native species	Distance between the invader and the closest native species	The similarity of species niches or traits is well captured by their phylogenetic distance, but relationship between coexistence potential and phylogenetic distance is stepwise (See Fig. 3) Community's biotic resistance (or facilitation) is driven by the native species that is the closest relative (or the most functionally similar) to the invader

distance-based metrics that can be computed from dissimilarity matrices (phylogeny or trait-based) and data of community structure (Table 2). If based on a phylogenetic tree, interspecific distances can be calculated using branch length information or by counting the number of nodes separating pairs of species when branch length information is missing. The following four metrics are adapted from or equal to metrics that are commonly used to depict the phylogenetic structure of natural communities (Kembel & Hubbell, 2006; Hardy & Senterre, 2007). First, the MDNS metric – Mean Distance of the introduced species relative to the Native Species – is the most straightforward one as it is directly derived from Ackerly & Cornwell's definition of α niche (2007). Second, one may hypothesize that all native species will contribute to the overall biotic resistance (or facilitation) of the community according to their relative abundances, because they most likely interact with the invader for resource competition and are more likely to attract natural enemies (or conversely, pollinators). This motivates the use of the WMDNS metric – Weighted Mean Distance from the invader to all Native Species – in the community (which is analogous to the measure of functional and phylogenetic diversity including species relative abundances, De Bello *et al.*, 2009). Third, when a limited number of dominant species play a central ecological role (so-called structuring or keystone species), one may use the DMANS metric – Distance to the single Most Abundant Native Species – in the community. Fourth, the biotic resistance (or facilitation) of a given community could be mainly driven by the native species that is most closely related to the invader because this close relative will most likely compete with similar resources, attract harmful enemies or conversely attract adapted pollinators or dispersers. In this case, an appropriate metric would just be the DNNS – Distance of the invader to its Nearest Native Species – in the native community (Table 2).

Each stage of species naturalization and invasion of native communities is certainly driven by a unique set of ecological mechanisms, and different mechanisms of biotic resistance (resource competition, apparent competition through natural enemies) may show different degrees of frequency dependence. Hence, we suggest that all four metrics should generally be calculated and compared when testing patterns of phylogenetic similarity and invasion success of introduced species.

Choosing an appropriate null model

The proposed reference set of (phylogenetic or functional) similarity metrics can be used to relate similarity patterns – at

different spatial scales ranging from local sites to continents – to invasion measures such as probability of naturalization (Diez *et al.*, 2008), probability of becoming a pest (Strauss *et al.*, 2006) or regional spread measures (Lambdon & Hulme, 2006). However, on its own the reference set of similarity metrics only describes patterns and does not test to which extent observed patterns of phylogenetic dissimilarity are important for invasion success. To properly test this question, the observed patterns of dissimilarity must be compared with null models to confront observed patterns with random expectations. Again, comparative tests of observed patterns against null model patterns only make sense if applied at the appropriate scale and within a proper randomization scheme. We argue that for testing Darwin's naturalization hypothesis, patterns should be analyzed at the local community scale where individuals interact. Finally, the remaining challenge is to determine the appropriate null model.

In order to test whether species invasions are favoured by their phylogenetic relatedness to native species, the employed null model must break down the phylogenetic relationship between introduced and native species but not the phylogenetic relationships between native species of recipient communities. In short, the question tested by the null model has to be why is the invader and not another species of the available pool of potential invaders entering the recipient community? Here, we are interested with testing the mechanisms of a single event of the process of community assembly (i.e. the immigration of a non-native species), and the implementation of the randomization algorithm must not change the other evolutionary and ecological mechanisms that led to the current structure of native communities. Thus, the null model that seems the most appropriate to us keeps the structure of native communities unchanged and instead swaps the invader along the phylogenetic tree (or the functional dissimilarity matrix) containing all the species of a given species pool. This step is repeated *N* times to get a probability distribution of the metric (Table 2) under random conditions, and use the cumulative probability of the observed metric given this random distribution to test the observed value. Note that other null models might be applied, such as swapping each invader between all possible communities or only between communities where it could occur given its niche, or alternatively keeping the invader unchanged and swapping all co-occurring species. But these models seem less desirable as they would preclude the use of abundance-based metrics of α niche (Table 2) or require more elaborate tests (i.e. Hardy & Senterre, 2007).

According to the hypotheses and assumptions, different null models can be generated, i.e. different algorithms can be used to swap the invader identity along the phylogenetic tree (Procheș *et al.*, 2008). Probably, the simplest algorithm is to draw these 'null' invaders from the entire regional species pool. When working on large environmental gradients, the species pool used for randomization in each given community can be constrained by previously inferred species niches along these gradients. Also, 'null' invaders could be drawn from a pool of all species that have been introduced in the study region but never naturalized. This would test for analogous patterns (but at a lower spatial scale) than the ones tested in (Duncan & Williams, 2002; Diez *et al.*, 2008, 2009).

However, the general approach we outline here may have some pitfalls. First, community data generally contain *a posteriori* information of invasion. Nothing is known about the community structure before the invader's arrival, and especially it is unclear whether native species have been displaced by the invader. One way to get around this problem may be to compare the structure of invaded communities to the one of non-invaded communities occurring nearby or under similar environmental conditions. Second, a problem may arise when native communities are potentially invaded by more than one species. When testing for the patterns of one invasive species, the other invasive species occurring in the same communities could be considered 'native' for running the randomizations. However, this could lead to erroneous interpretations of observed patterns of species similarities, especially when closely related invaders have strong facilitative interactions with each other (Simberloff & Von Holle, 1999). This is a critical area of research, which needs further improvements given that multi-species invasions are not uncommon. Developing appropriate null-model for such complex situation where multi-species invasions occur in a given community is a pre-requisite for understanding invasion patterns in highly invaded regions.

A MATTER OF IDENTIFYING NICHE SIMILARITY

Species phylogenetic relatedness and niche similarity

An important assumption of both hypotheses in Darwin's naturalization conundrum, implicitly made by Darwin (1859) himself, is that species niches are conserved over time, so that closely related species should tend to have more similar niches than distantly related ones (Wiens & Graham, 2005). Although evidence for niche conservatism has been reported before (Peterson *et al.*, 1999; Prinzing *et al.*, 2001; Losos & Glor, 2003), the scope of niche conservatism may not be as broad as previously thought (Wiens & Graham, 2005; Losos, 2008). The observation that ecological niches have been very labile in the evolutionary history of some taxa, with some evolutionary convergences towards similar niches in distinct taxa, severely challenges the conventional assumption of niche conservatism (Pearman *et al.*, 2007). So far, no clear consensus has been reached about whether phylogenetic niche conservatism is an appropriate baseline assumption or not.

One potential limitation of Darwin's naturalization hypothesis lies in the assumption of most phylogeny-based approaches that phylogenetic relatedness equally predicts niche similarity for any pair of species, i.e. that the strength of phylogenetic niche conservatism is constant over the phylogenetic tree relating all study species. In fact, although this assumption has clear computational advantages, deviations from it may potentially distort the observed patterns.

Diez *et al.* (2009) nicely demonstrated that although there is an overall positive effect of congeneric species occurrence on the naturalization of introduced species, the effect estimate is highly variable between different families and even negative in a few families. This suggests that the strength of phylogenetic niche conservatism, hence the strength of biotic resistance mediated by native species related to the introduced species, is variable between different clades and that in certain clades, biotic resistance is driven by species that tend to be distantly related to the invader – probably because for evolutionary convergence. We thus recommend that, to be completely heuristic, further tests of Darwin's naturalization hypothesis should quantify the strength of phylogenetic niche conservatism (Blomberg *et al.*, 2003; Ackerly, 2009), to assess whether deviations from this assumption in certain clades will likely blur the observed patterns of phylogenetic relatedness and invasion success in introduced species.

The major restriction of using phylogenetic relatedness as a proxy of niche similarity is also the difficultly of relating it directly to the multidimensional nature of species niches. This has been viewed, originally, as a benefit given the premise that it is relatively easier to find pattern with a conglomerate measure like phylogeny than with individuals' traits, which can bring noisy information when intra-specific variability is too large (Albert *et al.*, 2010). However, the multidimensionality nature of species niches may lead to opposite processes resulting in random patterns from a phylogenetic point of view. For example, if pollination or other mutualistic interactions cause introduced species to naturalize where allied native species also occur (increased phylogenetic similarity of invaders and recipient communities), competition for resources or natural enemies may alternatively cause introduced species to naturalize in zones where they are phylogenetically novel (decreased phylogenetic similarity of invaders and recipient communities). This can cause the overall effect of phylogenetic relatedness on species naturalization to be very low or null, even though meaningful ecological mechanisms are currently at work. While we share the view that a phylogenetic approach to biological invasions is highly insightful, we foresee that, as large databases of species traits are being elaborated, a trait-based approach will be an interesting approach to unravel the ecological mechanisms that make introduced species naturalize and spread.

Phylogeny and mechanisms of biotic resistance

Alien species naturalizations are potentially driven by a combination of ecological mechanisms, but it is not known which mechanisms of biotic resistance are likely to be modulated by phylogenetic relatedness between alien and native species. Invasive species interfere with a number of ecological processes within recipient ecosystems, including resource capture (Levine *et al.*, 2003, 2004), interactions with natural enemies such as herbivores or pathogens (Keane & Crawley, 2002; Hawkes, 2007) and mutualistic interactions such as with pollinators, seed dispersers or mycorrhizas

(Klironomos, 2002; Memmot & Waser, 2002; Milton *et al.*, 2007; Vilà *et al.*, 2009). Here, we review the relevant empirical work to assess the evidence for phylogenetic signals on how biotic resistance is mediated by resource capture, herbivory and pollination.

The breadth of environmental tolerance of closely related invasive and native species has been little investigated with experimental approaches (Brock & Galen, 2005; Braby & Somero, 2006; Geng *et al.*, 2006; Priddis *et al.*, 2009), so evidence for differences between invasive and native relatives in their response to large environmental gradients is limited. However, a larger number of studies support the hypothesis that ecophysiological traits can differ between closely related invasive and native plant species (Schierenbeck & Marshall, 1993; Mc-Dowell, 2002; Deng *et al.*, 2004; Willson *et al.*, 2008). Nevertheless, at least partial niche differentiation between congeneric species can be expected, suggesting that competition for resources between closely related plants may not be as intense as previously thought. To our knowledge, only one study tried to relate experimental measurements of competitive interactions to species phylogenetic relatedness (Cahill *et al.*, 2008). Based on a meta-analysis of competitive experiments involving 142 plant species, the authors show that Darwin's statement that competition should be stronger among closely related species is not supported and suggest that the outcome of interspecific competitive interactions should be better captured by species functional traits. Moreover, further experimental work suggest that competitive hierarchy between invasive and closely related native species can be reversed depending on resource availability (Burns, 2004; Garcia-Serrano *et al.*, 2007). Therefore, if the naturalization of introduced species is mainly driven by interspecific competitions, empirical evidence suggests that the importance of phylogenetic relatedness to native communities will be limited.

However, there is much more evidence that trophic or antagonistic interactions are influenced by species phylogenetic relationships, such as in prey–predator, prey–parasitoid, plant–parasitic fungi systems (Cattin *et al.*, 2004; Ives & Godfray, 2006; Vacher *et al.*, 2008; Rezende *et al.*, 2009). According to Darwin's naturalization hypothesis, biotic resistance of plant communities facing new invaders is predicted to be higher when native communities include species that are closely related to the introduced species. When natural enemies such as herbivores and pathogens mediate biotic resistance, it should be expected that introduced species that are phylogenetic novel to a native community should suffer less antagonistic interactions and ultimately be more likely to naturalize or increase in abundance. This prediction has actually received much support in the recent years. A number of studies have demonstrated that woody and herbaceous aliens tend to suffer less from herbivores attacks (mostly insects) when they were less related to the native flora (based on phylogenetic or taxonomic information), and this pattern seemed consistent between different bioclimatic contexts (Brändle *et al.*, 2008; Brown & Zuefle, 2009; Burton Hill & Kotanen, 2009; Dawson *et al.*, 2009; Pearse & Hipp, 2009), but

see Zuefle *et al.* (2008). Indeed, it seems that, for plant invasions, there is empirical support for a mechanism of Darwin's naturalization mediated by insect herbivores.

There is also some indication in the literature that networks of mutualistic interactions can be phylogenetically structured like for instance plant–pollinators, plant–frugivores and plant–mycorrhizal networks (Maherali & Klironomos, 2007; Rezende *et al.*, 2007). Concerning plant–pollinator interactions, there is evidence that closely related species may tend to have at least partly overlapping pollinator fauna and that pollinators can switch from native plants to congeneric aliens (Brown *et al.*, 2002; Vanparys *et al.*, 2008; Kandori *et al.*, 2009; Takakura *et al.*, 2009). However, these studies suggest that the negative effects of competition for pollinator service tend to be asymmetrical, that is alien species tend to have more negative effects on the reproductive success of their native congeners than native species on their aliens. Indeed, a recent meta-analysis showed that the negative effect of aliens on native species reproduction is consistently high and that this effect decreases with phylogenetic relatedness between alien and native species (Morales & Traveset, 2009). It generally seems that pollination mechanisms will tend to facilitate the naturalization of introduced species when species related to the invader occur within native communities, which goes against the prediction of Darwin's naturalization hypothesis. However, a proper test of this would be to examine whether pollinator limitation on reproductive success of alien species is increased when native communities are more related to the alien species. To our knowledge, such a test has not been published so far.

To conclude, naturalization of introduced species may result from varied ecological mechanisms of biotic resistance that are not necessarily affected by phylogeny. Although more empirical data are clearly needed especially on animal taxa, it appears that plant competitive hierarchies are poorly affected by species phylogenetic relationships. However, trophic interactions are strongly phylogenetically structured, and there are compelling evidences that biotic resistance through natural enemies may be affected by phylogenetic relatedness between invaders and native communities. Thus, there is a risk of observing no significant pattern of phylogenetic relatedness and invasion success of alien species, while varied mechanisms of biotic resistance might be truly acting, but in opposite directions.

Towards a trait-based measurement of species niche similarity

As outlined earlier, phylogenetic relatedness will not always be a good predictor for the ecological mechanisms that favour biotic resistance of native communities to particular alien species. A very promising alternative would be to quantify species niche similarity through a set of functional traits (Violle *et al.*, 2007) depicting the strategy of species in terms of resource use and interspecific interactions. Such an approach ties with the original proposition of Elton (1958) that successful invaders should harbour original traits relative to

native communities. Although highly promising, this approach will also have its own problems, which may be potentially overcome. First, the same scale issues than the ones highlighted here will still apply with a trait-based approach (e.g. Fig 3). More importantly, the choice of a set of relevant traits, that adequately depicts different niche characteristics and mechanisms of biotic resistance and are measurable on large number of species ('soft traits') will certainly be critical (Violle *et al.*, 2007).

In a recent extensive review, Pyšek & Richardson (2007) analyzed multiple papers on plant invasions to determine whether there were any consistent sets of traits that could explain and predict a potential invader. However, these traits do not necessarily match with previously listed traits that would be useful to quantify species niches' overlaps (Violle *et al.*, 2007). Although the past literature had not reached a consensus so far, Pyšek & Richardson (2007) concluded that successful invaders possess some traits that unsuccessful invaders do not have. They also pleaded for explicitly filtering out the effects of residence time and other biases to reveal inherent trait-related determinants of invasibility. They suggested that the role of traits in the invasion process is to a very large extent invasion stage- and habitat-specific. Traits that confer an advantage at a given stage of the invasion process (naturalization, spread) and in a particular habitat may be neutral or even detrimental in another phase and/or a different habitat (Pyšek & Richardson, 2007). Quite surprisingly, few papers have built on this review to also investigate whether a successful invader exhibit different traits than the native communities, which allows the use of different resources and avoid competition ('niche gap-filling'), or exhibit more or less the same traits and directly compete for resources (Cahill *et al.*, 2008).

CONCLUSION AND TAKE HOME MESSAGE

Biological invasions offer a unique opportunity to study the ecological and evolutionary mechanisms that drive species range expansion, species interactions and species coexistence within communities (Tilman, 2004; Callaway & Maron, 2006; Sax *et al.*, 2007). Ecologists have long separately studied species invasiveness and community invasibility. However, it is now increasingly recognized that both invader characteristics and community properties must be jointly accounted for if we ultimately want to predict invasion risks in the future (Richardson & Pyšek, 2006).

The long lasting quest for understanding community invasibility and resolving Darwin's invasion conundrum might be resolved if appropriate scales, metrics and statistical tests are thoroughly applied. Several considerations must be rigorously taken into account:

• Appropriate spatial scale: large spatial and grain scales are not appropriate to test co-existence mechanisms as drivers of community invasibility. An approach combining different scales is ultimately the best practice to disentangle all possible mechanisms driving species naturalization and spread (Fig. 2)

• Appropriate phylogenetic scale: the use of family and genera or more generally taxonomy-based relatedness metrics is not meaningful and tainted of strong unrealistic assumptions. Molecular phylogenies or supertree-based phylogenies should be favoured.

• Appropriate metrics: the alpha niche concept offers a framework to link invader characteristics and community properties in order to test Darwin's naturalization hypotheses. We strongly suggest the use of four different metrics connected to this concept (Table 2).

• Appropriate null models: past studies have not always used consistent statistical tests and null model hypotheses. Null models and the related species pool used to randomize should be carefully chosen based on the ecological mechanisms meant to be tested.

• Appropriate measure of (dis)similarity: although phylogenetic relationships offer a solid background to test patterns of community invasibility, they are based on strong assumptions. We further suggest that, when available, functional traits related to resource acquisition and biotic interactions should also be considered in the quantification of the dissimilarity between invaders and native communities. Ultimately, measurement of functional relatedness via the alpha niche concept should be more heuristic than measurements of phylogenetic relatedness.

The proper application of these above-mentioned criteria should foster the understanding of community invasibility and should generate comparable results from empirical tests of Darwin's naturalization hypothesis.

ACKNOWLEDGEMENTS

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BIOSKETCH

The EMABIO's team (Evolution, Modelling and Analysis of BIOdiversity) led by **Wilfried Thuiller** focuses at revealing the evolutionary mechanisms that have generated extant biodiversity and its spatial patterns, especially climatic niche evolution and its effect on species diversification. The EMABIO's team also aims to address the mechanisms governing the assembly of biotic communities, such as the genetic effects of keystone species on plant and microbial communities, but also the effects of dispersal limitation, environmental filtering, and resource competition. Finally, the EMABIO's team proposes new modelling tools and generate biodiversity assessments at various spatial scales (continental, national and regional).

Author contributions: All authors conceived the ideas and the structure of the paper. W.T. and S.L. led the writing.

Editor: David Richardson