

Review

Where we've been and where we're going: the importance of source communities in predicting establishment success from phylogenetic relationships

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The last two decades have seen growing use of phylogenetic patterns to test hypotheses predicting the success of introduced species. Nearly all of these tests have focused on hypotheses pertaining to phylogenetic relatedness between introduced species and those of the recipient community, largely neglecting hypotheses regarding phylogenetic relationships in the source region. We synthesize hypotheses regarding how phylogenetic relationships of both recipient and source regions together influence establishment success. We also detail how best to account for differences in source communities within phylogenetic frameworks of invasion. Existing studies have predominantly focused on the environmental filtering and competition-relatedness hypotheses, which deal with relatedness to the recipient community. We discuss how these recipient–region hypotheses can be integrated with three hypotheses focused on the relatedness between an introduced species and the source community in which it originated: the evolutionary imbalance, universal tradeoff and competitive constraint hypotheses. We detail important issues that arise when testing alternative hypotheses and interpreting results. We highlight a lack of tests of synthetic phylogenetic hypotheses including both the source and recipient community phylogenetic structure, as well as important covariates such as propagule pressure. Such synthetic tests may be valuable for identifying general phylogenetic patterns in establishment success, predicting future invasions, and for stimulating further exploration of the underlying mechanisms of invasibility. We conclude with recommendations for future studies that use phylogenetic relationships to predict invasions: including source and recipient communities, using complete phylogenies and accounting for phylogenetic uncertainty, considering multiple stages of invasion and conducting analyses across spatial and phylogenetic scales where possible.

Keywords: community phylogenetics, competition-relatedness, ecophylogenetics, environmental filtering, establishment, evolutionary imbalance, species invasions



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Introduction

As the human society has become increasingly interconnected there has been a concurrent increase in the transport of species beyond their native ranges (Jeschke and Strayer 2005, Seebens et al. 2017). A subset of these species has become established, persisting and reproducing within new regions. A portion of these established species have become ‘invasive’, spreading beyond the location of initial introduction to the detriment of the native community (Williamson and Fitter 1996, Kolar and Lodge 2001, Jeschke and Strayer 2005), causing major ecological and economic impacts (Pimentel et al. 2005, Vilà et al. 2010). The process of invasion is thus often conceptualized as a series of consecutive stages (transport, introduction, establishment and spread), in which a species can either succeed or fail at each stage (Blackburn et al. 2009a) and where the ecological processes that determine the outcome at each stage may differ (Lambdon 2008, Cadotte et al. 2009, Schaefer et al. 2011, Abellán et al. 2016). The question of whether establishment is predictable has naturally received considerable attention (Elton 1958, Vermeij 1996, Davis et al. 2001, Devin and Beisel 2007, Hayes and Barry 2008, Blackburn et al. 2009a, Lockwood et al. 2009, van Wilgen and Richardson 2012, Kempel et al. 2013). Despite a growing literature of clade-specific studies on traits that may increase success (Forsyth et al. 2004, Blackburn et al. 2009b, Kempel et al. 2013, Arndt and Schembri 2015, Mahoney et al. 2015, Peoples and Goforth 2017), few general correlates of establishment or invasion success have been found (Hayes and Barry 2008), with perhaps the most notable being propagule pressure (Blackburn et al. 2015). Due to this lack of general predictors of invasion success there is a growing interest in using the phylogenetic distance between introduced

and native species to predict the success of introductions (Strauss et al. 2006, Thuiller et al. 2010, Van Wilgen and Richardson 2011, Violle et al. 2011, Maitner et al. 2012, van Wilgen and Richardson 2012, reviewed by Ma et al. 2016). This approach rests on the assumption that closely-related species are similar in their competitive niches and environmental requirements, such that phylogenetic relatedness will predict ecological similarity and the impact of that similarity on establishment success (Webb 2000, Wiens et al. 2010).

Where we’ve been

Studies that use phylogenetic patterns to understand biological invasions have largely focused on testing two alternative hypotheses originally posited by Darwin (1859; Table 1): the competition–relatedness hypothesis (also known as Darwin’s naturalization hypothesis; Rejmánek 1996) and the environmental filtering hypothesis (also known as the pre-adaptation hypothesis; Ricciardi and Mottiar 2006). The competition-relatedness hypothesis assumes that stabilizing niche differences increase with phylogenetic distance, leading to increased competition and reduced establishment success among close relatives (Darwin 1859). Conversely, the environmental filtering hypothesis posits that differences in environmental tolerances increase with phylogenetic distance (Webb 2000). As such, introduced species that are closely-related to the species within a recipient community will most likely have the traits necessary to persist there (Darwin 1859). Darwin conducted the first test of these hypotheses, finding evidence in support of the competition–relatedness hypothesis (increased establishment success among species more

Table 1. Summary of hypotheses predicting establishment success from phylogenetic relationships.

	Hypothesis	Phylogenetic predictions	Hypothesized mechanisms	Citation
Recipient range	Environmental filtering (EFH, pre-adaptation)	Species closely-related to recipient community are more successful	• Shared environmental tolerances • Shared mutualists	• Darwin 1859 • Ricciardi and Mottiar 2006
	Competition-relatedness (CRH, Darwin’s naturalization)	Species distantly-related to recipient community are more successful	• Reduced competitive exclusion • Avoid shared natural enemies	• Darwin 1859 • Rejmánek 1996
Source range	Evolutionary imbalance (EIH, biogeographic superiority)	Species from regions with many/close relatives are more successful	• Increased phenotypic optimization due to high competition/apparent competition • Longer exposure to selection in a given environment • Competitive superiority	• Darwin 1859 • Fridley and Sax 2014
	Universal tradeoff (UTH)	Success is independent of source community phylogenetic structure	• Universal constraints limit species to a common tradeoff surface	• Niklas 1997 • Marks and Lechowicz 2006 • Tilman 2011
	Competitive constraint (CCH)	Species from regions with few/distant relatives are more successful	• Competition and/or apparent competition constrain adaptation	• de Mazancourt et al. 2008 • Meyer and Kassen 2007 • Wilson 2014

distantly related to the community). Since Darwin, these competing hypotheses have been tested across numerous taxa, regions and stages of the invasion process, using different metrics and methodologies (Daehler 2001, Duncan and Williams 2002, Ricciardi and Mottiar 2006, Strauss et al. 2006, Thuiller et al. 2010, Maitner et al. 2012, van Wilgen and Richardson 2012, Ma et al. 2016). However, reviews and meta analyses of such studies have found conflicting support for these two hypotheses, and the efficacy of predictive phylogenetic frameworks has yet to be demonstrated broadly (Procheş et al. 2007, Thuiller et al. 2010, Jones et al. 2013, Ma et al. 2016, Cadotte et al. 2018).

Thus, the approach of using relatedness as a proxy for ecological similarity has become the subject of active debate in the recent literature. Under modern coexistence theory (Fig. 2; Chesson 2000), species coexistence is dependent on the relative magnitude of stabilizing niche differences and species average fitness differences. Stabilizing niche differences promote coexistence by increasing intraspecific competition relative to interspecific competition. Conversely, species average fitness differences hinder coexistence by favoring one species to the exclusion of others. Mayfield and Levine point out that under modern coexistence theory, predicted patterns of coexistence are dependent on both the relative strengths of stabilizing niche differences and species average fitness differences and their correlations with phylogenetic distance (Mayfield and Levine 2010). Closely-related species are expected to co-occur more often only if stabilizing niche differences are relatively strong and accumulate faster with phylogenetic distance than do average fitness differences. Swenson (2013) defends the use of relatedness as a proxy for ecological traits, citing the contributions that this approach has made to our understanding of phylogenetic patterns in community assembly, but suggests that it is perhaps best used at large taxonomic or spatial scales. A recent meta-analysis (Ma et al. 2016) supports the generality of previous studies (Swenson et al. 2006) which indicate that the competition-relatedness hypothesis may best be supported at smaller spatial scales where the outcomes of biotic interactions should be most apparent. However, a literature review by Cadotte et al. (2018), failed to find greater support for the competition-relatedness hypothesis at smaller spatial scales.

Weber and Agrawal (2012) recommend that patterns of relatedness are best used to generate hypotheses that can then be tested experimentally. With this approach, phylogenetic patterns identify mechanisms that are expected to be relatively more important for a given region, taxon or spatial scale (Table 1). Once the set of candidate mechanisms are identified, targeted experimental work can focus on testing a specific set of potential mechanisms for phylogenetic patterns. For example, patterns consistent with environmental filtering have been attributed to both shared environmental tolerances and shared mutualists (Table 1). A study finding support for environmental filtering would then ideally be followed by experimental work manipulating mutualists and/or other environmental conditions.

Understudied hypotheses

In the midst of this discussion, a fundamentally different interpretation of phylogenetic novelty and its relationship with establishment success is garnering recent interest. Fridley and Sax have formalized the ‘evolutionary imbalance hypothesis’, which posits that the evolutionary history of a species in its native region could predict its ecological success in the introduced range (Fridley and Sax 2014). Two additional hypotheses, the ‘universal tradeoff hypothesis’ (Niklas 1994, 1999, Marks and Lechowicz 2006, Tilman 2011) and what we term the ‘competitive constraint hypothesis’ make alternative predictions about how native region evolutionary history should impact success in the introduced range, although they have not yet been integrated into a phylogenetic context.

These hypotheses and their associated mechanisms constitute a major departure from previous models of introduction success based upon recipient community relationships, with the potential to alter both inference of phylogenetic patterns and tests of specific mechanisms operating in the field (Table 1). These hypotheses pertain to species once they have been introduced into a novel region, and do not apply to the first two stages of the invasion process. However, many of the mechanisms which are proposed to promote establishment success may also promote the successful spread of a species once established, especially if we think of spread as an iterative process of establishment (Davis 2009). Schaefer et al. have also argued that the competition-relatedness hypothesis may be more applicable to the spread phase of invasions than the establishment phase, under the assumption that competition may play a relatively larger role in spread than establishment (Schaefer et al. 2011).

Source communities as predictors of introduction success?

It could be argued that predicting introduction success from the phylogenetic distance between an introduced species and a recipient community makes an implicit assumption that the community context of the donor region does not substantially influence ecological traits. There is evidence, however, that the ecological and evolutionary history that a species has experienced can influence its success as an invader, for example through interactions with competitors, natural enemies or the abiotic environment (Callaway et al. 2004, Lee and Gelembiuk 2008, Zenni et al. 2014, Buckley and Catford 2016). Species with different evolutionary histories at their origins might therefore be expected to differ in their ability to establish elsewhere, independent of (and confounding analyses based solely upon) their relationships to recipient communities. Thus, the outcome of an introduction could be expected to depend on the ecological characteristics predicted by phylogenetic relationships in both the source and recipient regions.

Under the evolutionary imbalance hypothesis (Box 1) regions characterized by more intense competition, relatively

Box 1. The evolutionary imbalance hypothesis

Upon close inspection, the use of native communities as predictors of a species' colonizing ability shows a long history in evolutionary biology: Darwin (1859) originally discussed this idea in *The Origin of species*. He hypothesized that, 'Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence', which he suggests is supported by the success of European species introduced in New Zealand. Elsewhere, Darwin notes that differential 'perfection' between regions may be driven by larger population sizes providing more material for natural selection to act upon. More recently, this general idea has been formalized as the 'evolutionary imbalance hypothesis' by Fridley and Sax (2014).

Under the evolutionary imbalance hypothesis, regions with many lineages and/or older lineages are hypothesized to have experienced more natural selection in a given environment, resulting in greater optimization of phenotypes and higher species average fitness (Fridley and Sax 2014). The mechanisms proposed to underlie such increases in species average fitness include: the duration of exposure to a set of environmental conditions, the intensity of interspecific competition and the increased efficacy of selection experienced when population sizes increase along with absolute fitness (Fridley and Sax 2014). If we assume that the intensity of interspecific competition increases with the number of competitors and the phylogenetic proximity of competitors (as assumed in the competition-relatedness hypothesis), then we should predict that establishment is most likely to be successful when species originating in regions with many, close relatives are introduced to containing fewer, relatively distantly-related species.

While the evolutionary imbalance hypothesis invokes competition as a mechanism, predation can also have similar effects (Chesson and Kuang 2008), and the hypothesis could be extended to include apparent competition through shared natural enemies. Experimental work testing for an influence of phylogenetic distance on the strength of competition has received mixed support (reviewed by Gerhold et al. 2015), but there is strong empirical support for a negative relationship between phylogenetic distance and the likelihood of sharing pathogens (Gilbert and Webb 2007, Liu et al. 2012, Parker et al. 2015). Introduced species may benefit generally from lower levels of natural enemies in the introduced range (Blossey and Notzold 1995, Keane and Crawley 2002, Colautti et al. 2004). Indeed, these effects might be the strongest when species come from regions characterized by many close-relatives, where many enemies are shared, and are introduced into recipient regions containing more distantly-related species (i.e. the same scenario where the evolutionary imbalance hypothesis predicts the strongest competitive superiority). To our knowledge such 'phylogenetic enemy release effects' have not been studied to date, but might provide a fruitful avenue of research.

Recent work has shown that plant families with higher diversification rates are associated with greater naturalization success, which the authors suggest may be due to shared traits within those families that increase the likelihood of both diversification and successfully passing through the stages of invasion (Lenzner et al. 2020). All else being equal, clades with high diversification rates will tend to co-occur with closely-related species. The phylogenetic patterns we expect if diversification rate is serving as a proxy for shared traits that drive invasion success is thus the same as we would expect under the evolutionary imbalance hypothesis, even though the mechanisms invoked differ. We also note that these two mechanisms need not be mutually exclusive, and that evidence for one does not preclude the other.

stable environments and larger population sizes will contain species that are relatively phenotypically optimized (Fridley and Sax 2014). These optimized species will thus be able to invade regions containing less-optimized species. This idea might be intuitive, but it need not be true or large enough in its effects to alter species establishment in new environments. For example, under the 'universal tradeoff hypothesis' (Niklas 1997, Marks and Lechowicz 2006, Tilman 2011) ecologically similar, potentially competing species are subject to the same set of fundamental tradeoffs, creating a universal limit to the optimization of phenotypes. Such tradeoffs ensure that competing species from different regions do not differ substantially in their relative fitness despite differences in traits and associated ecological and life history strategies. Under this hypothesis, the evolutionary experience of a given taxon in a region might have no influence on its establishment elsewhere, or might even go so far as to constrain success as a colonizer. The latter case could occur if the presence of

competitors (or apparent competitors) limits the phenotypic space that a lineage can explore (via character displacement; de Mazancourt et al. 2008), decreases diversifying selection (Meyer and Kassen 2007) or limits population sizes. Smaller populations will produce fewer beneficial mutations, experience reduced efficacy of natural selection and may experience decreased strength of diversifying selection (Wilson 2014). We refer to this idea as the 'competitive constraint hypothesis', under which we would expect that species originating in regions with few and/or distantly-related competitors (or apparent competitors) should be more successful when introduced into novel regions (Table 1).

While Darwin originally proposed the evolutionary imbalance hypothesis, he never tested it (Darwin 1859). Indeed, there have been relatively few tests on the role of source communities in establishment success. Fridley and Sax (2014) compared the probabilities of introduced and established species becoming invasive in three regions

(eastern North America, New Zealand, Czech Republic) as a function of the maximum phylogenetic diversity within the source regions of these species. They found a positive correlation between the maximum phylogenetic diversity of a species' source region and the probability of it becoming invasive. They also compared the number of species exchanged between historically separated regions following the construction of the Panama, Suez and Erie canals. They tested the ratio of species exchanged against that expected based on the number of species in each region, finding that regions with greater asymmetries in phylogenetic diversity showed a higher degree of asymmetry in the number of species exchanged (Fridley and Sax 2014). Both of these comparisons provide evidence that is consistent with the evolutionary imbalance hypothesis, though they do not compete the evolutionary imbalance hypothesis against other major hypotheses. Several subsequent studies have documented additional asymmetries in invasions between regions, as predicted by the evolutionary imbalance hypothesis (Kalusova et al. 2015, Fitzgerald et al. 2016, Visser et al. 2016, Mason Heberling et al. 2017). While these studies do not quantify evolutionary imbalance, the results suggest that the evolutionary imbalance hypothesis could explain aspects of establishment success and that the hypothesis merits rigorous incorporation into existing models to quantify its potential explanatory power.

The competitive constraint hypothesis has not been tested in a phylogenetic framework, but is supported by both simulation studies and experimental results (Meyer and Kassen 2007, de Mazancourt et al. 2008, Johansson 2008). In simulations that included both ecological and evolutionary dynamics, adaptive responses to environmental change were constrained in more diverse simulations (de Mazancourt et al. 2008). In these diverse simulations, environmental change was more likely to lead to changes in species' abundances rather than adaptation. Additional simulation work supports the ability of competition to limit adaptation by decreasing population sizes, in turn limiting both the number of beneficial mutations arising and the effectiveness of selection (Johansson 2008). A microcosm experiment shows that predation can also limit diversification by decreasing the strength of diversifying selection (Meyer and Kassen 2007).

Likewise, the universal tradeoff hypothesis has not been tested in a phylogenetic framework, but has received both theoretical and empirical support. Tilman (2011) developed the theory underlying the universal tradeoff hypothesis and provided support using examples drawn from the fossil record of taxa from different biogeographic regions coexisting for millions of years following colonization. Evidence for this hypothesis also comes from mechanistic models of evolution, which support the existence of multiple fitness peaks of equal (or approximately equal) fitness (Niklas 1994, 1999, Marks and Lechowicz 2006). However, even if species are indeed constrained to a common tradeoff

surface, human activities may in effect push species off of that surface (Catford et al. 2018). Catford et al. (2018) provide theoretical evidence that coexistence via the competition–colonization tradeoff may be hindered by biological introductions. Biological introductions may either decrease mortality of introduced species (e.g. via escape from natural enemies) and/or increase dispersal of introduced species (e.g. via human mediation). This anthropogenic effect essentially pulls species off of the tradeoff surface, making coexistence more difficult (Catford et al. 2018).

Going from patterns to mechanisms

Although phylogenetic patterns can provide support for hypotheses, they cannot identify the underlying mechanisms generating these patterns, as similar patterns may be driven by multiple processes (Cavender-Bares et al. 2009). Both the evolutionary imbalance hypothesis and competitive constraint hypothesis propose that 1) regions will differ in the degree of phenotypic optimization of their species; and 2) these differences in optimization are the result of differences in population size, environmental variability, range size and competitive environment (Table 1). These mechanisms could be explored further using a combination of ecological and evolutionary methods. Historical niche reconstruction and ancestral state reconstruction can be used to better understand the ecological conditions a lineage has experienced in the past (Moen and Wiens 2009, Kozak and Wiens 2010). Historical demography approaches could be used to understand past population sizes (Hung et al. 2014, Rogers and Slatkin 2017), and could potentially be used to infer past competitive dynamics. Methodological approaches that fit mathematical models to demographic and environmental data (Levine and HilleRisLambers 2009) may provide a useful approach for understanding the dynamics of competition between species from different regions. Experimental tests of establishment success have provided support for the competition-relatedness hypothesis at local scales (Jiang et al. 2010, Violle et al. 2011, Peay et al. 2012, Ma et al. 2016), and similar methods could be used to test the predictions of the evolutionary imbalance hypothesis and competitive constraint hypothesis. However, an ideal approach to testing these hypotheses would involve the experimental manipulation of both ecological and evolutionary factors. Experimental evolution (reviewed by Lenski 2017) seems to offer a valuable experimental framework in which the relevant factors (population size, lineage diversity, environmental heterogeneity, intensity of competition, intensity of predation) can be manipulated, and in which the relevant response variables (phenotypic optimization, competitive dynamics) can be measured. Previous experimental evolution studies have provided evidence in support of competitive constraint acting via apparent competition (Meyer and Kassen 2007), as well as evidence consistent with universal tradeoffs more generally (Korona 1996).

Phylogeny and traits

The use of phylogeny to predict establishment success rests on the assumption that phylogeny is indicative of ecologically meaningful differences between species, that is, their traits. Simulations have shown that as the number of traits considered increases, the convergence between phenotypic and phylogenetic distance metrics increases (Tucker et al. 2018). Where we are interested in the overall phenotypes of organisms, phylogenetic distances may serve as reasonable approximations of phenotypic distances. However, individual traits will differ in their degree of phylogenetic signal (Blomberg et al. 2003), and in situations where establishment success is determined by traits that do not show phylogenetic signal, phylogenetic metrics may not be useful predictors. Phenotypic plasticity in traits can also weaken the utility of phylogeny as a proxy for traits (Burns and Strauss 2012), even as plasticity itself can exhibit a phylogenetic signal (Relyea et al. 2018). Further, even where the traits underlying establishment do show substantial phylogenetic signal, we expect relationships between establishment success and phylogenetic metrics will not have high coefficients of determination, due to the variance inherent in the evolutionary process. Focusing on species traits instead of, or in combination with, phylogeny may eventually improve our ability to predict establishment success. Traits related to body size, reproduction, migration, environmental tolerances and diet have all been shown to influence establishment success (Forsyth et al. 2004, Blackburn et al. 2009b, Kempel et al. 2013, Arndt and Schembri 2015, Mahoney et al. 2015, Peoples and Goforth 2017). However, as with approaches based on phylogenetic metrics, trait-based approaches typically fall short of linking establishment success with a particular coexistence mechanism (but see Godoy and Levine 2014). Even in community assembly more broadly we suffer from a lack of studies that link species invasion or coexistence with niche differences or average fitness differences (but see Angert et al. 2009, Levine and HilleRisLambers 2009, Kraft et al. 2015).

Moving forward: testing alternative models

Testing the diverse phylogenetic models of invasion success that we introduced above requires the careful consideration of many factors, some of which we outline in detail below.

Relative phylogenetic structure

If both source and recipient community phylogenetic structures influence establishment, then ideally both would be included in the same model of establishment success where their relative predictive power could be quantified. Moreover, it might be important to evaluate the influence of differences between source and recipient community properties. For example, the evolutionary imbalance hypothesis predicts that source communities with greater phylogenetic diversity will supply more successfully establishing species than those

with lower diversity. We would therefore expect that recipient communities with lower diversity relative to a source community should experience a greater disadvantage in terms of reduced competitive ability or niche occupancy of resident species, and should therefore be more easily invaded. Conversely, the competitive constraint hypothesis predicts just the opposite: establishment should be most likely when species from a low-diversity source community are introduced into a high-diversity recipient community. Previous discussions of the evolutionary imbalance hypothesis have focused solely on the evolutionary history of source communities while previous discussion of the competitive constraint hypothesis have not fully considered a phylogenetic context. Extending these frameworks to consider the evolutionary history of both source and recipient communities would better quantify the change in species interactions experienced by an introduced species. Along these lines, Lovell et al. (2021) recently showed that invasive species spread can be better predicted when considering the species compositions of both source and recipient communities.

In models analysing multiple successful and unsuccessful invasions, with each species being a datapoint, a concern arises. When including both source community and recipient community phylogenetic metrics in the same model these metrics, particularly mean phylogenetic distance (MPD, Box 2), are likely to be correlated between communities. This correlation is a result of the sensitivity of MPD to deep branching events in a phylogeny (Mazel et al. 2016) and the degree to which higher taxa are shared between communities. Phylogenetic nearest neighbor distance (NND, Box 2) should show relatively little correlation between source and recipient communities because this metric is more sensitive to branching patterns towards the tips of a phylogeny (Mazel et al. 2016). A paired approach wherein differences in, or sums of, phylogenetic metrics between source and recipient communities are calculated explicitly and used as an explanatory variable will remove the issue of correlations between communities. Using the difference (or sum) between source and recipient communities as a measure of imbalance makes the assumption that source and recipient community structures contribute equally to establishment success, however. This approach would thus be unable to distinguish between e.g. a scenario with strong effects of source community phylogenetic structure coupled with weak effects of recipient community phylogenetic structure and a scenario with effects of intermediate strength for both source and recipient community phylogenetic structure.

We note that correlations between phylogenetic structure metrics in the source and recipient communities should also increase with spatial scale: larger areas will include more species, which means that more evolutionary history will be shared between communities, leading to increasing similarity in phylogenetic metrics. In this case, we would expect that including phylogenetic structure of both communities in a single model might reduce the effect of recipient region communities particularly at a large spatial scale, which is where we see the greatest support for environmental

Box 2. Phylogenetic metrics

Early tests of phylogenetic patterns of invasions utilized the number of congeners within a recipient region as a proxy for phylogenetic distance (Darwin 1859), under the assumption that species with more congeners in the recipient community will be more closely related to that community. However, this metric has been criticized as subjective and artificial (Thuiller et al. 2010), and has been shown to fail to predict establishment success where distance-based metrics succeed (Maitner et al. 2012). Common current approaches to measuring phylogenetic distance include Faith's phylogenetic diversity (PD; Faith 1992) of the entire community, and mean phylogenetic distance (MPD) or nearest neighbor phylogenetic distance (NND; Strauss et al. 2006) between a focal species and the rest of the community (Faith 1992, Strauss et al. 2006). These metrics capture different features of the evolutionary history of communities, and their use will test different ideas about the influence of phylogeny on ecological traits and establishment success (reviewed by Tucker et al. 2017). Going forward, it may be useful to consider higher moments of phylogenetic distance in addition to the mean, which capture different aspects of phylogenetic structure (Fig. 1). Variance in phylogenetic distance quantifies the spread of phylogenetic distances around the mean. Skewness reflects whether most species are relatively closely (positive skewness) or distantly (negative skewness) related to a focal species. Kurtosis indicates how long the tails of the phylogenetic distribution are, with higher values associated with a narrow range of phylogenetic distances, and lower values associated with a relatively-even distribution of phylogenetic distances. Including multiple metrics and interactions between metrics may be able to improve models or generate more nuanced predictions. However, we note that due to the topological constraints of phylogenies, phylogenetic distributions will also be constrained. For example, it isn't possible to have both a high mean and a high variance, since species descending from relatively long branches will necessarily be similarly distantly-related to all other species.

The accuracy of phylogenetic metrics will depend on the quality of the phylogenies used. Poorly-resolved (Swenson 2009, Molina-Venegas and Roquet 2014) or incomplete (Linder et al. 2005, Park et al. 2018, Jantzen et al. 2019) phylogenies can bias results and lead to incorrect inferences. Rather than omitting species, phylogenetic uncertainty can be accounted for to a degree by replicating analyses across a set of fully-resolved phylogenies that represent uncertainty (Park and Potter 2013, Rangel et al. 2015), adding missing species based on their taxonomic affiliation (Rangel et al. 2015, Jin and Qian 2019).

Phylogenetic corrections (Felsenstein 1985, Ives and Garland 2010) are statistical methods to account for the lack of non-independence among variables due to shared ancestry. Such methods should be applied when species are the unit of analysis, even when predictor variables include phylogenetic structure metrics. Phylogenetically-corrected versions of many common statistical models can be implemented with existing R (ver. 4.0.4; <www.r-project.org>) packages, such as phylogenetic linear models and generalized linear models (implemented in e.g. *phylolm* ver. 2.6.2; Ho et al. 2020), phylogenetic generalized mixed models (Ives and Helmus 2011, implemented in e.g. *pez* ver. 1.2.2; Pearse et al. 2015), and phylogenetic generalized least-squares models (Symonds and Blomberg 2014, implemented in e.g. *caper* ver. 1.0.1; Orme et al. 2018, *nlme* ver. 3.1.144; Pinheiro et al. 2020).

filtering (Ma et al. 2016). This highlights a critical need for theoretical work exploring the parameters under which we would expect to recover support for alternative phylogenetic hypotheses.

Competing multiple hypotheses for establishment success

Modern coexistence theory (Chesson 2000) provides one means to integrate the differing hypotheses discussed here into a more synthetic body of theory (Fig. 2). The environmental filtering hypothesis predicts that species closely-related to the recipient community share similar environmental tolerances with the recipient community (Darwin 1859), thereby using phylogenetic relatedness as a proxy of species mean fitness in a given environment (Fig. 2B). The competition-relatedness hypothesis predicts that resource use (or natural enemy) overlap between an introduced species and

the recipient community declines with phylogenetic relatedness to the recipient community (Darwin 1859), increasing the magnitude of stabilizing niche differences (Fig. 2C). The competitive constraint hypothesis predicts that species mean fitness should increase with phylogenetic novelty within the source region due to enhanced efficiency of selection and a greater number of mutations (Fig. 2D). The evolutionary imbalance hypothesis predicts that species mean fitness should decrease with phylogenetic novelty within the source region due to increased phenotypic optimization (Fig. 2D). The universal tradeoff hypothesis predicts that species mean fitness should be independent of relatedness to the source community, owing to a shared tradeoff surface that provides common limits to phenotypic optimization (Fig. 2D). Predictions of establishment success may be improved by considering the joint effects of both source and recipient region. For example, under the competitive constraint hypothesis a species originating in a community composed

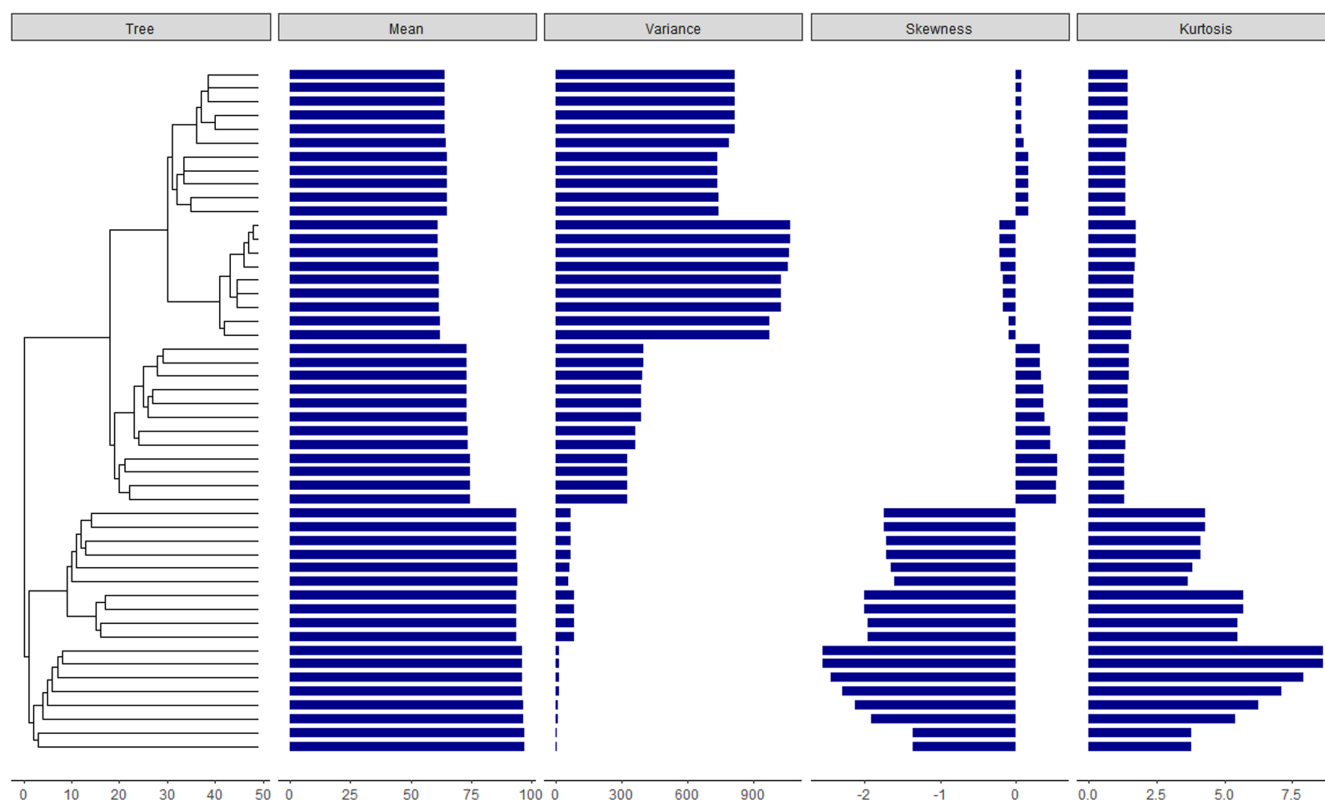


Figure 1. Statistical moments of phylogenetic distance. The distributions of phylogenetic distances relative to each species on this simulated phylogeny are quantified using the mean, variance, skewness and kurtosis.

of many close relatives may be at an average fitness disadvantage when introduced to a novel recipient region (e.g. white region of Fig. 2A). However, under the competition–relatedness hypothesis the species may still be able to establish by virtue of having a sufficiently large stabilizing niche difference to overcome that fitness difference (blue region below the x-axis of panel Fig. 2A). Conversely, the increased phenotypic optimization predicted by the evolutionary imbalance hypothesis may be enough to compensate for a relative fitness disadvantage of being poorly suited to a given environment (i.e. a shift from the white region to the grey region in panel Fig. 2A).

Native range size is known to be positively related to the likelihood of establishment success in some introductions (Blackburn et al. 2009a, Lenzner et al. 2020), but may itself be correlated with measures of phylogenetic structure. For example, species with larger ranges will tend to encounter more interacting species, which will increase PD and may decrease NND (Morlon et al. 2011). It is possible that these encounters will select for increased fitness or niche differentiation, as predicted by the evolutionary imbalance hypothesis. Alternatively, range size might reflect adaptations for success across a wide variety of environments, independent of encounters with other species. It has also been suggested that the same traits underlying high diversification rates, and hence relatively low NND and MPD, may be associated with an increased ability to adapt to novel environmental

conditions (Lenzner et al. 2020). If range size is included as a covariate in models of establishment success, the independent contributions of community phylogenetic structure and range size can be evaluated.

There is a longstanding interest in the ability of recipient community richness to predict establishment success (Elton 1958, Beaury et al. 2020), with the prediction that establishment success should decline with recipient community richness. However, there has been less emphasis on native range richness, which is expected to influence establishment success under both the evolutionary imbalance hypothesis and competitive constraint hypothesis. Tilman (2011) also notes that under the universal tradeoff hypothesis, establishment should be more difficult in more diverse regions. It may thus be useful to consider the inclusion of both source and recipient community richness as predictor variables in models of establishment success.

Finally, while many other covariates could be included in a phylogenetic model (keeping in mind that a goal of these models is to use phylogenetic relationships as a proxy for ecological traits), the single strongest known predictor of establishment success is propagule pressure (Holle and Simberloff 2005, van Wilgen and Richardson 2012, Blackburn et al. 2015). Both experimental and correlational evidence has made it clear that the introduction of a sufficient number of propagules is required for a high probability of establishment. Ideally, any analysis of the influence of species' traits on

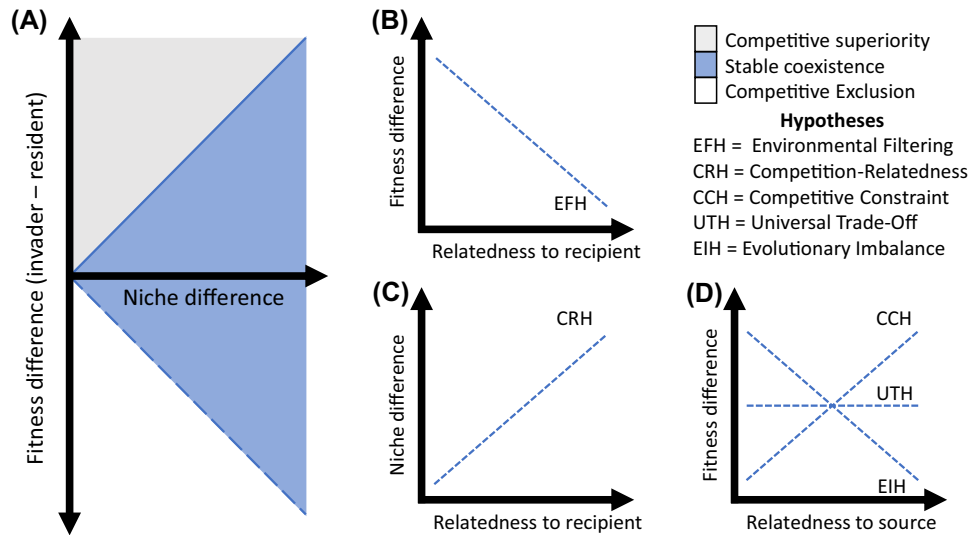


Figure 2. (A) depicts how species mean fitness differences and stabilizing niche differences contribute to coexistence. Species below the x-axis are at a mean fitness disadvantage and can only persist where the magnitude of the niche difference is large enough to compensate for their mean fitness disadvantage (the light blue region below the x-axis). Species above the x-axis have a mean fitness advantage and are expected to persist, with species in the grey region persisting predominantly due to their fitness advantages and species in the light blue region persisting predominantly due to niche differences. (B–D) depict how the source and recipient range hypotheses predict that stabilizing niche and mean fitness differences will differ with the phylogenetic relatedness of a species to the source or recipient communities.

establishment success would look for an effect of these ecological features beyond what can be explained by propagule pressure alone. The availability of information about propagule numbers poses a major limitation in this regard. Where detailed quantitative information about introduction effects does not exist, it may be useful to remove species where small introduction sizes were likely, based on known introduction pathways (Moulton et al. 2001). Nevertheless, the underlying importance of this effect should be considered when constructing and interpreting the predictive power of any new models of introduction success (Duncan et al. 2019).

As with all associations of evolutionary relatedness and ecological phenomena, how and whether patterns of relatedness among taxa predict the outcome of biological introductions can depend on the spatial and phylogenetic/taxonomic scales on which they are examined. In terms of spatial scale, it has long been hypothesized that closely related species exist in mutually exclusive patterns at smaller, local scales where direct competition occurs over the same pool of limited resources (MacArthur and Levins 1967, Swenson et al. 2006). Closely related species may be more likely to co-occur at larger, regional scales due to shared environmental preferences and less frequent direct interactions (Procheş et al. 2007). In the context of biological invasions, a meta-analysis of the literature showed that non-native introduced species tended to be more closely related to natives at the local scale, but less closely related to natives at the regional scale (Ma et al. 2016). The few empirical examinations of spatial scale effects on biological invasions have found similar patterns (Cavender-Bares et al. 2006, Davies et al. 2011, Carboni et al. 2013, Park and Razafindratsima 2019). Also, Park et al. (2020) demonstrated that the likelihood of observing the signature

of environmental filtering (i.e. phylogenetic clustering) over that of competition (i.e. phylogenetic overdispersion) in biological invasions increases with spatial scale at both local and regional levels across the flora of the United States. However, a recent review of the literature suggests that the effects of spatial scale may not be as clear cut, likely due to other confounding factors (Cadotte et al. 2018).

Scales of analysis

The phylogenetic and/or taxonomic scale of analyses can also affect the likelihood of observing certain signals of community assembly processes (Mayfield and Levine 2010, Graham et al. 2018). Studies of community assembly and biological invasions can span all levels of the tree of life, including genus (Cavender-Bares et al. 2006, 2009, Chalmardrier et al. 2013, Graham et al. 2018), tribe (Park and Potter 2015a, b), family (Daehler 2001, Strauss et al. 2006) and kingdom-scale (Schaefer et al. 2011, Marx et al. 2016) assessments, representing anywhere from a few to hundreds of millions of years of evolutionary time. Regardless of the hypothesis being tested, associating patterns of phylogenetic/taxonomic relatedness and community assembly processes depends on the assumption that the evolutionary distance between taxa correlates (negatively) with ecological similarity. However, this relationship does not always hold, especially across long divergence times. For instance, many species in the Cactaceae and Euphorbiaceae have colonized arid environments using similar adaptations to extreme drought despite being distantly related (Arakaki et al. 2011, Horn et al. 2014). At the same time, relatively closely related species in each respective family can be found in tropical rainforests and deserts

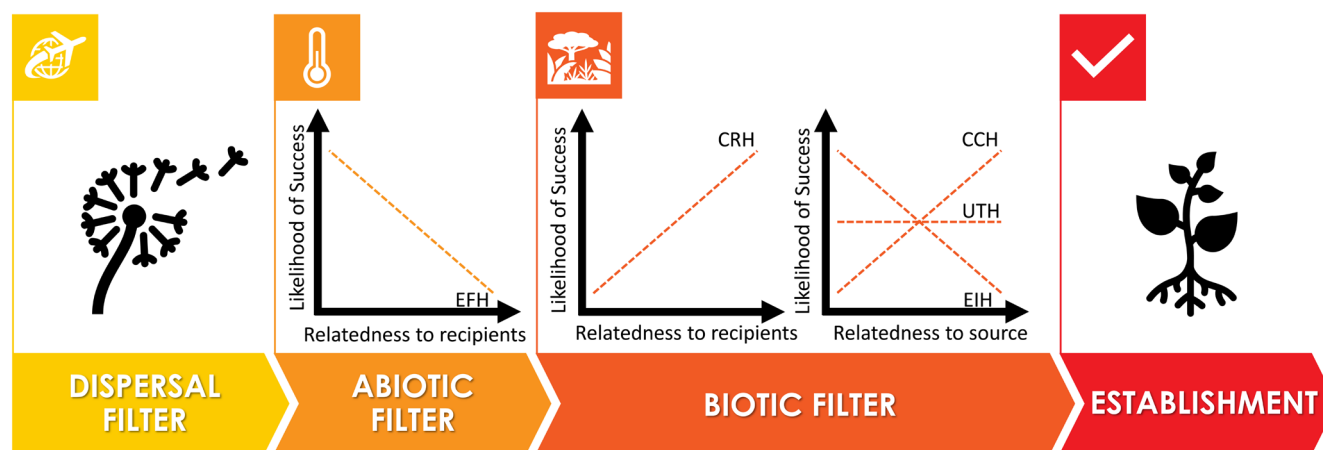


Figure 3. Potential changes in relevance of individual hypotheses over time. An introduced species must successfully pass through three filters in order to become established. The relevance of the environmental filtering (EFH), competition-relatedness (CRH), evolutionary imbalance (EIH), universal tradeoff (UTH), and competitive constraint (CCH) hypotheses may change as the species passes through these filters.

(Bruyns et al. 2011, Guerrero et al. 2019). Diversification rates and trait disparification rates vary across the tree of life; therefore, niches and traits are conserved over different phylogenetic scales (Ackerly 2009, Graham et al. 2018). Though generalizations about how these rates vary across phylogenetic scales have yet to be recognized, there is some evidence from the literature that analyses focused on larger phylogenetic/taxonomic scales (e.g. vascular plants) more often find that communities are structured through environmental filtering than those involving smaller phylogenetic scales (e.g. genus) (Cavender-Bares et al. 2006, 2009, Chalmandrier et al. 2013, Graham et al. 2018).

Along these lines, spatial and phylogenetic scale can be linked, and their individual effects may be difficult to separate. The presence and number of invaders (Stohlgren et al. 2002) as well as metrics of phylogenetic relatedness can be influenced by species richness (Swenson et al. 2006, Pavoine and Bonsall 2011), which increases with both phylogenetic and spatial scale. Thus, all else equal, increasing the spatial and/or phylogenetic extent of one's sampling will always increase the likelihood of observing more closely related species. Further, differences in ecological niches evolve over (geographic) space and (evolutionary) time (Peterson et al. 1999). Studies seeking to infer ecological processes from phylogenetic relationships among members of a community should therefore clearly communicate the evolutionary and spatial scales employed so that the results may be interpreted and applied at the appropriate scale and context. Further examining community structure at nested scales may provide insight into the roles and strengths of different ecological processes that distribute taxa across space and time.

As with phylogenetic and spatial scales, temporal scale may also be an important consideration when using phylogenetic patterns to understand introductions. Under both the competition-relatedness and the environmental filtering hypotheses only short time scales are relevant: the relatively recent time period which contains the set of potential competitors/

apparent competitors at the time of introduction (in the case of the competition-relatedness hypothesis) or over which the species occurring in an area provide a proxy for environmental suitability (in the case of environmental filtering). The evolutionary imbalance and competitive constraint hypotheses both invoke evolutionary changes that likely occur over a longer temporal scale, but it isn't clear what the relevant time scales might be. The incorporation of relatively long temporal scale data is hampered by the fact that communities are not static, and thus the usefulness of the current source community (which is often all that we have reliable data for) in representing the evolutionary context a species has experienced in the past may differ among species. The time scales over which assemblages persist and our ability to infer past communities are an active area of research (Williams and Jackson 2007, Ordonez et al. 2016, Knight et al. 2020) and the answers to these question have clear implications for our ability to use current assemblages or inferred past assemblages to represent the evolutionary context a species has experienced. Additionally, the support for different hypotheses may change over time during the course of a biological introduction (Fig. 3). If we conceptualize biological invasions as passing through a series of 'filters' in order to become established, a species must first pass through the dispersal filter, then abiotic filter and finally the biotic filter (Theoharides and Dukes 2007). Thus, the environmental filtering hypothesis might be more relevant earlier in introductions, with the other hypotheses becoming more relevant later in the course of an invasion (Fig. 3; Cadotte et al. 2018).

Conclusions

There have been many tests of the competition-relatedness and environmental filtering hypotheses (reviewed by Procheş et al. 2007, Thuiller et al. 2010, Jones et al. 2013, Ma et al. 2016, Cadotte et al. 2018), but they yielded conflicting support for the two hypotheses. Previous reviews of

these studies have pointed to differences in phylogenetic metrics, spatial scale and stages of invasion as possible reasons behind this lack of consensus. However, failure to consider where a species is coming from may be neglecting an important covariate that could help explain these inconsistencies among studies. Considering both source- and recipient-range phylogenetic metrics could improve our ability to predict the outcome of biological invasions, as well as providing insights into community assembly. If the phylogenetic structure of source regions has significant predictive power, then support can be identified for specific alternative hypotheses and their associated predicted mechanisms (Table 1). If species from different source regions do not differ systematically in their ability to establish in other regions, and if these invaders can stably coexist with the recipient communities, this would provide support for universal tradeoffs and encourage tests of its associated mechanisms. Such studies would be valuable steps to resolving the myriad possibilities for connections between phylogeny, evolutionary history and ecological interactions, but this process may also be complicated by a variety of additional interpretations of these results.

Tests of source-range hypotheses, or tests integrating both source- and recipient-range, stand to benefit from the lessons learned in studying the recipient range hypotheses. Many of the same issues that have been raised will remain important, and may even become more important. We recommend the following as key points to consider in future studies predicting invasion success using phylogeny:

- 1) Include both source and recipient community phylogenetic structure. This will allow us to test both sets of hypotheses, their predictive power and may help explain the lack of consensus in studies focused solely on recipient range.
- 2) Use a complete phylogeny and account for uncertainty. This will be of increased importance where incorporating multiple source and recipient ranges, as differences in phylogeny quality between regions may bias metrics.
- 3) Consider stages of the invasion process separately, and consider multiple stages where possible. Source and recipient range hypotheses invoke different mechanisms which may be more relevant at different stages of the invasion process. Source region hypotheses invoke species average fitness differences (which promote competitive exclusion), and may be especially relevant to predicting impacts of invaders.
- 4) Clearly state spatial and phylogenetic scales of analysis and conduct analyses across scales where possible. Support for different hypotheses may change with spatial or phylogenetic scale, potentially providing insights into the underlying ecological processes. In the case of source-range hypotheses, temporal scale may also be important.

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Data availability statement

This paper contains no original data.

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