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ECOLOGICAL SOUNDING

The imbalance of nature: revisiting a Darwinian framework for invasion biology

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ABSTRACT

Aim A major implication of natural selection is that species from different parts of the world will vary in their efficiency in converting resources into offspring for a given type of environment. This insight, articulated by Darwin, is usually overlooked in more recent studies of invasion biology that are often based on the more modern Eltonian perspective of imbalanced ecosystems. We formulate a renewed Darwinian framework for invasion biology, the evolutionary imbalance hypothesis (EIH), based only on the action of natural selection in historically isolated populations operating within a global network of repeated environments. This framework predicts that successful invaders are more likely to come from biotic regions of high genetic potential (with independent lineages of large population size), experiencing a given environment for many generations and under strong competition from other lineages.

Location Global.

Methods We test the predictive power of this framework by examining disparities in recent species exchanges between global biotic regions, including patterns of plant invasions across temperate regions and exchanges of aquatic fauna as a result of modern canal building.

Results Our framework successfully predicts global invasion patterns using phylogenetic diversity of the world's biotic regions as a proxy that reflects their genetic potential, historical stability and competitive intensity, in line with the Darwinian expectation. Floristic regions of higher phylogenetic diversity are more likely to be source areas of invasive plants, and regions of lower phylogenetic diversity are more likely to be invaded. Similar patterns are evident for formerly isolated marine or freshwater assemblages that have been connected via canals.

Main conclusions We advocate an approach to understanding modern species invasions that recognizes the potential significance of both the original Darwinian explanation and the more modern view that emphasizes novel ecological or evolutionary mechanisms arising in the introduced range. Moreover, if biological invasions are a natural outcome of Darwinian evolution in an increasingly connected world, then invasive species should continue to displace native species and drive widespread shifts in the functioning of ecosystems.

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Keywords

Biotic resistance, Darwin, Elton, empty niche, floristic regions, natural selection, phylogenetic diversity, pre-adaptation, species invasions.

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INTRODUCTION

Since Charles Elton's (1958) first modern treatment of the subject more than 50 years ago, the study of biological invasions has matured from one largely restricted to ecological processes – competition, predation, disturbance – to one that more fully acknowledges community assembly as driven by the interplay of ecological and evolutionary processes (Simberloff, 2000; Richardson, 2011). Although Elton's core mechanisms of enemy release (Keane & Crawley, 2002), biotic resistance (Levine & D'Antonio, 1999; Tilman, 2004) and disturbance (Hobbs & Huenneke, 1992; Davis *et al.*, 2000) remain key foci of invasion studies, evolutionary processes such as rapid adaptation of invaders to new selection pressures in the introduced range have emerged as a major feature of many invasions (Blossey & Nötzold, 1995; Callaway & Ridenour, 2004; Colautti & Barrett, 2013; Felker-Quinn *et al.*, 2013). Invasion biology today is therefore both 'Eltonian' and 'Darwinian', in the sense that Elton's perspective of imbalanced ecosystems (Cronk & Fuller, 1995) and the potential for evolutionary change in novel environments provide complementary frameworks for invasion studies. Moreover, these perspectives start from the same premise that there must be a strong explanation for why invading species (those with no evolutionary history in an invaded environment) can outcompete native species – species that are presumably finely adapted to local conditions (Sax & Brown, 2000).

Despite the increasing integration of evolutionary processes into invasion studies, it is remarkable that the original evolutionary explanation of species invasions, espoused by Darwin himself a century before Elton's publication, remains an afterthought in invasion theory. Darwin (1859) observed that because 'natural selection acts by competition, it adapts the inhabitants of each country only in relation to the degree of perfection of their associates', such that, 'we need feel no surprise at the inhabitants of any one country, although on the ordinary view supposed to have been specially created and adapted for that country, being beaten and supplanted by the naturalised productions from another land'. Darwin's view, one of the earliest on biological invasions, presents invasion as an expectation of natural selection – a view largely absent from modern invasion biology (Vermeij, 2005; Tilman, 2011). Darwin (1859) further suggested that species from larger regions, represented by more individuals, have 'consequently been advanced through natural selection and competition to a higher stage of perfection or dominating power' and therefore be expected to beat 'less powerful' forms found in other regions. Here we suggest that this basic insight can be used to develop a more holistic framework for understanding biological invasions as a fundamental product of Darwinian evolution, a framework we call the evolutionary imbalance hypothesis (EIH) of species invasions. This framework builds upon Darwin's observations, but also the work of others who recognized the role that evolutionary history, contingency and pre-adaptation can play in mediating the success or failure of invading species (MacArthur, 1972; Rejmánek, 1989; Tilman, 1999, 2011; Sax & Brown, 2000; Flannery, 2002; Mack, 2003; Stachowicz & Tilman, 2005; Vermeij, 2005; Leigh *et al.*, 2009; Fridley, 2013).

THE EVOLUTIONARY IMBALANCE HYPOTHESIS

The EIH is based on three postulates. First, *evolution is contingent and imperfect*. Evolution is a tinkerer (Jacob, 1977) rather than an engineer, working by modifying existing forms to meet new challenges. Thus, the characteristics of species in any biotic assemblage are subject to constraints posed by evolutionary history and past environments. Second, *the degree to which species are ecologically optimized increases as the number of 'evolutionary experiments' increases, and with the intensity of competition*. Each newly derived phenotype can be viewed as an evolutionary experiment, one that has some probability of having a selective advantage for a given set of environmental conditions. The number of such experiments should vary among regions that differ in spatial extent and biotic history, and their success should be influenced by the intensity of competition. Richer biotas of more potential competitors and those that have experienced a similar set of environmental conditions for a longer period should be more likely to have produced better environmental solutions (adaptations) to any given environmental challenge. Third, *similar sets of ecological conditions exist around the world*. Environmental conditions vary over the globe but similar habitats, including climate, soils and disturbance regimes, are repeated and separated by vast distances.

Given these postulates, it follows that once biotas of previously isolated habitats are mixed, some species should have a higher fitness than others for any given set of environmental conditions (Fig. 1). If the disparity in fitness is great enough, an introduced species becomes an 'invader'; i.e. it is able to become abundant within the ancestral habitat of resident species, based solely on an imbalance in the degree to which organisms are adapted to local environments (Stachowicz & Tilman, 2005; Vermeij, 2005). Superior adaptations to particular environmental circumstances by non-native organisms have long been implicated in ecophysiological and behavioural studies of invasive plants and animals (Table 1). If such adaptations were present in introduced species in their native range (what some invasion biologists have called 'pre-adaptation'; Mack, 2003), this becomes a basis for the EIH. In contrast, modern invasion studies often emphasize either the presumed advantages that invaders acquire by leaving their evolutionary context behind, such as hypotheses based on missing enemies (Colautti *et al.*, 2004), novel phenotypes (Callaway & Ridenour, 2004) or the evolution of increased competitive ability upon arrival to a newly occupied region (Blossey & Nötzold, 1995), or they depend on ecological explanations, such as reduced biotic resistance caused by disturbance or low native species diversity (Elton, 1958). We assert that the study of biological invasions should comprise a more balanced approach that acknowledges the full complement of mechanisms in both Darwinian and Eltonian frameworks, and specifically that divergent evolutionary histories of the donor and recipient regions are significant

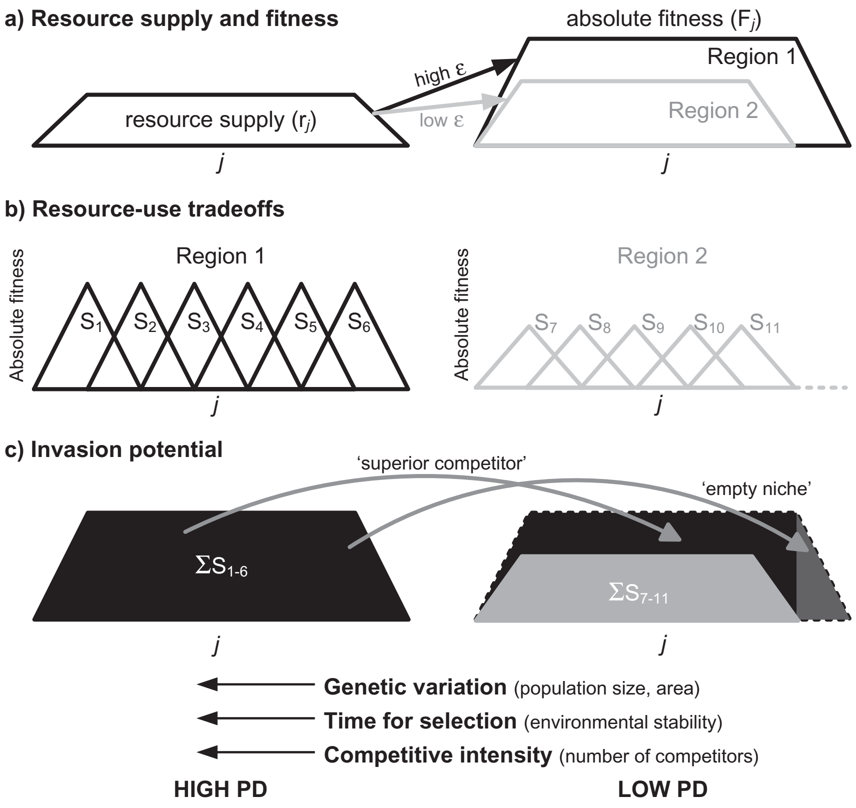

Figure 1 Invasion potential varies among biotic regions as a function of how species have evolved to convert resources into offspring. (a) Two isolated regions contain an identical resource gradient (r_j) (*sensu* Fig. 9-4 of MacArthur, 1972), but species of Region 1 convert the resource into offspring with greater efficiency (*reproductive power*, ε). (b) Tradeoffs along the resource gradient between species (S) in both regions allow for resource partitioning along the gradient, but the absolute fitness of species of Region 1 is higher, due to the greater resource-to-offspring conversion of (a). (c) Once barriers to dispersal are removed, species from Region 1 (black) are superior competitors under equal resource conditions due to higher fitness, and may additionally colonize 'empty niches' that species of Region 2 (gray) did not evolve to fill. The evolutionary imbalance hypothesis argues that region phylogenetic diversity (PD), a proxy for evolutionary advancement, can predict the asymmetry of invasions among regions.

Table 1 Examples of superior abiotic tolerances or metabolic or foraging efficiencies driving the establishment or spread of invading species. Introduced, non-native species can be better adapted for local environmental conditions than native species. We argue this may be a consequence of evolutionary pressures that vary globally, which tend to produce organisms that vary in their absolute fitness for any given set of environmental conditions.

Behaviour or adaptation	Manifestation	Invaded region	Exemplars
Cold tolerance	Tree line elevation	Southern Hemisphere, islands	Northern conifers (e.g. *Picea engelmannii*); Körner & Paulsen (2004)
Salt tolerance	Coastal grassland dominance	California	Iceplant (*Mesembryanthemum crystallinum*); Vivrette & Muller (1977)
Shade tolerance	Rain forest dominance	Hawaii	Strawberry guava (*Psidium cattleianum*); Pattison *et al.* (1998)
Inundation tolerance	Tidal mud-flat colonization	Western USA	Cordgrass (*Spartina anglica*); Mack (2003)
Tolerance of shifting sands	Coastal dune colonization	South Africa, New Zealand, western USA	European beachgrass (*Ammophila arenaria*); Mack (2003)
Drought, fire tolerance of tree growth form	Tree colonization of arid or fire-prone grasslands	Brazil, central Europe, South Africa, Pacific islands	Trees including pines (*Pinus* spp.) and black locust (*Robinia pseudo-acacia*); Rejmánek (1989) and Mack (2003)
Mating system and cooperative social organization	Supercoloniality ('invasive ant syndrome')	Global	Invasive garden ant (*Lasius neglectus*); Cremer *et al.* (2008)
Foraging efficiency	Ant invasions	Islands	Little fire ant (*Wasmannia auropunctata*); Le Breton *et al.* (2005)

for understanding global patterns of invasion (Vermeij, 2005). Indeed consideration of the evolutionary history of a potential invader's home region has been a surprisingly neglected aspect of invasion biology (Fridley, 2013, cf. Catford *et al.*, 2009), even for those studies that highlight the superior adaptations of some invaders (e.g. the 'global competition hypothesis'; Alpert, 2006).

The EIH can also be placed within a modern species interaction framework where competitive outcomes are the result of both niche and fitness differences between species (Chesson, 2000; Stachowicz & Tilman, 2005; MacDougall *et al*., 2009). For example, Tilman (2011) showed that even small differences in absolute fitness between resident and introduced species inhabiting the same niche could lead to the rapid dominance of invaders. Although he used this approach in the context of extinction data to come to different conclusions about the mechanisms underlying historical biotic exchanges, his 'biogeographic superiority hypothesis' describing the evolution of different tradeoff surfaces among biotic regions is an expression of the EIH using resource ratio theory. Differences in average absolute fitness among regions as a result of contrasting tradeoff surfaces are a major implication, but they are not the only explanation for invasion under the EIH, as species from one region can also evolve to exploit resource conditions that species from another region cannot (an 'empty niche'). From this perspective, invasion mechanisms that invoke a 'superior competitor' (Rejmánek, 1989) or 'empty niche' (Mack, 2003) are both manifestations of a higher absolute fitness of the invader, in that empty niches are simply conditions under which natives cannot sustain self-supporting populations (Fig. 1).

QUANTIFYING EVOLUTIONARY IMBALANCE

The EIH is based on the insight provided by Darwin that regions of the world should vary in the degree to which natural selection has been able to optimize the conversion of resources into offspring by organisms under competition, or what Brown *et al*. (1993) called 'reproductive power'. For this insight to explain global invasion patterns, we must first understand the factors that vary among regions and produce differences in reproductive power for organisms inhabiting a given set of environmental conditions. We suggest that this process could be driven by three primary factors: (1) the amount of genetic variation within populations; (2) the amount of time a population or genetic lineage has experienced a given set of environmental conditions; and (3) the intensity of the competitive environment experienced by the population.

Spatially extensive regions of contiguous habitat contain species with larger populations, and thus allow for a greater array of genetic variation to be acted upon by natural selection over time (Darlington, 1959; MacArthur, 1972; Leigh *et al*., 2009). We would thus expect a population's reproductive power to scale with the size of its habitat. This was the original mechanism of invasion invoked by Darwin (1859) in consideration of the apparent bias in plant invasions between the Northern and Southern Hemispheres. Darlington (1959) invoked a similar mechanism for global patterns of environmental adaptation in mammals, and Tilman (1999, 2011) considered the consequences of larger plant population sizes and genetic variation for the evolution of resource-based tradeoff surfaces. In general, the correlation of population size and genetic diversity is a well-tested tenet of conservation genetics (Leimu *et al*., 2006), and genetic variation is well recognized as a key driver of long-term adaptation. We apply this basic evolutionary process to the assessment of species invasiveness: all else being equal, we expect species with a high reproductive power in a given environment to come from regions where that environment is more extensive, supporting larger population sizes for a given selection regime.

We also expect evolutionary lineages in older, more stable environments to have had more opportunities to be honed by selective pressures than those occupying new environments (e.g. young oceanic islands) or those more disturbed in the recent past (e.g. formerly glaciated regions) (Dobzhansky, 1950; Cody & Mooney, 1978). This mechanism is a direct consequence of the significance of time in the process of natural selection, where adaptation occurs continually through the accumulation of beneficial mutations, even in a constant environment (Lenski *et al*., 1991). The tendency of the fitness of a population to increase in response to a constant selection pressure, even after thousands of generations, has been well demonstrated in microbial systems in the laboratory (Elena & Lenski, 2003; Barrick *et al*., 2009) and is consistent with quantitative genetics theory (Fisher, 1930). Extending this process to the biogeography of species invasions, we suggest that organisms with high reproductive power (and thus invasiveness) for a given environment should tend to be those that in addition to having large populations have been exposed to that condition for more generations.

A third mechanism promoting disparities in reproductive power is differences in interspecific competitive intensity among regions that vary in the complexity and diversity of their communities (Dobzhansky, 1950; MacArthur, 1972; Leigh *et al*., 2009; Schemske, 2009), a mechanism often invoked to explain the apparent competitive superiority of tropical lineages. MacArthur (1972) extended this idea to species invasions, arguing that 'emigrants from species-rich continents in tropical climates have had much practice in competing . . . they certainly should be good at invading a new community of competitors'. This idea has also been invoked to explain biases in past biotic exchanges (Vermeij, 1996, 2005) and the competitive superiority of mainland over island species (Leigh *et al*., 2009). Although separating this mechanism from other regional differences underlying diversity patterns may not be feasible in many cases, we expect that populations facing a greater array of competing species historically have evolved a higher reproductive power and will therefore be more likely to invade regions of lower competitive intensity.

The challenge for applying regional variation in these factors – larger population sizes, relative environmental stability or habitat age and competitive intensity – to global invasion patterns is finding a straightforward way to measure them. Even seemingly simple measurements like habitat area as a proxy for population size require decisions about what constitutes a 'habitat', or how environmental constancy or competitive intensity should be quantified. As a first attempt to evaluate the predictive power of the EIH we suggest an alternative approach of using a proxy variable, one that is likely to correlate with the above factors but is relatively easy to estimate for the biota of a given region. One such candidate is phylogenetic diversity (PD), which, broadly speaking, is an index of the number of unique lineages in a region (Faith, 1992) and should bear a strong relation to the range of phenotypic innovation available and the level of competitive intensity experienced by extant species (Vermeij, 1996, 2005; Leigh *et al.*, 2009). Because PD is more reflective of deep divergences than recent diversification, we further expect it to be a rough indicator of environmental constancy or habitat age, in that it can distinguish between recent adaptive radiations (e.g. on island archipelagos) and longer-term trends in diversity driven by adaptation through specialization (e.g. Safi *et al.*, 2011, for global mammalian assemblages) whereas species diversity cannot. All else being equal, our expectation is that biotas represented by lineages of greater number or longer evolutionary history should be more likely to have produced a more optimal solution to a given environmental problem, and it is this regional disparity, approximated by PD, that allows predictions of global invasion patterns. We emphasize, however, that we consider PD to be the best available surrogate for describing how species assemblages should vary in reproductive power for a given environment, and do not imply any direct causal relationship between PD and the invasibility of a region.

PHYLOGENETIC DIVERSITY AND GLOBAL INVASION PATTERNS

The EIH suggests that species with a disparate evolutionary history inhabiting similar but spatially isolated environments should vary in reproductive power, and thus exhibit differential fitness in a common environment. If, as we suggest, PD is a suitable proxy for differences in reproductive power between biotic regions, then the EIH predicts that *when introduction attempts are held constant among donor regions, the number of successful invaders in a recipient region should vary positively with the PD of each donor region, and recipient regions with lower PD should be easier to invade.* In other words, the EIH presents global invasion patterns as a function of the biological characteristics of both a recipient region and potential donor regions, which we suggest can be predicted using regional PD. Unfortunately, the condition of equal introduction attempts among potential donor regions is rarely met, such that simple comparisons of invader richness and PD of the donor region across different recipient regions are not appropriate tests of the EIH. Instead, we demonstrate two alternative approaches to evaluating this prediction that control for variation in introduction attempts between regions.

First, we examine whether native region PD can predict whether a species will become invasive in a region after it has been introduced. This is an approach used in invasive species risk assessments (Pheloung *et al.*, 1999; Daehler *et al.*, 2004), where non-native species of a certain region are separated into ‘invasive’ or ‘non-invasive’ groups, and traits or other species-level variables are sought that are predictive of whether a species belongs in the invasive group. The approach is useful here because it does not depend on equal introduction attempts from each potential donor region; rather, it examines the probability that species from different regions will be successful invaders once introduced, as a function of the PD of their native range. We examined this prediction for plants by estimating PD for the 35 floristic regions of the world identified by Takhtajan (1986), and assigning each introduced species in a region a PD value according to the region of largest PD that overlaps with their native range. We did this for three geographic areas that have well-documented non-native floras, including Eastern North America (Fridley, 2008), the Czech Republic (Pysek *et al.*, 2002) and New Zealand (Howell & Sawyer, 2006; Howell, 2008). For example, eastern North America (Fig. 2, top panel) contains

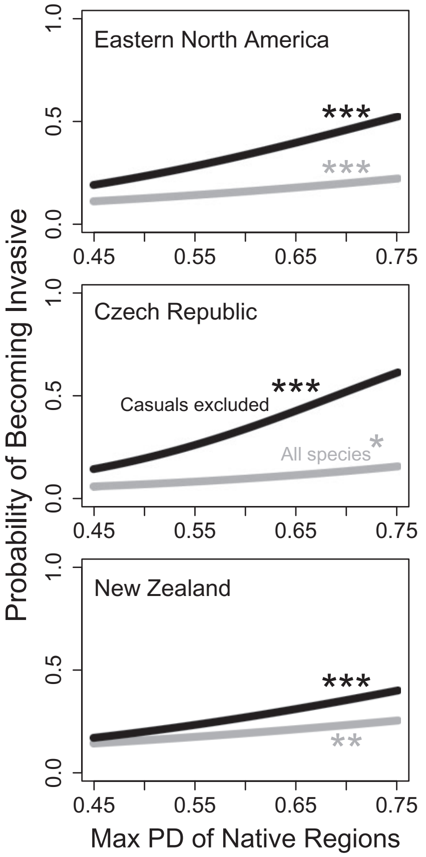

Figure 2 The probability of an introduced (grey) or fully naturalized (black) species becoming invasive increases according to the associated phylogenetic diversity (PD) of its native range, consistent with the evolutionary imbalance hypothesis. Fitted lines are from logistic regression of the model $P(\text{invasive}) = N_{\text{regions}} + \text{PD}_{\text{max}}$, where $P(\text{invasive})$ is whether an introduced or fully naturalized species is recorded as invasive, N_{regions} is the total number of floristic regions that overlap a species’ native range and PD_{max} is the maximum (Faith’s) PD of its native floristic regions (*sensu* Takhtajan, 1986). N_{regions} controls for the tendency of PD_{max} to increase with native range size. PD_{max} is a significant predictor across all six models (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$), and its effect size increases when casual (not fully naturalized) species are excluded. Models are based on samples sizes of 2433 aliens and 1275 fully naturalized aliens for Eastern North America, 1199 and 454 species for the Czech Republic, and 2235 and 1639 species for New Zealand. Pseudo-R^2s for each regression, top to bottom, are: 0.014, 0.030, 0.005, 0.055, 0.003 and 0.0126.

approximately 2433 introduced plant species, of which 431 have become invasive (Fridley, 2008; Table S1 in Supporting Information). Using native distribution information from world floras (Appendix S1), we assigned one or more native floristic regions to each introduced species and estimated the PD of each region using mapped occurrences of 504 angiosperm families (Heywood *et al*., 2007) in a phylogenetic analysis of relative total branch lengths across regions [Faith's (1992) PD; see Appendix S1 for details]. We then took the maximum PD of all regions overlapping a species' native range (PD_{max}) and used PD_{max} as a predictor variable in a logistic regression of whether an introduced species was regarded as invasive. Importantly, because those species native to many regions would by chance have greater PD_{max}, we also used the number of native regions as a predictor in the regression to evaluate the power of PD_{max} independently of native range size. Finally, our datasets allowed us to perform two regressions for each invaded region: one using all introduced species regardless of whether they were fully naturalized, and a more restrictive analysis that disregarded 'casuals' – species of low introduction effort that often regenerate only near parent plants – that should add noise to the PD_{max} signal. Our hypothesis is that PD_{max} will be a more powerful predictor of invasiveness for the subset of fully naturalized species.

For all three regions we examined, PD_{max} was a strong predictor of invasiveness, significantly more so than native range size (Table S1), and increased in effect size when casuals were excluded, as predicted (Fig. 2). The effect size of PD_{max} was largest in the Czech Republic (Fig. 2, middle panel), the region with the longest invasion history, and lowest in New Zealand (Fig. 2, bottom), the most recently invaded region and, as expected for such an isolated flora, the region with the highest total invasion rate. The power of native region PD as a predictor of invasiveness across regions is evidence in support of the EIH and a strong rationale for including properties of the native region of an introduced species in invasive species risk assessments. One can also address the relationship of native range PD and invasiveness at the regional level by modelling the proportion of all naturalized species from a region that become invasive as a function of regional PD, which we present as Fig. S1. To meet independence assumptions, however, this requires us to limit the analysis to only those naturalized species native to a single floristic region. Even with this limitation, the EIH is supported by patterns of invasion in Eastern North America and the Czech Republic (Fig. S1).

Second, we evaluate the EIH by examining the exchange of species between newly connected biotic regions, reasoning that the exchange should be symmetrical when the difference in PD between regions is small and asymmetrical when it is large. All else being equal, there should be a bias of invasion in the direction from regions with a high PD to regions with a low PD. By 'newly connected' we refer to biotic regions that were historically isolated but became connected as a result of shifting land masses, sea level changes or modern canal building. These exchanges provide a strong test of the EIH whenever there is an equal opportunity for dispersal across the connection. The EIH predicts that any bias (or degree of asymmetry) in exchange between regions should be greater than the simple proportional difference in species among regions, the so-called 'null pattern of diversity' (Vermeij, 1991). Vermeij (2005) suggests that this is true in many cases of biotic exchanges that occurred in the palaeontological record, such as in the Trans-Arctic Interchange, when marine molluscs passed from the Pacific to the Atlantic following the submersion of the Bering Land Bridge. In this case, many more genera migrated from the relatively rich Pacific region to the relatively poor Atlantic region than would be expected based purely on proportional sampling of the number of genera (Vermeij, 1991).

Modern connections between previously isolated biotic regions allow for the direct examination of species exchanges. These exchanges vary from highly asymmetrical to symmetrical in relation to differences in PD between regions and the areas to which they are naturally connected (Table 2). Following the construction of the Suez Canal, the biota of the Red Sea, which had been historically connected to the hyper-diverse Indo-Pacific region, became connected to the Mediterranean Sea (Por, 1978). While there are various complications in interpreting all modern species exchanges as a function of species interactions, as opposed to canal flow rates and regional differences in harvest pressure (Ben-Tuvia, 1966; Daniels, 2001; Galil, 2006; Belmaker *et al*., 2013), the flow of species has been almost exclusively from the Red Sea to the Mediterranean, greatly exceeding null expectations for both fishes and molluscs (Table 2). In contrast, the Erie Canal across New York State (USA) connects regions that are likely to have had periodic connections in the Pleistocene (Strayer & Jirka, 1997) and which differ only modestly in the number of species that are unique to each region (Table 2). Consequently, interchanges across the Erie Canal for both fishes and molluscs were not expected to be, and indeed have not been, asymmetrical (Table 2). Similarly, the Panama Canal connects the Atlantic and Pacific freshwater drainages of Panama, which have similar environmental histories and faunas (Aron & Smith, 1971). No asymmetry in exchange of freshwater fishes was expected and none was observed (Table 2).

REFOCUSING INVASION RESEARCH

Invasion biology as a discipline has been largely defined by its search for proximate explanations of species invasions. This exploration has been productive, leading to advances in our understanding of a myriad of basic aspects of ecology and evolutionary biology. This search has occurred, however, largely in the absence of an appropriate biological null model. Recasting invasions as a process that includes not only the interaction of a novel species and a resident community – the classic Eltonian perspective – but also the interaction of species with disparate evolutionary histories – the original Darwinian perspective – should allow for a more comprehensive understanding of modern biological invasions as only the latest chapter in the Earth's long history of biotic interchanges (Vermeij, 1991, 1996; Mack, 2003; Fridley, 2013). It also allows the use of a greater array of predictive tools, including the ecological properties of

Table 2 Species exchanged between formerly isolated regions. Regions naturally connected to phylogenetically diverse regions show asymmetrical exchanges of species with regions that have been historically more isolated, whereas exchanges between regions with more similar histories show symmetrical exchanges. The first two examples were expected and shown to be asymmetrical, defined as a significant difference between the observed and expected ratios of exchange.

Exchange group	Exchange regions	Total number of native species	Exchange pools† (expected ratio)	Species exchanged (observed ratio)
Suez canal				
Marine fishes	Red Sea: Mediterranean Sea	1071:604	1015:548 (1.8:1)	49:7 (7:1)*
Marine molluscs	Red Sea: Mediterranean Sea	1765+:1959§	1765+:1959§	80:0 (80:0)*
Erie canal				
Freshwater fishes	Lake Ontario: Hudson River	110:69	59:18 (3.3:1)	11:3 (2.75:1)¶
Freshwater molluscs	Lake Ontario: Hudson River	62:52	22:12 (1.8:1)‡	10:3 (3.3:1)‡
Panama canal				
Freshwater fishes	Rio Chagres: Rio Grande	36:23	22:9 (2.4:1)	7:5 (1.4:1)

*Asymmetrical exchange ($P < 0.05$).

†Exchange pools reflect the total number of species in each region minus those species shared between regions.

§The number of species recorded for the Red Sea is out of date and underestimates the true count; consequently the number of shared species could not be calculated and the total numbers known were used for the exchange pool.

¶The number of fish invaders in Lake Ontario is contested, with estimates ranging from two to four species (see Appendix S1).

‡Only species in Gastropoda and Unionoida were considered.

an invader's region of origin, which have been largely neglected under the Eltonian paradigm (Fridley, 2011).

Predictions of the EIH also contrast with those of the core Eltonian perspective in several ways. Biotic resistance, an important component of the Eltonian view (Fridley *et al.*, 2007), predicts that a similar number of invaders should be exchanged between regions that have a similar diversity of species, regardless of differences in region age, size or PD, which form the basis of the EIH predictions. For example, an Eltonian view would predict a largely symmetrical exchange of species across the Suez Canal, as the difference in species pools is small, whereas the EIH predicts the large asymmetry that is actually observed (Table 2). Further, because the core Eltonian framework does not consider the origin of an invader, it cannot explain why the identity of problematic invaders is typically shared among regions with similar abiotic conditions (Richardson & Thuiller, 2007), or why the best predictor of invasiveness in a region is whether a species is invasive elsewhere (D'Antonio *et al.*, 2004), both predicted under the EIH. Perhaps most significantly, the EIH does not highlight disturbance or anthropogenic change to ecosystems as precursors to invader dominance, as Elton (1958) and others (Davis *et al.*, 2000) have advocated, which we argue better reflects the reality that disturbance is associated with many (Hobbs & Huenneke, 1992) but by no means all (Rejmánek, 1989; Holm, 1991; Pysek *et al.*, 2002; Mack, 2003) current invasions.

We emphasize that the EIH does not predict outcomes for individual species, but instead predicts trends among species and regions. For example, the EIH predicts that island species should be relatively poor invaders of mainland environments; although this is generally true, there are nonetheless a small number of island species that have invaded continental regions (such as the New Zealand ngaio tree, *Myoporum laetum*, invasive in California). Similarly, the EIH predicts an asymmetry in biotic exchanges, but it is mute on which particular species should invade. The EIH defines a statistical expectation about source areas of invaders and the sensitivity of regions to invasion, and does not imply that all species from a phylogenetically rich region will outcompete those from a phylogenetically poor region in a common environment, or vice versa. Consequently, the EIH provides a framework for estimating risk of invasion among species and regions, but cannot be used to predict the outcome of invasions for particular species in the absence of relevant fitness data. Nonetheless, comparisons of the characteristics of successful invaders and the natives they disadvantage should give great insight into the nature of adaptation for particular environmental conditions. Further, the EIH provides an alternative framework for understanding why the performance of species can change between recipient and donor regions and so is valuable in contextualizing recent integrative frameworks in invasion biology (e.g. Colautti *et al.*, 2014).

IMPLICATIONS FOR CONSERVATION AND ECOSYSTEM FUNCTIONING

The EIH has two important implications for species conservation and the functioning of ecosystems. First, if species invade because they are more finely tuned by natural selection for a particular environment, then over the long term these species are expected to displace native species through competitive dominance. However, whether this process inevitably results in the extinction of native species is unclear, given that competition (as opposed to predation) has yet to be implicated as the sole factor causing the extinction of any species, despite more than five centuries of human-mediated species introductions (Sax & Gaines, 2008). For biotas that inhabit all but the smallest land masses it may well be that sufficient space or marginal habitat exists to stave off competition-induced extinction for centuries, perhaps via further habitat-based selection in native populations. This would additionally explain why there are such large disparities in both historical and modern exchanges between biotas (Vermeij, 1991, 2005) yet subsequently few extinctions (Tilman, 2011). Nonetheless, to prevent severe reductions in native population sizes, particularly on islands but on continents as well, relatively costly control programmes may be the only alternative in lieu of strict introduction controls.

Second, to the extent that the fitness advantage of invaders stems from more efficient conversion of resources into biomass (Funk & Vitousek, 2007), invaders may significantly alter the rates of productivity and nutrient cycling in invaded ecosystems (Liao *et al.*, 2008). This should lead to increases in net rates of biomass production, with possible ramifications for future carbon storage (Wardle *et al.*, 2007), hydrological processes (Sala *et al.*, 1996) and biogeochemistry (Liao *et al.*, 2008). Some of these ecosystem changes may prove detrimental to native species (Burghardt *et al.*, 2010), raising additional hurdles for conservation. In the context of a rapidly changing global environment, balancing conservation risks with the potential functional benefits of invasive species may prove especially challenging.

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Additional references concerning sources of the data used in this study are found at the end of Appendix S1 at [website URL].

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Presentation of an alternative analysis to Fig. 2 using floristic region rather than species as the unit of analysis.
Table S1 ANOVA tables of logistic regressions associated with Fig. 2.
Appendix S1 Detailed methods.

BIOSKETCHES

Jason Fridley is a plant ecologist interested in the assembly of plant communities from local to global scales.

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Editor: Gary Mittelbach

Supporting Information

Fridley, J.D. & Sax, D.F., *The imbalance of nature: revisiting a Darwinian framework for invasion biology*

Appendix S1: Detailed methods

1. Floristic summaries of Takhtajan's floristic regions

Boundaries of the 35 world floristic regions of Takhtajan (1986) were mapped onto a world atlas using Takhtajan's Map 1 and associated text descriptions of regional boundaries. Takhtajan did not describe the floristic richness of each region or the occurrences of particular plant families. Instead, maps of the global distributions of the 504 angiosperm families recognized by Heywood (2007) were used to assign family occurrences to each of the 35 Takhtajan regions. Family occurrences on many small or insular Takhtajan regions, including Uzambara-Zululand (region 11), Karoo-Namib (13), St. Helena and Ascension (14), Fijian (19), Polynesian (20), Hawaiian (21), Neocledonian (22), Guayan Highlands (24), Cape (28), Fernandezian (32), and South Subantarctic Islands (34) could not be accurately identified by the scale of the Heywood (2007) maps and were not included in our analysis. Very few global invaders are endemic to these regions. Because floristic region boundaries are often associated with the spatial turnover of plant distributions at the family level, limits to some family distributions as illustrated by Heywood (2007) were too close to region limits to accurately determine region membership; in these cases regional family membership was assigned conservatively such that small transgressions beyond boundaries were not counted.

Estimates of floristic region phylogenetic diversity

We used family occurrences to calculate Faith's (1992) PD for each Takhtajan floristic region. Faith's PD calculates the total branch length of a particular subset of taxa relative to the total branch length of the full phylogeny, including the root node. PD calculations were performed in Phylocom 4.1 (Webb *et al.* 2008). We standardized the above list of familial occurrences to the taxonomy of the best available angiosperm phylogeny for mega-tree analysis (Stevens 2009), which included removing 101 families that were not recognized in the most recent mega-tree (R20100701.new). The phylogeny of several orders (Dipsacales, Dioscoreales, Fabales) were further revised to reflect updates to the Stevens tree (up to Aug 14, 2010). We calculated Faith's PD with and without aged nodes using the "ages" file supplied in Phylocom (Wikstrom *et al.* 2001) and the 'bladj' algorithm. The use of node ages made little difference to our regional PD estimates (Pearson correlation = 0.97) so we show only un-aged branch lengths. PD and family richness data for each selected region are presented in Table S1.

2. Invasive and naturalized plant data of the Eastern U.S., Czech Republic, and New Zealand

We constructed a database on all naturalized vascular plant taxa present in the Eastern Deciduous Forest of the Eastern USA (state occurrences from MN to LA, east to the coasts of ME to GA, excluding presences unique to FL), broadly coincident with Takhtajan's floristic region 3 (North American Atlantic region). Naturalized species are all those listed as "Introduced" by USDA PLANTS (USDA, NRCS 2008) residing in the above states, and omitting multiple taxa below the species level. Taxa such as *Phragmites australis* with native and exotic populations listed as "Native and Introduced" were not included. Note that naturalized plant species in the U.S. are only tracked by PLANTS if their native range is wholly outside the contiguous U.S., preventing analysis of the contribution of naturalized plants in the Eastern U.S. from Takhtajan's region 4 (Rocky Mountain region). Naturalized plants were categorized as "invasive" if they were represented on the USDA PLANTS Weedy and Invasive Plants list for particular Eastern U.S. regions, including the Northeast U.S. (Uva *et al.* 1997), Kentucky (Haragan 1991), Tennessee/Southeast U.S. (Southeast Exotic Pest Plant Council 1996), or Wisconsin (Hoffman & Kearns 1997), plus any remaining naturalized taxa that were indicated as present in the selected states in the WeedsUS database maintained by the U.S. National Park Service (Swearingen 2008). Our invasive plant definition for ENA is thus a naturalized plant in the Eastern U.S. of significant management concern. Although introduced plants of the Eastern U.S. have not been categorized as 'casual' versus 'fully naturalized' as they have been in other non-native floras, we created a 'casuals' category of non-invasive introduced species as those present in fewer than 10 U.S. counties or those with no herbarium occurrences. The final dataset contained 2433 introduced species, of which 1158 were only casuals and 431 were invasive.

Naturalized and invasive plant taxa of the Czech Republic were obtained from Pyŝek *et al.* (2002), using their status designations of 'casual', 'naturalized', and 'invasive', eliminating hybrids or species of unknown origin. This produced a list of 1199 introduced species, including 745 casuals and 85 invaders. Casual (596) and fully naturalized (1639) plant species of New Zealand were obtained from Howell & Sawyer (2006), with a subset of 399 invaders from Howell *et al.* (2008), after restricting the analysis to species-level taxa and removing species of unknown, hybrid, or cultivation origin.

All naturalized taxa for each dataset were assigned regions of origin (nativity) according to the Takhtajan scheme through online queries to the Germplasm Resources Information Network (USDA, ARS 2008), a central location of floristic distribution information compiled from world floras for listed taxa. In a small but significant number of cases where GRIN records were unavailable or did not clarify species distribution with respect to Takhtajan boundaries, a number of other floras were consulted, including (but not limited to) Flora of North America (FNA Committee 1993+), Flora of China (Wu & Raven 1994+), Flora of Japan (Ohwi *et al.* 1965), Flora Europea (Tutin *et al.* 1964-1980), Flora of the U.S.S.R. (Komarov 1934-1964), and, when necessary due to absence in a flora, specimen distribution information available online at TROPICOS (version 1.5, Missouri Botanical Garden, http://mobot.mobot.org/W3T/Search/vast.html). Online databases were accessed between and 2007 and 2011.

3. Methods for biotic interchanges across the Panama, Erie and Suez Canals

Ascribing with certainty the movement of species by natural means across a canal is rarely possible (Daniels 2001). Instead, we have considered species that are likely to have dispersed across a canal or been moved by ships using these canals. Similarly, differences in physical conditions on either side of a canal, as well as conditions within canals, are likely to serve as a strong filter on which species are capable of dispersing or becoming established (Aron & Smith 1971). Nevertheless, the differences or similarities in numbers of species exchanged across such artificial bodies is instructive, particularly in aggregate across several canals, in evaluating whether such evidence is consistent with the predictions of EIH. In each case we examined evidence of an asymmetry between observed and expected frequencies with a binomial model that tested the null hypothesis that the actual number of exchanged species in one region (N) is consistent with that expected from N random draws from the overall (exchanged) species pool. We describe each of our five cases below.

Suez Canal – Marine Fishes: The number of native species of fishes for the Red Sea is from Golani & Bogorodsky (2010), whereas the number for the Mediterranean was tabulated from FishBase (Froese & Pauly 2008). The number of shared native species between regions was determined by comparing species lists generated from FishBase for both regions. The number of non-native species in the Mediterranean of Red Sea origin were tabulated by cross-checking the total list of established exotic fishes in the Mediterranean (Zenetos *et al.* 2010) against those native to the Red Sea (Golani & Bogorodsky 2010). The number of fishes of Mediterranean origin in the Red Sea are from Golani (1999). If we had compared Red Sea invaders against only those species in the Eastern Mediterranean, the numbers of species would have changed relatively little and the significant asymmetry of the result presented in Table 2 would still be below a P value of 0.05. The number of native species in the Eastern Mediterranean is 408 and the number of non-natives from the Red Sea is 48. Finally, although we listed seven species as being established in the Red Sea, several are restricted to the Northern Gulf of Suez region, in relatively close proximity to the Canal; four species are found in other parts of the Red Sea (Golani 1999), but none of these species appear to be widely distributed (Por & Dimentman 2006). This is in sharp contrast to fishes that have invaded the Mediterranean, which have become so abundant that they are now commercially important (Boudouresque 1999).

<u>Suez Canal – Marine Mollusks</u>: The number of native species of mollusks for the Red Sea is from Dekker & Orlin (2000), whereas the number for the Mediterranean is from Coll *et al.* (2010). The number of shared native species between regions was not evaluated, but is likely to be small; however, given the observed exchange values, even a large number of shared species would not change the significance of the asymmetry observed. The number of non-native species in the Mediterranean of Red Sea origin was tabulated by cross-checking the total list of established exotic mollusks in the Mediterranean (Zenetos *et al.* 2010) against those native to the Red Sea, as determined by accessing one or more of several online databases, including A Biotic Database of Indo-Pacific Marine Mollusks, CIESM.org, World Register of Marine Species, and other sources. The presence of Mediterranean invaders in the Red Sea was evaluated by consulting Barash & Danin (1987), Dekker & Orlin (2000), and Rusmore-Villaume (2008). From these publications,

four candidate invaders arise, but each can be shown to be species already present in the Red Sea before the opening of the Suez Canal or not clearly having established populations in the Red Sea. The number of native species recorded for the Red Sea is an underestimate of the actual number (Dekker & Orlin 2000). The true number is difficult to determine and will only become apparent with further study. Nevertheless, even a doubling of this number would not change the statistical significance of the asymmetry indicated in Table 2. Finally, as in the fishes described above, some mollusk species invading the Mediterranean have become abundant and invasive (Gofas & Zenetos 2003).

<u>Erie Canal Freshwater Fishes</u>: The numbers of native species of fishes for the Lake Ontario Basin and for the Hudson River Basin, which includes the Hudson and Mohawk drainages, are from Carlson & Daniels (2004). Species that were exclusively estuarine in distribution were excluded from these counts. The number of non-native species are from Mills *et al.* (1993, 1997) and Owens *et al.* (1998). The number of species of fishes established in the Lake Ontario Basin that are from the Hudson River Basin is disputed; we indicated 3 species in Table 2, but there are four potential candidates and we believe that the actual number is likely to be 2 or 3 species. One species, *Morone americana* (white perch), clearly dispersed from the Hudson River Basin to Lake Ontario through the Erie Canal (Mills *et al.* 1993). A second species, *Alosa aestivalis* (blueback herring), was first observed in Lake Ontario in 1995 (Owens *et al.* 1998). The only other known observation in Lake Ontario was an adult caught in 2006 (Robert O'Gorman, pers. comm.), but the length of time between sightings suggests that this species might be established in Lake Ontario in low numbers. A third species, *Alosa pseudoharengus* (alewife), while of contested origin in Lake Ontario (Mills *et al.* 1993), appears based on allozyme variation, to have invaded Lake Ontario from the Hudson River Basin (Ihssen *et al.* 1992). The status of fourth species, *Petromyzon marinus* (sea lamprey), is debated in the literature (Eshenroder 2009; Waldman *et al.* 2009), but the preponderance of data seems to indicate that it is native to

Lake Ontario. Even if the final tally of invaders to the Lake Ontario Basin is only two species, the exchange is still not significantly asymmetrical; consequently the results shown in Table 2 are robust to the range of possible invaders reported in the literature.

Erie Canal Freshwater Mollusks: Freshwater species in the family Sphaeriidae (order Veneroida) were excluded from consideration because of the limited information available on the their current and historical distributions. The numbers of freshwater species of Gastropoda and Unionoida that are natives and invaders were determined from several sources (Strayer 1987, 1990; Jokinen 1992; Strayer & Jirka 1997); Strayer, pers. comm.). Species that invaded through the Erie Canal, but which are not native to one of the two basins were excluded from all counts; this excludes Eurasian invaders, as well as species native to North America that invaded the Lake Ontario Basin and subsequently invaded the Hudson River Basin. Species only observed once within the invaded range were also excluded. Species observed at two or more locations with an invaded basin were considered to have been established and hence included in the species counts. Many of the native and invader species may no longer be established in these basins due to changes in environmental conditions, including pollution of aquatic environments (Strayer & Jirka 1997). The numbers of species listed in Table 2 represent a best estimate, but there is some uncertainty in these numbers as a consequence of limited current and historical distribution data, as well as disagreements over the taxonomy of some species (Jokinen 1992; Strayer & Jirka 1997). Two additional species not included in our counts, *Alasmidonta undulata* and *Lampsilis cariosa*, may have invaded the Lake Ontario Basin, although they may have arrived under their own power prior to the establishment of the Erie Canal (Strayer & Jirka 1997). Similarly, one additional species, *Elimia livescens*, that did invade the Hudson River Basin through the Erie Canal, was not included in our counts because it is probably not native to the Lake Ontario Basin (Jokinen 1992). However, the results presented in Table 2 are robust to the decision to exclude these species, because if we had included them the observed exchange ratio would have become even closer to the expected ratio, i.e., even more symmetrical.

Panama Canal Freshwater Fishes: The numbers of native and naturalized species from both drainages are from Smith *et al.* (2004).

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Table S1. ANOVA tables for logistic regressions shown in Fig. 2 (***P<0.001, **P<0.01, *P<0.05).

ENA

Using all alien species (N = 2433)

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -3.40041    0.42970  -7.913  2.5e-15 ***
totregions   0.09783    0.03270   2.992 0.002774 **
maxPD        2.72830    0.75779   3.600 0.000318 ***

Null deviance: 2272.6; Residual deviance: 2235.8
```

Using only fully naturalized aliens (N = 1275)

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -3.72095    0.50284  -7.400 1.36e-13 ***
totregions  -0.02513    0.03900  -0.644    0.519
maxPD        5.11084    0.90102   5.672 1.41e-08 ***

Null deviance: 1544.3; Residual deviance: 1507.8
```

Czech Republic

Using all alien species (N = 1199)

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -4.28486    1.03872  -4.125  3.7e-05 ***
totregions  -0.19005    0.09072  -2.095   0.0362 *
maxPD        3.70079    1.87994   1.969   0.0490 *

Null deviance: 613.8; Residual deviance: 607.6
```

Using only fully naturalized aliens (N = 454)

```
Estimate Std. Error z value Pr(>|z|)
(Intercept)  -4.7579     1.1405  -4.172 3.02e-05 ***
totregions   -0.4382     0.1061  -4.129 3.65e-05 ***
maxPD         7.5368     2.1040   3.582 0.000341 ***

Null deviance: 437.8; Residual deviance: 415.1
```

New Zealand

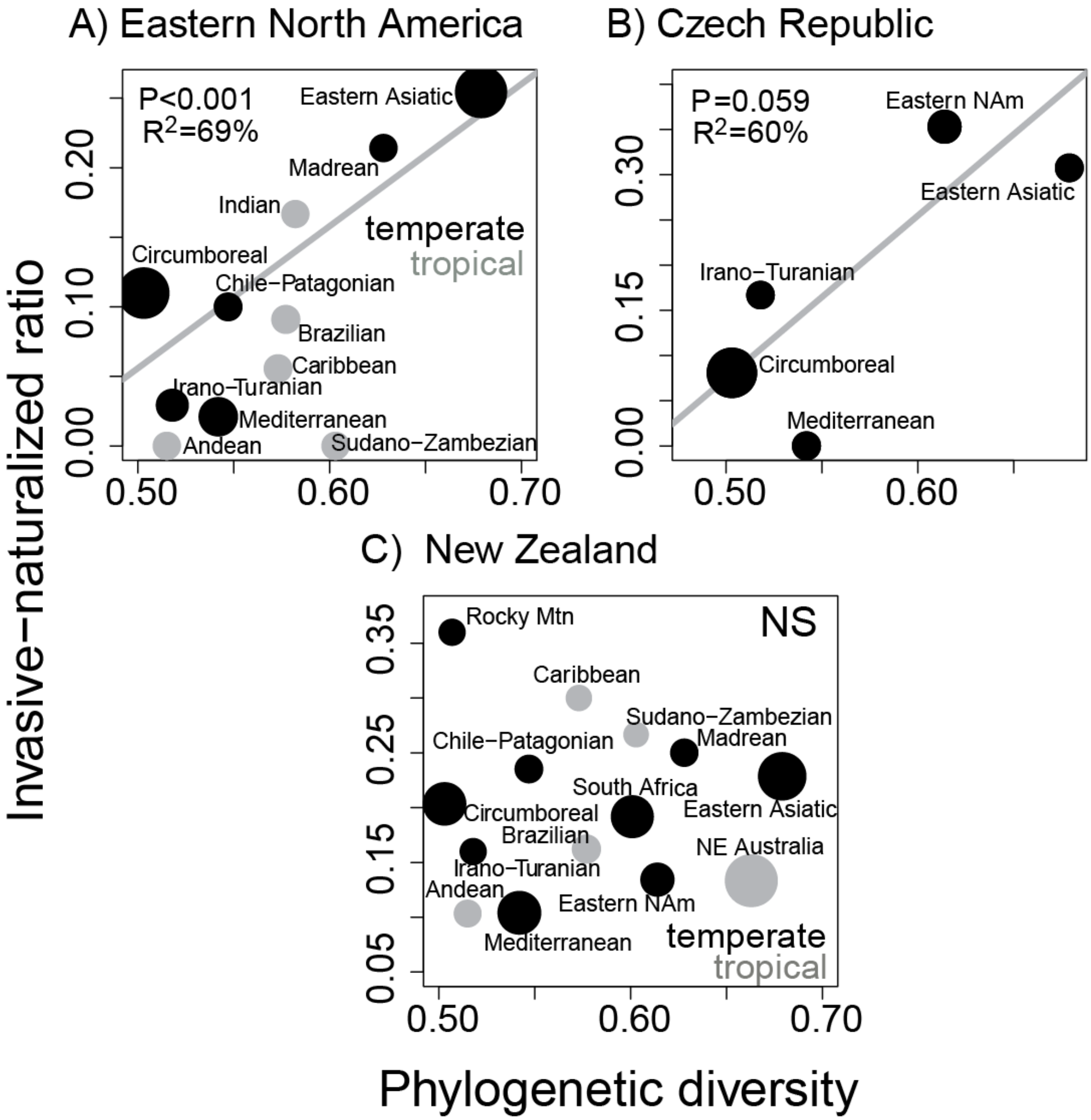
Using all alien species (N = 2235)

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -2.73514    0.49511  -5.524 3.31e-08 ***
totregions  -0.00733    0.02804  -0.261  0.79375
maxPD        2.19877    0.84608   2.599  0.00936 **

Null deviance: 2179.9; Residual deviance: 2172.4
```

Using only fully naturalized aliens (N = 1639)

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -3.13999    0.52662  -5.963 2.48e-09 ***
totregions  -0.07062    0.03157  -2.237   0.0253 *
maxPD        3.69220    0.90612   4.075 4.61e-05 ***

Null deviance: 1819.3; Residual deviance: 1799.0
```

Figure S1. Floristic region-based analysis of global invasion patterns as a function of phylogenetic diversity (PD). An alternative analysis to that presented in Fig. 2 examines the relationship of native range PD and species invasiveness at the level of global floristic regions (Takhtajan 1986) rather than at the individual species level. To allow for statistical independence between regions, this analysis only considers the subset of species introduced to a region that are endemic (as natives) to a single floristic region. Further, for all three invaded regions examined, an invader donor region was included only if represented by 10 or more naturalized species. Analyses include 906 naturalized species endemic to a single floristic region for Eastern North America (ENA), 172 for the Czech Republic, and 1007 for New Zealand. (A) In ENA there is a positive relationship between the phylogenetic diversity (Faith's [1992] PD) of particular floristic regions (Takhtajan 1986) and the percentage of naturalized plants endemic to those regions that are invasive, with points scaled to the total number of naturalized species represented in the ENA flora. Regions are categorized as temperate (black circles) or tropical (grey circles) according to whether they are principally above or below 23.5° latitude (N or S); for those regions that overlap these latitudes, plant families found only in the tropics were excluded from calculations of PD. Dashed line is least squares regression weighted by total naturalized species in the ENA flora contributed by each region. (B) A similar pattern is found for the naturalized and invasive floras of the Czech Republic, using the same methods as in (A), with a further restriction of species found in natural or semi-natural habitats. (C) PD does not predict a region's invasiveness in New Zealand when limited to endemics (as described above), using the same methods as in (A).


A) Eastern North America
P<0.001
R2=69%
Eastern Asiatic
Madrean
Indian
temperate
tropical
Circumboreal
Chile−Patagonian
Brazilian
Caribbean
Irano−Turanian
Mediterranean
Andean
Sudano−Zambezian
0.00
0.10
0.20
0.50
0.60
0.70
B) Czech Republic
P=0.059
R2=60%
Eastern NAm
Eastern Asiatic
Irano−Turanian
Circumboreal
Mediterranean
0.00
0.15
0.30
0.50
0.60
C) New Zealand
NS
Rocky Mtn
Caribbean
Sudano−Zambezian
Chile−Patagonian
Madrean
South Africa
Circumboreal
Eastern Asiatic
Brazilian
NE Australia
Irano−Turanian
Andean
Eastern NAm
Mediterranean
temperate
tropical
0.05
0.15
0.25
0.35
0.50
0.60
0.70
Invasive−naturalized ratio
Phylogenetic diversity