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.

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, \(\varepsilon\)). (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.

<table>
<thead>
<tr>
<th>Behaviour or adaptation</th>
<th>Manifestation</th>
<th>Invaded region</th>
<th>Exemplars</th>
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</thead>
<tbody>
<tr>
<td>Cold tolerance</td>
<td>Tree line elevation</td>
<td>Southern Hemisphere, islands</td>
<td>Northern conifers (e.g. <em>Picea engelmannii</em>); Körner &amp; Paulsen (2004)</td>
</tr>
<tr>
<td>Salt tolerance</td>
<td>Coastal grassland dominance</td>
<td>California</td>
<td>Iceplant (<em>Mesembryanthemum crystallinum</em>); Vivrette &amp; Müller (1977)</td>
</tr>
<tr>
<td>Shade tolerance</td>
<td>Rain forest dominance</td>
<td>Hawaii</td>
<td>Strawberry guava (<em>Psidium cattleianum</em>); Pattison et al. (1998)</td>
</tr>
<tr>
<td>Inundation tolerance</td>
<td>Tidal mud-flat colonization</td>
<td>Western USA</td>
<td>Cordgrass (<em>Spartina anglica</em>); Mack (2003)</td>
</tr>
<tr>
<td>Tolerance of shifting sands</td>
<td>Coastal dune colonization</td>
<td>South Africa, New Zealand, western USA</td>
<td>European beachgrass (<em>Ammophila arenaria</em>); Mack (2003)</td>
</tr>
<tr>
<td>Drought, fire tolerance of tree growth form</td>
<td>Tree colonization of arid or fire-prone grasslands</td>
<td>Brazil, central Europe, South Africa, Pacific islands</td>
<td>Trees including pines (<em>Pinus</em> spp.) and black locust (<em>Robinia pseudo-acacia</em>); Rejmánek (1989) and Mack (2003)</td>
</tr>
<tr>
<td>Mating system and cooperative social organization</td>
<td>Supercoloniality (‘invasive ant syndrome’)</td>
<td>Global</td>
<td>Invasive garden ant (<em>Lasius neglectus</em>); Cremer et al. (2008)</td>
</tr>
<tr>
<td>Foraging efficiency</td>
<td>Ant invasions</td>
<td>Islands</td>
<td>Little fire ant (<em>Wasmannia auropunctata</em>); Le Breton et al. (2005)</td>
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J. D. Fridley and D. F. Sax tested tenet of conservation genetics (Leimu et al., 2010) that the correlation of population size and genetic diversity is a well-supported phenomenon. In general, tenets of larger plant population sizes and genetic variation have a higher reproductive power. This was the original mechanism of invasion invoked by Darwin (1859) in consideration of 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.

PHYLLOGENETIC 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 \( P(\text{invasive}) = N_{\text{region}} + PD_{\text{max}} \), where \( P(\text{invasive}) \) is whether an introduced or fully naturalized species is recorded as invasive, \( N_{\text{region}} \) is the total number of floristic regions that overlap a species’ native range and \( PD_{\text{max}} \) is the maximum (Faith’s) PD of its native floristic regions (sensu Takhtajan, 1986). \( N_{\text{region}} \) controls for the tendency of \( PD_{\text{max}} \) to increase with native range size. \( PD_{\text{max}} \) 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’s 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 (PDmax) and used PDmax 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 PDmax, we also used the number of native regions as a predictor in the regression to evaluate the power of PDmax 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 PDmax signal. Our hypothesis is that PDmax will be a more powerful predictor of invasiveness for the subset of fully naturalized species.

For all three regions we examined, PDmax 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 PDmax was largest in the Czech Republic (Fig. 2, middle panel), the region with the lowest 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.

<table>
<thead>
<tr>
<th>Exchange group</th>
<th>Exchange regions</th>
<th>Total number of native species</th>
<th>Exchange pools† (expected ratio)</th>
<th>Species exchanged (observed ratio)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suez canal</td>
<td>Marine fishes</td>
<td>Red Sea: Mediterranean Sea</td>
<td>1071:604</td>
<td>1015:548 (1.8:1)</td>
</tr>
<tr>
<td></td>
<td>Marine molluscs</td>
<td>Red Sea: Mediterranean Sea</td>
<td>1765+1959§</td>
<td>1765+1959§</td>
</tr>
<tr>
<td>Erie canal</td>
<td>Freshwater fishes</td>
<td>Lake Ontario: Hudson River</td>
<td>110:69</td>
<td>59:18 (3.3:1)§</td>
</tr>
<tr>
<td></td>
<td>Freshwater molluscs</td>
<td>Lake Ontario: Hudson River</td>
<td>62:52</td>
<td>22:12 (1.8:1)‡</td>
</tr>
<tr>
<td>Panama canal</td>
<td>Freshwater fishes</td>
<td>Rio Chagres: Rio Grande</td>
<td>36:23</td>
<td>22:9 (2.4:1)</td>
</tr>
</tbody>
</table>

*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 (Hobb & Hueneke, 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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REFERENCES


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

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