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# Diversification, Biotic Interchange, and the Universal Trade-Off Hypothesis

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**ABSTRACT:** Competition theory predicts that multispecies coexistence requires that species have traits that fall on the same interspecific trade-off surface. Fossil records for mollusks, mammals, trees, and other taxa show that with rare exception, ecologically similar species have coexisted for a million years or more after interchange between formerly isolated realms. This coexistence suggests the possibility, termed the universal trade-off hypothesis, that ecologically similar species of different realms have been bound to the same interspecific trade-off surface despite millions of years of independent evolution. Such persistence fails to support the biogeographic superiority hypothesis, which posits that genetic drift, recombination, mutation, and selection would cause taxa of one realm to gain superiority over those of another realm during long periods of isolation. Analysis of the lengths of time that species have persisted once in contact suggests that the trade-off surfaces of realms differed by <0.1% at the time of interchange. This implies that macroevolutionary patterns of differentiation and speciation within and between realms were more likely the movement of traits on a common trade-off surface rather than directional selection achieved without compensatory trade-offs and costs. The existence of transrealm trade-offs, should further work support this possibility, has deep implications for ecology and evolution.

*Keywords:* coexistence, invasion, trade-offs, speciation, biotic interchange.

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## Introduction

The tree of life, founded about 3 billion years ago by a single ancestral species, now contains on the order of 5 million species (May 2010). The fossil record shows that diversity has been generally increasing throughout the history of life on earth, albeit with bursts of both speciation and extinction and periods of stasis (e.g., Sepkoski 1984, 1996; Benton and Emerson 2007). This article compares the paleontological patterns of displacement or coexistence that occurred as new taxa arose and migrated between

biogeographic realms with the predictions of competition theory in order to address several fundamental questions. In particular, does the ongoing accumulation of species imply that existing and novel species frequently coexisted during life's diversification (e.g., Vermeij 1991*b*; Benton 1995, 1996)? If so, what underlying mechanisms might explain why natural selection and vicariance events generally produced species incapable of displacing existing taxa? What mechanisms could explain why taxa that had evolved in different biogeographic realms with little, if any, gene flow for millions to tens of millions of years or that had markedly different phylogenetic origins might coexist with each other when brought into contact?

A central tenet of evolutionary theory is that individuals within a species accumulate traits that let them better deal with the hostile forces of their environment. It might seem reasonable to assume that within individuals of a species, selection would continually favor any traits that increased competitive ability and/or resistance to predation, pathogens, and disease and that accumulation of such traits within a species would consequently allow it to displace other species with which it had been coexisting but which had not acquired comparable advantages. In this regard, it is important to note that individuals can gain competitive ability not only through increased abilities to acquire or efficiently use limiting resources but also through increased resistance to predation, pathogens, disease, or any other sources of loss, since lower loss rates decrease the mean levels of limiting resources required for survival and reproduction (Tilman 1982; Louda et al. 1990; Keane and Crawley 2002; Shea and Chesson 2002). Similarly, species that gained increased dispersal and colonization ability without a cost to competitive ability could displace competing species with which they had been coexisting because of a competition-colonization trade-off (Tilman 1994).

Although Darwin described interspecific interactions such as competition and predation as hostile forces of nature that shaped the evolution of species, little was known then about their prevalence or underlying mech-

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anisms. We now know that competition, predation, and mutualism are major forces determining the presence and abundances of species (Connell 1983; Schoener 1983). Competition is a prevalent force. For example, for species of land birds, Ricklefs (2010) showed that both the range of habitats occupied and the local abundances of bird species were lower in geographic regions that had more bird species. Moreover, mechanistic theories of interspecific interactions predict that the long-term stable persistence of trophically and ecologically similar species results from interspecific trade-offs that couple superiority for some environmental and/or biotic conditions with inferiority for others (e.g., MacArthur 1972; Levin et al. 1977; Levins 1979; Tilman 1982, 1988, 1994; Tilman and Pacala 1993; Holt et al. 1994; Leibold 1996; Molofsky et al. 1999; Chesson 2000; Rees et al. 2001; Bever 2003; Chase and Leibold 2003; Rudolf and Antonovics 2005; Chesson and Kuang 2008). In contrast, as theoretically developed later, the emergence in one realm of novel species that had traits that fell on an interspecific trade-off surface superior to that of a second realm could lead to the extinction of the established species of the second realm.

Might we expect natural selection to have consistently generated new species with traits and trade-offs that caused them to persist with established species? Or might new species have traits that made them superior overall to established taxa of their own or other realms? Let us consider two alternative possibilities. The biogeographic superiority hypothesis posits that the biota of two or more biogeographic realms would slowly diverge one from the other over the course of millions of years following their isolation. Divergence would result from the random forces of recombination, mutation, isolation, and drift; from selection in response to environmental differences among the realms; and from different coevolutionary dynamics within each realm. Divergence would be accelerated if realms differed in their sizes, since larger populations should accumulate greater genetic diversity, allowing selection to lead to more rapid evolution and eventually to superiority relative to initially similar taxa of the smaller realm. The end result of such divergence could be that the trade-off surface of taxa from one realm became superior to that of taxa from another. Thus, the biogeographic superiority hypothesis predicts that longer periods of isolation and greater differences in the size of realms would lead to greater divergence and thus to greater species displacements if realms came back into contact.

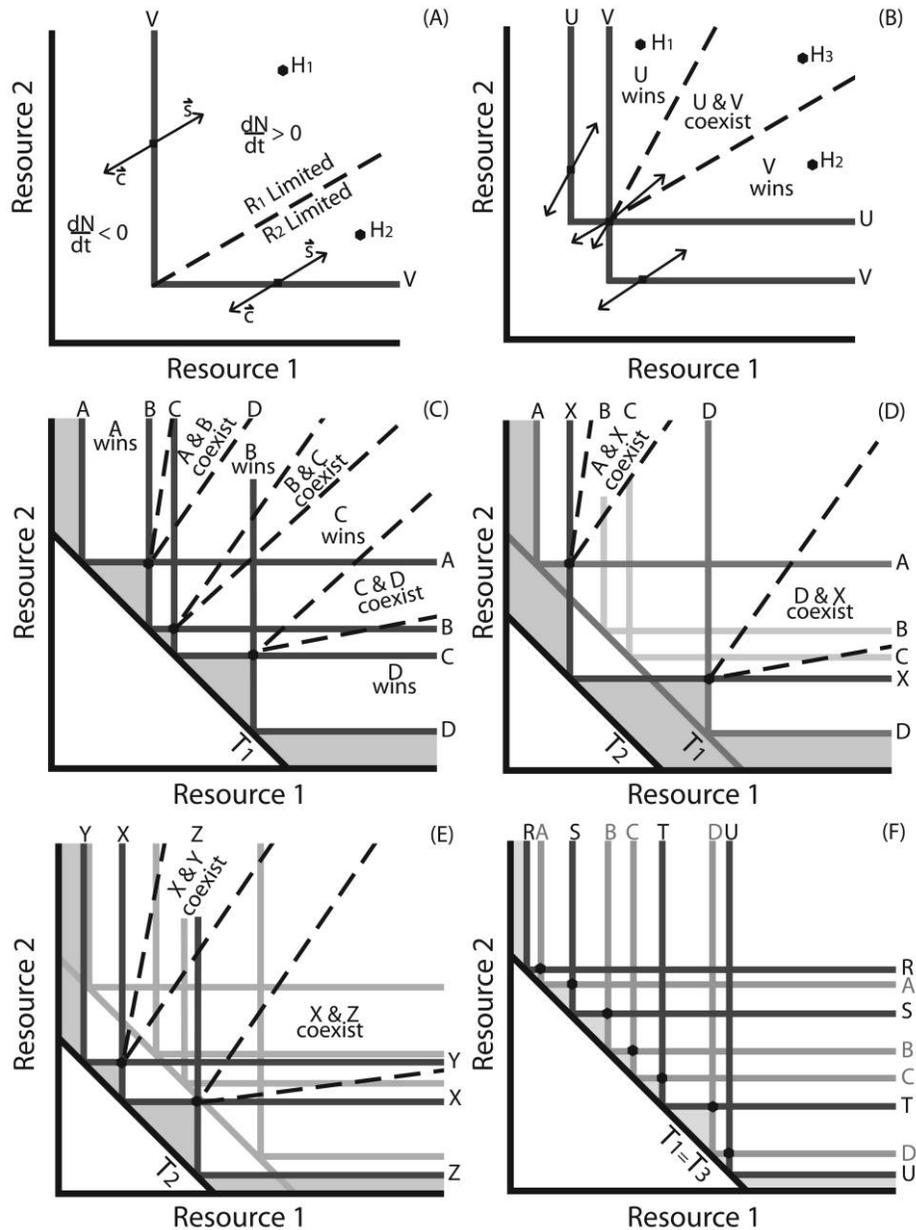
At the other end of the spectrum, the universal trade-off hypothesis posits that all ecologically similar taxa of all realms and of all phylogenetic histories share the same deep constraints and unavoidable trade-offs, causing all trophically similar species of all realms to have traits that fall at various points on the same trade-off surface (e.g.,

Tilman 1988, 2004; Chase and Leibold 2003). The trade-off surface reflects the full range of evolutionarily sustainable interspecific differences in the responses of species to limiting factors. The growth isoclines of species are constrained to being no better than tangent to the interspecific trade-off curve (fig. 1C, 1F). The universal trade-off hypothesis predicts that the appearance of novel species from other realms would not cause extinction of trophically and ecologically similar species. Rather, established and invading species, while affecting each other's abundances, would persist with each other within a realm despite millions of years of separation and independent evolution and radiation, precisely because all had evolved while bound to the same universal trade-off surface.

In this article, I first review published studies to evaluate the prevalence of species persistence, displacement, establishment, or exclusion following experimental species additions, anthropogenic introductions during the past 5 centuries, and speciation and interchange events as documented in the fossil record. I use these data to determine whether, in general, species from one biogeographic realm have invaded into and coexisted with the established species of other realms, as predicted by the universal trade-off hypothesis, or whether they displaced species of other realms once in contact and resisted invasion themselves, as predicted by the biogeographic superiority hypothesis. I then develop an expanded theory of interspecific trade-off surfaces that allows a more mechanistic interpretation of the results reviewed. Finally, I must note that this article evaluates the causes and implications of patterns of multispecies persistence or exclusion at the spatial scale of entire biogeographic realms precisely because consistent patterns at this scale would be strong evidence of major factors that structured the evolutionary process and its impacts on diversity and community composition.

### Short-Term Studies

Experimental additions of seed of new plant species to sites have generally increased plant diversity and rarely displaced established species (e.g., Cavers and Harper 1967; Thompson and Baster 1992; Tilman 1997; Turnbull et al. 2000; Myers and Harms 2009). For birds, Cassey et al. (2004) report a median success rate of 38% for 646 introduction attempts, in which a total of 149 bird species became established in new regions. These introduced species did not lead to any reported extinctions of established bird species; rather, they coexisted with the native species. The construction of the Suez Canal joined together the Red Sea and the Mediterranean Sea, which had been separated for millions of years. The subsequent movement of about 250 marine species over the past 140 years from the Red Sea into the Mediterranean has not led to any reported



**Figure 1:** Competition for two resources. *A*, The right-angle line labeled *V* is the resource-dependent zero net growth isocline ( $dN/dt = 0$ ) for species *V*. It shows the concentrations to which  $R_1$  and  $R_2$  are reduced by an equilibrated population of species *V*.  $R_1$  and  $R_2$  are essential resources. Species *V* is limited by  $R_1$  for supply points, such as  $H_1$ , above the dashed line and by  $R_2$  below it. Consumption vectors,  $\mathbf{c}$ , of a species are parallel to its dashed line. Supply vectors,  $\mathbf{s}$ , point at their associated supply point. *B*, Competition between species *U* and *V*, showing supply points for which species *U* displaces species *V*, species *U* and *V* coexist, or species *V* wins. *C*, Competition between four species (*A*, *B*, *C*, and *D*) that are bound to the same trade-off curve,  $T_1$ . Species *A* is the best competitor for  $R_1$  and the worst for  $R_2$ , and species *D* is the worst competitor for  $R_1$  and the best for  $R_2$ . Species *B* and *C* have intermediate trade-offs. There are regions of resource supply ratios for which each species persists and coexists. *D*, Competition between species of two realms that have different trade-off curves. Species *X*, bound to superior trade-off curve  $T_2$ , would displace species *B* and *C*, but there are resource supply ratios where species *A* and species *D* coexist with it. *E*, Competition as in *B* but where three species (*X*, *Y*, and *Z*) from realm 2 invade realm 1. Species *X*, *Y*, and *Z* would displace species *A*, *B*, *C*, and *D*. *F*, Competition between species of two realms that have identical trade-off curves  $T_1$  and  $T_3$ . There are regions of resource supply ratios for which each species (*A*, *B*, *C*, *D*, *R*, *S*, *T*, and *U*) persists and coexists with another species (unmarked). See Tilman (1982, 2004) for further details.

extinctions (Por 1978; Mooney and Cleland 2001). Similarly, the introduction of five molluscan species to the North Sea during historic times also did not lead to extinctions (Vermeij 1991*b*).

Because oceanic islands are far from mainland habitats, novel plant species rarely invaded until large-scale human-mediated oceanic transport began about 500 years ago. The introduced plant species that have become naturalized have essentially doubled plant diversity on oceanic islands, with the mean increase in species numbers being 97% across 13 islands, including New Zealand and the Hawaiian Islands (Sax et al. 2002). This doubling was associated with a loss of 3.3% of native plant species. Data are insufficient to determine the extent to which introduced and native species coexist in truly undisturbed habitats, but their seeming persistence has occurred despite the introduced species coming from a variety of biogeographic realms and phylogenetic groups and often having had millions of years of evolutionarily distinct histories. Similarly, within the 49 continental United States, naturalized exotic plant species introduced during the post-Columbian era have increased plant species numbers per state by an average of 20% (Sax and Gaines 2003). Davis (2003) also noted that invasive species have rarely caused extinction of native species on their same trophic level. Blackburn et al. (2005) showed that some predators that have invaded islands have led to extinctions of their prey species, especially prey species that had evolved on islands devoid of such predators. Although no North American tree species have been driven to extinction by introduced diseases, some once-dominant tree species have experienced massive declines in abundance from exotic diseases or pests, including chestnut and elm.

On a longer timescale, the poleward movement and intermingling of tree species in North America following glacial recession showed that many species that had lived in geographically separated refuges during glacial periods have coexisted over the 5,000–10,000 years that they have been together (Davis 1986). Pielou (1991) reported similar patterns of coexistence in North American vertebrate taxa as they expanded poleward after glacial recession. In total, these cases show a surprising persistence of species after they come to occupy the same regions or realms.

## Paleontological Studies

### *Marine Interchanges*

A longer-term perspective is provided by the fossil record. At about 450 Ma, during the Upper Ordovician, a major invasion of midcontinent North American subtidal marine ecosystems, called the Richmondian invasion, occurred (Patzkowski and Holland 1993). Species of corals, bryo-

zoans, arthropods, echinoderms, mollusks, and brachiopods from a western tropical region invaded eastward. More than 27,000 subtidal organisms from 490 samples were collected from fossil sites within a 150 × 250-km portion of the invaded eastern region, with the collection focusing on four stratigraphic levels, each separated by ~1 million years (Patzkowski and Holland 1993, 2007). Comparison of preinvasion communities with postinvasion communities revealed three major patterns. First, invasion caused a denser packing of species along the nearshore to offshore gradient, with species diversity increasing by more than 40%. Second, established species and invaders subsequently coexisted for at least 1 million years. Third, invading species were neither disproportionately rare nor abundant; rather, they attained about as wide a range of relative abundances as established taxa. Although some invaders were locally dominant and displaced established taxa from particular sites, they were rare in other regions, and their invasion did not lead to regional extinctions. Indeed, the rate of species extinction (turnover) was indistinguishable before and after the invasion event (Patzkowski and Holland 2007).

At about 3.5 Ma, the Bering Strait opened, allowing movement between the north Pacific and Atlantic oceans (Vermeij 1991*a*). From ~30 Ma until then, these oceans had been separate realms, each containing invertebrate taxa that had evolved during that period of separation. Of ~300 species of mollusks that moved between realms, ~85% were from the Pacific into the Arctic and Atlantic (Vermeij 1991*a*). This biased migration corresponded to a large number of premigration extinctions in the Atlantic. Vermeij (1991*a*) found no evidence that North Sea (Atlantic) bivalves experienced extinctions caused by the Pacific invaders. Indeed, when comparing five different periods from the early Pliocene (5.3–3.6 Ma) through the Late Pleistocene (120–10 Ka), there was no positive dependence of extinction on the number of invading species but rather a weak and nonsignificant trend in the opposite direction. Thus, invading and established species coexisted with each other after a massive interchange at ~3.5 Ma and continue to coexist today. Vermeij (1989, p. 275) concluded, “Although biotic interchange may have many important biological consequences for species in the recipient biota, extinction is an unlikely consequence in marine biotas involved in marine interchange.”

Intervening warm tropical waters generally prevented biotic interchanges between Northern Hemispheric and Southern Hemispheric temperate or arctic marine regions (Lindberg 1991). However, during the Pliocene (~5 Ma) and then the Pleistocene (~2 Ma), there were two major periods of transequatorial interchange of marine mammals, mollusks, and macro algae for both polar and temperate marine ecosystems. In reviewing these interchanges,

Lindberg (1991, p. 319) concluded that endemics coexisted with invaders in the invaded realms and that “none of the antitropical distributions reviewed here suggests that the arrival of a taxon in the adjoining hemisphere resulted in the extinction of an endemic taxon.”

In total, the Richmondian, Bering, and transequatorial interchanges show that marine organisms that had evolved in isolation for millions of years coexisted once in contact. Given the large numbers of species that migrated, the relatively short life spans of invertebrates and macroalgae taxa, the millions of years that they had evolved in separate realms, and the millions of years they coexisted postmigration, these results and others (e.g., Gould and Calloway 1980) suggest a universality of coexistence of marine taxa rather than of competitive displacement.

#### *Terrestrial Land Bridges*

During the Miocene (~24–5 Ma), Asia and North America were periodically joined by the Bering land bridge. Repeated reciprocal migrations of mammals across this land bridge contributed to diversity in Eurasia, Africa, and North America (Flynn et al. 1991; Webb 1991, 2006). North America, for instance, accumulated ~60% greater mammalian diversity than South America, which had been isolated during most of the Miocene (Webb 1978, 1991). North American taxa, including grazers and browsers (such as horses, oreodonts, dromomerycids, and camels) and predators and scavengers (such as cheetahs, short-faced bears, running hyenas, and dogs/wolves), coexisted with their Eurasian and African counterparts when they entered those continents (Flynn et al. 1991). Similarly, mastodonts, gomphotheres, cats, rhinos, pronghorn antelope, and bears entered North America from Asia and coexisted with the resident fauna (Webb 1991, 2006; Benton 1995, 1996; Flannery 2001). For instance, Flynn et al. (1991) found that well-documented arrivals of mammals from North America, Africa, and Europe were not associated with changes in the extinction rates of extant Asian mammals. Similarly, in reviewing global patterns of diversification, Benton and Emerson (2007, p. 37) concluded that there “is no evidence that rapidly speciating clades have reached a limit, nor that they are driving other clades to extinction.”

South America was isolated from all other realms from ~32 Ma until the Isthmus of Panama connected it to North America at ~3 Ma. From ~9 to 4 Ma, some South American birds and ground sloths migrated into and persisted in North America (Vrba 1992). Similarly, some North American birds, mainly *Icteridae* (blackbirds), migrated to the south (Weir et al. 2009), as did some *Procyonids* (raccoons), of which some then speciated into bearlike animals (Webb 1991). The major flow of taxa between the Amer-

icas, called the Great American Interchange, began with the closure of the Isthmus of Panama. For both bird species (Weir et al. 2009) and land plants (Gentry 1982; Burnham and Graham 1999), many more taxa migrated from south to north than vice versa. Some South American bird taxa radiated to form new families of warblers, flycatchers, and vultures in the north. Taxa of South American origin now comprise the majority of the plant and bird diversity of the Central American tropics. For neither land plants nor birds—and for neither direction of movement—are migrations reported to have increased extinction rates in the recipient realm.

Immigration of trees that had evolved in other realms had already contributed to the diversity of the South American tropical flora before closure of the Isthmus. From the separation of South America from Gondwana until ~76 Ma, additional African plants migrated to South America, likely across a series of islands (Goldblatt 1993). The proto-Antilles subsequently allowed some migration of the Laurasian or North American boreotropical flora to South America (Morley 2003). About 20% of tree species and 30% of tree genera of the current Peruvian Amazon were migrants from the African paleotropics and the North American boreotropics (Pennington and Dick 2004). Species that arrived at more than 3 Ma seem to have coexisted for millions of years after coming into contact, despite tens of millions of years of prior separation.

Unlike birds and land plants, mammalian migration was greater from North America to the south. This southerly migration included species of *Ursidae* (bears), *Equidae* (horses), *Mustelidae* (skunks and weasels), *Tayassuidae* (peccaries), *Gomphotheriidae* (gomphotheres), *Canidae* (dogs), *Tapiridae* (tapirs), *Camelidae* (camels), *Cricetidae* (mice), *Cervidae* (deer), *Felidae* (cats), and other taxa (Webb 1976; Marshall et al. 1982; Vrba 1992). Some of these taxa had major radiations in South America. Almost all persisted until the Pleistocene mass extinction event at ~10 Ka (Marshall et al. 1982; Vrba 1992). While these northern invaders “insinuated, and raised total generic diversity from 77 to 120 genera” of mammals in South America (Benton 1996, p. 203), the extinction of some marsupial carnivores has been attributed to competition with North American placental carnivores (Patterson and Pascual 1968). Moreover, during a >3-million-year period, 12 genera of South American ungulates were lost as 20 ungulate genera of North American origin invaded into or radiated within South America. The temporal dynamics of the appearances of northern ungulates and of the loss of southern ungulates seems suggestive of slow competitive displacement being a cause of the extinctions (Webb 1991). Alternatively, these ungulate extinctions might have been caused by “northern carnivores, the likes of which southern ungulates had never before experienced” (Webb 1976,

p. 229). Patterson and Pascual (1972) suggested that their disappearance was just the continuation of a pattern of species loss that began before the arrival of northern ungulates. Vrba (1992) suggested that the ungulate extinctions were caused not by interspecific interactions but by the dramatic cooling that occurred at 2.5 Ma and the resultant great reduction in the areal extents of the ungulate habitat in South America.

The southern mammals that migrated north after formation of the Isthmus included the *Trichechidae* (manatees), *Megatheriidae* (giant ground sloths), *Megalonychidae* (large edentate mammals), *Dasypodidae* (armadillos), *Didelphidae* (opossums), *Mylodontidae* (sloths), *Erethizontidae* (porcupines), *Glyptodontidae* (a group related to armadillos), *Myrmecophagidae* (giant anteaters), *Hydrochoeridae* (capybara), and *Toxodontidae* (rhino-like ungulates; Vrba 1992). These mammals became well established in North America; South American mammals still dominate the mammal fauna of Central America (Webb 1991). These invasions did not cause extinctions but rather increased the mammalian diversity of North America. Most of the southern taxa that no longer persist in North America did persist from their time of arrival at ~2–7 Ma until being driven to extinction during the Pleistocene mass extinction at ~10 Ka. Similarly, the establishment of large predaceous South American ground birds (*Phomrhadidae*) in North America was not associated with extinctions of either other large predators or their prey (Flannery 2001).

In total, coexistence of trophically and ecologically similar species long has been the norm following speciation or migration among realms. This evidence suggests that coexistence is not merely a local phenomenon associated with coadapted organisms but an evolutionarily deep and frequent feature of diversification and interrealm movement of marine and terrestrial flora and fauna. A presumptive reason for coexistence would be that the taxa of all realms evolved in response to the same underlying trade-offs. The potential universality of interspecific trade-offs is reinforced by convergent evolution in isolated biomes. Distantly related phylogenetic groups, such as the *Euphorbiaceae* (succulents) and *Cactaceae* (cacti), evolved remarkably similar plant physiologies and morphologies as they radiated in the deserts of Africa (*Euphorbiaceae*) and the Americas (*Cactaceae*; Bennici 2003). Movement of these groups between realms resulted in coexistence, not displacement. These cases of competitive coexistence beg for ecological and evolutionary explanation. The theory presented below is used to develop and explore such explanations.

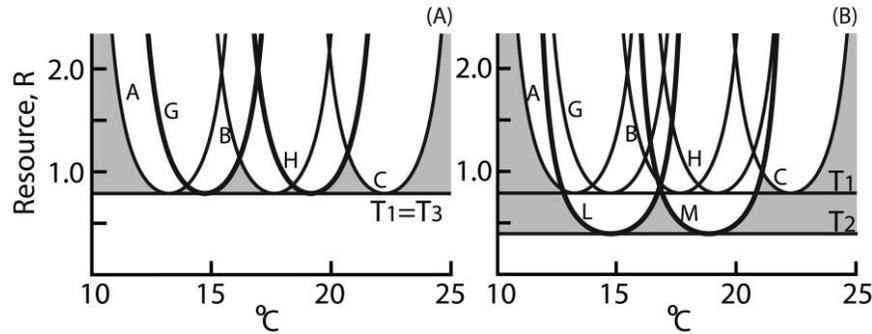
#### Theoretical Considerations

It is instructive to consider more formally the assumptions and implications of the biogeographic superiority hypoth-

esis and the universal trade-off hypothesis, which could be explored with any of the numerous models that predict the stable persistence of many interacting species. I use a model of competition for two essential resources and a model of temperature-dependent competition, both of which directly incorporate interspecific trade-offs (Tilman 1982; Lehman and Tilman 2000).

The model of competition for two essential resources can be illustrated graphically (fig. 1A). The zero growth isocline of species V shows the resource levels at which its  $dN/dt = 0$ . Vectors show resource consumption and supply, which must balance each other at equilibrium. A habitat is defined by its resource supply point, such as  $H_1$  or  $H_2$ , which determines the direction and length of the resource supply vector. If two species have a trade-off where species V is a better competitor for resource 2 ( $R_2$ ) and species U is a better competitor for resource 1 ( $R_1$ ), both species would stably coexist in habitats that have intermediate resource supply points (fig. 1B). A potentially unlimited number of species could coexist in a realm if resource requirements of all species were constrained to the same interspecific trade-off surface and if the realm had sufficient spatial heterogeneity in resource supply rates. Throughout this article, I assume that all realms have spatial heterogeneity such that the supply points of all the habitats within a realm span the full range of conditions above the trade-off curves. Interspecific trade-offs would mean that both within and between species, traits that increased competitive ability for one resource necessarily decreased competitive ability for the other resource. Specifically, all species would have resource requirements, as defined by the corners of their isoclines, that were bound to the same interspecific trade-off curve (for two resources) or surface (for three or more resources; Tilman 1982, 1988). In figure 1C, species A, B, C, and D of realm 1 are bound to the trade-off curve  $T_1$  and could coexist with each other when living in a realm with sufficient habitat-to-habitat spatial heterogeneity in the supply rates of these resources. These species can persist, even though the presence of any given species may displace similar species from some particular habitat types. Although this model predicts local coexistence of only two species, the addition of small amounts of dispersal from other habitats (i.e., places with different supply points) can allow many species to persist locally (Amarasekare and Nisbet 2001).

What would be predicted to occur if species from a second realm invaded? Let us first assume that the biogeographic superiority hypothesis held, with the species of realm 2 being superior and having trade-off curve  $T_2$  (fig. 1D, 1E).  $T_2$  shows that species from realm 2 would increase in abundance on the resources left unconsumed by the taxa of realm 1 and eventually reduce resources below the levels, shown by  $T_1$ , required for the survival of taxa of



**Figure 2:** Temperature-dependent resource competition. *A*, Competition between species from two realms that have identical trade-off curves. Curves labeled with species' names are the zero net growth isoclines for the respective species, indicating the concentration to which the resource is depleted by an equilibrium population. Species A, B, and C are bound to trade-off curve  $T_1$ , and species G and H are bound to trade-off curve  $T_3$ . *B*, Competition with superior competitors, species L and M, on trade-off curve  $T_2$ . Species L and M would displace species B, G, and H, but there are temperature ranges at which species A and C would persist. See Lehman and Tilman (2000) and Tilman (2004) for further details.

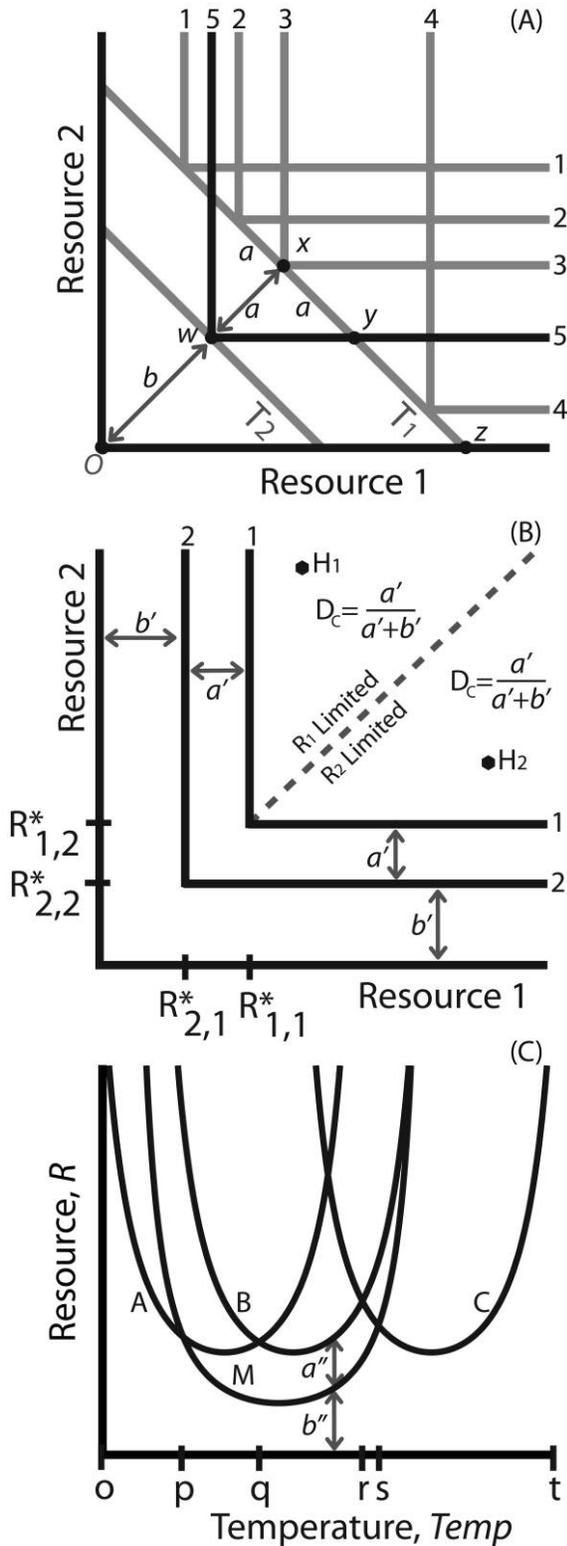
realm 1. Depending on the traits of the invading and established taxa, a single invading species from realm 2 might not displace any established species or could displace several. In figure 1*D*, invading species X displaces species B and C. Several superior invaders from realm 2—such as species X, Y, and Z in figure 1*E*—could displace many (in this case, all) established species in realm 1. Conversely, species from realm 1 would be unlikely to invade realm 2, especially if realm 2 were species rich. For instance, if realm 2 contained only species X of figure 1*D*, species A and D could invade and persist with it. However, if realm 2 contained species X, Y, and Z, then species A, B, C, and D of realm 1 could not invade. Moreover, invading species from a realm with an inferior trade-off curve are never able to fully displace the established species of a realm with a superior trade-off curve.

What is predicted to occur if the universal trade-off hypothesis were to hold? Let the taxa of realm 3 be bound to the same exact interspecific trade-off curve as those of realm 1; that is, let  $T_1 = T_3$ . Then when species R, S, T, and U of realm 3 invade realm 1 (fig. 1*F*), the established and invading species would all persist. Specifically, each invading species from realm 3 would have regions of the spatially heterogeneous habitat where resources left unconsumed by established species of realm 1 allowed a rare invader to increase in abundance. The stable two-species equilibria (Tilman 1982) allow any number of such invading species to persist with the established species in the heterogeneous realm. Results would be identical if species from realm 1 invaded realm 3. In all cases, established and invading species would persist across the realm, though the range of habitats occupied by each species—and thus its abundance—would decrease after the interchange. The

only case in which an invading species from one realm would not deterministically increase when rare would be if the invader were environmentally identical to an established species of realm 1, that is, had its isocline exactly on top of that of the established species. Such identical species would be neutral (*sensu stricto* Hubbell 2001) and undergo the stochastic dynamics associated with neutrality (Hubbell 2001).

In total, the universal trade-off hypothesis predicts that migration between realms would result in coexistence and not competitive extinction. Even though invaders would decrease the abundances of some established species and could fully displace them from certain types of habitat conditions, established and invading species are predicted to coexist across the wide spectrum of heterogeneous habitat conditions that occur within a realm. About the same proportion of the resident taxa of each realm would be expected to migrate to the other realm, except that a realm that has a greater diversity of species should be more difficult to invade than one that is less diverse (Shea and Chesson 2002; Tilman 2004; Fargione and Tilman 2005).

Such results are not unique to the particular type of resource competition illustrated in figure 1. Qualitatively similar outcomes are predicted for the wide class of other models in which multispecies coexistence hinges on interspecific trade-offs (e.g., Tilman and Pacala 1993; Rees et al. 2001). For instance, consider cases in which species compete for a single resource in a habitat that has spatial heterogeneity in a physical factor, such as temperature (fig. 2; Lehman and Tilman 2000). The different optimal temperatures represent a trade-off, since each enzymatic or physiological system has a temperature optimum, and an organism would have to make a different system to change



**Figure 3:** A, Species 1, 2, 3, and 4 are established species of an invaded realm, bound to trade-off curve  $T_1$ . Species 5, an invading

its optimum. If taxa of two realms, realms 1 and 3, have the same interspecific trade-off curve ( $T_1 = T_3$ , as in fig. 2A), species from realm 3 (species G and H) would increase when rare, become established in realm 1, and coexist with their established species (species A, B, and C) and vice versa. However, species L and M from realm 2, which has the superior trade-off curve,  $T_2$ , would displace species B, G, and H. No species from realms 1 or 3 could displace any species in realm 2 (fig. 2B). Clearly, though, dispersal and stochastic forces acting on rare invaders could make it more difficult for a species on the same trade-off surface as an established species to invade if its traits were more similar to those of established species (e.g., Tilman 2004).

#### Trade-Off Differences and Extinction Rates

Further analysis of the relationships illustrated in figure 1 provides a useful approximation to the quantitative effects of both the number of invading species and the magnitude of their trade-off superiority on the magnitude of the resultant extinctions (fig. 3). Let the trade-off difference  $D_T$  between two trade-off curves, such as curves  $T_1$  and  $T_2$  of figure 3A, be defined as  $D_T = a/(a + b)$ , where  $a$  is the orthogonal distance between the two parallel trade-off

species, is bound to superior trade-off curve  $T_2$ . The trade-off difference between these two curves,  $D_T$ , is defined as  $D_T = a/(a + b)$ . The invaded realm has habitat-to-habitat spatial heterogeneity in the supply rates of the two resources that is assumed to span the full range of requirements of all species shown. Species 5 would displace any and all species that had isoclines tangent to the segment of  $T_1$  enclosed within the isocline of species 5. For analytical simplicity, the trade-off curves of established and invading species have been chosen to be parallel, and the units of resources 1 and 2 have been linearly scaled such that the line  $ox$  is perpendicular to  $T_1$  and  $T_2$  and bisects them at points  $x$  and  $w$ , respectively. B, The rate of competitive displacement when species 2 invades an established competitively inferior but otherwise ecologically similar species 1 depends on  $D_c$ , which is their relative interspecific competitive difference for the resource that limits their growth. Here  $D_c = a'/(a' + b') = (R_{1,1}^* - R_{2,1}^*)/R_{1,1}^* = (R_{1,2}^* - R_{2,2}^*)/R_{1,2}^*$ , where  $R_{i,j}^*$  is the resource requirement of species  $i$  for resource  $j$ .  $D_c$  is the difference between the  $R^*$  of the inferior competitor and the superior competitor divided by the  $R^*$  of the inferior competitor. If isoclines are offset,  $D_c$  differs between habitats, depending on which resource is limiting which species (fig. A2 in the online edition of the *American Naturalist*). The time to displacement from a spatially heterogeneous realm would be determined by the lowest of all such  $D_c$  values, since this gives the longest time to displacement. C, Temperature-dependent resource competition, as in figure 2. Species A, B, and C are bound to the same trade-off curve. Species M is a superior invading species that would displace species B. Before invasion by species M, species A dominates the temperature range ( $o, q$ ), species B dominates ( $q, r$ ), and species C dominates ( $r, t$ ). After invasion by species M, species A dominates the temperature range ( $o, p$ ), species M dominates ( $p, s$ ), and species C dominates ( $s, t$ ). The arrows illustrate how  $D_c$  is determined at a given temperature, with  $D_c = a''/(a'' + b'')$ .

curves and  $b$  is the orthogonal distance from the superior trade-off curve (the one closer to the origin) to the origin.

Simple geometry shows that, given random distributions of established species on their trade-off curve  $T_1$ , an invader randomly chosen from the superior trade-off curve  $T_2$  would on average displace a proportion  $D_T$  of all established species. For example, species 5 would displace all species whose isocline corners intersect the segment of  $T_1$  enclosed by the isocline of species 5. This segment of  $T_1$  has a length of  $2xy$ . Because the total length of  $T_1$  is  $2xz$ , the average proportion of species from trade-off surface  $T_1$  displaced by species 5 is  $2xy/2xz$ , or  $xy/xz$ . Because  $\Delta wxy$  and  $\Delta oxz$  are similar right triangles,  $xy = a$ ,  $ox = xz = a + b$ , and thus  $xy/xz = a/(a + b) = D_T$ , where  $xy/xz$  is the proportion of  $T_1$  species driven to extinction by a single invader with superior trade-off  $T_2$ . Thus  $1 - D_T$  is the probability that a randomly chosen established species would not be driven to extinction by a randomly chosen invader of trade-off superiority  $D_T$ . The term  $1 - D_T$  raised to the power  $N$  is the probability that a randomly chosen established species would not be driven to extinction by  $N$  randomly chosen invaders. This means that  $E$ , the average proportion of existing species driven to extinction by  $N$  randomly chosen invaders with a trade-off superiority of  $D_T$ , would be

$$E = 1 - (1 - D_T)^N. \quad (1)$$

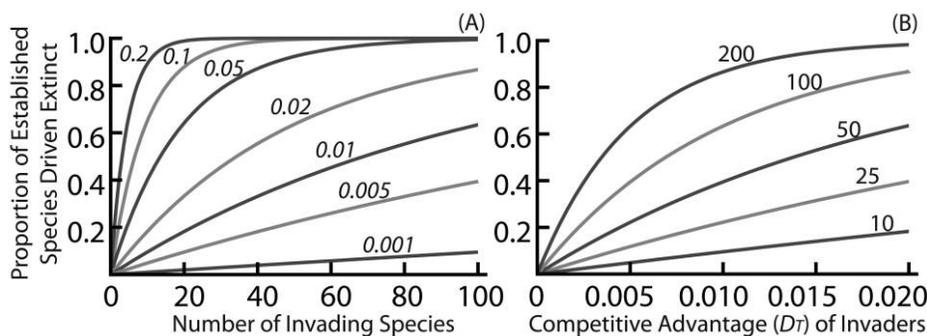
This equation has two major features. First, the greater the number of species from a superior realm that invaded an inferior realm, the greater would be the proportion of established species driven to extinction (fig. 4A). Second, a greater trade-off difference  $D_T$  between two realms would result in greater extinction (fig. 4B). Even when two realms have trade-off curves that differ by only 1% ( $D_T = 0.01$ ), a moderately sized interchange, such as invasion by 25

species, is expected to cause the extinction of about one-fifth of the species of the inferior realm. A relationship qualitatively similar to equation (1) and figure 4 would hold for temperature-dependent resource competition (as in fig. 2). In this case, the proportion of established species displaced by an invader would not be simply  $D_T$  but rather an inverse Gaussian function of  $D_T$ .

#### Displacement Times and Trade-Off Differences

Sepkoski (1996) suggested that ecological competitive displacement should be rapid relative to the geologic record of life on earth, with competitive displacement occurring “in a geological instant” when similar taxa (which would have relatively similar adult body sizes, mortality rates, and maximal growth rates) interact (Savage et al. 2004). A differential equation model of the dynamics of resource competition (see appendix in the online edition of the *American Naturalist*; Tilman 1982) was numerically solved to simulate a spectrum of 179 different invasion events, with each case using a unique combination of species parameters (maximal growth rates, half-saturation constants, mortality rates, and initial abundances) for the invading competitively superior species and the displaced inferior species (as in figs. 1–3).

While  $D_T$  is used to determine the proportion of established species displaced by invasive species, a distinct variable  $D_C$  that summarizes the relative competitive difference between two species is needed to estimate the time required for displacement. In particular, when two species compete for two essential resources, with species 2 being the superior competitor,  $D_C = (R_{1,1}^* - R_{2,1}^*)/R_{1,1}^*$  when  $R_1$  is limiting, and  $D_C = (R_{1,2}^* - R_{2,2}^*)/R_{1,2}^*$  when  $R_2$  is limiting (fig. 3B; appendix). Note that  $R_{ij}^*$ , and thus  $D_C$ , depend on the values of the species traits (eq. [A3] in the ap-



**Figure 4:** Species displacement contours:  $E = 1 - (1 - D_T)^N$ . A, Proportion of established but competitively inferior species displaced by various numbers of randomly chosen, competitively superior invading species for values of  $D_T$  ranging from 0.001 (bottom line) to 0.2 (top line). B, Proportion of established species displaced by invaders with a given competitive advantage,  $D_T$ , for cases in which the number of superior invader species ranges from 10 (bottom line) to 200 (top line).

pendix).  $D_C$  is similarly defined for each temperature along a temperature gradient as the  $R^*$  difference between two species at that temperature divided by the  $R^*$  of the inferior competitor at that temperature (fig. 3C).

Multiple regression analyses of the dependence of the time to displacement,  $t_d$ , on the species parameters used in the numerical solutions showed that all parameters affected the time to displacement. Most effects came from how these parameters determined the values of  $R_{i,j}^*$  and thus  $D_C$ . In particular, regressions that included  $D_C$  explained the vast majority of the observed variation in displacement times ( $R^2 > 0.99$ ; appendix). In contrast, regressions that included all model parameters or their log-transformed values but not  $D_C$  provided much poorer fits ( $R^2 \leq 0.5$ ). Two models provide useful abstracts of the essence of these relationships (eqq. [A2], [A3] in the appendix). Let  $m_x$  be the per capita adult mortality rate of the competitively inferior species and  $t_d$  be the time required for a superior invader to increase from rarity (defined here as 1% of its potential equilibrium density) to at least 99% of this equilibrium density and for the established species to have its abundance decrease to 1% of its preinvasion abundance. Multiple regression analysis of the results of all numerical solutions gave

$$t_d = \frac{14.4}{D_C m_x^{0.9}} \quad (2)$$

( $R^2 = 0.993$ ,  $P < .0001$ ). Because adult mortality rates ( $m$ ) scale roughly as the  $-1/4$ th power of body mass (Savage et al. 2004), the time to displacement is predicted to increase as about the fifth root of body mass; for a given value of  $D_C$ , taxa with body masses that are 40,000-fold larger would take about 10 times longer to be displaced.

A fuller description of the dynamics of competitive displacement is provided by fitted equation (3). The time to displacement is

$$t_d = \frac{10.0}{I^{0.118} D_C m_x^{0.80} r_y^{0.20}} \quad (3)$$

( $R^2 = 0.997$ ,  $P < .0001$ ), where  $I$  is the ratio of the initial abundance of a competitively superior invader to its eventual equilibrium abundance and  $r_y$  is the maximal per capita growth rate of the superior invader (appendix).

Terms with larger exponents have greater effects on  $t_d$ . For instance, a 10-fold increase in  $D_C$ ,  $m_x$ ,  $r_y$ , or  $I$  would reduce the time to displacement by about 9/10, 5/6, 2/5, or 1/4, respectively. When  $D_C$  is properly interpreted, equations (2) and (3) apply to cases such as those of figures 1 and 2 (appendix).

Equations (2) and (3) describe the time to displacement in a particular habitat (i.e., resource supply point or temperature) in which a single invader has a competitive ad-

vantage of  $D_C$  over the species that would be displaced. Because geographic realms are spatially heterogeneous, the  $D_C$  for the species being displaced may have a range of values dependent on habitat characteristics (supply point or temperature) and the traits of its superior competitors. The habitat types from which a species would be most slowly displaced would be the ones with the smallest  $D_C$ . Thus, it is the minimum value of  $D_C$  across a realm that determines the realm-wide time for its displacement. For figure 3A, when species 5 invades, it would displace some individuals of species 2 quickly and others more slowly. The greatest time to displacement (smallest  $D_C$ ) would be for those habitats in which both species 2 and 5 were limited by  $R_1$ . Because the realm-wide minimum value of  $D_C$  for species 2 is about one-third that of the minimum for species 3, species 5 would displace species 3 from the realm in about one-third of the time required for it to displace species 2.

An invader may displace several species, each with its own realm-wide time to displacement. To estimate the displacement times when multiple species are displaced by a single superior invader, let us assume that established species are randomly spaced on their trade-off curve (fig. 3A). If a superior invader is otherwise ecologically similar (i.e., requires the resources in the same ratio) to an established species on an inferior trade-off curve, then for this pair of species  $D_C = D_T$ . For instance, in figure 3A, species 3 has the same optimal  $R_2 : R_1$  ratio as invading species 5 (i.e., a line through the corners of their isoclines hits the origin), and thus the  $D_C$  of species 3 would be the  $D_T$  for these two trade-off curves. Geometry suggests that on average, approximately 50% of all the resident species that were destined for extinction because of invasion by a given superior species would have a minimum  $D_C$  value of  $D_T/2$  or greater and thus would be driven to extinction within a time period  $t_{50}$ , where

$$t_{50} = \frac{28.8}{D_T m_x^{0.9}} \quad (4)$$

Similarly, approximately 90% of extinctions resulting from invasion by a single superior species would have a  $D_C$  value of  $D_T/10$  or greater and occur within  $10t_d$  years, giving

$$t_{90} = \frac{144}{D_T m_x^{0.9}} \quad (5)$$

Displacements could be faster than in equations (4) and (5) if more than one species of superior competitors invaded. For example, if  $N$  is the number of superior invading species, if invaders are evenly spaced on their trade-off curve, and if  $N > (1 + 2/D_T)$ , then all susceptible species (not just 50% or 90%) would be driven to extinction within time  $t_{50}$  or less (eq. [4]). Since interchanges

between realms generally included movement by many species,  $t_{90}$  is a reasonable upper bound estimate of the expected time to displacement, and  $t_{50}$  might be a reasonable lower bound. This implies that following a species interchange between two realms, if established and invading taxa were to persist for a time  $t_{\text{persist}}$  after invasion, then an upper bound for the value of  $D_T$ , obtained from equation (5), would be

$$D_T < \frac{144}{t_{\text{persist}} m_x^{0.9}}. \quad (6)$$

Let us also consider a community of species that are competing for a single resource in a habitat with spatial heterogeneity in temperature, which is invaded by species from a realm with a superior trade-off curve (fig. 2). In this case, the “bottoms” of the isoclines (regions tangent or close to the trade-off curve) are broader and more flattened than the right-angle corners of the isoclines for the prior case (fig. 1). This then gives each invader a broader region of more rapid displacement than for the cases in figure 1. The equations defining the shapes of the isoclines of figure 2 (Lehman and Tilman 2000) show that, on average for small values of  $D_T$ , ~95% of resident species would experience a resource reduction of at least  $D_T/10$  and thus be displaced within  $t_{90}$  (10 times the  $t_d$  calculated for their  $D_T$ ). In total, for both types of resource competition considered,  $t_{90}$  is an upper bound on the time for ~90% of the extinctions resulting from an invasion event, with extinctions being faster when there were more invading species.

### Discussion

The dynamics of biotic interchanges show that species from different realms generally persist for millions of years once in contact. In contrast, equation (1) predicts that a moderate number of invading species (e.g.,  $N = 25$ ) that have a small trade-off advantage, such as  $D_T = 0.01$  (superiority of 1%), should displace a readily observable proportion of established species (~20%). Equation (5) predicts that such displacements will be rapid relative to observed times of persistence. The slowest predicted displacement times are for taxa with large body sizes, such as rain forest trees (mortality rate of ~0.02 year<sup>-1</sup> for canopy species and ~0.03 year<sup>-1</sup> for subcanopy species; Condit et al. 1995) or elephants (postjuvenile mortality rate of ~0.025 year<sup>-1</sup>; Moss 2001). For such taxa, ~90% of displacements resulting from invasion by species with a superiority of  $D_T = 0.01$  are predicted to occur within an upper bound of ~340,000–490,000 years. For taxa the size of large shrubs (mortality rate of ~0.06 year<sup>-1</sup>; Condit et

al. 1995) and wild horses (mortality rate of ~0.08 year<sup>-1</sup>; Turner and Morrison 2001), displacement times for  $D_T = 0.01$  have an upper bound of ~140,000–180,000 years. For taxa such as wild sheep ( $m = 0.16$  year<sup>-1</sup>; Caughley 1966), eagles ( $m = 0.3$  year<sup>-1</sup>; Harmata et al. 1999), and large corals ( $m = 0.2$  year<sup>-1</sup>; Harriott 1985), displacement times for  $D_T = 0.01$  would be ~40,000–75,000 years. For  $D_T = 0.01$  and even smaller taxa (such as mollusks, barnacles, small birds, and small mammals with adult mortality rates of ~0.4 to 0.8 year<sup>-1</sup>; e.g., Connell 1961; Sullivan 1989), ~90% of displacements resulting from invasion would occur within ~18,000–33,000 years. These displacement times are much shorter than the reported persistence times after invasion for taxa with body sizes spanning those involved in major interchange events (table 1).

The reported times that established and invading taxa have been observed to persist and their approximate mortality rates can be used, in combination with the inequality derived above (eq. [6]), to estimate upper bounds on  $D_T$  for major interchange events (table 1). The estimates of  $D_T$  are extremely small, ranging from 0.002 to 0.00008, with a mean of 0.0007 and a median of 0.0003. The mean corresponds with trade-off surfaces that had relative differences of just 0.07%. These estimates are upper bounds on the values of  $D_T$  because the resident and invading taxa of table 1 (1) are still coexisting, as for rainforest trees and smaller mammals of the Great American Interchange and the mollusks of the Bering Migration; (2) were still coexisting when a major extinction event occurred, as for the large mammals of the Great American Interchange that were lost in the Pleistocene extinction; or (3) were still coexisting at the last reported sampling time, as for the invertebrates of the Richmondian invasion. Equation (4) can be used to calculate approximate lower bounds for  $D_T$  for these invasions since each involved movement of many species. These lower bound values for  $D_T$  would be one-fifth of the  $D_T$  values of table 1. Looked at another way, for trade-off differences as small as those in table 1, equation (1) predicts that only a large number of invading species would cause sufficient extinctions to be detectable in the fossil record. For instance, when  $D_T = 0.001$ , 2% of native species are predicted to be lost in response to 20 invading species and 20% lost from 220 invading species.

The mutual invisibility repeatedly observed when taxa moved between realms and the long-term persistence observed after most interchange events support the universal trade-off hypothesis and suggest that even taxa that evolved in realms isolated from each other for millions of years had interspecific trade-off surfaces so similar as to be essentially indistinguishable. Theory predicts that for a given invader trade-off advantage ( $D_T$ ), extinctions of resident taxa should have been both more numerous and

**Table 1:** Calculated trade-off differences,  $D_T$ , between taxa of two realms involved in selected interchange events

	Approximate mortality rate (year <sup>-1</sup> )	Coexistence ( $t_{\text{persist}}$ ; year)	Trade-off difference between realms (upper bound) $D_T^a$
Great American Interchange:			
North to south:			
Mastodons	.025	2,000,000	.0020
Raccoons	.18	4,000,000	.00017
Small mammals	.4	2,000,000	.00016
South to north:			
Rain forest trees	.02	2,000,000	.0024
Giant ground sloths	.04	7,000,000	.00038
Armadillos, opossums, and porcupines	.2	2,000,000	.00031
Llama-like camels	.1	2,000,000	.00057
Bering land bridge:			
Equids	.08	5,000,000	.00028
Richmondian marine invasion:			
Corals	.2	1,000,000	.00061
Mollusks	.5	1,000,000	.00027
Bering Strait mollusk migration	.5	3,500,000	.00008
Neotropical rain forest invasions:			
Trees (Paleotropical)	.02	>10,000,000	.00049
Trees (North American)	.02	2,000,000	.0024
Transhemisphere marine invasions:			
Mollusks and macro algae	.5	2,000,000	.00013

Note: Taxa grouped by body size.

<sup>a</sup> Based on equation (6).

more rapid when there were more invading species and higher mortality rates (smaller body sizes). Thus, the most robust test of the universal trade-off hypothesis comes from the Bering interchange. Following invasion by more than 200 mollusk species, the extinction rate for established mollusks of the North Atlantic declined slightly, though not significantly, from the preinvasion rate (Vermeij 1991a), strongly supporting the universal trade-off hypothesis.

The extinction of notoungulates in South America in the aftermath of the Great American Interchange is a notable case that seems to support the biogeographic superiority hypothesis, though the cause of these extinctions is debated (Patterson and Pascual 1972; Webb 1976, 1991; Vrba 1992). However, most South American mammal taxa persisted after invasion, as did South American bird, fish, and tree species. These and other South American taxa invaded into North America and persisted for millions of years with their North American counterparts. Bidirectional invasion and persistence are consistent with the universal trade-off hypothesis but not the biogeographic superiority hypothesis.

Although most interchange events have species dynamics that support the universal trade-off hypothesis, three

alternative hypotheses merit consideration. First, it is possible that some potential invaders had niche requirements matching unexploited environmental conditions in the new realm ("empty niches"). If so, they should have readily invaded. The dimensionality of the trade-off surface on the scale of a realm seems likely to be high. Plant species, for instance, may be limited by water, various nutrients, light, dispersal, temperature, mutualists, herbivory, disease, and other conditions, although only a subset may apply in a given habitat. If novel species are able to exploit a new niche dimension, competitive displacement of existing taxa should be rare because the cost of different or added structures needed to do so would likely impose a trade-off. For instance, the emergence of new life forms, such as branching corals, could have allowed them to exploit empty portions of the water column but to face trade-offs associated with higher allocation to structural tissues.

The theoretical implications of high niche dimensionality for invasibility are poorly understood. Because of adaptation to local conditions, each species might be expected to have heritable variation that led it to occupy a portion of the trade-off surface (Tilman 1982) and not just a single point, as is graphically illustrated in this article. This could decrease the tendency for what might otherwise

be higher invasibility at higher niche dimensions. On the surface at least, the possibility of coexistence after interchange being caused by numerous open niches seems to be contradicted by the dynamics of speciation. The occurrence of novel conditions in a realm is often associated with initially rapid speciation followed by long periods of stasis (e.g., Eldridge and Gould 1972; Sepkoski 1984, 1996; Benton 1996). Sepkoski (1996) suggests that interspecific competition was a major force structuring such macroevolutionary patterns of species radiation, noting that the Early Cambrian evolutionary explosion did not dampen until a rich fauna had evolved; that Phanerozoic diversification rates were much higher after extinction events than before; and that between extinction events there were intervening intervals, some more than 50 million years, of relatively high and stable taxonomic diversity.

Such diversity-dependent speciation has been interpreted as showing that speciation is limited by ecological opportunity and slows as there are fewer “open niches,” thus implying that the dimensionality of realms is small enough that speciation often “fills” most niches in a realm (Schluter 2001). If this is so, though, why is so much of the diversity of each realm the result of interchanges between realms? One possibility is that speciation requires both ecological opportunity (Sepkoski 1996; Schluter 2001) and genetic isolation and that isolation becomes more limiting to speciation than ecological opportunity as diversity increases within a realm. Then, assuming that the universal trade-off hypothesis held, species from a different realm would often be able to invade a niche position that would have been difficult for in situ speciation to fill. There are, however, alternative explanations (e.g., McPeck 2008; Ricklefs 2010).

Environmental filtering is a second potential explanation for the observed persistence of species after interchange events. Although biotic interchanges involve the movement of numerous taxa among realms, most taxa do not migrate. It is plausible that the taxa that have lower invasion success are those that have greater environmental similarity to the resident taxa of the other realm. Such environmental filtering would decrease invasion-caused extinctions relative to cases that lacked such filtering. With or without filtering, no extinctions are predicted to occur if resident and invading taxa share the same interspecific trade-off surface. However, if two realms have different trade-off curves, the filtering by the superior realm should exclude most species and mainly allow invasion by those species adapted to open niches. Filtering by the taxa of the inferior realm would also favor invasion by niche-differentiated species, which would reduce extinctions, but the inferior realm could also be invaded by taxa that caused displacements. Although interchanges rarely have the same number of species moving in both directions, they do seem

to have about the same proportion of the resident taxa doing so and may have equally low extinction rates in both realms, as expected for the universal trade-off hypothesis.

Finally, predators, parasitoids, and disease may exert species-specific and frequency-dependent effects that could influence both speciation and coexistence (e.g., Janzen 1970; Connell 1971; Ricklefs 2010). This coexistence mechanism requires trade-offs that favor the persistence of species-specific predators, pathogens, or disease that have stronger negative effects against stronger competitors. A variety of studies in tropical forests are consistent with this possibility. However, the trans-Atlantic dispersal of tropical tree species, the source of 20% of the Amazonian rain forest taxa of equatorial Peru (Pennington and Dick 2004), would likely have introduced new taxa without their natural enemies. The enemy release hypothesis predicts that some invading tree species should have become highly abundant and perhaps displaced their competitors (Keane and Crawley 2002) unless or until some predators, pathogens, or diseases of the new habitat evolved to attack them. The same logic would seem to apply to the taxa introduced into new realms as ornamental plants or pets. But the vast majority of these do not become highly abundant; displacements of existing species are rare (Sax et al. 2002). The work of Chesson and Kuang (2008) offers a resolution to this issue by showing how theory that includes both competition and predation interactions can explain multispecies coexistence.

The universal trade-off hypothesis does not necessarily contradict the assertion that invasive species are a factor contributing to the extinction risk of some species. Although past interchanges among biotic realms were rarely associated with extinctions, invaders did reduce the abundances of some established species. In combination with the effects of current anthropogenic habitat destruction and fragmentation, nutrient loading, or climate change on rare species, such reductions could increase extinction risk.

The universal trade-off hypothesis differs in several significant ways from neutral theory (Hubbell 2001). Species that occur at different points on a trade-off surface are neither, *sensu stricto*, ecologically identical nor neutral and are predicted by theory to persist with each other precisely because of competitive stabilizing forces (Chesson 2000), not slow random walks constrained to the unlikely case of fitness-equalizing trade-offs (Purves and Turnbull 2010). Neutral theory combines the simplest possible mechanism of competition—that a new individual can establish only when an existing one dies—with a rigorous treatment of stochasticity, thus demonstrating the important role that stochastic processes play in nature. Analytical theory that combines the stochastic processes of neutral theory with the competitive stabilizing forces of the uni-

versal trade-off hypothesis would seem to hold great promise (Hubbell 2001; Tilman 2004).

The long-term persistence of taxa after biotic interchanges and the trade-off-based explanation offered here suggest that adaptation and diversification have resulted more from the evolution of species traits on a trade-off surface and less commonly from the evolution of species that are superior overall. Taxa with truly superior trade-offs should have swept through ecosystems, displacing established taxa, contrary to the vast majority of observations reported here. Large extinction events have occurred throughout the fossil record, but they have been attributed mainly to external causes, such as meteor impacts, massive volcanism, or major shifts in climate. Some taxa that entered a new realm eventually did become dominant, and some original taxa have been lost, but the millions of years required for such replacements are more consistent with a new clade "outevolving" an existing clade than with ecological competitive displacement (Sepkoski 1996).

The simple hypothesis that all of life may be bound to the same trade-off surface raises many questions, of which perhaps the most fundamental is this: Is it evolutionarily plausible for all taxa, despite differing phylogenetic histories and millions to tens of millions of years of evolutionary diversification while isolated on different continents, to be bound to essentially the same trade-off surface? I support a tentative "yes" by noting the following.

Laboratory selection experiments on prokaryotes have observed the rapid emergence of seemingly new species (Lenski et al. 1991; Elena and Lenski 2003). Consider, then, the impacts of the first 2 billion years of the evolutionary history of life on Earth, when morphologically simple, often single-celled organisms were predominant. Even small selective forces from intra- and interspecific interactions would have strongly shaped their traits. For instance, for a microbe that reproduced once per day, a variant with a heritable selective advantage of only  $10^{-9}$  would have increased  $10^{12}$ -fold relative to the wild type within 76 million years, which is only 3.8% of this 2-billion-year period. Any novel trait or trait combinations that gave even the slightest advantage without an offsetting cost (trade-off) should have swept to fixation. The end results of this immensely long period of evolution of single-celled organisms would have been the common cellular and organelle biochemistry, molecular genetics, and physiology that higher taxa share.

The evolution of modern plants and animals was likely highly constrained by the traits of their single-celled eukaryotic progenitors. Most differences among higher taxa might then result from trade-offs that arose from the allocation of limiting factors (e.g., amino acids, phosphorus, sugars) to one structure or metabolic function, which meant that these factors could not simultaneously be al-

located to a different structure or function. Differences within and among species would thus be based largely on traits that had allocation-based trade-offs. Major innovations have swept the world, such as structural tissues that had low metabolic costs (bones, chitin, lignocellulose, calcium carbonate shells) and vascular or other transport tissues that redistributed resources from points of origin to points of need within an individual. Interestingly, such innovations have been major causes of increased diversity, not extinction (Benton 1996), suggesting that the superiority gained from such structures imposed costs and trade-offs that allowed much preexisting diversity to persist.

Unavoidable allocation-based trade-offs at the biochemical, cellular, tissue, and behavioral levels may explain another seeming universal of life: the scaling relations between species traits reported in comparisons among various species (e.g., Enquist et al. 1998, 1999; West et al. 1999; Brown et al. 2004). For instance, relative growth rates of species scale inversely with body size (McMahon and Bonner 1983; Enquist et al. 1999). This corresponds with greater proportional allocation to structural and transport tissues in larger organisms and the lower proportional allocation to basic growth functions (leaves in plants, feeding structures in animals; McMahon and Bonner 1983; Enquist and Niklas 2002). The fastest growing plants, after all, are single-celled algae, which do not allocate any specialized cells to stems, roots, or seeds.

In total, the pattern of diversification of life within realms and the results of biotic interchanges between realms have more often been consistent with the universal trade-off hypothesis than with the biogeographic superiority hypothesis. Should it be supported by further research, the existence of a commonly shared suite of trade-offs within and across realms could have deep implications for ecology and evolution. If the traits of all environmentally similar species do fall on essentially the same trade-off surface, the task of estimating species-specific parameters is greatly simplified once the relevant axes and dimensionality of the system are known. Trade-off-based models of resource competition that include stochasticity predict patterns of invasion, community diversity, and species relative abundances (Tilman 2004) that are reminiscent of speciation, invasion, and diversity patterns from the fossil record. Moreover, if life has long been bound to essentially the same trade-off surface, then species formation may be better viewed as movement along an interspecific trade-off surface than as directional selection achieved without compensatory costs. These possibilities suggest that further exploration of the universal trade-off hypothesis may be informative.

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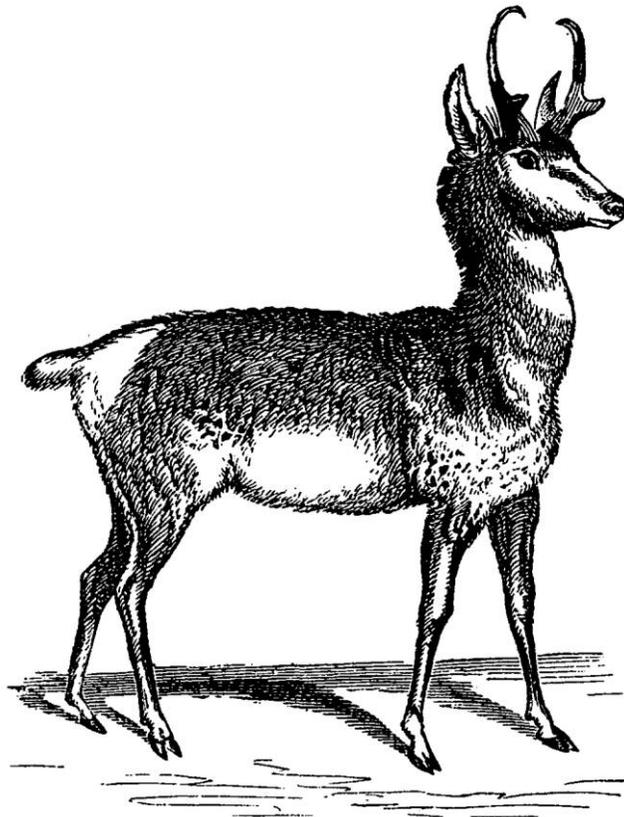
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Prong-horn antelope. “The new horn continues to grow from the tip downwards, and generally to curve inwards; at the same time the thick skin below continues to harden, at first assuming the appearance of black leather. It is flexible, so that the tip may be bent in any direction; a prong sprouts from the base, and, by the middle of summer, the horns are fully developed, to be dropped and again renewed in the autumn.” From “The Prong-Horn Antelope” by W. J. Hays (*American Naturalist*, 1868, 2:131–133).