Biotic Globalization: Does Competition from Introduced Species Threaten Biodiversity?

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The introduction of new predators and pathogens has caused numerous well-documented extinctions of long-term resident species, particularly in spatially restricted environments such as islands and lakes. However, there are surprisingly few instances in which extinctions of resident species can be attributed to competition from new species. This suggests either that competition-driven extinctions take longer to occur than those caused by predation or that biological invasions are much more likely to threaten species through intertrophic than through intratrophic interactions. The likely threat of introduced species to resident controphics (species in the same trophic level) can be assessed with the help of existing biodiversity and extinction data sets and of two recent theories: (1) the fluctuating resource availability hypothesis, developed to account for changes in the invasibility of communities, and (2) the unified neutral theory, proposed to account for patterns of biodiversity at the community and metacommunity levels. Taken together, theory and data suggest that, compared to intertrophic interactions and habitat loss, competition from introduced species is not likely to be a common cause of extinctions of long-term resident species at global, metacommunity, and even most community levels.

Keywords: biological invasions, unified neutral theory, fluctuating resource availability hypothesis, extinction threats, competition

The globalization of Earth's biota is transforming local and regional floras and faunas. From the smallest, most remote islands to the largest continents, the intentional or accidental introduction of new species is altering the composition and ecology of long-established biological communities (Wilson 1992). As evidenced by the recent introductions of the Asian longhorned beetle *(Anoplophora glabripennis)* and the West Nile virus into the United States, some species introductions can inflict economic harm and threaten human health. In addition, it is widely reported that introduced species are threatening many resident species with extinction (Elton 1958, Wilcove et al. 1998).

There have been numerous well-documented extinctions of long-term resident species caused by the introduction of predators and pathogens, particularly in spatially restricted environments such as islands and lakes (King C 1984, Gill and Martinson 1991, Kaufman 1992, Fritts and Rodda 1998, Loope 1999). However, there are surprisingly few instances in which extinctions of resident species can be attributed to competition from new species, either on continents or islands (Mooney and Cleland 2001, Sax et al. 2002). For example, more than 4000 plant species introduced into North America north of Mexico during the past 400 years are naturalized (established to various degrees), and these new species now represent nearly 20% of the continent's vascular plant species. Yet there is no evidence that even a single long-term resident species has been driven to extinction, or even extirpated within a single US state, because of competition from an introduced plant species (John T. Kartesz, Biota of North America Program, University of North Carolina, personal communication, 2002).

The paucity of documented extinctions caused by competition from new species could mean that extinctions of this type simply take longer to occur. Or it could mean that, compared to intertrophic interactions and habitat loss, competition from introduced species is not likely to be a common cause of extinctions of long-term resident species. The likely threat of introduced species to resident controphics (species in the same trophic level) can be assessed with the help of existing biodiversity and extinction data sets and of two recent theories, one focusing on biological invasions and the other focusing on geographic patterns of biodiversity. The first theory, the fluctuating resource availability theory (Davis et al. 2000), was developed to account for changes in the invasibility of communities (susceptibility to being colonized by new species). The second theory, the unified neutral theory of biodiversity and biogeography (Hubbell 2001), was proposed to account for patterns of biodiversity at the community and metacommunity levels.

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The fluctuating resource availability theory

The fluctuating resource availability theory of invasibility holds that a mechanistic relationship exists between invasibility and resource availability and that changes in invasibility often result from changes in the competition intensity from residents, which in turn result from fluctuations in resource availability (figure 1). This theory is supported by field data showing that short-term increases in resource availability in plant communities can temporarily reduce or suspend competition from resident vegetation, thereby increasing the invasibility of the environment (Davis and Pelsor 2001). The theory assumes that whatever individual arrives first at a pool of unused resources is able to co-opt them. Whether that individual represents a species new to the region or one that has resided in the community for a long period of time, it now has the opportunity to become established in the community. Under the fluctuating resource availability theory, communities are equal opportunity employers, not discriminating among species based on their geography of origin. An important component of this theory is that it does not require new species to be ecologically different from resident species in order to successfully colonize a new environment, as has been argued in the past (Thompson 1991). In this way, the theory is similar to that presented by Moyle and Light (1996), who also emphasized the importance of fluctuating environmental conditions on invasion success, and to lottery-based models of community assembly (Sale 1977) and other nonequilibrium models that emphasize the role played by disturbances and fluctuating resources in forestalling competitive exclusion (Huston 1994).

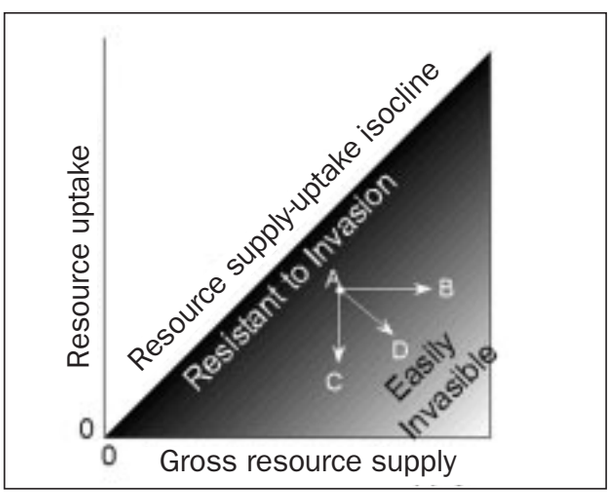

Figure 1. The theory of fluctuating resource availability holds that a community's susceptibility to invasion increases as resource availability (the difference between gross resource supply and resource uptake) increases. Resource availability can increase because of a pulse in resource supply (A→B), a decline in resource uptake (A→C), or both (A→D). In the plot, resource availability, and hence invasibility, increases as the trajectory moves farther to the right or farther below the supply/uptake isocline (where resource uptake = gross resource supply). Image modified from Davis and colleagues (2000).

The unified neutral theory of biodiversity and biogeography

The unified neutral theory of biodiversity and biogeography established that biodiversity patterns at multiple scales can be accurately predicted using a model based on random but limited migration, random speciation, and random fluctuations in species abundances (the latter a process Hubbell referred to as "ecological drift"). In this model, individuals of all species within a community trophic level are considered to be "per capita ecological equivalents," meaning they exhibit the same probabilities of giving birth, dying, and migrating. In Hubbell's model, individual organisms interact in a zero-sum game in a biotically saturated landscape, meaning that, although disturbance may create small patches of resources for a brief period, no significant amount of space or other limiting resource goes unused for long.

Using a two-tiered model consisting of communities within a metacommunity, Hubbell showed how changes in dispersal rates among local communities would be expected to affect biodiversity patterns at both levels. He concluded that high rates of dispersal among local communities should increase the diversity at the local level while reducing the diversity at the metacommunity level as abundant and widespread species drive some rare and local species extinct. Conversely, Hubbell argued that although low dispersal rates result in low diversity in local communities, the infrequent introduction of new species to these communities allows many rare local endemic species to survive, thereby sustaining a high diversity at the metacommunity level (figure 2).

In the development of his theory, Hubbell defined a "fundamental biodiversity number," θ, described by Hubbell as a "dimensionless, fundamental quantity that appears pervasively [in the unified neutral theory] at all spatio-temporal scales." The variable θ is calculated as $2J_M\nu$, where J_M = the size of the metacommunity and ν = the speciation rate within the metacommunity. Species richness and relative abundance patterns in local communities and in metacommunities are believed to be a function of θ and dispersal rates, m, among local communities (Hubbell 2001).

Commonalities of the two theories

A fundamental similarity of both theories is that they are dispersal rather than niche based. Neither theory requires that new species possess traits different from those of the resident species to colonize and become established in a community. Both theories emphasize spatiotemporal variability in habitat characteristics (e.g., availability of resources). Both theories emphasize the importance of stochastic events and processes, particularly the coincident synchronization of dispersal episodes with the availability of underutilized resource-rich patches. Both theories focus on diversity issues within individual trophic levels, and both were developed using data

primarily from plant communities, although Hubbell also uses a number of animal examples to support his unified neutral theory.

Extension of the unified neutral theory to incorporate global biological invasions

Although Hubbell (2001) mentioned introduced species in the context of the unified neutral theory, he did not try to incorporate the phenomenon of global biological invasions into his two-tiered model. Owing to the structural and logical similarities of the two theories, one can explicitly incorporate biological invasions at the global level into Hubbell's neutral model by adding a third tier, creating a hierarchical system comprising local communities and metacommunities (the two tiers of Hubbell's model) plus one meta-metacommunity, the entire Earth. In this simple extension of the unified model, the metacommunities (e.g., continents and large island groups) can be treated as local communities within the meta-metacommunity, and global "invasions" can be treated as dispersals among metacommunities.

The introduction of a new species from outside a metacommunity is equivalent to an increase in the speciation rate within the metacommunity. (If these introductions are rare events and typically involve only one or a very few number of individuals, the introductions are equivalent to what Hubbell describes as speciation occurring by point mutation mode. If species introductions occur frequently or if introductions typically involve large numbers of individuals, the introductions are equivalent to fission mode speciations.) In accordance with the fluctuating resource availability theory, once an introduced species has entered a local community through an invasion window (i.e., by usurping available space and resources before one of the residents could do so), it is now a player in the game just as much as any of the long-term residents. From that point on, the new species will simply be part of the local ecological system, being defined by the size (total number of individuals) of the metacommunity, J_M; by the speciation rate, v; and by the dispersal rate within the metacommunity, m. None of these defining factors are changed by the introduction of the new species.

To explicitly incorporate global invasions into the neutral theory, one could redefine v (defined as speciation rate within a metacommunity in Hubbell's original model) as the species proliferation rate (V), which equals the sum of the speciation rate occurring within the metacommunity, v, and the immigration or invasion rate, i, of new species into the metacommunity from other metacommunities. (In a similar extension of Hubbell's model, Chave and colleagues (2002) combined immigration and speciation rates in the same way and referred to the collective term as the speciation rate.) Thus, Hubbell's fundamental biodiversity number, θ, originally defined as $2J_M v$, would now be defined as $2J_M V$, where $V = v + i$. Owing to the ongoing and rapid globalization of Earth's biota, the invasion rates experienced by most metacommunities will normally be quite high relative to their speciation rate. As a result, under today's conditions (where $i \gg v$), Hubbell's fundamental biodiversity number, θ, would be largely defined by a metacommunity's size and invasion rate. This means that biological invasions occurring on a global scale—that is, dispersal taking place among Hubbell's metacommunities (continents and island groups)—have significantly increased the value of θ, and, as described below, would be expected to significantly alter the biodiversity and biogeographic patterns at the local, metacommunity, and global scales.

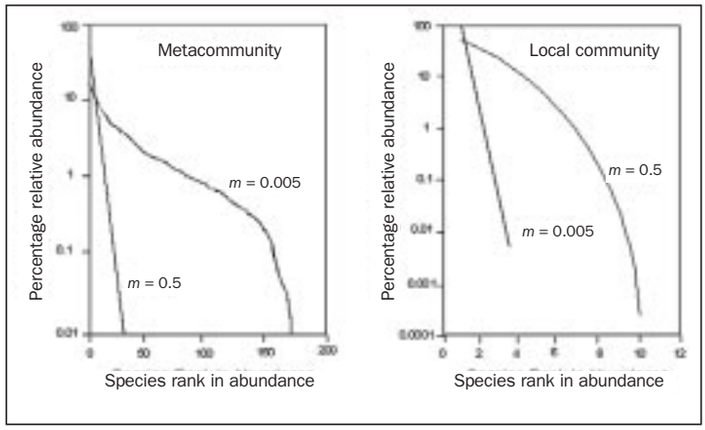

Figure 2. Steady-state dominance–diversity distributions for simulated metacommunities and local communities experiencing low and high dispersal rates (m) among the local communities (m = 0.005 and m = 0.5, respectively). The graph at left shows that metacommunity diversity declines with increasing dispersal rates, while the graph on the right shows that diversity at the local community level increases with increasing dispersal rates. In the simulation shown, metacommunity size (J_M) = 7056, the fundamental biodiversity number (θ) = 10, and the size of local communities is 16 individuals. Redrawn from Hubbell (2001).

Biodiversity at the community and metacommunity levels

In a three-tiered system, dispersal limitation can be apportioned among the three levels in four different ways (table 1). In a Type 1 dispersal system, highly limited dispersal among local communities and metacommunities would result in a high degree of endemism at both the local and regional levels, because new species appear at both levels primarily through speciation events rather than immigration. The metacommunity, being the sum of many endemic-dominated communities, would be very diverse. However, individual communities would be expected to exhibit low levels of biodiversity, because their species pools depend almost entirely on speciation events for recruitment of new species. A good example of a Type 1 dispersal system would be the terrestrial communities of South Pacific islands before human colonization. During this time, there was very little dispersal among the islands or between the Pacific archipelago and metacommunities (continents) in other parts of the world. The result was that the species-poor communities of

Table 1. Four dispersal systems involving communities and metacommunities and the biodiversity patterns predicted by the extended unified neutral theory.

Dispersal system type		Predicted biodiversity patterns
Type 1	Dispersal highly limited among local communities and among metacommunities	High degree of endemism at both the local and metacommunity levels; local communities exhibit low diversity; metacommunities exhibit high diversity
Type 2	Dispersal not highly limited among local communities; dispersal highly limited among metacommunities	High degree of endemism at the metacommunity level but not at the local community level; high diversity at the local level; diversity at the metacommunity level lower than in a Type 1 system
Type 3	Dispersal highly limited among local communities; dispersal not highly limited among metacommunities	Low degree of endemism at both the local and metacommunity levels; higher diversity at both local and metacommunity levels than in a Type 1 system
Type 4	Dispersal not highly limited among either local communities or metacommunities	Lowest degree of endemism at both local and metacommunity levels of the four dispersal systems; high diversity at metacommunity level; highest diversity at the local community level of the four dispersal systems

individual islands comprised a large number of endemics (Loope 1999). Although individual island diversity was low, the total number of endemics from the many Pacific islands meant that the archipelago itself was quite species rich. For example, it is estimated that before human colonization, the Pacific islands (including New Guinea and New Zealand) were home to between 15% and 20% of the world's bird species (Pimm et al. 1994, Steadman 1995), despite representing less than 1% of the world's landmass.

In a Type 2 dispersal system, dispersal is not highly limited within tier 2 (among local communities) but is highly limited within tier 3 (among metacommunities). As described by Hubbell, frequent dispersal among local communities will drive up and sustain diversity at the local level. However, this same dispersal pattern will suppress metapopulation biodiversity (tier 2) compared to a Type 1 dispersal system because of the extinctions of some rare species within the respective local communities (tier 1). In the Type 2 system, endemism would be expected to be common at the metacommunity, but not at the local community, level.

An example of a Type 2 dispersal system would be continental biotas up to approximately a thousand years ago, before humans began to travel regularly between continents, transporting other species with them. Because dispersal among continents more than a thousand years ago normally would have been exceedingly rare, endemism at the continental level would be expected to be common, as is known to be the case in most plant and animal groups (Cox and Moore 2000). Although endemism would be expected to be common at the metacommunity level in a Type 2 system, the frequent dispersals among local communities would homogenize the composition of these communities. Thus, endemism at the local level would be expected to be lower than in a Type 1 dispersal system. This is borne out by the ranges of most continental species, including vascular plants, birds, and mammals, whose ranges typically extend broadly east to west provided suitable habitat is present. This contrasts with the ranges of most long-term terrestrial residents of the South Pacific archipelago, whose home ranges, until the arrival of humans, were often restricted to one island or to a few nearby islands because of severe dispersal limitation, even though suitable habitat existed on other islands in the archipelago (Loope 1999).

In a Type 3 dispersal system, dispersal is highly limited within tier 2 but is not highly limited within tier 3. In this situation, species would disperse regularly between metacommunities but seldom between local communities. Given the influx of new species into both local communities and metacommunities, biodiversity would be expected to increase at both levels. At the same time, the global exchange of species would drive down endemism rates at both the local and the metacommunity level. This is probably an unlikely combination of dispersal patterns, although it seems to describe the South Pacific archipelago since the time the first European explorers reached the islands in the 16th century. An analysis of 410 plant species that are listed by the Pacific Islands Ecosystems at Risk project as invasive or potentially invasive in different Pacific islands (PIER 1999) reveals that 81% of the species originated in continental floras, while only 19% originated from the floras of other Indo-Pacific islands (table 2). These data show that species introduced to the Pacific islands during the past 400 years principally involved introductions from outside the archipelago rather than from other islands. Captain Bligh, the notorious English sea captain, is responsible for dispersing at least two species between metacommunities. He is credited with introducing papaya *(Carica papaya,* native to Central America) to the Cook Islands in 1792 and then introducing breadfruit *(Artocarpus altilis,* native to Tahiti) to Jamaica and the West Indies in 1793 on his return trip.

In a Type 4 dispersal system, dispersal would not be highly limited within either tier 2 or tier 3. This probably describes, to varying degrees, most regions in the world today. As in a Type 3 dispersal system, biodiversity should increase at both

Table 2. Origin of 410 plant species listed by the Pacific Island Ecosystems at Risk (PIER) project as invasive, or potentially invasive, in Indo-Pacific island ecosystems.

Area of origin	Number of invasive or potentially invasive species	Percentage of total (410 species)
North America, Central America, South America, and Caribbean	193	47.1
Eurasia	52	12.7
Africa, Madagascar	50	12.2
Australia, New Zealand	21	5.1
Multiple continents	17	4.1
Indo-Pacific islands, including Java, New Guinea, Indonesia, and Philippines	77	18.8

Note: Species listed as originating both in the Indo-Pacific islands and in one or more continents were listed in the Indo-Pacific islands column.

the community and metacommunity levels. However, the increase at the community level would be expected to be greater in the Type 4 dispersal system, because communities would regularly receive new species from other communities within their metacommunity as well as from other metacommunities. Owing to the high rates of dispersal among both local communities and metacommunities, endemism at both levels would be expected to be the lowest among the four dispersal systems.

Of course, some long-term resident species have gone extinct on both island and continental landmasses during the past several hundred years. Has the number of new species actually exceeded the number of extinctions, thereby supporting the model's prediction that biodiversity should be increasing at the community and metacommunity levels in a Type 4 dispersal system? In the vast majority of cases, the answer is yes (Mooney and Cleland 2001, Rosenzweig 2001, Sax et al. 2002). Where good data sets exist, regional biodiversity levels have almost always increased during the past few centuries. For example, the introduction and naturalization of new vascular plant species into the state of Minnesota (from outside the Midwest) during the past several hundred years have increased the state's vascular plant diversity by almost 25% (Owenby and Morley 1991). Naturalized species have increased the diversity of the California flora by 20% (Randall et al. 1998). Considering all of North America, naturalized species have increased the continent's vascular plant diversity by more than 20% (BONAP 1999). Introductions of new species have had an even larger impact on the biodiversity of islands. For example, the naturalization of introduced vascular plants on Pacific islands has doubled the species richness of the flora on most of these islands (Sax et al. 2002).

As is the case with plants, the most dramatic increases in local and regional animal biodiversity caused by species introductions occur on islands, the fauna of which have sometimes lacked entire classes of animals. For example, Hawaii, which had no terrestrial amphibian or reptile species and only one species of mammal (a bat) before the arrival of humans, now has a terrestrial fauna including 4 amphibian, 21 reptile, and 44 mammal species (Miller and Eldredge 1996).

The primary cause of extinctions at the local and metacommunity levels in most areas of the world is habitat loss (Mooney and Cleland 2001, Rosenzweig 2001). However, in most cases, this loss in habitat (which translates to a decline in J_M in Hubbell's original theory), has been more than compensated by the substantial increase in V, the metacommunity species proliferation rate, resulting from the high invasion rates (i) among metacommunities. Thus, except in areas where natural environments have all but disappeared through habitat destruction, the fundamental biodiversity number, θ (defined using V), and overall species richness have been increasing in most regions of the world.

Are competition-driven extinctions likely to increase in the future?

Recent past extinctions of long-term residents can seldom be attributed to competition from new species (Mooney and Cleland 2001, Sax et al. 2002). The six bird species that have gone extinct in North America during the past 150 years (passenger pigeon, great auk, Labrador duck, Carolina parakeet, Bachman's warbler, and ivory-billed woodpecker) succumbed to overhunting, habitat loss, or both (Pimm and Askins 1995, Montevecchia and Kirk 1996, Chilton 1997). In the Cook Islands, no plant extinctions can be definitely attributed to competition from introduced species. Likewise, none of the extinctions of bird or land snails in the Cook Islands were caused by competition from introduced species; instead, these extinctions resulted from overharvesting and habitat alteration (in the case of the birds) and from predation by an introduced ant species (in the case of the land snails) (Gerald McCormack, Cook Islands Natural Heritage Project, personal communication, 2002). Warren B. King (1980) lists competition as a contributing factor in only 11% of the extinctions of birds from oceanic islands since 1600, whereas predation and habitat loss are listed as causes in 70% and 30% of the cases, respectively. Tompkins and colleagues (2003) have argued that the decline in the abundance of the European red squirrel is due less to competition from the introduced North American gray squirrel, once thought to be the primary cause for the red squirrel's decline, than to disease from the parapoxvirus carried by the gray squirrel. As already mentioned, no introduced plant species are known to have caused any North American long-term resident plant species to go extinct.

Extinctions often result from the combined effects of multiple processes, and thus, although competition may not be the primary cause of most extinctions, it may prove to be

a contributing factor in some cases (King WB 1980). For example, if habitat fragmentation on continents continues, some long-term resident species, particularly those with limited ranges to begin with, may end up persisting in just one or a few fragments of habitats. With populations reduced in size and confined to geographically restricted habitats, these species—much like species inhabiting oceanic islands—will be more vulnerable to extinction. That competition-driven extinctions have been uncommon even on oceanic islands suggests that factors other than competition are likely to cause extinctions in these fragmented continental habitats as well. Given that small populations are vulnerable to extinction resulting from a wide variety of causes, the fact that a long-term resident species goes extinct in the presence of an introduced controphic will not be enough alone to justify a claim of competition as the cause.

In most instances where an introduced species has exterminated a resident, the species interactions have been between trophic levels, e.g., predator–prey, pathogen–host (King C 1984, Gill and Martinson 1991, Kaufman 1992, Fritts and Rodda 1998, Loope 1999). The fact that competition-driven extinctions have been so uncommon during the past few centuries suggests that, compared to habitat loss and intertrophic interactions, competition is a relatively weak extinction threat. For example, although introduced freshwater fish have been shown to reduce the population sizes of long-term resident species through competition, these interactions seldom cause extinctions (Herbold and Moyle 1986, Ross 1991). If competition is a relatively weak extinction threat, extinctions caused by competition should take longer than those caused by predation and habitat loss. If this is the case, then the reason so few competition-driven extinctions have been documented may be that not enough time has passed for competitive exclusion to occur. This would suggest that we might expect more competition-driven extinctions in the future. However, the increased time frame needed for these extinctions also provides more time for other factors to disrupt the competitive asymmetry between the new and long-term resident species, thereby reducing the likelihood that such extinctions would ever occur. These factors would include events and processes that would reduce the abundance of the new species, such as disturbances, disease, environmental fluctuations, or even a new introduced species. To illustrate, Marchetti (1999) concluded that although the Sacramento perch *(Archoplites interruptus)* is threatened by the aggressive dominance of an introduced bluegill *(Lepomis macrochirus),* competitive exclusion of the perch may never occur because of fluctuating environmental conditions.

A longer time frame also means that the resident species may have time to adapt to the new competition pressure in their environment and thereby reduce the intensity of competition to a level that permits coexistence. For example, as described by Mooney and Cleland (2001), the introduction of more than 250 new fish species into the Mediterranean Sea following the completion of the Suez Canal has resulted in only a single extinction (Por 1978). This has been attributed to the ability of the long-term residents to respond to the competitive interactions with the Red Sea species by adjusting their foraging depths. This niche adjustment enabled the long-term residents, which prefer to feed in the warmer surface waters of the Mediterranean (Spanier and Galil 1991, Golani 1993), to accommodate the introductions. Similar niche adjustments in response to introduced species have been documented for freshwater fish (Ross 1991).

For these reasons, it seems unlikely that competition will emerge as a primary, or even frequent, cause of future extinctions. It is significant that interspecific variation in competitive abilities is not incorporated into the extended unified neutral model presented here. The fact that biodiversity data sets from around the world are consistent with the predictions of such a theory, and at multiple spatial scales, is an additional argument against the notion that competition from introduced species constitutes a major extinction threat for long-term residents. Thus, the observed increases in local and regional biodiversity resulting from species introductions are not likely to be a temporary phenomenon, but represent real increases that, in the absence of future habitat loss, will likely persist indefinitely into the future (Rosenzweig 2001).

Biodiversity at the meta-metacommunity (global) level

Biodiversity is declining at the global level (Wilson 1992). This is indisputable. The extended unified neutral model presented here predicts that increased dispersal among metacommunities will be responsible for some of the species extinctions at the global level. A theorem of Hubbell's model, which is based on a biotically saturated landscape, is that any increase in the population size of one species must be accompanied by a corresponding decrease in the collective number of individuals of all other species in the community. Thus, any new species that become dominant and widespread in communities would be expected to depress the populations of resident species, making already rare and local species particularly vulnerable to extinction from stochastic processes (i.e., ecological drift). The result of these extinctions would be that total meta-metacommunity biodiversity (i.e., global biodiversity) would decline, even though local communities and metacommunities may be experiencing a net increase in diversity. Nevertheless, it is habitat loss, and not the globalization of Earth's biota, that principally threatens a substantial and permanent reduction in global biodiversity (Rosenzweig 2001).

Caveats and exceptions

Even if new species seldom drive long-term residents to complete extinction through competition, they can sharply reduce the numbers of once abundant long-term residents (Porter and Savignano 1990, Petren and Case 1996, Carlton et al. 1999). However, it does not necessarily follow that changes in the dominance–abundance distribution of a community, or even local extirpations of long-term residents, constitute an ecological or evolutionary catastrophe, although there may be

other compelling reasons to prefer the long-term residents over the new species, including aesthetic, economic, cultural, and historical preferences (Gould 1998). While the arrival of new species often disrupts ecological and evolutionary relationships among the long-term residents, it also creates opportunities for the development of new ecological and evolutionary relationships (Mooney and Cleland 2001).

It is important to reemphasize that the extended unified neutral model proposed here addresses species within the same trophic level. Without question, introduced species can drive resident species in other trophic levels to extinction, even quite quickly, as illustrated by the introductions of predators and pathogens to islands (figure 3). The expected impacts on biodiversity of such intertrophic interactions might be effectively addressed using approaches based on food web theory and trophic cascades (Winemiller and Polis 1996, Polis et al. 1997).

In addition, it must be stressed that both the fluctuating resource availability theory and the unified neutral theory were developed primarily with the ecology of plant communities in mind. Although the predictions presented here seem to hold for many animal groups as well, it is possible that competition-driven extinctions might be more likely higher on the food web. For example, some predators (e.g., wolves) are known to drive other predators (e.g., coyotes) out of an area with their aggressive behavior (Peterson 1995). Thus, the introduction of a dominant predator into a region, particularly a geographically isolated region such as an island or lake, potentially could cause the extinction of one or more resident predators through competition. Although the reasons behind the extinction two to three thousand years ago of the thylacine *(Thylacinus cynocephalus)* in Australia are not fully known, it is suspected that competition from the dingo was a major factor (King C 1984, Guiler 1985). Overhunting, habitat loss, and disease are believed to have driven the last remaining thylacine populations to extinction in Tasmania in the early 1900s (Bryant and Jackson 1999).

One problem that arises from extending the spatial scale of Hubbell's unified neutral theory is that the species neutrality assumed by Hubbell at the local and regional scale is less likely to hold at the global scale. Hubbell recognized this, pointing out that while species evolving in different regions would have evolved neutrality (equivalence of per capita fitness) with respect to the other controphic species in their local communities, there would be no reason to expect neutrality among controphics from different regions. Thus, some introduced species may enjoy a pronounced competitive advantage in their new environment. Hubbell (2001) refers to such species as "rule breakers." These are species capable of substantially reducing the abundance of many long-term resident species. However, the paucity of documented cases of competition-driven extinctions indicates that, even in instances where considerable interspecific variation in competitive ability exists between new species and long-term residents, extinction is seldom the outcome. Furthermore, the introduction of these "rule breakers" would alter the selection regimes in the host environment, which would be expected to lead, over time, either to an increase in the relative competitive ability of the long-term residents (Hubbell 2001) or, as explained above, to a niche shift that would reduce the intensity of competition (Ross 1991, Spanier and Galil 1991, Golani 1993).

Figure 3. The brown tree snake,* Boiga irregularis*, introduced into Guam around 1950, is believed to have caused the extinction of more than 10 bird species, some endemic to Guam, in only a few decades. Biological invasions are more likely to threaten long-term resident species with extinction through intertrophic interactions, such as predation and pathogenic infection, than through competition. Photograph: Gordon Rodda, US Geological Survey.

Although introduced species seldom drive resident controphics to extinction through competitive interactions, they can bring with them new pathogens that may cause extinctions among the resident species (Loope 1999). Also, introduced species may significantly alter disturbance regimes, as in the case of flammable grasses introduced to Hawaii (D'Antonio and Vitousek 1992); such alterations could lead to substantial enough changes in habitat to result in the extinction of long-term resident and controphic species. Richardson and colleagues (2000) refer to species that can change the character or condition of an ecosystem over a substantial area as "transformers."

Conclusions and recommendations

Few new species are returning to the metacommunities from which they came, and thus it is inevitable that communities of the future will consist of a mixture of new and long-term residents. However, that we cannot turn back the ecological clock (except possibly in small restoration efforts requiring perpetual vigilance and intensive management) does not mean that we should cease all efforts to protect long-term residents or that we should welcome all introduced species with open arms. The serious health and economic problems caused by a small percentage of introduced species certainly demand aggressive action, including efforts to prevent the

Figure 4. A diverse Fiji reef community. Shown are both hard and soft corals (the prominent red soft coral is* Dendronephthxa *sp.), some crinoids, sponges, and several species of fish—fairy basslets* (Pseudanthias *spp.) and damselfish* (Chromis *sp.). Because of the long-distance dispersal capabilities of many reef organisms, endemism is not common in most reefs. Historically, Pacific island reef communities were more homogenous in their species composition than the respective terrestrial island environments. However, although homogeneous, the reef communities were very diverse, whereas the terrestrial island communities, which were largely isolated from one another and thereby composed of many endemic species, were comparatively species poor. The diverse homogeneity illustrated by coral reefs may aptly characterize the world's biota in the future. Increasingly connected as a result of biological invasions, different regions of the world will become more similar in their floras and faunas. At the same time, they will become more diverse, in some cases much more diverse. Photograph: Copyright © Brandon Cole.

spread of these species and to eradicate them in regions where they are already a threat. Some new species, such as introduced predators on islands, are clearly capable of exterminating resident species, and most ecologists would probably regard such extinctions as undesirable and hence support the use of society's resources to protect these species.

Globalization of Earth's biota will not lead to a world composed of zebra mussels, kudzu, and starlings. One need only look to one of the most diverse communities in the world, coral reefs, to see the consequence of regular long-distance dispersal (figure 4). As a result of ocean currents that regularly transport immature corals and fish hundreds or even thousands of miles, reefs exhibit comparatively low rates of endemism and instead are typically composed of fish and coral species with large geographic ranges (Hughes et al. 2002). As predicted by the extended unified neutral theory, reefs throughout the Indian and Pacific Oceans share a common fauna (Bellwood and Hughes 2001), a biogeographic pattern that contrasts sharply with that exhibited by historic terrestrial communities in the same archipelago.

Comprehensive analyses of coral and reef fish communities suggest that community composition of reefs throughout the Indo-Pacific region is primarily dispersal rather than niche driven (cf. Bellwood and Hughes 2001), consistent with Hubbell's original theory. Although the extensive dispersal patterns homogenize reef faunas to some extent, the diverse coral and fish communities are fundamentally the product of these high dispersal (invasion) rates, and these same high dispersal rates currently help to maintain, not threaten, the high species richness among corals and reef fish communities (Hughes et al. 2002). Thus, although it is true that the breakdown of the world's dispersal barriers will result in a homogenization of Earth's biota, homogenization is not synonymous with low diversity. In the future, different regions of the world will be more similar than they are now. They will also be more diverse.

Because conservation priorities and management plans involving introduced species are largely based on ecologists' assessments of biological invasions and their effects, it is vital that these judgments be scientifically sound, that is, well grounded in theory and robustly supported by field data. In addition, given the limited human and financial resources available to deal with the biodiversity impacts of the large number of introduced species throughout the world, it is important that conservationists focus their efforts wisely. The biogeographic analysis and data presented here and elsewhere (Mooney and Cleland 2001, Rosenzweig 2001, Chave et al. 2002, Sax et al. 2002) suggest that ecologists and habitat managers striving to protect and maximize biodiversity will be able to maximize their effectiveness by focusing principally on intertrophic interactions between introduced species and long-term residents. Taken together, theory and data suggest that, compared to the effects of intertrophic interactions and habitat loss, competition from introduced species is not likely to be a common cause of extinctions of long-term resident species at global, metacommunity, and even most community levels.

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