

New Pangea: Homogenizing the Future Biosphere

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The literature discussing future human impacts on the biosphere has tended to focus on the metaphor of the next (sixth) mass extinction. I outline some benefits of another metaphor, that of the New Pangea. Conceptualizing human impacts in this way not only emphasizes the inevitable loss of global biodiversity but also includes the loss of regional diversity that occurs through homogenization, when unique native species are replaced by a relatively limited pool of widespread exotic species. The New Pangea metaphor thus emphasizes not only the “losers” of the next extinction but also the “winners”, those species that will inevitably thrive. This metaphor specifies how human impacts are operating to alter the biosphere because biotic homogenization is a two-step process consisting of human-accelerated: (1) long-distance dispersal including removal of barriers; and (2) replacement of diverse natural habitats with a much smaller diversity of human-dominated habitats that will support a smaller global diversity of species. The process is enhanced even more by the highly selective nature of human transport and habitat creations so that species from certain groups disproportionately become winners or losers. The ultimate outcome will likely be a superhomogenized biosphere, with biotic intermixing on a scale far greater than any time in Earth’s history. Conservation efforts to slow down the extensive species intermixing will be impeded by the fact that exotic species often increase species richness and spatial diversity (species turnover) at local scales. The general public and their policymakers, who typically perceive the world only at local scales and often value exotic species for crops, pets and many other utilitarian reasons must be educated about the global and long-term consequences of biotic exchanges.

Comparison of current human impacts on the biosphere to diversity patterns in the fossil record is essential for conservation biology (Purvis et al. 2000a, 2000b). Without some kind of natural baseline, it is impossible to understand the radical changes being made to our current biosphere by humans. Examples of crucial baseline parameters include extinction rates, rates of biotic interchange, extinction selectivity (which taxa are more extinction-prone) during background and mass extinctions, and recovery patterns following mass extinctions (Jablonski 2001).

However, an important message of the fossil record is that it is often difficult to generalize about these baseline parameters (Woodruff 2001). One reason is that the sheer complexity of the biosphere does not make it easy to find simple rules. Increasing this complexity is that the drastic and rapid changes being wrought by humans are probably even more rapid, unique and varied than any physical changes that have occurred in geological history (Western 2001). Still other obstacles to fossil versus modern comparisons are pragmatic, such as the practical difficulty of measuring extinction rates now or in the past (Regan et al. 2001).

Despite these problems, there is a substantial literature relating modern extinctions to the fos-

sil record. Perusal of this literature reveals two major metaphors that have emerged. One is that of the Sixth Mass Extinction (Leakey and Lewin 1995; Pimm and Brooks 2000), which relates the impending biotic crisis to the previous five global catastrophes that eliminated a large proportion of species. The second metaphor is the New Pangea (Rosenzweig 2001a, 2001b), which relates the impending crisis to the biotic reorganizations that occurred during the assembly of the Pangea supercontinent in the late Paleozoic Era.

In this paper, I discuss the New Pangea metaphor, and some of its advantages. Unless humans disappear, the impending biotic crisis will apparently be a prolonged one. The Sixth Mass Extinction metaphor implies that the impending crisis is some kind of single event. Also, the New Pangea metaphor focuses on both winners and losers of global environmental change. Extinction is nearly always selective (McKinney 1997) with some groups being selectively removed whereas other groups selectively benefit (McKinney and Lockwood 1999). In discussing a New Pangea, it is possible to conceptualize certain groups as beneficiaries. The Sixth Mass Extinction emphasizes only one side of this ledger, the losers. A final advantage of the New Pangea metaphor is its explicitly geographic component. As Jablonski (2001) noted, considerations of the current biotic crisis need to incorporate the reality that extinction rates now vary substantially among regions, just as they often have in the past. The New Pangea metaphor includes this, by noting that the winners of the impending global changes will tend to undergo geographic range expansion, replacing the losers whose ranges will shrink or disappear.

Like most metaphors, the New Pangea one is not perfect, and it certainly is not my own idea. Pangea is not a perfect metaphor for the future biosphere in part because the end-Permian mass extinction resulted from a combination of many factors, of which continental assembly was only one (Erwin 1993). In addition, human alterations of the biosphere are so rapid and are occurring in so many ways that any comparison with the comparatively simple natural dynamics of the past must be considered as speculative.

To my knowledge, Rosenzweig (2001a, 2001b) was the first to use this metaphor in its current context, although Brown (1995) reviews some very relevant species-area calculations predicting biotic homogenization from the removal of geographic barriers. Also, several related allusions to the future homogenized biosphere have acquired some currency in the literature. The term "Homogocene" has made its appearance in several places (e.g., Guerrant 1992) to describe the next geologic epoch. David Quammen (1998) has labeled the future biosphere as the "planet of weeds". Although this latter metaphor is certainly colorful, I suggest that the New Pangea concept is more informative because future winners of the human-dominated biosphere will consist of more than only "weedy" species, most notably pets, ornamental plants and other species that we cultivate for our own uses. The Pangea concept also conveys much about the processes that will shape our future biosphere.

NEW PANGEA: TRANSPORTATION PLUS INCREASING HABITAT UNIFORMITY

The extinction of local native species and their replacement with widespread species from another locality are ongoing processes that promote biotic homogenization (Olden and Poff 2003; Olden et al. 2004). The mixing process has only just begun but its effects are visible to anyone who travels very far, especially to islands, where biotic homogenization is most apparent in such groups as birds (Harrison 1993) and snails (Cowie 2001).

Homogenization is probably an inevitable trend of a globalized modern world, occurring with culture and technology as well. Commentators in several fields of study often note the increasing uniformity of the world by the loss of local and regional distinctiveness (Quammen 1998; Western

2001; Olden et al. 2004). In the social realm of economics and culture there is growing concern over “globalization,” whereby the wide diversity of the world’s cultures is becoming replaced by a globalized mass culture (Goldsmith and Mander 2001).

Although humans are obviously not forcing the continents together, we are recreating many of the major conditions found in ancient Pangea that promoted species mixing. Specifically, modern species mixing is promoted by two distinct steps: increasing dispersal and the spread of habitat uniformity. In the past, increased dispersal occurred by the removal of barriers. Now, humans not only remove barriers (e.g., the Panama Canal) but we also accidentally or intentionally transport species all over the globe.

The second step in the mixing process, habitat uniformity, is perhaps less obvious and is given less discussion in the scientific literature on species mixing. But this second step is very important because any species immigrating into an area cannot become established unless the area provides suitable habitat. In the future, the widespread creation of human-dominated habitats, such as cities and farmland, will provide the habitat used by introduced species (Woodruff 2001, and see below).

It is commonly noted that current extinction rates are orders of magnitude higher than those of the past (Woodruff 2001). In contrast, I know of no one who has compared rates of exotic species introductions to biotic exchanges in the past. Clearly, this is a difficult comparison to make, especially in light of our lack of knowledge of current species introductions in the marine realm where fossil data are most complete. However, what we do know about marine introductions from the global shipping industry (Ruiz et al. 2000) makes it evident that current rates of introduction are very high, on the order of hundreds of species introductions per year for most large geographic regions, and probably increasing exponentially.

Thus, as with extinctions, modern introductions are orders of magnitude higher than natural background rates, and they probably also exceed introduction rates even during past natural catastrophic episodes. In other words, rates of biotic homogenization are also orders of magnitude higher than at any time in earth’s history. This is because of the high rate of dispersal (transportation) plus the high rate of habitat creation for exotic species. Ultimately, for reasons I discuss next, the overall extent of homogenization also seems likely to exceed that of the past.

SUPERHOMOGENIZATION: CREATING WIDESPREAD HABITAT FOR A FEW NEWCOMERS

Most human activities transform natural ecosystems in ways that reduce habitat for native species, and create habitat for nonnative species (Williamson 1996). There are many examples, so I will focus on three of the most obvious and widespread activities: urbanization, pollution, and other “disturbances” and cultivation.

Urbanization is one of the fastest-growing causes of habitat loss for native species (McKinney 2002). To the frequent traveler, homogenization is probably most visible in the increasing physical sameness of cities of the world. As James Kunstler (1995) describes so well in his popular book, *The Geography of Nowhere*, the rise of modern industry in the 1800’s was accompanied by the spread of advanced technologies, such as steel-reinforced concrete, that allowed the construction of skyscrapers to house increasing numbers of people. Although they may differ in stylistic details, large office buildings tend to converge in their appearance. Kunstler (1995) also describes the post-World War II mass production of suburban housing subdivisions in the United States. Since 1945 American suburban housing has become dominated by development corporations that buy large parcels of land that are subdivided into small plots for houses based on a very small number of basic design schemes.

This widespread physical uniformity promoted by urbanization is accompanied by an increase

in biological uniformity. For example, well over 50% of the plant species found in most major cities around the world are not native to the region where the city is located (Pysek 1998). Similarly, urban-rural gradient studies show that the proportion of exotic species increases from the countryside to reach a peak in the highly urbanized downtown areas. This pattern has been documented for many groups, including plants, birds, mammals, and insects (Blair 2001; McKinney 2002). As a result, synanthropic species, well adapted to intensively urbanized city areas, are among the widespread and homogenized biota in the world (Johnston 2001).

Another kind of widespread habitat change would include pollution and many other ways that humans degrade natural ecosystems. Extreme pollution of air, water, and land often degrades those media to the point that only a few nonnative species are able to tolerate habitats in them. An example would be carp and other freshwater fishes adapted to polluted waters (Rahel 2002). Similarly, fragmentation of forests by logging, roads and human settlements increases the exotic plant invasion rate (MacQuarrie and Lacroix 2003).

Finally, cultivation of species is a major mechanism of homogenization. Monocultures for food, timber and many other plant products are increasingly widespread in many parts of the world. Examples where homogenization by these activities has been discussed would include coffee plantations (Marcano-Vega et al. 2002) and agricultural land use in Puerto Rico (Grau et al. 2001).

MEASURING BIOTIC HOMOGENIZATION

Despite the increasing biotic homogenization caused by human activities, there have been surprisingly few attempts to study, and especially measure it. In those few studies where biological homogenization is actually measured (e.g., Rahel 2000, 2002; Blair 2001), the most common method is Jaccard's similarity index. This index measures the proportion of species that are shared between two locations:

$$\text{Jaccard's Index } (JI) = c/(a + b + c)$$

where c = number of species in common to both locations, a = number of species only found at site a, and b = number of species only found at site b. JI can vary between 1 (all species shared) to 0 (no species shared) between the two locations.

A basic null hypothesis for homogenization studies to test is that humans should generally increase Jaccard's Index, or similarity of species among locations. When humans remove unique native species, we increase JI by decreasing a and b in the denominator. Conversely, when we add widespread non-native species that are shared between both locations, we increase the numerator. For example, using Jaccard's Index, Rahel (2000, 2002) found that the fish faunas of states in the U.S. have become more similar, largely because of introductions of game fishes plus the widespread alteration of aquatic habitats from dams, dredging and many other human activities. A similar pattern was found by Marchetti and others (2001) for fishes in California. They demonstrated that the JI increased through time, as humans increasingly modified water bodies. I found the same pattern with plants among various locations in the United States, where increasing species richness of exotics tended to increase the JI (McKinney 2004).

We might expect that, as humans increasingly modify environments, we should find increasing similarity among these modified locations. The most intensively altered environments, such as highly urbanized areas, should thus show the greatest amount of homogenization. Evidence for this has been especially well documented by biologists studying birds. Blair (2001), for example, used Jaccard's Index to show that the birds of downtown Palo Alto, California are relatively similar to

the birds of downtown Oxford, Ohio. In contrast, when he compared the birds living in the natural environments outside those cities, they were very dissimilar (Blair 2001).

In addition to similarity indices such as Jaccard's Index, another way to measure homogenization is the species-area curve. Rosenzweig (2001a, 2001b) discusses how the slope of the species-area curve tends to be higher when sampling areas with many unique species, such as islands, mountains, or highly diverse tropical rainforests. Conversely, as humans homogenize islands, and all other habitats, new species will accumulate more slowly on species-area curves because locally unique species are lost and more species are shared among areas. In other words, homogenization tends to lower the slope of the species-area curve. This was found, for example, by Flather (1996) when comparing curves of bird species in intensively farmed regions of the United States (which are very homogenized) versus bird species in more natural areas of the United States. In his book *Macroecology*, James Brown (1995) uses species-area patterns to predict that between 35–70% of species now on Earth will disappear if humans completely homogenize the global biota. I used this method to predict the loss and homogenization of marine species from the building of the Panama Canal, and concluded that it seems to be fairly accurate (McKinney 1998).

I hasten to add that the species-area method to predict species homogenization is fraught with many problems and assumptions. These problems have been discussed at length by Collins and others (2002) and they make a persuasive case that such predictions are very tentative. However, the species-area curve is well known, and it is a good way to at least conceptually visualize how homogenization affects large-scale patterns, especially where such complexities as habitat diversity are also factored in.

Thus far, I have focused on measuring homogenization as the number of shared elements. Jaccard's Index measures the number of shared species between ecosystems, and the species-area curve tabulates species accumulation along a sampling gradient. One important limitation on this method is that it assumes that the elements counted are individual and distinctive units. But many of these elements can be blended with one another. Cultural items including architectural styles and languages, for instance, are often blended, as evidenced by such dialects as Creole. This is also true of biological homogenization, where distinct but related species can sometimes interbreed when exotic species are introduced.

Sometimes called "genetic or biological pollution," this genetic intermixing between native and a related introduced species has become increasingly common (Petit 2004). Many examples are documented in a review by Rhymer and Simberloff (1996). Some of the more familiar examples would include the genetic mixing of many introduced crop plants with their wild relatives. Among animals, mallard ducks (often introduced for hunting) are infamous for interbreeding with native ducks. For instance, hybridization with introduced mallards has contributed to the decline of the endangered, endemic Hawaiian duck. Mating with feral housecats has contributed to the genetic decline among several species of wildcats native to Africa and Europe, and the bobcat of North America. A similar decline has occurred among several native wild species of canids, through interbreeding with domesticated dogs. Examples include many populations of wolves. In Europe, what had been considered pure wolf (*Canis lupus*) populations have turned out to be largely hybrids between wolves and domestic and feral dogs (*Canis familiaris*). Genetic blending among species not only dilutes the gene pool of native species and subspecies, it also affects the evolutionary process (Olden et al. 2004).

Even if we set aside the problem of blending among elements, a more thorough measurement of homogenization requires that we look beyond tabulating the number of elements (such as species, architectural styles, or languages) that are shared. We also should try to examine the relative abundance of each element where we can. For example, suppose we compare two cities and

find that they share all ten species of non-native birds in them. But what if all ten species are very common in one city and they are all very rare in another? We might not even see the birds in the city where they are rare. In other words, the similarity among cities is even greater where species are not only shared, but where each species has similar abundances in each city. Ecologists have the ability to incorporate abundance data into such comparisons by using the Bray-Curtis and several other indices (Waite 2000). However, I am not aware of any studies of homogenization that have included abundance data thus far.

In addition to homogenization from the exchange of species and genes, we should also consider other ways that the biosphere is becoming more uniform. Olden and others (2004), for instance, have noted the potential importance of functional homogenization. This examines the increasing similarity among human-disturbed ecosystems in such community traits as energy flow, food web structure and complexity, and chemical cycles. These new homogenizing human-dominated ecosystems tend to be more simplified than natural ones (Western 2001). From an energy perspective, one may see this as a process whereby the few species that can exploit sources of food increasingly provided by human activities become widespread. Examples include species that exploit cultivated plant communities such as crops or suburban ornamental plants, and species that thrive on garbage, bird seed and other forms of imported foods. In many cases, these “subsidized” species attain population densities far above their natural abundance, such as documented in coyotes of southern California (Fedriani et al. 2001).

THE CONSERVATION CHALLENGE OF LOCAL DIVERSITY BUT GLOBAL MONOTONY

An important consequence of biotic exchanges in the past is that they sometimes have led to increases in local and regional diversity (Vermeij 1991). This is also often true today, as human activities increase the number of species in an area. Sax and Gaines (2003) have reviewed the literature to document such local and regional increases produced by exotic species for many groups, especially plants and freshwater fishes. In such cases, the number of exotic species gained exceeds the number of native species that become extinct (Mooney and Cleland, 2001; Rosenzweig, 2001a, 2001b). A main explanation for this species enrichment is that increasing modification of the environment not only degrades habitats of native species but also creates a diversity of habitats for many exotic species that are imported by humans (Sax et al. 2002). Cities, for example, often have a greater richness of plant species than surrounding areas for this reason (Pysek 1998) because cities have a rich variety of land-use and habitat mosaics (McKinney 2002). Similarly, suburban landscapes are very rich in lawn grasses, shrubs, flowers and trees that are cultivated by homeowners (Hope et al. 2003).

The problem for biodiversity conservation is that despite these local species enrichments, global biodiversity continues to decline. Furthermore, because these locally diverse exotic species are typically widespread species, there is a global trend of increasing homogenization (Rosenzweig 2001a, 2001b). Harrison (1993) documented this process on Pacific islands. She showed that the extinction of native birds by exotic birds introduced by humans has increased the net local (alpha) bird diversity on those islands. However, the total regional bird diversity of those islands has declined because the introduced birds tend to be the same species that are shared among many islands. From a genetic perspective (Petit 2004), this process represents the loss of unique genes and genomes which are replaced by more common ones.

This pattern of local enrichment but global decline is a crucial one for conservation biology because it may divert public attention away from the more global problem of global species decline. The general public, and most policymakers, tend to think mainly at local scales (Ornstein

and Ehrlich 1989). This is illustrated by the fact that, although people often value species diversity, most of the general public cannot identify whether a local species is exotic (McKinney 2002) and, even when they do know it is exotic, they still place a high value on that species if it is aesthetically pleasing (Reichard and White 2001), good for sport or has some other utilitarian value (Brown et al. 1979; McKinney 2002).

ENHANCING HOMOGENIZATION: WINNERS AND LOSERS ARE CLUMPED IN GROUPS

Extinction is almost never random. Ecologists and paleontologists have accumulated a large literature documenting how certain traits make some species more prone to extinction (McKinney 1997, Purvis et al. 2000a, 2000b). In general, these traits are correlated with a higher risk of extinction in the past, and in today's human-dominated world. Examples of such extinction-promoting traits include: low abundance, large body size, slow reproduction, specialization (such as a specialized diet or habitat), and adaptation to island life.

In addition, traits such as body size and reproductive rate tend to be shared by closely related species so that some phylogenetic and taxonomic groups tend to contain more species at risk (McKinney 1997; Purvis et al. 2000a, 2000b). Birds are among the best studied in this respect. For instance, Lockwood and others (2000) found that certain bird families, including the pigeon family and the parrot family, have a higher concentration of globally threatened species than would be expected if globally threatened bird species were randomly distributed among families. In accord with the extinction-biasing traits noted above, pigeons and parrots tend to be large and slowly reproducing birds. In addition, they are also often harvested for food and pets. In contrast, the woodpecker family has fewer threatened species than expected. Similarly, a study of threatened vertebrates of the United States showed that threatened species of mammals, birds, reptiles, amphibians and fishes tended to be concentrated within certain genera (Lockwood et al. 2002). This concentration of species losses in certain groups can accelerate biodiversity loss, essentially by disproportionately pruning certain branches on the phylogenetic tree (Purvis et al., 2000a, 2000b).

The concentrated loss of species also can enhance biological homogenization. By removing species that belong to unique groups, biological communities lose their most distinguishing elements. Homogenization is enhanced if those species that expand their geographic ranges (the winners) are not randomly distributed among groups but are concentrated within the same few groups. For example, Lockwood (1999) found that bird species purposely introduced and established by humans are not randomly distributed among families but have been concentrated in certain families. The duck and pheasant families are examples. In their case, these species have been mainly introduced for their value as game birds. Aside from human preference (such as sport for game birds), another key reason for clumping is that species in certain groups have, by evolutionary chance, evolved adaptations for exploiting the kinds of habitats that humans often create. Species in the grass family, for example, tend to be well adapted as weeds and have often spread widely for that reason (Daehler 1998). Among insects, flies and beetles (among others) seem to be overrepresented (Vazquez and Simberloff 2001).

The important outcome is that humans not only replace locally unique species with the same few species, but those same few species tend to be from the same few taxonomic groups, such as the duck family (among birds) and the grass family (among plants). Clumping enhances homogenization because our biota not only consists of the same few species, but, because they are from the same few groups, even these few tend to be similar to one another (McKinney and Lockwood 1999).

Clumping is not limited to taxonomic groupings. Winners and losers are often nonrandomly distributed among ecological groupings as well. Species adapted to the forest edge and species that are generalists and have a broad diet, for example, are often favored in human-dominated environments (McKinney and Lockwood 1999; Western 2001). Again, this enhances homogenization because the world becomes dominated by species in these categories.

CONCLUSIONS: HOW BLENDED THE FUTURE BIOSPHERE?

How far will the mixing process go in the future? Efforts to answer this are impaired by the lack of study of homogenization. Most of the few homogenization studies thus far have analyzed freshwater fishes, perhaps because this group has experienced some of the most extensive homogenization of all groups. These studies include fishes in the United States (Radomski and Goeman 1995; Rahel 2000, 2002; Marchetti et al. 2001; Scott and Helfman 2001) and in the state of Tennessee (Duncan and Lockwood 2001). In addition, homogenization has been studied in Pacific island snails (Cowie 2001), Pacific island birds (Harrison 1993) and urban birds in the United States (Blair 2001). McKinney (2004) found that exotic species increase homogenization among North America flora. The main metric of homogenization in all these studies has been to compare the species composition of communities before and after human disturbance and the introduction of exotics. In all cases, these studies conclude that human activities have significantly increased the amount of homogenization by increasing the proportion of shared species among human-disturbed communities.

It seems likely that homogenization will continue for many decades and will eventually produce a biosphere that is more homogenized than any in Earth's history. In the first place, there is enormous potential for species movement in today's world, with modes of transportation that can easily leapfrog over all natural barriers. In the second place, there is a greater potential in today's Pangea for homogenization of the physical environment. As humans destroy unique natural environments, they tend to replace them with the same types of artificial environments throughout the world. For reasons of efficiency and human tastes, cities, farms, roads, airports, and most other human environments tend to have much more in common with similar human environments elsewhere in the world than with their original natural environment. In the third place, human selectivity, by concentrating the winners and losers of the next mass extinction into certain higher taxa and ecological categories (e.g., early successional species), will likely enhance homogenization.

Will the entire biosphere ultimately become completely and uniformly homogenized? It seems unlikely. Natural limits on species ranges include physical geographic gradients such as climate and soil. For example, one can speculate that the tropical South American exotic species that now thrive in the cities of South Florida will probably not persist in the cities of Canada. Human-imposed limits to homogenization may also exist. Conscious efforts to reduce native species extinction, non-native species transport and establishment, and many other conservation efforts could, in theory, curb the ultimate extent of biological homogenization.

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