Biotic homogenization: a few winners replacing many losers in the next mass extinction

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Human activities are not random in their negative and positive impacts on biotas. Emerging evidence shows that most species are declining as a result of human activities ('losers') and are being replaced by a much smaller number of expanding species that thrive in human-altered environments ('winners'). The result will be a more homogenized biosphere with lower diversity at regional and global scales. Recent data also indicate that the many losers and few winners tend to be non-randomly distributed among higher taxa and ecological groups, enhancing homogenization.

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Biotic homogenization is an increasingly common phrase used in discussions of the modern biodiversity crisis[1–5]. Although rarely precisely defined, homogenization generally refers to the replacement of local biotas with non-indigenous species, usually introduced by humans. Because homogenization often replaces unique endemic species with already widespread species, it reduces spatial diversity. Although biotic homogenization is a rapidly growing conservation issue in both biology[6] and the public arena[7], understanding the dynamics of homogenization will be challenging because it subsumes many complex aspects of the biodiversity crisis such as extinction and species introductions.

Environmental disturbances are often viewed only in terms of their harmful impacts on the affected species. However, in any disturbance some species will benefit[8]. If that disturbance is widespread and persistent, the beneficiary species will expand their range and replace those that cannot survive. Thus, biotic homogenization occurs when a widespread environmental change promotes the geographic expansion of some species ('winners') and the geographic reduction of others ('losers')[6]. Previous mass extinctions, for example, show that global climatic and geological disturbances often produce low-diversity biotas dominated by a few widespread, broadly adapted species[9].

This same process is now occurring on a global scale as a result of two influences: environmental modification and transportation of exotic species[3,4,10]. Environmental modification promotes the loss of local endemic species that cannot tolerate human activities. Meanwhile, increasing global transport promotes the spread of non-indigenous species[4,10,11]. Although many of these non-indigenous species thrive in disturbed environments, some also invade, and thus homogenize, relatively undisturbed natural areas[10]. The homogenization process is seen in island biotas where the loss of endemic species and their replacement by widespread exotic species result in decreased beta diversity among the islands[2]. The projected rise in species extinctions[5,12] and species introductions[10] will almost certainly increase homogenization at continental scales as well. As Brown[13] stated, 'geographically restricted native species with sensitive requirements will continue to have high extinction rates while those widespread broadly tolerant forms that can live with humans, and benefit from their activities, will spread and become increasingly dominant'.

How many losers and winners?

A common source for estimating the number of probable losers can be found in lists of threatened species[14]. However, this almost certainly underestimates the true number of losers as many (probably most) species are in decline but their abundance is not yet low enough to warrant current listing. A compilation of observed declines at many spatial scales and as a result of many types of human activities (Table 1) supports the suggestion that many species (usually >50%) are adversely affected by human activities, but are not yet listed[14]. About 11% of all global bird species, for example, are listed on the IUCN (The World Conservation Union) Red List compared with a much higher proportion (70%) of species in decline[14]. In the five major fossil mass extinctions, over 50% of all species became extinct[5,9]. If all, or even most, species now in decline eventually become extinct then a mass extinction on the scale of previous events would occur. This is all the more striking given that humans have not yet fully impacted some remaining ecosystems (and their endemic species) so that the total number of declining species will probably grow. Interestingly, the percentages of declining species (Table 1) are similar to species–area curve predictions of a homogenized biosphere, which project the eventual extinction of about half the living species in most major taxa[3,4,15].

Winners are species that not only resist geographic range decline, but also expand their ranges. Thus, estimating the total number of winners requires directly measuring the number of species that are currently, or will eventually, expand their ranges. The rapidly growing literature on biotic introductions is a useful starting place for data about species range expansions. About 2% of bird[11] and 1% of mammal[16] species, worldwide, are currently identified as having been successfully introduced into new environments. About 2% of plant species are considered successful invasive weeds[17], indicating an even larger percentage of successful introductions if non-weed (economically benign) plant species are counted. For many reasons, such tiny fractions of estimated successful biotic introductions probably underestimate the true number of ultimate winners. One reason is the woefully inadequate data on current species introductions, which under-report species expansions because of lag times and cryptic species[10,18]. In addition, many species that could be successfully introduced have not yet been transported to the appropriate habitat. Perhaps most important is that many winners are not perceived as invasive because they are undergoing only localized expansion in, or near, their native ranges.

One way to estimate the number of winners as a result of human disturbances is to examine the percentages of biotic beneficiaries of human activities at smaller scales, where all the winners and losers in a formerly natural biota can be identified. For example, agroforestry in Sumatra negatively impacts population size in 56% of rainforest bird species but positively impacts population size in only 22% (Table 1). Similarly, in California (USA), conversion of a natural ecosystem

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to a residential area caused population declines in 52% of bird species but an increase in 29%. Taken as a preliminary indication, the eight studies shown in Table 1 suggest that the percentage of native species that are winners in localized disturbances ranges from 5% to 29%, with numbers of winners decreasing as the severity of disturbance increases. In birds, deforestation and urbanization apparently produce fewer winners than agroforestry and suburbanization. Many more examples such as these need to be collected. However, in general, these studies seem to be consistent with past mass extinctions where the loss of over 50% of all species was accompanied by the expansion of a much smaller fraction (<< 50%) of the original biota[9].

Table 1. Estimated proportions of species declining (losers) or increasing (winners) in range and abundance

Group[a]	Proportion of species affected (%)	Disturbance(s)	Refs
Losers			
Birds (global)	70	Many	26
Birds (Sumatran rainforest)	56	Agroforestry	27
Birds (Atlantic rainforest)	68	Deforestation	21
Birds (Californian preserve, USA)	52	Suburbanization	28
Fishes (California, USA)	64	Many	29
Butterflies (The Netherlands)	46	Many	30
Amphibians (Maine, USA)	93	Deforestation	31
Amphibians (Amazon)	64	Deforestation	24
Butterflies (UK)	74	Many	32
Bees, wasps, ants (UK)	70	Many	33
Moths (Borneo)	83	Deforestation	34
Plants (excluding trees; Singapore)	60	Forest fragmentation	35
Winners			
Birds (Californian preserve, USA)	5	Urbanization	28
Birds (Indonesia)	11	Deforestation	36
Birds (Borneo)	15	Deforestation	36
Birds (Sumatran rainforest)	22	Agroforestry	27
Birds (California, USA)	29	Suburbanization	28
Foxes (North America)	20	Urbanization	37
Butterflies (UK)	9	Many	32
Bees, wasps, ants (UK)	10	Many	33

[a] Habitats are given in parentheses.

Taxonomic and ecological enhancement of homogenization

The replacement of many endemic species by a few widespread species could, by itself, promote large-scale homogenization[2,3]. However, this effect can be enhanced if the winning and losing species are not randomly distributed among taxonomic and ecological categories.

Selective extinction of species within higher taxa can accelerate biodiversity loss[19]. This is especially true if losses are concentrated in species-poor taxa. The accelerated loss of higher taxa removes the unique genetic morphological and behavioral diversity that these taxa represent[19]. Emerging evidence suggests that species extinction is taxonomically non-random at local and global scales; some families are reported to contain substantially higher percentages of threatened species (global) or declining species (local) than others (Table 2). Globally, the high percentage of threatened species in the parrot family (Psittacidae) has been attributed to their larger size and, especially, their lower fecundity[20]. These traits make parrots more prone to extinction from a variety of human disturbances including overexploitation and habitat loss. On a local scale, Goerck[21] suggests that parrots are more prone to extinction from deforestation in Brazil because they tend to be larger and more frugivorous. Such clustering of extinction-biasing traits within higher taxa is apparently a very common result of the non-random way that traits are shared among closely related species[19].

Similarly, homogenization might be enhanced to the extent that the relatively few winning species are also concentrated within certain higher taxa. The biosphere could be increasingly dominated not only by the same few species,

Table 2. Taxonomic patterns among local and global winners and losers

Group[a]	Over-represented families	Biasing traits[c]	Refs
Losers (global)			
Threatened birds[b]	Parrot, pheasant	Large size, low fecundity	20
Threatened mammals[b]	Ape, rhinoceros	Large size, low fecundity	12
Threatened plants	Cactus	Small range	38
Losers (local)			
Birds (Sumatran forest)	Babbler	Large, forest specialist	27
Birds (Brazilian forest)	Parrot	Large, frugivore	21
Birds (USA urban)	Vireo	Migratory, insectivore	37
Frogs (Amazon forest)	Leptodactyl	Inner forest specialist	24
Insects (Boreal forest)	Fungus gnat	Diet (forest)	39
Salamanders (Maine forest, USA)	Plethodontid	Skin respiration	31
Plants (Singapore forest)	Rubiacid (shrub)	Shade-tolerant	35
Winners (global)			
Invasive plants[b]	Grass, roses	Rapid growth, ornamental	22
Serious weeds[b]	Grass, pondweed	Rapid dispersal/growth	17
Widespread weeds[b]	Grass, cattail	Rapid dispersal/growth	17
Natural area plant invaders[b]	Grass, legume	Broadly tolerant	17
Introduced birds[b]	Duck, pheasant	Good for sport/pets	11
Domesticated mammals	Bovids	Non-territorial, broad diet	40
Winners (local)			
Birds (agroforestry)	Warbler	Small, omnivore/granivore	27
Moths (Borneo forest)	Sphingid	Open-habitat, generalist	34
Frogs (Amazon forest)	Hylids	Temporary pond breeder	24
Spiders (S. African forest)	Wolf spider	Plant-independent webs	25

[a] Habitats are given in parentheses.

[b] Groups were analyzed statistically to document non-random concentrations of loser or winner species within families.

[c] Reported traits that are common in a family and apparently promote the geographic spread or decrease of many species in the family.

Table 3. Traits influencing whether species are winners or losers in a human-dominated world[a]

Traits promoting range expansion	Traits promoting extinction
r-selected traits (small size, high fecundity)	*K*-selected traits (large size, low fecundity)
High variability	Low variability
Widespread	Rare
Rapid dispersal	Slow dispersal
Generalist (eurytopy)	Specialist (stenotopy)
Human commensalism	Poorly adapted to human activities

[a]Modified from Refs 1,11,15.

but also by the same closely related species. Table 2 shows examples of families that have globally and locally high percentages of species showing range expansion. Globally, statistical testing shows that families such as the grasses (Poaceae)[17,22] and ducks (Anatidae)[11] have more successfully introduced species than would be predicted if such species were randomly distributed among families. This over-representation can have drastic taxonomic homogenizing effects where species-rich taxa have a very large concentration of exotic species. For example, the large grass family (Poaceae) contains 180 more weed species than it would if 'weediness' were distributed randomly among plant families[17]. These represent 180 closely related winners (almost 10% of those analyzed) that would otherwise represent many other plant families within the set of global weeds. Taxonomic over-representation also occurs in local winners [e.g. hylid frogs (Hylidae); Table 2].

As with extinction-biasing traits, such clustering of winning species in certain families can be attributed to the non-random way that traits are shared among closely related species[19]. Such taxonomic clumping of invaders can occur because closely related species tend to share traits that promote successful transport and establishment in new environments[23]. However, the specific traits that are clustered seem to fall into two different categories (Table 2). One category represents those traits that promote survival and spread in alien environments. In plants, for example, invaders of croplands and other highly disturbed areas are concentrated in herbaceous families with rapid growth and wide environmental tolerances[17,22,23]. By contrast, invaders of undisturbed natural areas are over-represented in a variety of woody families, including nitrogen-fixers that can live in nitrogen-poor soils[17].

A second category of trait clustering relates not to establishment in an alien environment but transportation to the alien environment. Many bird and plant families with a significantly high concentration of exotic species have traits that encourage purposeful human transport such as birds for sport (pheasants, Phasianidae), pets (parrots, Psittacidae)[11] and plants as ornamentals (roses, Rosaceae)[22]. Shared family traits that promote transport should thus be distinguished from shared family traits that promote establishment after transport, such as rapid reproduction in crop weeds and nitrogen fixation in natural area invaders.

Similarly, families with many local winners apparently have clusters of traits that promote establishment in environments produced by human activities. Deforestation benefits moths (Sphingidae) with generalist adaptations to an open habitat, frogs (Hylidae) that breed in temporary ponds[24], and spiders (Lycosidae) with webs not confined to certain kinds of vegetation[25]. In all cases, species with these traits are not randomly distributed among families, but tend to be concentrated in specific families (Table 2).

It is perhaps not surprising that traits commonly reported as promoting successful introduction into alien environments and local range expansion by disturbance are often the reverse of traits commonly suggested as promoting extinction (Table 3). Winners are characterized by omnivory, rapid growth and dispersal or breeding in ephemeral habitats, whereas extinction-prone groups have a predominance of traits associated with specialization, slow reproduction and other traits not associated with opportunism (Table 2). Interestingly, the same pattern has been suggested for mass extinctions, wherein widespread generalist (eurytopic) and opportunistic species not only survive major crises, but often expand their ranges[9].

Homogenization can also be enhanced by selectivity among ecological categories. Specifically, spatial homogenization in the future biosphere (as in previous prolonged mass extinctions) could be exaggerated by the local replacement of ecological specialists with the same widespread generalists and opportunists. This would produce ecological homogenization by the replacement of many (often more complex) functional and ecological systems by the same few simpler ones.

Conclusions and future prospects

As with past mass extinctions, the impending global crisis has many biotic losers being replaced by a few increasingly widespread winners. Previous mass extinctions eliminated over 50% of all species on earth[9] and this appears to be the likely outcome of current trends with over 50% of species in most groups in decline. Even if these species (losers) do not become completely extinct, they will probably be reduced to tiny fragments of undisturbed habitat[5] and become virtually invisible components of the biosphere. Conversely, the number of definite winners is currently a much smaller fraction of the earth's biotas at 1–2% (known invasive species) and 5–29% (species expanding their ranges locally). Addition of domesticated species as a category of winners does not significantly change this conclusion because less than 1% of all plant and animal species are domesticated and many are already counted among invasives[10,16,17].

The replacement of many losing species with a relatively small fraction of widespread winners will likely produce a much more spatially homogenized biosphere. This spatial homogenization might be taxonomically and ecologically enhanced to the degree that winners and losers continue to be increasingly clustered in certain higher taxa and ecological groups. Taxonomic clustering of losers and winners occurs when evolutionarily shared traits bias some groups towards extinction and other groups towards range expansion. As in past extinctions, species with broad diets and tolerances, rapid dispersal and high reproduction seem to occur disproportionately among winners. This implies that ecological homogenization might also occur because many ecological specialists are replaced by the same widespread and broadly adapted ecological generalists. The result would be fewer and simpler ecosystems in our newly homogenized biosphere. The ultimate degree of homogenization, if unchecked, will probably exceed even that seen in the largest past mass extinctions. This is because humans transport many species to isolated, distant areas that they would never have reached on their own, even if the earth were re-assembled into a single supercontinent[9].

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Hopeless monsters

Sudden Origins: Fossils, Genes, and the Emergence of Species

by Jeffrey H. Schwartz

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Are monsters hopeful, hopeless or simply a figment of our evolutionary imagination? In yet another attempt to re-establish the saltatory views of that decidedly mixed bag of anti-Darwinians, notably Richard Goldschmidt and Otto Schindewolf, the anthropologist Jeffrey Schwartz trawls the waters of developmental biology to argue that the discontinuities in the tree of life are not only real, but also can actually be explained. To get there, however, the reader is faced by a circuitous route that occupies most of the book. This is in the form of an extended historical essay that moves from the story of the hominid discoveries to a well-written and absorbing account of the rise and rise of genetics, via such luminaries as Galton, Haldane and Wright. All this is well-told, and can be read with profit and enjoyment. But the purpose of this section is also to soften us for the book's crescendo so, not surprisingly, there is an underlying tone of rancour. As with those who bleat about the 'hardening' of the neo-Darwinian thesis, here too there is a brooding sense of conspiracy: of those brave men, for example, who somehow 'were not cowed into complete silence'.

This is by no means the first attempt to topple the neo-Darwinians, but, as Schwartz correctly observes, only recently have the full implications of developmental genetics and embryology begun to emerge. The central problem with *Sudden Origins*, however, is that the main thesis is fatally flawed. To restore credibility to a saltatory mode of evolution, whereby the morphological discontinuities between even species are real and monsters are decidedly hopeful, Schwartz wades into the rapidly emerging story of *Pax*, *Hox*, *Otx*, *dpp* and other developmental genes. The extent of Schwartz's misunderstanding is evident simply by quoting him: 'If a mutation were to activate a homeobox gene or gene cluster, it would already possess the potential to create a complete structure. Although, of course, there could be an increase in output of the homeobox gene from the time of its activation, this, as indicated by the fossil record on the emergence of new kinds of organisms, was not the case.' These claims are not simply theoretical. On the contrary, Schwartz can be very specific: 'the model … demonstrates how a mutation involving the expression of homeobox genes can produce a morphological, physiological, or behavioral novelty that would emerge in a full-blown and viable state. Consider … the consequences of the experiment in which the [*Pax-6*] gene is altered from the