Species diversity: from global decreases to local increases

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Current patterns of global change can strongly affect biodiversity at global, regional and local scales. At global scales, habitat destruction and the introduction of exotic species are contributing to declines in species diversity. At regional and local scales, evidence for declines in diversity is mixed, and recent work suggests that diversity might commonly be increasing. In spite of these trends, considerable research continues to consider explicitly the effects of declines in diversity on processes that operate at regional and local scales (such as ecosystem functioning), without explicitly considering the converse set of questions, namely the effects of increases in diversity. Here, we examine evidence that indicates how species diversity is changing across spatial scales and argue that global decreases in diversity are commonly contrasted by increases in diversity at regional and local scales.

Habitat destruction and the introduction of exotic species are causing the extinction of many native species [1]. At a global level, these losses are causing a decrease in total biodiversity [1–4]. At sub-global scales, losses of native species can be offset by the establishment of exotic species, which can sometimes cause a net increase in diversity for specific regions or locations [5]. In spite of the complexity of net changes in diversity across different spatial scales, the assumption of much current research is that diversity is declining at all spatial scales. Nowhere has this view been more apparent than in the recent body of research addressing the 'diversity–ecosystem function' debate. The premise for most of this work has been to examine the consequences of declines in diversity on ecosystem functioning [6,7]. Because of this, many experiments have reduced 'natural' levels of diversity within species assemblages and then measured the consequences of these reductions on one or more measures of ecosystem functioning (e.g. [8]). This approach is only sufficient, however, if most species assemblages are declining in diversity. Recently published empirical studies have shown that the level of diversity of many species assemblages is actually increasing or remaining unchanged. Here, we examine the generality of this result by exploring how diversity has changed across spatial scales from the entire globe to small local areas.

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Global change in diversity

Many ecologists and evolutionary biologists expect global diversity to decrease dramatically in the years ahead, likening these reductions to the mass extinction events that occurred in past geological eras [1–4]. Some projections estimate that more than half of current species could become extinct as a consequence of current patterns in global change [2]. Many types of global change can cause species extinction, but two are believed to be particularly important [9]. First, habitat loss can cause species extinction when the entire habitat occupied by locally endemic species is destroyed; habitat loss can also facilitate extinctions when historically wide-ranging species have their populations fragmented or reduced [10]. Second, the introduction of exotic species can cause or facilitate extinctions of native species by initiating species interactions that lead to declines in the abundance and distribution of native species (e.g. [11]). These introductions of exotic species, and the associated decline in the importance of barriers that previously isolated distinct regions, have been likened in the extreme case to the creation of a 'new Pangea' or supercontinent, in which all landmasses are interconnected [12,13]. This conceptual model overemphasizes the importance of human-mediated transport of species; nevertheless, it provides an upper limit to what the anticipated effects of exotic species could be. Not surprisingly, strong disagreement exists in the literature over the long-term consequences of such a change, but there is general agreement that, in the short term, the consequence will be a decrease in global diversity [12–14].

Besides affecting rates of species extinction, current patterns of global change might also affect rates of speciation. Although we know much less about how patterns of global change can affect speciation patterns, there are several reasons why speciation events might become more likely in the current regime of global change. First, speciation events should become more likely (particularly with plants) when previously isolated species are brought together and given the opportunity to hybridize. Many hybridization events fail to produce fertile taxa, but a significant proportion do so, and some of these, following changes in chromosome arrangement or number, are able, in turn, to form new genetically isolated and distinct species [15]. Although reports of such speciation events following hybridizations between native and exotic species are not common, they are nonetheless well documented in the literature [15,16]. Second, speciation events might be

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promoted (for both plants and animals) by modern-day vicariance events, such as habitat destruction, that cause allopatric distributions, in which populations are isolated from on another. Isolated populations, such as those within a reserve that is surrounded by a sea of suburban development, that can survive over the long term and adapt to changing conditions might ultimately form new species. Third, the introduction of small founder populations of exotic species, and the subsequent genetic changes that they experience in their naturalized range, could lead to the formation of new species. Undoubtedly, other unanticipated global changes that cause species to be brought together or split apart might also lead to the formation of new species.

At a global scale, the opposing processes of speciation and extinction determine net change in species diversity (Box 1). Although many speciation and extinction events will have gone unnoticed, available evidence from this past century indicates that the number of extinction events has greatly exceeded the number of speciation events [2,16]. Therefore, it is more than likely that species diversity is currently decreasing globally.

Regional changes in diversity

Within regions (by which we mean the broad set of areas that are intermediate in extent between the entire globe and small study plots of less than a few dozen hectares), determining changes in species diversity is more complicated than determining those at the global scale (Box 1). At these 'regional' scales, speciation, extinction and extirpation (regional-level extinction events) are important.

Box 1. Processes determining changes in species diversity across disparate spatial scales

Species diversity is affected by a variety of different processes, only some of which operate across spatial scales. At a global scale, change in species diversity is only affected by two processes, extinction and speciation, and the net balance between these two processes determines whether diversity is increasing or decreasing on Earth.

At regional scales, diversity is also increased by speciation and decreased by extinction. These decreases in diversity include those caused by regional extinction events that extirpate species from the region in question but not necessarily from all other regions. In contrast to the global scale, regional diversity can also increase when species immigrate between regions. The immigration of 'new' species to a region causes net diversity to increase when these species become established. However, these same species can cause decreases in diversity if they cause or facilitate the extinction of species that were previously present. So, net change in regional diversity is determined by speciation, extinction, extirpation and immigration.

At local scales, diversity is affected by the same processes that operate at larger scales, except that the process of speciation is rarely important. At local scales, however, biological and physical interactions become extremely important in determining diversity. This is because interactions between species, and interactions between species and their physical environment, will have a significant effect on the total number of species within a local area. Finally, at local scales, diversity is often measured not only as species number, but also by indices that consider measures of species relative abundance. Using diversity indices does not change the range of possible outcomes of changes in local diversity, because the addition of species can cause relative abundances of species to become more or less evenly distributed, resulting in increases or decreases in diversity.

However, an additional process, species immigration, is also important. Species immigration involves the import of species to regions where they were not present historically. This occurs naturally when species increase the extent of their native range via long-distance dispersal. More often, however, this occurs when species are transported by humans [17]. Regardless of their means of introduction to a region, when these 'new' species (hereafter referred to as exotics) become established, they can affect species diversity in two ways. First, they can decrease diversity if they cause extinctions (or extirpations) of native species. Second, they can increase diversity by becoming established and contributing to the total number of species present in a region. Therefore, the net effect of exotic species on species diversity is determined by the balance between the species extinctions (or extirpations) that they cause or facilitate and the number of exotic species that become established. Essentially, the issue is whether, on average, more (or less) than one native species is extirpated per exotic that becomes established.

Theoretical work that uses species area and isolation relationships to consider expected changes in diversity at regional scales predicts that regional diversity should increase as barriers to isolation are removed, and the world comes closer to resembling a single supercontinent [12,13]. Similarly, a recent conceptual synthesis of invasion theory with the unified neutral theory also suggests that regional species diversity should increase [18].

The conclusions of these theoretical and conceptual approaches are corroborated by evidence from the fossil record. In the past, there have been many times when regions that were previously isolated from one another were later connected as a result of changes in sea level, the formation of land bridges, and other tectonic events. In most cases, there is clear evidence that net species diversity increased following faunal mixing ([19] and references therein).

Empirical evidence also suggests that net species diversity has increased, both on islands (since the arrival of humans within the past few thousand years) and within regions on continents (since the arrival of Europeans within the past few centuries). Some of the largest net increases in diversity have been observed with vascular plants. On oceanic islands, many plant species have become naturalized, whilst few native species have become extinct, such that the total number of species has approximately doubled on most islands [5] (Figure 1). Qualitatively similar increases in richness have been recorded in continental regions. Plant richness has increased within US states by an average of $\sim 20\%$ [20,21] (Figure 1) and by a similar amount within Australian states [22,23]. These qualitative increases in plant richness also hold at smaller regional scales; for example, the Vice-county of West Lancaster in the UK has increased dramatically in species diversity over the past 200 years, with the loss of <40 native species and a gain of nearly 700 exotic species [24].

Empirical evidence from animals also commonly shows a pattern of increased diversity. Reptile and amphibian diversity have increased slightly in California [25]. Mammal diversity has increased on many oceanic islands, in California, in Western Australia and in their

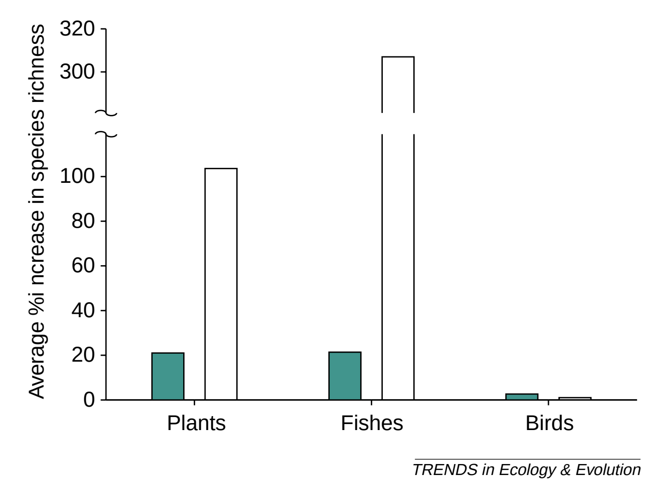

Fig. 1. Change in species richness at regional scales. Species richness of plants and fishes has increased dramatically, whereas species richness of birds has remained relatively unchanged, on oceanic islands (white bars), since the arrival of humans within the past few thousand years, and within continental regions (green bars), since the arrival of Europeans within the past few centuries. Continental regions used for plants and birds are the 49 continental states of the USA, whereas continental regions used for fishes are 125 drainages in North America. The value reported for fishes from oceanic islands is based on data from only: Hawaii, New Zealand and the Falkland Islands; data from islands where there were no native species (e.g. Kerguelen) are excluded. Changes in plant richness reported here for US states underestimate actual increases, because data used to calculate extinctions also included threatened species that are still extant. Data sources: plants and birds on islands [5], fishes from islands [27,30,31], fishes in North American drainages [32], plants from American states [20,21], birds from American states ([20] and uncollated data from [37], and references cited therein).

respective continents of North America and Australia [25–29]. Freshwater fish diversity has increased dramatically on oceanic islands [26,27,30,31] (Figure 1), where diversity of fishes has historically been strongly limited by barriers to dispersal. Freshwater fish diversity has also increased significantly within drainages of the USA [32] (Figure 1), and within drainages of California [33]. At the scale of individual lakes, changes in diversity of freshwater fishes (over the past 50–150 years) have been more idiosyncratic, with examples of increased, decreased and relatively unchanged diversity (e.g. [34–36]). In contrast to most other vertebrates, net bird diversity (in spite of large changes in species composition) has remained largely unchanged on oceanic islands [5] (Figure 1) and within US states ([20] and uncollated data from [37]; Figure 1). In one study, over a 50-year period within two counties in Michigan, net bird diversity remained almost the same in spite of large changes in species composition [38]. For invertebrates, few data are available at regional scales; marine invertebrates along littoral environments are believed to have increased in diversity [39], whilst species diversity of butterflies in California is not believed to have changed significantly [25].

The one consistent pattern among all these groups is that no general decreases in diversity are known to have occurred at regional scales. The only exceptions to this conclusion are species that occupy regions that are becoming increasingly isolated by patterns of global change. For example, in National Parks of the USA, mammal diversity has decreased slightly [40], although the magnitude of these changes is small relative to the total mammalian diversity of these areas. This difference, however, between mammals in US National Parks and plants in US states indicates that conditions that might isolate one group at one spatial scale might provide increased connectedness for other groups at other spatial scales; this suggests that relative differences in connectedness (and dispersal ability) will strongly influence future changes in species diversity among groups.

Local changes in diversity

At local scales (by which we mean small study plots of less than a few dozen hectares with respect to plants, or slightly larger areas with respect to animals), diversity is expected to have changed in very different ways within anthropogenic environments versus native ecosystems that are more or less intact. Within anthropogenic environments, such as parking lots, housing developments and agricultural fields, diversity of species (at least of those able to persist without human assistance) has clearly decreased dramatically from conditions before human disturbance. Within local systems that are more or less intact, however, net changes in diversity are not as well understood.

Although ‘intact’ local systems are perhaps the most studied of all ecological systems, ironically it is at these small scales that we have the poorest conception of how diversity has changed. This is due, in part, to the added complexity in the way that diversity is often defined at local scales, which includes concepts of species evenness (Box 1). The primary difficulty in determining how diversity has changed at local scales, however, is the lack of repeated sampling of small-scale plots. To measure how species diversity has changed, we need to know how many species were present within a specific local area at some point in the past as well as how many species are present there now. With the exception of very short timescales (e.g. on the scale of a few dozen years), we rarely have such information.

To circumvent this deficiency, we can examine indirect evidence from studies of local changes in species diversity owing to species invasion or introduction events. Most of this evidence comes from paired comparisons of systems that have and have not been invaded by particular exotic species. Such comparisons are generally made, or at least reported in the literature, only within systems in which exotic species are believed to have had significant impacts. Although many of the most notorious exotic species, including salt cedar *Tamarix* sp., blue gum tree *Eucalyptus globulus* and purple loosestrife *Lythrum salicaria* commonly do not reduce species diversity relative to native systems [41–43], there are nevertheless cases in which reductions in species diversity are apparent [44]. It is these latter cases that have perhaps most strongly coloured the popular view that diversity is decreasing at local scales. Remarkably, this view has formed in spite of the fact that most exotic species are not known to have major detrimental effects on native biota [45] and that many studies show no reductions in diversity [41–43]. Additional sources of indirect evidence for local changes in diversity come from studies that examine how sets of native and exotic species vary in diversity across multiple local sites. This work has shown that native and exotic diversity are often positively correlated [46–48], which suggests that species richness has increased. However, without historical reference points, it is impossible to test this relationship conclusively, because an unknown number of native species might have been displaced by the exotic species present.

Fortunately, some direct evidence of local change in diversity is available from long-term studies and from work that has resurveyed older study plots. Most of this work has been done with plants, but a few studies of other groups provide relevant information. A study of rodents on a several hectare plot in southeastern Arizona that has been ongoing for >20 years has shown little change in species diversity, in spite of large changes in species composition [49]. Resurveys of 54 small lakes in Minnesota (after an average of 43 years before initial surveys) showed that freshwater fish diversity had increased in many lakes, but had decreased or remained relatively unchanged in others [50]. Resurveys of the Channell Islands off the coast of California (after 50 years) showed little change in species diversity (in spite of significant changes in species composition) on most islands, including three smaller ones that were each approximately one square mile in size [51]. With plants, some studies have shown that changes in limiting resources or disturbance regimes can increase local diversity in spite of a relatively constant number of species in the larger aggregate or regional pool of species [52,53]. Here, however, we are most concerned with how local diversity has changed within regions where the number of species available to occupy local sites has been increased by the addition of exotic species; several studies provide such information. At Tumamoc Hill in Arizona, where long-term plots of vegetation have been studied since 1909, the net number of species has increased significantly, with >50 exotic species becoming established [54,55]. At Carnac Island (a 16-ha island reserve <10 km from the Australian mainland), studies since 1951 have shown large oscillations in net plant diversity, but the most recent survey shows nearly twice as many plant species as were found originally, and much of this increase is associated with an increasing number of exotic species [56]. In Uruguay, long-term grassland plots established in 1935 and re-sampled in 1990 show that local diversity has increased dramatically; this has presumably occurred because of the addition, not just of species exotic to Uruguay, but also of species native to Uruguay that might not have been present in this region historically [57]. Of course, not all historical records indicate increasing local diversity. In a resurvey of the vascular plants in 25 small lakes in Finland, species diversity was found to be relatively unchanged after 62 years [58]. Furthermore, in small parks or reserves that have been completely isolated by surrounding urban development, net species diversity has often declined (e.g. [59]). In summary, at local scales, the empirical evidence available suggests that diversity of intact systems has often increased, but that diversity has decreased and remained relatively unchanged as well.

Future changes in diversity

Whether we are in the early stages of the next mass extinction is difficult to determine conclusively, but present rates of species extinctions are not inconsistent with this notion [1–4]. Certainly, in the next few centuries, global species diversity is expected to continue to decline. This should occur because of continued habitat destruction and the introduction of additional exotic species. However, even if these activities were stopped today, many more species extinctions would still be expected because of changes that have already occurred; that is, there might be an 'extinction debt' [60]. This extinction debt is expected, because the process of species extinction could operate slowly for some species or become apparent only over relatively long periods. At regional scales, it is therefore conceivable that current increases in species diversity are transient and that diversity might eventually reach levels that are equal to or even lower than those known historically. Although such an outcome is possible, much ecological theory suggests that the net effect of removing isolating barriers will be to cause continuing increases in species diversity at regional scales [12,13,18]. Reconciling these different perspectives, and predicting the magnitude of future extinctions, is one of our great challenges. We believe that this challenge can be met best by examining the specific manner in which habitat loss and exotic species impact the abundance of native species. Finally, at local scales, we anticipate that future changes in diversity should generally correspond with changes at regional scales. At the local scale, however, we expect these changes to be more idiosyncratic, regardless of the general patterns of change at larger spatial scales.

Conclusions

Global diversity appears to be decreasing and should continue to do so as long as the rate of species extinction exceeds the rate of speciation. By contrast, regional diversity appears to be increasing for many taxonomic groups and remaining relatively unchanged for others; in only a few cases do we see evidence of regional declines in diversity. At local scales, diversity has often declined in anthropogenic environments. By contrast, in more or less intact systems we have a poorer understanding of how diversity has generally changed, but it is clear that there are many examples of increases in local diversity (particularly in plant communities). Future work should attempt to characterize more adequately how local diversity has changed, as the implications of these changes might be of paramount importance to the functioning of ecological systems. Certainly, these changes are more complicated than have been generally appreciated, and the potential ecological implications of these changes should be explored further at all spatial scales (Box 2).

Current evidence clearly shows the shortcomings of continuing to focus ecological research exclusively on the effects of decreasing local or regional diversity. Instead, future research should also consider the flipside of these same questions; namely, it should address how increases in diversity might affect ecological systems. The patterns described here highlight the need for more carefully defined concepts of native and exotic species diversity [61], for the use of metrics besides diversity to measure the changing state of natural systems [62], and for the need to educate the public about how diversity is changing at different spatial scales (Box 3). Increases in species diversity cannot be assumed to be beneficial to community or ecosystem

Box 2. Changes in diversity across spatial scales: why it matters

The problems caused by declines in global diversity have been known for some time. They include both practical concerns over the loss of genetic diversity (e.g. loss of potential future sources of medicine) and ethical concerns over the loss of the natural heritage of the Earth [10].

At regional scales, declines in diversity, and particularly the loss of endemic species, pose the same concerns as those described above for global losses. In addition, there is increasing concern regarding the process of biotic homogenization, in which distinct regional biotas are sometimes replaced largely or entirely by sets of species that are gaining ever-broader distributions and global abundances [4]. Much empirical evidence for these species replacements exists for birds, fishes and other vertebrates, whereas the evidence for these same processes in plants is less apparent, as comparatively few native plant species have gone extinct in spite of the establishment of many exotic species [5,63]. Besides the threat of species replacement, patterns of increasing regional diversity raise several potentially equally important concerns. First, are these increases in diversity permanent or transient? If they are transient, will there be many native species that are eventually driven to extinction? Second, will increases in diversity affect ecosystem functioning? Do processes relevant to ecosystems operate at these scales? Third, will increases in diversity of the kind described here affect local patterns of diversity? Addressing these questions will do much to help us understand the implications of current patterns of regional change in diversity.

At local scales, all of the processes and concerns described above for global and regional scales are also relevant. It is at local scales, however, that processes relative to ecosystem functioning might be most relevant and most important. Changes in local diversity are expected to have strong influences on a variety of ecosystem processes and services, including productivity, nutrient cycling and nutrient retention. Certainly, processes operating at local scales can scale up to affect global carbon budgets, global climate change, and the production of clean air and water. It is in part because of these concerns that much of the 'diversity–ecosystem function' debate has occurred. However, this debate has largely focused on the effects of decreases in diversity [6–8]. Nevertheless, increases in local diversity, which might be more common than decreases (at least within many intact plant communities), should also be considered, because these increases in diversity could cause unknown and quite possibly detrimental effects upon ecosystem functioning and community processes.

Box 3. Contrasts in changing species diversity across disparate spatial scales: an educational challenge

Species diversity is changing in fundamentally different ways at different spatial scales. At a global scale species diversity is decreasing, whereas at smaller spatial scales diversity is often increasing. This empirical pattern presents an educational challenge to conservation managers, NGOs and others who are concerned with preserving our natural heritage. This challenge arises from the current emphasis (and public adoption) of the view that conserving diversity is important. Because declines in diversity at global and local scales are undesirable, it is likely that many will perceive an increase in local or regional diversity as desirable. Part of the solution to this conundrum is to continue to educate the lay-public about exotic species, and to distinguish between native and exotic diversity.

This solution is probably not sufficient, however, because at local scales increases in diversity can often be attributed to species that are native to the region (e.g. [57]). It might be important, therefore, to begin to stress the importance of spatial scale in the context of changing species diversity. Such an understanding could help to cultivate a more mature understanding of the threats to the integrity of biological systems at disparate spatial scales.

functioning, and the ultimate consequences of these changes can only be determined by carefully constructed research efforts.

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