Causes and Consequences of Biodiversity Declines

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What natural and anthropogenic processes influence biodiversity, ecosystem functioning, and ecosystem stability? How can ecology increase our ability to understand and manage ecosystems?

Biodiversity is the diversity of life on Earth. This includes the richness (number), evenness (equity of relative abundance), and composition (types) of species, alleles, functional groups, or ecosystems. Biodiversity is rapidly declining worldwide, and there is considerable evidence that ecosystem functioning (e.g., productivity, nutrient cycling) and ecosystem stability (i.e., temporal invariability of productivity) depend on biodiversity (Naeem *et al.* 2009). Thus, biodiversity declines may diminish human wellbeing by decreasing the services that ecosystems can provide for people (Millennium Ecosystem Assessment 2005).

Although the causes and consequences of contemporary biodiversity declines have been extensively explored in ecology, several questions deserve further consideration. For example, what natural processes influence biodiversity; what anthropogenic processes influence biodiversity; what are the consequences of biodiversity declines? Thus far, these questions have been considered separately within several ecological fields. Here, I briefly describe previous progress in each of these fields and then offer a conceptual and mechanistic synthesis across these fields. I conclude by suggesting novel questions and hypotheses that could be considered in future studies to increase our ability to understand, conserve, and restore ecosystems.

What Natural Processes Influence Biodiversity?

Theoretical and empirical studies have identified a vast number of natural processes that can potentially maintain biodiversity. Biodiversity can be maintained by moderately intense disturbances that reduce dominance by species that would otherwise competitively exclude subordinate species. For example, selective grazing by bison can promote plant diversity in grasslands (Collins *et al.* 1998). Additionally, biodiversity can be maintained by resource partitioning, when species use different resources, or spatiotemporal partitioning, when species use the same resources at different times and places. For instance, plant species in the tundra can coexist by using different sources of nitrogen or use the same sources of nitrogen at different times of the growing season or at different soil depths (McKane *et al.* 2002). Furthermore, biodiversity can be maintained by interspecific facilitation, which occurs when species positively influence one another by increasing the availability of limiting resources, or by decreasing the limiting effects of natural enemies or physical stresses. Although previous theoretical and empirical studies have identified numerous processes that can maintain biodiversity, ecologists and conservationists rarely know which of these mechanisms actually maintains biodiversity at any particular time and place. Thus, further investigation is needed to identify the natural processes that actually maintain biodiversity in intact ecosystems.

What Anthropogenic Processes Influence Biodiversity?

Human actions have resulted in multiple changes on a global scale that often drive contemporary biodiversity declines. In particular, land use changes, exotic species invasions, nutrient enrichment, and climate change are often considered some of the most ubiquitous and influential global ecosystem changes (Vitousek *et al.* 1997, Chapin *et al.* 2000, Benayas *et al.* 2009, Butchart *et al.* 2010). Unfortunately, the mechanisms by which global ecosystem changes influence biodiversity and ecosystem processes, and the combined effects of multiple changes, are often unclear. This greatly reduces the ability to predict future changes in biodiversity and ecosystem processes. Therefore, further investigation is needed to predict the consequences of global ecosystem changes.

In some cases, human actions have promoted biodiversity. Conservation strategies, such as creating parks to protect biodiversity hotspots, have been effective but insufficient (Bruner *et al.* 2001). For example, although biodiversity is often greater inside than outside parks, species extinctions continue. Similarly, restoration strategies, such as reinstating fire as a natural disturbance, have been effective but insufficient. Specifically, biodiversity and ecosystem services are greater in restored than in degraded ecosystems but lower in restored than in intact remnant ecosystems (Benayas *et al.* 2009). Despite the positive effects of conservation and restoration efforts, biodiversity declines have not slowed (Butchart *et al.* 2010). Thus, further investigation is needed to determine new conservation and restoration strategies.

What are the Consequences of Biodiversity Declines?

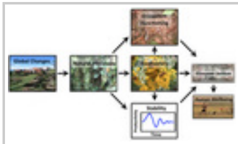

Figure 1

There is considerable evidence that contemporary biodiversity declines will lead to subsequent declines in ecosystem functioning and ecosystem stability (Naeem *et al.* 2009). Biodiversity experiments have tested whether biodiversity declines will influence ecosystem functioning or stability by manipulating some component of biodiversity, such as the number of species, and measuring various types of ecosystem functioning or stability. These studies have been conducted in lab, grassland, forest, marine, and freshwater ecosystems. From these studies, it is clear that ecosystem functioning often depends on species richness, species composition, and functional group richness and can also depend on species evenness and genetic diversity. Furthermore, stability often depends on species richness and species composition. Thus, contemporary changes in biodiversity will likely lead to subsequent changes in ecosystem properties. Further investigation at larger spatiotemporal scales in managed ecosystems is needed to improve our understanding of the consequences of biodiversity declines.

Synthesizing Biodiversity Research

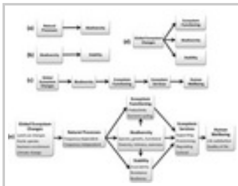

Figure 2

A synthesis across four ecological fields may increase our ability to understand, conserve, and restore ecosystems by providing a framework for considering the causes and consequences of biodiversity declines (Figure 1). First, maintenance of biodiversity research has focused on the effects of natural processes on biodiversity (Figure 2A). Second, biodiversity–stability research has focused on the effects of biodiversity on various measures of stability (Figure 2B). Third, biodiversity–ecosystem functioning research has focused on the effects of biodiversity on ecosystem functioning and how this relationship mediates the effects of global ecosystem changes on human wellbeing (Figure 2C). Fourth, global change ecology has focused on the effects of global ecosystem changes on biodiversity, ecosystem functioning, and stability (Figure 2D). Combining the relationships explored in each of these four fields produces an inclusive framework (Figure 2E) and elucidates two novel questions: What natural processes promote biodiversity, ecosystem functioning, and stability; do global ecosystem changes influence ecosystems by altering these natural processes?

What Natural Processes Promote Biodiversity, Ecosystem Functioning, and Stability?

The natural processes that are predicted to locally promote biodiversity, ecosystem stability, and ecosystem functioning have commonly been considered separately, but are quite congruent (Loreau 2010). Theoretical and empirical studies have identified mechanisms that can promote biodiversity

Figure 3

(Figure 3A), ecosystem stability (Figure 3B), and ecosystem functioning (Figure 3C). Interestingly, stabilizing species interactions, which cause a species to limit itself more than it limits other species, are predicted to promote biodiversity, ecosystem stability, and ecosystem functioning (Figure 3). Previous studies have found that stabilizing species interactions can promote biodiversity, ecosystem stability, and ecosystem functioning (Isbell *et al.* 2009). Stabilizing species interactions occur when interspecific interactions (i.e., between individuals from different species) are more favorable than intraspecific interactions (i.e., between individuals of the same species). This results in a rare species advantage, common species disadvantage, or both. Species interactions are stabilizing when interspecific resource competition is less than intraspecific resource competition (McKane *et al.* 2002), interspecific apparent competition is less than intraspecific apparent competition (Chesson & Kuang 2008), interspecific facilitation is greater than intraspecific facilitation (Cardinale et al. 2002), or some combination of these mechanisms. For example, when species consume different resources or consume the same resources at different times or places, resource competition will be stronger between two individuals from the same species than between two individuals from different species. Consequently, species have an advantage when rare because competition is relatively weak and a disadvantage when common because competition is relatively strong. This can maintain biodiversity because it prevents any particular species from competitively excluding all other species. This can promote ecosystem stability in diverse ecosystems because it results in species asynchrony, wherein decreases in the abundance of some species are compensated for by increases in the abundance of other species. This can promote ecosystem functioning in diverse ecosystems because it results in overyielding, in which species perform better when they are rare and other species are present than when they are common and other species are absent.

Figure 4

Future studies can be designed to determine the relative importance of various types of stabilizing species interactions (Figure 4). The relative importance of competition v. facilitation can be determined by manipulating the density of individuals. Competition is greater than facilitation when individuals perform better at low than high density. Adding resources and removing natural enemies can elucidate the relative importance of resources and natural enemies, respectively. Ecologists have often focused on resource competition, but recent studies suggest that facilitation (Brooker *et al.* 2008) and natural enemies (Chesson & Kuang 2008) have been under-appreciated in ecology. Thus, further study is needed to determine which types of stabilizing species interactions commonly promote biodiversity, ecosystem functioning, and ecosystem stability.

Do Global Ecosystem Changes Influence Ecosystems by Altering these Natural Processes?

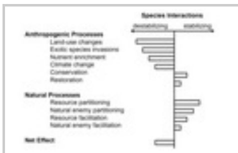

Figure 5

It may be possible to predict future changes in biodiversity, ecosystem functioning, and ecosystem stability by considering how global ecosystem changes are currently influencing stabilizing species interactions. The United Nations is currently developing an Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) to monitor biodiversity and ecosystem services worldwide (Marris 2010). The IPBES will be modeled after the Intergovernmental Panel on Climate Change (IPCC), and there is great potential for ecologists to borrow strategies that have been successfully employed by climatologists. For example, climatologists have modeled the effects of natural and anthropogenic processes on radiative forcing (i.e., the change in the difference between the amount of radiation entering and exiting Earth's atmosphere) to determine the causes and consequences of climate change (IPCC 2007). Radiative forcing is central to this discussion because it is influenced by both natural and anthropogenic processes and it influences many climate variables. Future ecological studies could take a similar approach to determine the causes and consequences of changes in biodiversity. Stabilizing species interactions are central to this discussion because they can be influenced by both natural and anthropogenic processes, and they can influence both biodiversity and ecosystem properties (Figure 1). I hypothesize that global ecosystem changes are currently destabilizing species interactions (Figure 5) and that this will lead to future declines in biodiversity, ecosystem functioning, and ecosystem stability. Collaborations among investigators considering one or more of the relationships in Figure 1 are becoming increasingly common (Naeem *et al.* 2009), and this will continue to be an active area of research.

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