Biodiversity and Ecosystem Stability
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Introduction: Biodiversity, Stability, and Ecosystem Functioning
Climate change and other human-driven (anthropogenic) environmental changes will continue to cause biodiversity loss in the coming decades (Sala et al. 2000), in addition to the high rates of species extinctions already occurring worldwide (Stork 2010). Biodiversity is a term that can be used to describe biological diversity at a variety of different scales, but in this context we will focus on the description of species diversity. Species play essential roles in ecosystems, so local and global species losses could threaten the stability of the ecosystem services on which humans depend (McCann 2000). For example, plant species harness the energy of the sun to fix carbon through photosynthesis, and this essential biological process provides the base of the food chain for myriad animal consumers. At the ecosystem level, the total growth of all plant species is termed primary production, and — as we’ll see in this article — communities composed of different numbers and combinations of plant species can have very different rates of primary production.

This fundamental metric of ecosystem function has relevance for global food supply and for rates of climate change because primary production reflects the rate at which carbon dioxide (a greenhouse gas) is removed from the atmosphere. There is currently great concern about the stability of both natural and human-managed ecosystems, particularly given the myriad global changes already occurring. Stability can be defined in several ways, but the most intuitive definition of a stable system is one having low variability (i.e., little deviation from its average state) despite shifting environmental conditions. This is often termed the resistance of a system. Resilience is a somewhat different aspect of stability indicating the ability of an ecosystem to return to its original state following a disturbance or other perturbation.

Species Identity, Functional traits, and Resource-Use
Species diversity has two primary components: species richness (the number of species in a local community) and species composition (the identity of the species present in a community). While most research on the relationship between ecosystem diversity and stability has focused on species richness, it is variation in species composition that provides the mechanistic basis to explain the relationship between species richness and ecosystem functioning. Species differ from one another in their resource use, environmental tolerances, and interactions with other species, such that species composition has a major influence on ecosystem functioning and stability.

The traits that characterize the ecological function of a species are termed functional traits, and species that share similar suites of traits are often categorized together into functional groups. When species from different functional groups occur together, they can exhibit complementary resource-use, meaning that they use different resources or use the same resources at different times. For example, two animal predators may consume different prey items, so they are less likely to compete with one another, allowing higher total biomass of predators in the system. In the case of plants, all species may utilize the same suite of resources (space, light, water, soil nutrients, etc.) but at different times during the growing season — for example, early- and late-season grasses in prairies.

Increasing species diversity can influence ecosystem functions — such as productivity — by increasing the likelihood that species will use complementary resources and can also increase the likelihood that a particularly productive or efficient species is present in the community. For example, high plant diversity can lead to increased ecosystem productivity by more completely, and/or efficiently, exploiting soil resources (e.g., nutrients, water). While primary production is the ecosystem function most referred to in this article, other ecosystem functions, such as decomposition and nutrient turnover, are also influenced by species diversity and particular species traits.

Diversity-Stability Theory
Theoretical models suggest that there could be multiple relationships between diversity and stability, depending on how we define stability (reviewed by Ives & Carpenter 2007). Stability can be defined at the ecosystem level — for example, a rancher might be interested in the ability of a grassland ecosystem to maintain primary production for cattle forage across several years that may vary in their average temperature and precipitation. Figure 1 shows how having multiple species present in a plant community can stabilize ecosystem processes if species vary in their responses to environmental fluctuations such that an increased abundance of one species can compensate for the decreased abundance of another. Biologically diverse communities are also more likely to contain species that confer resilience to that ecosystem because as a community accumulates species, there is a higher chance of any one of them having traits that enable them to adapt to a changing environment. Such species could buffer the system against the loss of other species. Scientists have proposed the insurance hypothesis to explain this phenomenon (Yachi & Loreau 1999). In this situation, species identity — and particular species traits — are the driving force stabilizing the system rather than species richness per se (see Figure 2).
Each rectangle represents a plant community containing individuals of either blue or green species and the total number of individuals corresponds to the productivity of the ecosystem. Green species increase in abundance in warm years, whereas blue species increase in abundance in cold years such that a community containing only blue or green species will fluctuate in biomass when there is interannual climate variability. In contrast, in the community containing both green and blue individuals, the decrease in one species is compensated for by an increase in the other species, thus creating stability in ecosystem productivity between years. Note also that, on average, the diverse community exhibits higher productivity than either single-species community. This pattern could occur if blue or green species are active at slightly different times, such that competition between the two species is reduced. This difference in when species are active leads to complimentary resource utilization and can increase total productivity of the ecosystem.

In contrast, if stability is defined at the species level, then more diverse assemblages can actually have lower species-level stability. This is because there is a limit to the number of individuals that can be packed into a particular community, such that as the number of species in the community goes up, the average population sizes of the species in the community go down. For example, in Figure 2, each of the simple communities can only contain three individuals, so as the number of species in the community goes up, the probability of having a large number of individuals of any given species goes down. The smaller the population size of a particular species, the more likely it is to go extinct locally, due to random — stochastic — fluctuations, so at higher species richness levels there should be a greater risk of local extinctions. Thus, if stability is defined in terms of maintaining specific populations or species in a community, then increasing diversity in randomly assembled communities should confer a greater chance of destabilizing the system.
Simple communities are represented by a box; in this case, these communities are so small that they can only contain 3 individuals. For example, this could be the case for a small pocket of soil on a rocky hillslope. There are 3 potential species that can colonize these communities — blue, dark green, and light green — and for the sake of this example let’s assume that the blue species has traits that allow it to survive prolonged drought. Looking at all possible combinations of communities containing 1, 2 or 3 species, we see that, as the number of species goes up, the probability of containing the blue species also goes up. Thus, if hillslopes in this region were to experience a prolonged drought, the more diverse communities would be more likely to maintain primary productivity, because of the increased probability of having the blue species present.

Experiments and Observations Can Evaluate the Diversity-Stability Relationship

A wealth of research into the relationships among diversity, stability, and ecosystem functioning has been conducted in recent years (reviewed by Balvanera et al. 2006, Hooper et al. 2005). The first experiments to measure the relationship between diversity and stability manipulated diversity in aquatic microcosms — miniature experimental ecosystems — containing four or more trophic levels, including primary producers, primary and secondary consumers, and decomposers (McGrady-Steed et al. 1997, Naeem & Li 1997). These experiments found that species diversity conferred spatial and temporal stability on several ecosystem functions. Stability was conferred by species richness, both within and among functional groups (Wardle et al. 2000). When there is more than one species with a similar ecological role in a system, they are sometimes considered “functionally redundant.” But these experiments show that having functionally redundant species may play an important role in ensuring ecosystem stability when individual species are lost due to environmental changes, such as climate change.

More recently, scientists have examined the importance of plant diversity for ecosystem stability in terrestrial ecosystems, especially grasslands where the dominant vegetation lies low to the ground and is easy to manipulate experimentally. In 1995, David Tilman and colleagues established 168 experimental plots in the Cedar Creek Ecosystem Science Reserve, each 9 x 9 m in size (Figure 3A), and seeded them with 1, 2, 4, 8 or 16 species drawn randomly from a pool of 18 possible perennial plant species (Tilman et al. 2006). Plots were weeded to prevent new species invasion and ecosystem stability was measured as the stability of primary production over time. Over the ten years that data were collected, there was significant interannual variation in climate, and the researchers found that more diverse plots had more stable production over time (Figure 3B). In contrast, population stability declined in more diverse plots (Figure 3C). These experimental findings are consistent with the theory described in the prior section, predicting that increasing species diversity would be positively correlated with increasing stability at the ecosystem-level and negatively correlated with species-level stability due to declining population sizes of individual species.

Figure 3: A biodiversity experiment at the Cedar Creek Ecosystem Science Reserve (a) demonstrates the relationship between the number of planted species and ecosystem stability (b) or species stability (c).

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Experiments manipulating diversity have been criticized because of their small spatial and short time scales, so what happens in naturally assembled communities at larger spatial scales over longer time scales? In a 24-year study of naturally assembled Inner Mongolia grassland vegetation, Bai et al. (2004) observed variation in the biomass of species, functional groups, and the whole community in response to strong interannual variation in growing-season precipitation. They found that while the abundance of individual species fluctuated, species within particular functional groups tended to respond differently such that a decrease in the abundance of one species was compensated for by an increase in the abundance of another. This compensation stabilized the biomass productivity of the whole community in a fluctuating environment (see Figure 1). These findings demonstrate that local species richness — both within and among functional groups — confers stability on ecosystem processes in naturally assembled communities.

Experiments in aquatic ecosystems have also shown that large-scale processes play a significant role in stabilizing ecosystems. A whole-lake acidification experiment in Canada found that although species diversity declined as a result of acidification, species composition changed significantly and ecosystem function was maintained (Schindler 1990). This suggests that given sufficient time and appropriate dispersal mechanisms, new species can colonize communities from the regional species pool and compensate for those species that are locally lost (Fischer et al. 2001). This observation emphasizes the importance of maintaining connectivity among natural habitats as they experience environmental changes.

**Summary**

Evidence from multiple ecosystems at a variety of temporal and spatial scales, suggests that biological diversity acts to stabilize ecosystem functioning in the face of environmental fluctuation. Variation among species in their response to such fluctuation is an essential requirement for ecosystem stability, as is the presence of species that can compensate for the function of species that are lost. While much of the evidence presented here has focused on the consequences of changes in species diversity on primary production in natural ecosystems, recent research has found similar relationships between species diversity and ecosystem productivity in human-managed ecosystems (e.g., Jactel et al. 2005).

**References and Recommended Reading**


