

Response diversity, ecosystem change, and resilience

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Biological diversity appears to enhance the resilience of desirable ecosystem states, which is required to secure the production of essential ecosystem services. The diversity of responses to environmental change among species contributing to the same ecosystem function, which we call response diversity, is critical to resilience. Response diversity is particularly important for ecosystem renewal and reorganization following change. Here we present examples of response diversity from both terrestrial and aquatic ecosystems and across temporal and spatial scales. Response diversity provides adaptive capacity in a world of complex systems, uncertainty, and human-dominated environments. We should pay special attention to response diversity when planning ecosystem management and restoration, since it may contribute considerably to the resilience of desired ecosystem states against disturbance, mismanagement, and degradation.

Front Ecol Environ 2003; 1(9): 488–494

“Nature is not fragile . . . what is fragile are the ecosystems services on which humans depend”.
(Levin 1999)

Ecosystems are complex, adaptive systems characterized by historical dependency, non-linear dynamics, and multiple basins of attraction (Levin 1999). We are part of ecosystems and alter their dynamics through activities that change the atmosphere and climate, land surface, and waters. In the future, we are likely to face different, more variable environments, and there will be greater uncertainty about how ecosystems will respond to the inevitable increases in levels of use (Folke *et al.* 2002). At the same time, our activities have already reduced the capacity of ecosystems to cope with distur-

bance and change (Jackson *et al.* 2001; Scheffer *et al.* 2001). Here we highlight the often neglected but essential role of diversity within functional groups in the adaptive capacity of ecosystems.

Ecosystem resilience may be an essential factor underlying the sustained production of natural resources and ecosystem services in complex systems faced with uncertainty and surprise (Gunderson and Holling 2002). Ecosystem resilience is defined as the amount of disturbance a system can absorb and still remain within the same state or domain of attraction (Holling 1973, 1996; Figure 1). Resilience also encompasses the ability of an ecosystem subject to disturbance and change to reorganize and renew itself. The definition includes the degree to which the system is capable of self-organization (versus a lack of organization, or organization forced by external factors), and how much it expresses a capacity for learning and adaptation (Carpenter *et al.* 2001).

Biological diversity appears to play a substantial role in ecosystem resilience and in sustaining desirable ecosystem states in the face of change (Peterson *et al.* 1998). This role is related to the diversity of functional groups in a dynamic ecosystem undergoing change, and the species diversity within these groups (Walker 1992, 1997; Norberg *et al.* 2001). Luck *et al.* (2003) point to the importance of diversity in species and populations within functional groups in helping to maintain ecosystem services (ie ecological redundancy). In particular, we hold that the variability in responses of species within functional groups to environmental change is critical to ecosystem resilience, a property that we call “response diversity”, and define as the diversity of responses to environmental change among species that contribute to the same ecosystem function.

Response diversity is not an entirely new concept, and has been used in several other biological disciplines. In

In a nutshell:

- As humanity has altered the capacity of ecosystems to buffer disturbance, we can no longer take for granted a sustained flow of ecosystem services essential to our well-being
- Resilience is necessary to sustain desirable ecosystem states in variable environments and uncertain futures
- Response diversity, defined as the range of reactions to environmental change among species contributing to the same ecosystem function, is critical to resilience, particularly during periods of ecosystem reorganization
- Management of both functional and response diversity at large scales and across scales will be required to sustain and enhance the flow of ecosystem services

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neurology, for example, it describes the diverse reactions among cells to a specific stimulus (Burrows *et al.* 1997), while in oncology it reflects the variable response of tumor cells to therapeutic treatment with ionizing radiation (Hlatky *et al.* 1994).

Most ecosystems are subject to disturbance regimes that operate across a range of temporal and spatial scales. Natural disturbances tend to be pulse disturbances with a characteristic magnitude and frequency distribution. Human activities tend to transform pulse disturbances into press or chronic disturbances (Bengtsson *et al.* 2003) and contribute to the creation of compounded perturbations (Paine *et al.* 1998). Sustaining desirable states of an ecosystem in the face of compounded perturbations requires that functional groups of species remain available for renewal and reorganization (Lundberg and Moberg 2003). Given the present human simplification of the biosphere and the ensuing loss of species, we cannot take this capacity for renewal and reorganization for granted (Chapin *et al.* 2000). The role of biological diversity in providing capacity for renewal and reorganization of desirable ecosystem states following change, and preventing shifts to undesirable ecosystem states, has not been the focus of previous studies on the relationship between biodiversity and ecosystem function (Loreau *et al.* 2001; Kinzig *et al.* 2002). Although the insurance aspect of biodiversity has been discussed, the focus has mainly been on biomass productivity, or on the compensatory effects of species interactions on random population fluctuations in single equilibrium systems at the aggregate level (eg Tilman and Downing 1994; Ives and Hughes 2002; Loreau *et al.* 2002).

The insurance metaphor needs to be revived with a focus on how to sustain ecosystem capacity to cope with and adapt to change in the context of multiple-equilibrium systems and human-dominated environments (Folke *et al.* 1996; Norberg *et al.* 2001; Luck *et al.* 2003). The concept of response diversity does not imply that high species diversity necessarily entails high ecosystem resilience or vice versa, and species-rich areas may be highly vulnerable to environmental change. Furthermore, equating resilience with species richness also ignores the reality that species loss is often non-random.

In the following sections we elaborate on patterns of species loss in relation to ecosystem functioning and response diversity. We then provide examples of the role of response diversity in ecosystem resilience in relation to disturbance and human-induced environmental change from both terrestrial and aquatic ecosystems. In the third section of this paper, we examine the temporal and spatial

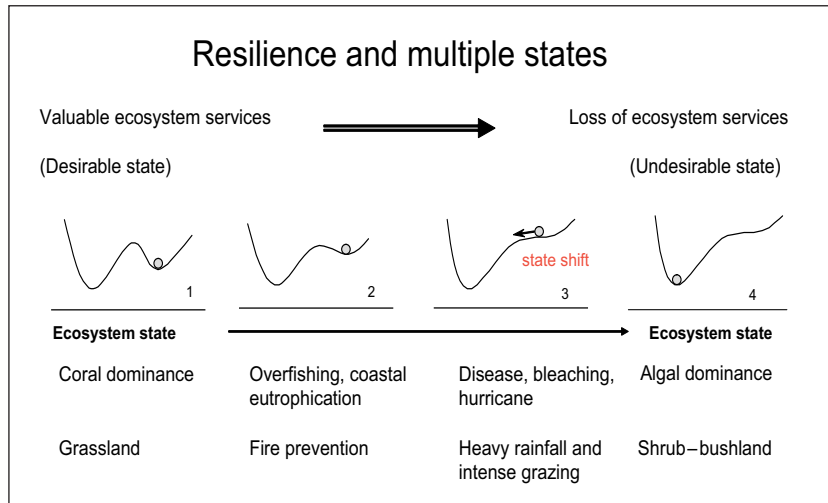


Figure 1. Shifts in coral reef and rangeland ecosystems from a more to a less desirable state as a consequence of human-induced erosion of resilience. The stability landscapes depict the basins of attraction at different conditions. If the size of the attraction basin is small, resilience is small, and even a moderate perturbation may bring the system into the alternative basin of attraction. The actual shifts in coral reefs and grasslands are caused by disturbance events, which resilient ecosystems would have absorbed through reorganization supported by response diversity (modified from Deutsch *et al.* 2003).

context of response diversity, and finish with a discussion of the management implications.

■ Ecosystem functioning and patterns of species loss

Ecosystems can be strikingly conservative in their organization and function, despite differing histories and species compositions. For example, lake studies have demonstrated that similar ecological functions can be maintained over a wide mix of species and population densities (Schindler 1990). Mediterranean climate regions are similar in ecological structure and function, despite the geographic and evolutionary isolation that has produced radically different floras and faunas (Kalin Arroyo *et al.* 1995). Other work has shown that an ecosystem's patterns of function (Forys and Allen 2002), diversity (Brown *et al.* 2001), and body mass (Havlicek and Carpenter 2001) can be conserved despite considerable species turnover.

However, ecosystems can change drastically when sets of key species are lost (Estes and Duggins 1995; Terborgh *et al.* 2001) or when new species invade (Vitousek and Walker 1989). When species go extinct locally as a result of natural or anthropogenic disturbance, they often do so in a non-random sequence as a consequence of varying body size, trophic position, habitat specialization, physiology, morphology, and life history. For example, when continuous forest areas were fragmented as the sea level rose at the end of the most recent ice age, the species that went extinct on islands around the Malay Peninsula were predominantly larger ones, at higher trophic levels (Heaney

1984). Studies have shown that predators, which were lower in abundance, were more prone to go extinct with fragmentation (Gonzalez and Chaneton 2002). Fragmented systems like archipelagos generally seem to lose specialized species and have a disproportionately large share of generalist species.

The sequence of species loss following disturbances may have important implications for ecosystem functioning and the sustained flow of ecosystem services. The loss of megaherbivores at the end of the most recent ice age had a profound influence on boreal and tundra ecosystems (Zimov *et al.* 1995), and overfishing seems to have had similar effects on coastal ecosystems (Jackson *et al.* 2001). The loss of specialist species may entail lower rates of ecosystem processes, and some functions performed by specialists may not be carried out at all – for example, the decomposition of particular substrates or the pollination of certain species. Systems where whole functional groups go extinct or become ecologically insignificant as a result of environmental change are characterized by low response diversity. This is of particular importance when such functional groups contribute to ecosystem services that are essential for human well-being.

■ Examples of response diversity

Seed dispersers in tropical forest systems

On islands in Western Polynesia, a large proportion of the tree species produce fleshy fruits that are dispersed by vertebrate frugivores. The diversity of species within the functional frugivore group has been substantially reduced since the arrival of humans. Many species have gone extinct, with only one species left on the island of Mangaia and six to eight species remaining on larger islands (Steadman 1997). In Samoa, the majority of trees produce fleshy fruits that are consumed by two species of flying foxes (*Pteropus tonganus* and *Pteropus samoensis*) and three species of fruit pigeons and doves (*Columba vitiensis*, *Ducula pacifica*, and *Ptilinopus porphyraceus*) (Rainey *et al.* 1995; Pierson *et al.* 1996; Banack 1998). These vertebrate frugivores show a 60–80% overlap in fruit consumption. Cyclones and a fire in the early 1990s caused extensive changes to lowland forests, with colonization and regeneration limited by seed dispersal (Hjärpe *et al.* 2001).

The frugivorous species, particularly the flying foxes, showed striking differences in response to the cyclones in behavior and mortality. While species such as *P tonganus* and *D pacifica* showed greater than 90% reductions in population size, others such as *P samoensis* were much less affected (<10% reduction) (Pierson *et al.* 1996). Thus, while previously dominant species declined drastically, other subdominant species in the same functional group survived and maintained the seed dispersal functions (Elmqvist *et al.* 2001) – they provided response diversity. If this response diversity had been low or absent, ecosystem development may have been redirected into a different

pathway, dominated by wind-dispersed and passively dispersed plants, with a great risk of invasion by wind-dispersed exotic opportunistic species and a changed resource base for humans.

Population fluctuations in a given seed disperser may not have a great effect on the rate of short-distance seed dispersal if a decline in seed dispersal by one species leaves more seeds available for others. An increase in seed availability allows other species to increase their seed dispersal, compensating for the initial decline (a negative covariance effect). For example, seed dispersal persists in the forests of Africa and the Neotropics, despite intensive hunting, due to the differential responses to hunting among seed dispersers (Wright 2000). In West Africa, primates and hornbills disperse a different yet overlapping set of tropical plant species (Poulsen *et al.* 2002).

Plants in rangelands

The significance of both functional diversity and response diversity in grass species were highlighted in an example from the Australian rangelands (Walker *et al.* 1999). The species abundances followed the typical distribution, with the bulk of the biomass accounted for by a few dominant species and a long “tail” of minor species with low abundances. Five functional attributes of each of the 22 perennial grass species in the rangeland – height, biomass, specific leaf area, longevity, and leaf litter quality – were measured or estimated. These attributes were ones involved in water and nutrient cycling and for which there were data or estimates. The species were plotted in a five-dimensional space using a similarity index, such that species close together were very similar in terms of these particular attributes.

The dominant grass species were functionally dissimilar and therefore complementary; this is functional diversity. Most of these dominant species had one or more minor species that were very similar to them in terms of the function they performed. At a heavily grazed site, a number of the species that were dominant in the ungrazed community had been lost or substantially reduced. In four out of five cases, the minor species that replaced these lost ones were their functional analogues. Therefore, despite the fact that grazing reduced the populations of dominant grazing-sensitive species, formerly less dominant but functionally analogous grazing-tolerant species increased in abundance and contributed to the maintenance of ecosystem functions; this is response diversity.

Both functional and response diversity are important in the rangeland. Functional diversity increases the performance of the plant community as a whole, bringing together species that take water from different depths, grow at different speeds, store different amounts of carbon and nutrients, and thus complement each other. Response diversity enables the community to keep performing in the same complementary way in the face of stresses and disturbances such as grazing and drought.

Freshwater detritivores

Anthropogenic disturbances such as acidification and organic pollution have strong but different effects on the functional group of detritivorous macroinvertebrates found in streams (Metcalf 1994). Crustaceans are sensitive to acidification, while plecopterans (stoneflies) tend to be tolerant (Dangles and Gu erold 1999). In organically polluted streams, plecopterans tend to be sensitive and crustaceans tolerant (Woodwiss 1964). Jonsson *et al.* (2002) found that species loss among detritivorous insects and crustaceans resulted in reduced litter breakdown rates. Their experimental design allowed alternative interpretations of the effects of species loss based on the known species differences in sensitivity to acidity and organic pollution. Under different scenarios of anthropogenic impacts on freshwater systems, response diversity among detritivores contributes to the maintenance of that function.

Similarly, the importance of response diversity in maintaining lake resilience has been illustrated by experiments in which lakes have been stressed by toxic chemicals and acidification (Carpenter and Cottingham 1997). Ecosystem processes persist in lakes with low levels of stress, due to variation in the response of plankton and bacteria species. Populations of stress-sensitive species decline, but compensatory growth of less sensitive species results in minimal changes in ecological processes (Schindler 1990; Frost *et al.* 1995). At higher stress levels, response diversity deteriorates and the remaining individuals are not sufficient to maintain ecosystem processes. For example, lake acidification has eliminated a group of bacteria critical to maintaining the nitrogen cycle (Rudd *et al.* 1988).

Coral reef grazers

Coral reefs support a diverse assemblage of functional groups, including framework-builders, primary producers, herbivores, and numerous predators (Done *et al.* 1996; Figure 2). Herbivores grazing on algae are important for maintaining reefs in coral-dominated states (Carpenter 1990). In the absence of herbivores, algae can overgrow and eventually kill adult coral colonies and inhibit coral larval settlement (Glynn 1990). The latter is vital for the reorganization of the reef after disturbance events such as mass bleaching, crown-of-thorns outbreaks, and hurricanes that open up large areas for fast-growing algae. Once algae have grown large enough, they become unpalatable to most herbivores (McClanahan *et al.* 1999), and a regime shift from coral to algal dominance (Hughes 1994) or bioeroders (McClanahan and Shafir 1990) may take place.

Reefs around Jamaica have been subject to just such a large-scale shift (Hughes 1994). Decades of overfishing, progressing from large predators to smaller herbivorous fish, eroded response diversity in the functional group of grazers. The loss of robustness of the function was camou-



Figure 2. Coral reefs support a wide diversity of life.

flaged by a dramatic increase in numbers of the black long-spined sea urchin *Diadema antillarum*. To some extent, the urchin's grazing compensated for the loss of the other herbivores and sustained the coral-dominated state. However, the grazing function was not resilient to change (Nystr om *et al.* 2000). When a species-specific pathogen dramatically reduced the sea urchin population (Lessios *et al.* 1984) and the reefs were hit by a hurricane, there were no herbivores left to prevent the algal invasion and regime shift (Figure 1).

These cases illustrate how human-induced erosion of response diversity within functional groups may lead to vulnerability and shifts between states, as illustrated in Figure 1. A diverse group of abundant species with a wider range of responses can help to absorb disturbance events. The diversity of responses to events among species within a functional group is a critical component of resilience.

■ Response diversity and interactions across scales

Response diversity across scales exists through species operating at different spatial and temporal scales. Ecological disruption usually occurs across a limited range of scales, allowing ecological functions that operate at

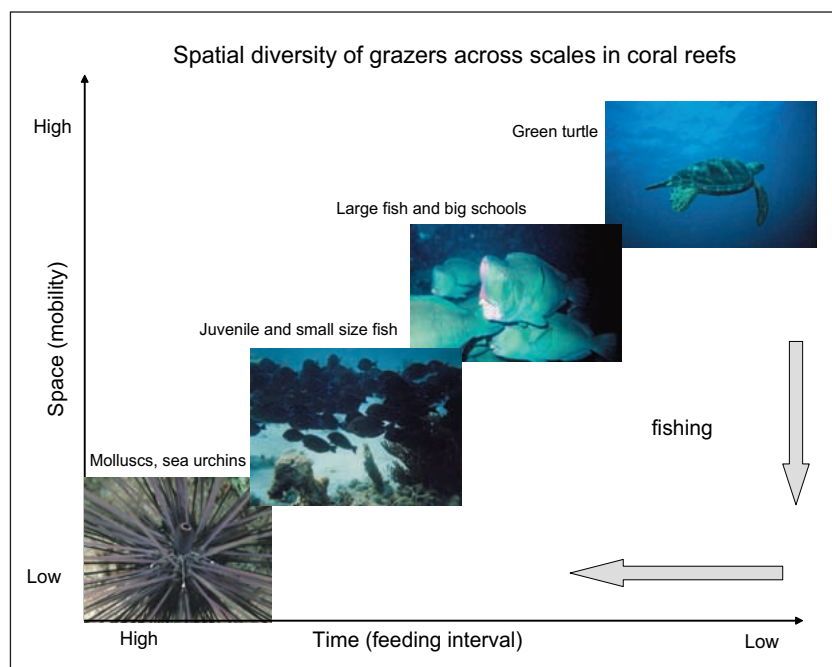


Figure 3. The multiple-scale nature of response diversity in the functional group of herbivores of coral reefs. Response diversity is enhanced by species operating over a broad range of scales. However, overfishing of large, economically attractive species has resulted in a situation where grazing is maintained by a set of smaller species operating more intensively at faster intervals.

other, undisturbed scales to persist. Ecological functions that are replicated across a range of scales can withstand a variety of disturbances. In Brazil's Maracá Island Ecological Reserve, Fragoso (1997) has shown that palm seeds are dispersed across a range of scales by a variety of species of seed dispersers, ranging in size from small rodents, which typically leave seeds within 5 m of parent trees, to tapirs (*Tayassu tajacu*), which move seeds up to 2 km. Seed dispersal at multiple scales allows the palm population to persist, despite a variety of small- and large-scale disturbances. Small-scale dispersal maintains palm patches, while larger scale dispersal bypasses barriers at small scales to create new palm patches.

Coral reef grazers live at a wide range of spatial and temporal scales. Some herbivores operate intensively on a small scale, from centimeters to tens of meters, including molluscs, amphipods, sea urchins, and territorial, juvenile, and other small fish species. Other grazers feed less intensively on larger scales, from hundreds to thousands of meters (eg large adult fish species such as parrot fish, surgeon fish, and rabbitfish), or very large scales, from hundreds to thousands of kilometers, (eg green turtles; Figure 3). Although these grazing organisms have different impacts, by feeding on different algae they all contribute to the same function. Since they operate at different spatial and temporal scales, competition between species within the grazer guild is minimized, and robustness over a wider range of environmental conditions is enhanced (Peterson *et al.* 1998). Thus, the distribution of grazers in space and time is an important component, con-

tributing to response diversity in coral reefs, and reef resilience.

Similarly, in the forests of eastern Canada, five distinct size classes prey upon spruce budworm (*Choristoneura fumiferana*), a defoliating insect. The predators prey upon budworms which are aggregated at different scales, maintaining predation pressure across a broad range of budworm densities (Holling 1988, 1992).

Overexploitation has resulted in long-lived species with large home ranges, such as large fish and sea turtles, being heavily reduced in numbers (Jennings *et al.* 1999). Human removal of species within the same functional group tends to reduce response diversity across scales, as illustrated by Jackson *et al.* (2001). Performance of the grazing function contracts from a set of species covering a diversity of scales to a few smaller species, with smaller home ranges, grazing at shorter intervals (Figure 3). This poses a threat not only to the evolutionary characteristics (Pauly *et al.* 2002), with potentially negative cascading effects (Carr *et al.* 2002), but also to the cross-scale distribution of species within functional

groups. Removal of mobile link species (Lundberg and Moberg 2003) and contraction of spatial resilience (Nyström and Folke 2001) seem to increase the spectrum of disturbance and compounded perturbation that will be seen as "catastrophic" from our perspective. It suggests that the vulnerability of desired ecosystem states increases as the home ranges of the remaining organisms in a functional group narrow. Response diversity for ecosystem resilience therefore has an important cross-scale component.

■ Managing response diversity

We must explicitly account for the role of biodiversity in ecosystem resilience for sustained social and economic development in formulating management and policy. Managing for resilience is critical for coping with uncertainty and surprise in a biosphere shaped by human action (Folke *et al.* 2002). Human homogenization of landscapes and seascapes has altered disturbance regimes (Paine *et al.* 1998) and eliminated entire functional groups of species (Jackson *et al.* 2001). The persistence of these groups appears to help prevent shifts to ecosystem states that are unable to sustain the desired level of ecosystem services.

Focusing on response diversity helps increase the effectiveness of ecosystem management. Ecosystems with high response diversity provide a buffer that insures the system against the failure of management actions and policies based on incomplete understanding. This allows managers to learn and actively adapt their resource management policies. In other words, response diversity increases the

tolerance for management mistakes. In some systems, it may also be possible to test and analyze the degree of response diversity through non-random removal experiments, as suggested by Diaz *et al.* (2003).

In this paper we have stressed the essential link between ecosystem services, functional groups, and response diversity. We have focused on the role of response diversity in sustaining and enhancing desirable ecosystem states in the face of disturbance and human-induced environmental change, and highlighted its cross-scale nature. Bengtsson *et al.* (2003) suggested that in the future, dynamic refugia and reserve networks may serve a key role in management and the restoration of response diversity. Interestingly, there are several examples of local groups and societies worldwide that appear to have managed for response diversity for a long time (Berkes *et al.* 2003). The erosion of response diversity may increase the vulnerability of specific functional groups, or even result in the loss of entire groups. This may, in turn, lead to social and economic vulnerability, changes in nature's capacity to supply human society with essential ecosystem services, and ultimately degraded socioecological systems.

■ Acknowledgements

This article is the result of stimulating discussions within the Resilience Alliance (www.resalliance.org). We thank Björn Malmqvist for constructive comments and Buzz Holling for inspiration. Research has been supported by grants from the Swedish research councils Vetenskapsrådet and Formas.

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