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18 Global change and ecological complexity

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The aim of the Global Change and Terrestrial Ecosystems (GCTE) core project has been to assess the effects of global change on the functioning of ecosystems and how these changes feed back to the atmosphere and the physical climate system. The drivers of global change, which are changes in land use, atmospheric composition, and climate, also directly affect ecological complexity which in turn affects ecosystem functioning (Fig. 18.1). How important is this indirect effect? Focus 4, Global Change and Ecological Complexity, is a new programme launched by GCTE to answer this question. The objective of this new Focus is to assess the effects of global change on ecological complexity and on the relationship between ecological complexity and ecosystem function (the dotted arrow in Fig. 18.1).

Ecological complexity represents biological diversity but in a broad sense, including not only species diversity but also diversity of ecosystems and landscapes, as well as genetic diversity within species. In addition, ecological complexity involves the diversity of trophic pathways and interactions. We can envision systems with similar diversity but contrasting complexity as a result of different organizational structures. Ecosystem functioning represents the collection of processes including primary production, decomposition, and nutrient cycling and their interactions.

Ecologists are intrigued by the diversity of organisms which inhabit the earth and, therefore, have studied the mechanisms that may account for this wealth of diversity. There is currently evidence supporting several available hypotheses which explain diversity as a function of ecosystem properties. However, less effort has been concentrated in understanding the effect on the opposite direction (Fig. 18.1): the effects of ecological complexity (or changes in ecological complexity) on ecosystem functioning. SCOPE (Scientific Committee on Problems of the Environment) has just finished a project led by H. A. Mooney which synthesized our current understanding of effects of biodiversity on ecosystem functioning (Schulze & Mooney, 1993).

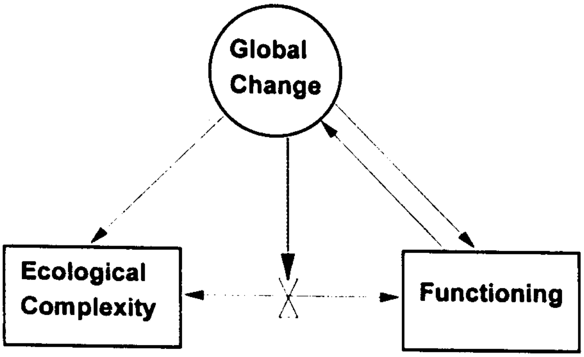

Figure 18.1 *The relationship between global change, ecological complexity and ecosystem functioning.*

This project consisted of a series of parallel workshops around the globe for different biomes and a final synthesis conference which attempted to identify similarities and differences among biomes regarding this issue. The reports from each biome and the cross-biome comparisons helped identify gaps in our understanding. There is a close connection between the ending SCOPE project and the starting GCTE Focus 4 Global Change and Ecological Complexity. The SCOPE project synthesized our knowledge and identified gaps which are the base of the research project which will be carried out by the new Focus 4. This agrees with the missions of SCOPE (synthesis) and of IGBP (fostering and coordinating research).

Several models of the relationship between ecological complexity and ecosystem functioning have been suggested, ranging from one which proposes that each species plays a unique role in the functioning of ecosystems and that therefore deletion of any species results in a change in ecosystem functioning, to those which consider that most species are redundant and that changes in ecological complexity should not result in changes in functioning (Vitousek & Hooper, 1993). A recently developed model relates previous diversity–function models with rank dominance models (Sala *et al.*, 1996). The effects on ecosystem functioning depend not only on changes in complexity but how these changes occur, and on which species are added or deleted. The model suggests a way of identifying those species which will have maximum effect on ecosystem processes.

Experiments scattered around the world provide evidence to support or reject the different diversity–function models. These include a range of studies from field to controlled environment conditions (McNaughton, 1993; Naeem *et al.*, 1994). Primary production and its relationship to plant species diversity has been one of the best-studied relationships. For example, in the Serengeti grasslands, removal of grasses with different contributions to total productivity shows the limits of ecosystems to compensate for the deletion of different species (McNaughton, 1983). Removal of rare plant species resulted in full compensation of production by remaining species, removal of species of intermediate abundance resulted in partial compensation, whereas removal of dominant species resulted in a significant reduction in production.

Ecological complexity may affect not only average ecosystem functioning but also the system response to extreme conditions. The diversity–stability hypothesis suggests that perturbations will result in a larger change in ecosystem functioning in simple systems than diverse systems. In old fields in New York, McNaughton (1993) described the response of ecosystems with different diversity resulting from being at different successional stages to a perturbation caused by fertilization. In the USA tall grass prairie, Tilman and Downing (1994) analysed the effects of a severe drought along a diversity gradient created as a result of an experimental fertilization where diversity was maximum in the native system and decreased as fertility increased. In both cases, the effect of perturbation on production was maximum in simple systems and minimum in the most diverse systems. Some of the conclusions drawn from these experiments have been criticized because fertilization simultaneously modified diversity and selected for species with lower root–shoot ratio, higher leaf conductance, and greater photosynthetic capacity, which are characteristics which result in lower drought resistance (Givnish, 1994). Consequently, the lower productivity during the drought year in low-diversity plots could have been the result of those plots being dominated by drought-sensitive plants. The critical experiment to disentangle the effect of diversity from the effect of individual species has not been performed yet.

The chapters presented in this section provide an excellent overview of the current understanding of global change and ecological complexity. Heal *et al.* note that a major part of the world's biodiversity lies unseen in the soil. However, it is important for many key ecosystem functions, such as organic matter decomposition, nutrient transformation and translocation, greenhouse gas formation and breakdown, and pedogenesis and soil morphology. They explore the following questions in their chapter: How diverse is the soil biota? How is it structured? How does diversity affect individual ecosystem functions? What are the research priorities?

Chapin *et al.* provide a useful link between below-ground processes and above-ground diversity by focusing on the direct and indirect effects of individual species on ecosystem processes, such as litter decomposition. They note that it is individual organisms that carry out essential ecosystem processes, and thus the traits of the individuals and their abundances should be important in determining the pool sizes and rates of energy and material fluxes in ecosystems. Their chapter addresses two general questions about the ecosystem significance of species traits and species diversity. If we know the traits of key organisms in an ecosystem, can we predict (1) the ecosystem impacts of species invasions or losses, and (2) the rates and patterns of processes in intact ecosystems? How does species diversity influence ecosystem processes?

Focus 4 is also concerned with diversity at the landscape level and its impacts on ecosystem functioning. The chapter by Holling *et al.* highlights recent advances in understanding the spatial and temporal functioning of terrestrial ecosystems at the landscape scale. It shows how contagious processes such as disturbances (e.g. fire and insect outbreaks) can self-organize vegetation patterns to create mosaics that are persistent over time and are resilient to broad ranges in variation in vegetation species composition, topography, and climate. These patterns in vegetation entrain discontinuous patterns in the body sizes of resident mammal and bird communities. The chapter concludes that when change in vegetation pattern occurs, perhaps as a result of global change, it will be sudden and extensive. Such dramatic change will probably have significant effects on ecological complexity and ecosystem functioning.

Chapters in this section describe our current understanding of the effects of ecological complexity on ecosystem function at different scales and from different standpoints. At the same time as reviewing what is known, they have highlighted gaps in our understanding. In order to fill those gaps the starting Focus 4 of GCTE will seek problems which are best solved collectively. It will avoid tasks which can be accomplished individually by investigators or groups and will concentrate on those studies which yield more than the sum of individual experiments.

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