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Biodiversity effects on ecosystem functioning: insights from aquatic systems

Mark O. Gessner, Pablo Inchausti, Lennart Persson, David G. Raffaelli and Paul S. Giller

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Unprecedented rates of species extinctions have prompted extensive research into the consequences of biodiversity losses on ecosystem functioning. While aquatic species are most threatened, research with freshwater and marine model systems has lagged behind progress made in terrestrial environments. This editorial to a special feature summarizes the main outcomes of a conference aimed at setting the stage for exploring the potential of aquatic systems to assess the role of biodiversity in ecosystem functioning. This series of papers proposes fresh approaches to the study of biodiversity effects on ecosystem functioning, outlines a new way of analyzing experimental data, presents a model that considers scale as an important factor determining outcomes, explores the effects of multiple stressors on species richness and ecosystem processes, and develops a food-web perspective that relates ecosystem properties to biodiversity. An insightful synthesis of lessons learned from aquatic systems is premature at present, but the papers clearly demonstrate the role that marine and freshwater systems can play in resolving open questions. The implications go well beyond the biodiversity in, and functioning of, ecosystems shaped by free-flowing or standing water.

M. O. Gessner, Dept of Limnology, EAWAG/ETH, Limnological Research Center, CH-6047 Kastanienbaum, Switzerland. (gessner@eawag.ch). – P. Inchausti, UMR CNRS 6553, Université de Rennes 1, campus de Beaulieu, bât 14, FR-35042 Rennes, France. – L. Persson, Dept of Ecology and Environmental Science, Umeå Univ., Sweden. – D. G. Raffaelli, Environment Dept, Univ. of York, Heslington, York, YO10 5DD, UK. – P. S. Giller, Dept of Zoology, Ecology and Plant Science, Univ. College Cork, Lee Maltings, Prospect Row, Cork, Ireland.

The consequences of species loss for the functioning of ecosystems has been addressed through several major research programmes in recent years, mostly in terrestrial environments (Kinzig et al. 2001, Loreau et al. 2002). The effects of species loss in aquatic environments, in contrast, have received much less attention, yet the nature of these ecosystems and their biota differ markedly from those on land (Giller et al. 2004). This raises the question as to whether, and how far, insights from terrestrial research programmes can be extrapolated to lakes and open oceans, rivers and freshwater wetlands, coastal marine and deep-sea ecosystems. The series of papers in this special feature seeks to address this question. In addition, it explores whether research on aquatic communities and ecosystems can in turn make a general contribution to the understanding of the functional consequences of biodiversity changes.

The papers included in this feature are the outcome of an international workshop held from 4–7 April 2002 at Ascona, Switzerland, which brought together aquatic ecologists working in theoretical and empirical areas and having an interest in a range of systems (marine and freshwater, benthic and pelagic), taxa (microbes to vertebrates) and focus (populations, communities and ecosystems). The papers focus on the effects of biodiversity changes on ecosystem functioning, rather than

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the reverse relationship of how ecosystem processes may affect species diversity, which has been the subject of recent reviews (Mittelbach et al. 2001).

Teasing apart the polarity of causation is important, as the failure to do so has clouded the debate on the biodiversity-ecosystem functioning issue (Loreau et al. 2001). Claims that changes in biodiversity can influence rates of ecosystem processes, such as primary production, are based on evidence from experiments involving deliberate manipulation of biodiversity levels (Fig. 1A). Observational evidence, in contrast, has typically shown a hump-shaped relationship between these two variables (Fig. 1B). These seemingly opposing findings can be reconciled by recognizing that they represent in fact two-dimensional projections of a three-dimensional relationship among site fertility, primary productivity and species diversity (Schmid 2002). Site fertility governs both plant species diversity and primary productivity. This results in a correlation between the last two variables although a mechanism that would convincingly explain a dependence of diversity on productivity is lacking. Consequently, abandoning the incorrect 'productivity' shorthand for site fertility would put to rest part of the ongoing controversy (Loreau et al. 2001) and allow gathering forces to scrutinize the implications of biodiversity loss on ecosystem processes and properties, as is done in the following series of papers.

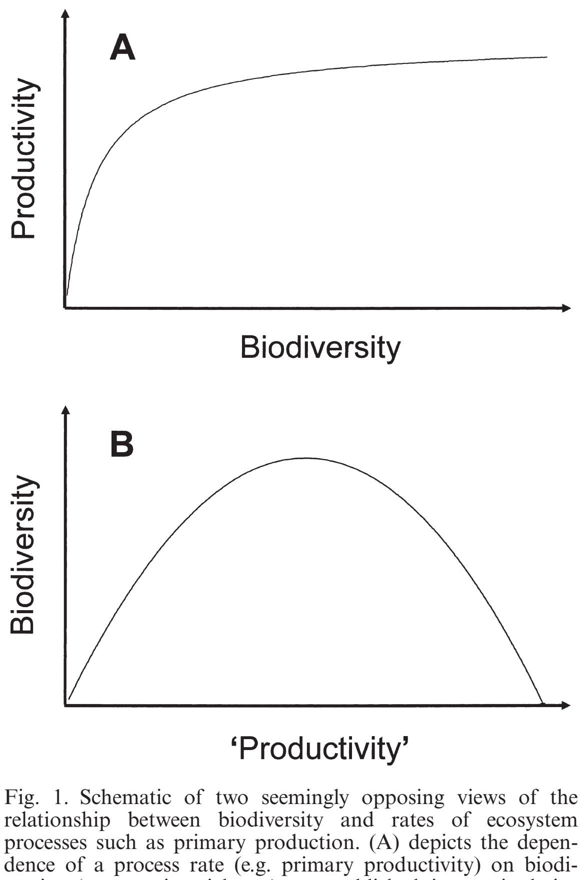

Fig. 1. Schematic of two seemingly opposing views of the relationship between biodiversity and rates of ecosystem processes such as primary production. (A) depicts the dependence of a process rate (e.g. primary productivity) on biodiversity (e.g. species richness) as established in manipulative experiments conducted primarily in terrestrial grasslands (Kinzig et al. 2001). Primary productivity is defined as the average rate of total autotrophic biomass production in an ecosystem over an extended period such as a year. (B) shows the correlation between plant productivity and biodiversity typically observed over broad spatial scales (Loreau et al. 2001, Mittelbach et al. 2001). The seeming contradiction between the relationships shown in (A) and (B) can be reconciled by acknowledging that 'productivity' is a convenient and often used, but incorrect substitute for site fertility, on which both biodiversity and productivity depend while there is no causal dependence of biodiversity on productivity.

To what extent can aquatic biota and ecosystems provide insights into the functional consequences of species loss? Giller et al. (2004) argue that the unique features of marine and freshwater systems provide ample opportunities for testing whether the principles emerging from research in some terrestrial ecosystems hold generally true and for addressing currently unresolved questions of the biodiversity-ecosystem functioning issue. To this end, four novel experimental designs are proposed. These include (1) the functional consequences of non-random as opposed to random species loss, to be investigated by manipulating the sequence and magnitude of species loss by means of dilution experiments; (2) the significance of spatial heterogeneity by manipulating biodiversity in interconnected habitat patches; (3) the relative importance of local demographic processes and species exchanges across ecosystem boundaries by manipulating recruitment rate and diversity both within patches and within the supply propagule pool; and (4) the effects of species extinctions following exposure to multiple stressors.

Much criticism on previous biodiversity-ecosystem functioning experiments relates to the limited spatial and temporal scales at which experiments have been conducted. Some would argue this limitation precludes inferences about phenomena in natural ecosystems and thus the experimental findings would bear little relevance to the real world. Extending Giller et al.'s (2004) proposal to consider habitat diversity in the context of biodiversity-ecosystem functioning relationships, Cardinale et al. (2004) develop a patch-dynamics model that assesses biodiversity effects when accounting for large spatial and temporal scales. Their modelling results suggest that the effect of biodiversity on an ecosystem process, plant production, grows stronger with successional time. Significantly, biodiversity effects do not necessarily change across spatial scales, even though the mechanism underlying the effects can indeed vary with scale of observation. When built into the model, regional processes such as dispersal and disturbance could amplify the biodiversity effect on ecosystem functioning.

A new conceptual framework to analyse the impact of multiple stresses on the functioning of ecosystems is proposed by Vinebrooke et al. (2004). It is based on the idea that the sensitivities of species to any two stressors can be correlated. The direction and strength of this correlation would determine what proportion of the species persists when both stressors have an effect and hence determine the potential of the persisting, tolerant species to compensate for the loss of sensitive taxa and thus to maintain ecosystem functioning. Evidence from planktonic communities in temperate lakes affected by multiple stressors provides initial support for the proposed framework. It appears, therefore, that predicting the impacts of global environmental change on biodiversity loss and ecosystem functioning is enhanced by a consideration of the possible interactive effects among multiple stressors as mediated by correlated species sensitivities to different stressors.

A key problem to demonstrate biodiversity effects on ecosystem functioning is the large number of experimental units typically required for experimentation (Giller et al. 2004). Hence the manipulation of microbial communities in microcosms has been instrumental in investigating relations between various aspects of aquatic ecosystem functioning and changes in biodiversity. Even the use of simple microcosms, however, may entail problems with the analysis of data (Schmid et al. 2002). Morin and McGrady-Steed (2004) present a remedy by proposing novel analytical methods based on resampling statistics to separate the contributions of temporal and spatial variation to overall variation in ecosystem functioning. Their reanalysis of published data confirms the negative relationship found previously between species richness and the temporal variability of an ecosystem process, the flux of carbon dioxide measured in a microcosm. This negative relationship reflects high variation among communities of low species richness, rather than high temporal variation within communities of low richness.

Most experiments and theory that dominate investigations into the functional consequences of biodiversity loss are based on model communities comprising a single trophic level (Loreau et al. 2002). This simplification represents a major weakness in the current attempts to understand effects of biodiversity loss on ecosystems, especially for some aquatic habitats where strong trophic interactions tend to impinge on the fluxes of energy and matter. Based on the distribution of species richness and the patterns of species extinction of different trophic levels observed in a range of case studies, Petchey et al. (2004) develop a Lotka–Volterra predation model to assess whether the trophic level from which species go extinct matters for the functional consequences of biodiversity loss. Their modelling results indicate that species belonging to higher trophic levels are more likely to be lost than species at lower trophic levels and, more importantly, that the impact of species loss on an important ecosystem property (total biomass) depends on both food-web structure (the occurrence of omnivory and distribution of species richness among trophic levels) and the trophic level from which species are eliminated.

In conclusion, the papers of this special feature highlight a number of hitherto unresolved issues in the pursuit of understanding biodiversity effects on ecosystem functioning. A comprehensive synthesis of evidence linking changes in biodiversity to ecosystem functioning and the mechanisms underlying the relationships is not attempted, since assessing the ecosystem-level consequences of species loss has just begun in aquatic systems and pertinent information is still limited at present. However, the papers published both here and elsewhere (Bolam et al. 2002, Cardinale et al. 2002, Jonsson et al. 2002) show that aquatic biota and ecosystems may serve as excellent testing grounds for exploring the biodiversity-ecosystem functioning issue with both experimental and theoretical approaches, offering significant potential for the results of studies in aquatic environments to contribute to general theory building. As our understanding of biodiversity effects on ecosystem functioning improves, predictions on the consequences of species loss will enable scientifically informed, integrative management of aquatic organisms and ecosystems. This ultimate goal will conceivably continue to be the key driver for research on the functional implications of biodiversity change, overshadowing the scientifically motivated interest to grasp how the structure of communities in general affects ecosystem processes and properties. In face of the current record rates of species losses and invasions, clearly a thorough understanding of the functional consequences of changing community structure at large, and the mechanisms underlying them, is critically needed.

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