PREFACE

Editorial Commentary: Monitoring, Manipulation and Modelling of Ecological Responses to Global Change in Multispecies Systems

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Our understanding of the ecological consequences of global change for multispecies systems has come a long way in recent years, reflecting the considerable research effort that has been devoted to this area. This volume of *Advances in Ecological Research* is the last of a three-part compendium on this theme, which, when taken together, covers both aquatic and terrestrial systems, as well as addressing different components of global change and the various different ways of studying them, from monitoring to manipulation and modelling (e.g. Hagen et al., 2012; Hannesdóttir et al., 2013; Jeppesen et al., 2012; Ledger et al., 2012, 2013; McLaughlin et al., 2013; Meerhoff et al., 2012; Mintenbeck et al., 2012; Möllmann and Diekmann, 2012; Moya-Larano et al., 2012; Mulder et al., 2012; O'Gorman et al., 2012a,b; Raffaelli and White, 2013; Rossberg, 2012; Stewart et al., 2013; Struebig et al., 2013). There is now a significant body of global change research that spans multiple levels of biological organisation and approaches that include laboratory microcosms (e.g. Beveridge et al., 2010), outdoor mesocosms (Ledger et al., 2012, 2013), surveys (Jeppesen et al., 2012; Meerhoff et al., 2012) and natural experiments (e.g. O'Gorman et al., 2012b). Throughout these three volumes, the papers have been linked by a common theme: to understand the real-world impacts of global warming, acidification, habitat fragmentation or land-use change, we cannot simply consider individual- or population-level effects. All ecosystems contain a complex suite of interactions and interdependencies, which can produce emergent properties at the whole-system scale that could not be predicted by only examining lower organisational levels.

A case in point is the contribution by Hannesdóttir et al. (2013) to the current volume. This study adds important new data from a "sentinel system" (the geothermally heated Hengill region of Iceland) that formed the

focus of a monograph by O'Gorman et al. (2012b) in the preceding volume. The stream system in this volcanically active area has been identified as a natural global warming experiment for gauging potential future impacts of warming at higher latitudes (Friberg et al., 2009; Woodward et al., 2010). Hannesdóttir et al. (2013) measured the secondary production of benthic stream invertebrates and found that warming increases secondary production. They related this to increased resource availability supplied by primary producers (Demars et al., 2011; Gudmundsdottir et al., 2011) that ultimately support much larger apex predators in the warmer streams, in apparent contrast to the predictions of metabolic theory (Brown et al., 2004) and temperature–size rules (Atkinson, 1994; James, 1970). However, these predictions have often only been tested in a controlled laboratory environment with single species or grossly simplified communities, or inferred from correlational data that are prone to confounding variables (e.g. substituting latitude for temperature): Hannesdóttir et al. (2013) thus highlights how complex biological interactions may bend seemingly general rules in the real world.

McLaughlin et al. (2013) also present the results of a natural experiment into the ecosystem-level effects of global change in this volume. This is a rare example of a natural study that captures the impacts of an extreme event—severe flooding—with sufficient pre- and post-disturbance data at the ecosystem level to draw viable conclusions about the consequences. Such effects can typically only be simulated in a controlled environment due to their rarity making them, by definition, difficult to anticipate (e.g. Ledger et al., 2013 for drought), so capturing them in a natural context provides an invaluable glimpse of their impacts in the real world. Additionally, McLaughlin et al. (2013) study severe flooding in the context of another element of global change—habitat fragmentation—which has rarely been studied at the food-web level (Hagen et al., 2012; but see Ledger et al., 2012, 2013). It is now widely recognised that different aspects of global change do not act in isolation and there is great potential for multiple stressors to interact synergistically or antagonistically, although we still know very little about how this might be manifested (Crain et al., 2008; O'Gorman et al., 2012a; Ormerod et al., 2010). In the McLaughlin et al. (2013) study, habitat isolation had no effect on food-web structure during much of the year, but after severe flooding, the complexity and temporal stability of the islands were reduced the further they were from the mainland. This is a valuable example of how debilitating erosion of ecosystem stability may be missed if the drivers of global change are studied in isolation.

This volume also sees Struebig et al. (2013) tackle the topic of habitat fragmentation, this time in the rainforests in Borneo. This study examines the impact of logging as part of the Stability of Altered Forest Ecosystems (SAFE) project to understand how forest modification ramifies through the web of life (www.safeproject.net). This may be described as a semi-natural experiment, where human alteration of the forest is examined in real time, with different levels of conservation within the Kalabakan Forest Reserve creating a mosaic of logging disturbance and associated biological impacts. The authors use a gradient approach to address this issue, looking at the effect of different levels of logging intensity on the biodiversity of bat assemblages within the reserve. They combine this with a more conventional comparative approach to show that changes in assemblage structure are strongly related to canopy height, but that heavily logged forests still retain some biodiversity value, suggesting we may still be able to derive important ecosystem goods and services through careful management of our natural resources.

Raffaelli and White (2013) follow up on this last point with a comprehensive review of how mainstream ecological theory and research have contributed to the rapidly developing area of ecosystem services, which currently sits at the juncture of the natural and social sciences. They trace the development of ecosystem ecology from a purely biophysical science to the evaluation and management of human benefits derived from nature. They relate the concepts of capital stocks and flows to ecosystem ecology, articulating the different values that can be placed on an ecosystem and clearly delineating ecosystem processes, services and goods, which have previously often been used in a looser, interchangeable manner, which has allowed accusations of a lack of rigour to be levelled at this emerging field. The limited temporal and spatial scale of many experiments in biodiversity and ecosystem functioning research is highlighted (see Cardinale et al., 2012), again illustrating the value of temporally resolved natural experiments (Hannesdóttir et al., 2013; McLaughlin et al., 2013). Raffaelli and White (2013) also recognise the need for ecosystem ecologists to expand beyond the comfort zone of their own discipline, by collaboration with social scientists, in general, and economists, in particular. Only through such interdisciplinarity can we grapple with the complex challenge of managing the planet's natural resources effectively in the face of rapid global change (Mace et al., 2012).

This shift to a more integrated approach has been promoted increasingly, for instance, by the Stockholm Environment Institute in Sweden and the

recently established York Environmental Sustainability Institute in the United Kingdom, as a means of developing innovative approaches to sustainable development that bridge science and policy by recognising that humans are part of the ecosystems that we study and nature is inherently linked to our future socio-economic well-being (Naeem et al., 2009; Raffaelli and White, 2013). These initiatives are critical to our success at quantifying and maintaining planetary boundaries—the safe operating space for humanity in the earth system (Rockstrom et al., 2009)—and there is a pressing need for long-term monitoring of multispecies systems in the context of global change, using approaches like the NSF-funded Long Term Ecological Research (LTER) network in the United States (www.lternet.edu).

As early-warning indicators of the effects of global change, Arctic ecosystems will experience some of the most rapid warming over the next century, as predicted by the Intergovernmental Panel on Climate Change's Fourth Assessment Report (IPCC, 2007). Thus, long-term studies in such sentinel systems, such as the Hengill catchment in Iceland (Friberg et al., 2009; O'Gorman et al., 2012b), provide important baseline monitoring data for tracking future change due to warming as well enabling natural experiments to be blended with *in situ* manipulations and models. For example, a long-term whole-stream warming experiment allows transient effects of rapid warming to be compared with equilibrial responses (see Hannesdóttir et al., 2013; Woodward et al., 2010), which is rarely possible with most current mesocosm experiments, as highlighted by Stewart et al. (2013). Further, by coupling theory with experiments, the right kinds of data, such as those that consider species interactions, can be collected to enhance the currently poor predictive power of bioclimate envelope models (Araújo and Peterson, 2012).

Only limited conclusions can be drawn from isolated natural experiments, however, and replicate sets of such systems need to be identified in future, as well as finding candidates for other natural experiments spanning a range of environmental and anthropogenic stressors, including habitat fragmentation (e.g. McLaughlin et al., 2013; Struebig et al., 2013) and acidification (e.g. Hall-Spencer et al., 2008; Layer et al., 2010). By establishing a global network of such 'sentinel systems' and engaging the collaboration of a wide range of interdisciplinary scientists (as called for by Raffaelli and White, 2013), we can maximise our chances of understanding, predicting and coping with future change. Such initiatives will require investment from research councils around the world and such cross-border collaborations

are not always the easiest to realise, although useful parallels and lessons can be drawn from the physical sciences (e.g. the Large Hadron Collider at CERN) as well as from the past (e.g. the 10-year International Biological Program of the 1960s and 1970s).

Long-term monitoring and manipulation of natural experiments should be viewed as complementary to smaller scale manipulative experiments, and if integrated with the rapidly growing number of mesocosm studies, this united approach is greater than the sum of its parts. Predictive ecology is best informed by a continuous gradient of approaches, spanning the full spectrum of simplicity and control to complexity and naturalness (see Fig. 1). While long-term natural experiments can help us to validate and refine our models in the real world, initial formulation and testing of theories require shorter-term, controlled experiments. A pertinent example of this is the synthesis of drought experiments by Ledger et al. (2013) in this volume. Like severe flooding, droughts are an unpredictable climatic event that can be difficult to capture in a natural setting, especially in combination with sufficient baseline data at the study site for detectable ecosystem-level changes (even though the frequency and severity of droughts is increasing all the time: Easterling et al., 2000; Hoerling and Kumar, 2003; IPCC, 2007). Ledger et al. (2013) circumvent this unpredictability by setting up a series of artificial stream channels, with food webs of complexity similar to those found in natural systems (Brown et al., 2011). They exposed a subset of channels to periodic drying out to simulate the effects of drought, while controlling for this perturbation with channels that always remained wet. Important alterations to species diversity and composition were evident, with a distinctive functional switch among the primary producers and a promotion of *r*-selected species in the drought treatments. These changes led to significant losses of standing biomass and secondary production, and a suppression of consumer-resource biomass flux. These experiments now provide us with the first important assumptions about the system-level consequences of repeated droughts, the generality of which must be tested not only with similar controlled experiments in various aquatic (and indeed terrestrial) ecosystems but also long-term monitoring of natural environments exposed to different forms of drought (e.g. acute vs. chronic).

While the experiments of Ledger et al. (2013) are the first to simulate the ecological network-level effects of drought in a controlled environment in fresh waters, they are complemented by a growing body of mesocosm research into other aspects of climate change. Stewart et al. (2013) take the first steps in searching for general patterns (and important exceptions),

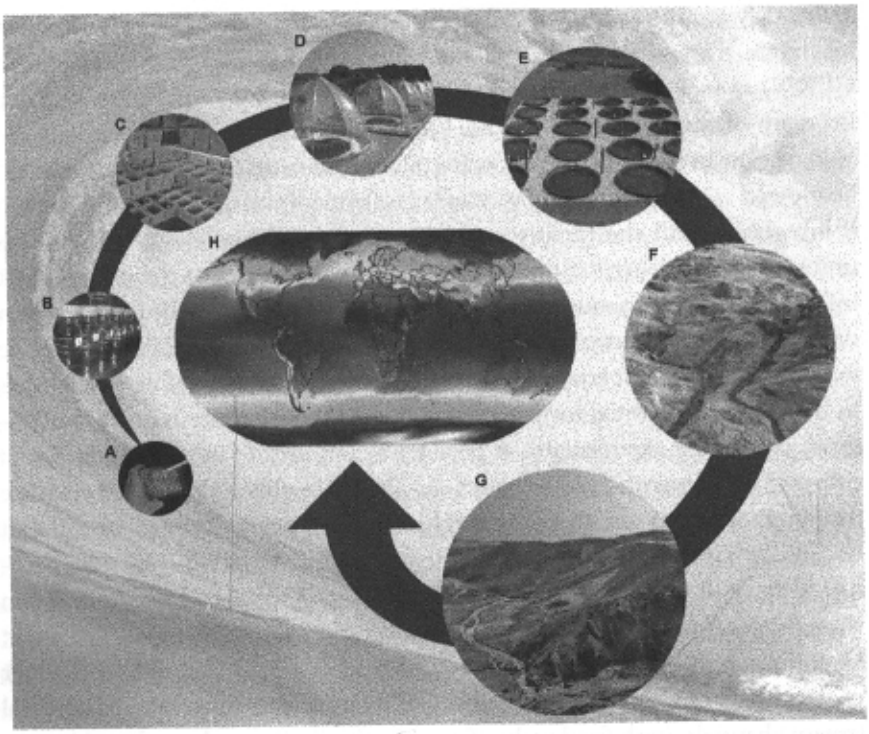

Figure 1 The spectrum of simplicity and control to complexity and naturalness employed in current research into global change in multispecies systems. Experimental manipulation of microbial communities in 96-well plates (A) or protist communities in glass microcosms (B) represents the tightest level of control, at small spatial scales, allowing intergenerational responses to be measured. Laboratory mesocosms (C) with multicellular organisms in a controlled environment, but often at temporal scales that are too short to reach equilibrium conditions (Stewart et al., 2013). Ecotrons (D) are highly instrumented chambers that can increase the scale of mesocosm research further, while allowing simultaneous manipulation and measurement of complex ecological processes. Outdoor mesocosms (E) introduce natural variability, increasing the realism of the response to global change stressors, while still maintaining a high level of control. Natural experiments, such as the geothermal catchment in Iceland (F and G), provide a natural manipulation of global change impacts (e.g. warming) at the landscape scale (G) in a natural setting but without the control of the laboratory environment. Combining *in situ* experimental manipulation with natural experiments (F) offers an optimal combination, especially if replicated at a global scale (H), to create an international network of sentinel systems to monitor, manipulate and model ecological responses to global change. *Image: Phil Sanders.*

with their review of almost 300 controlled mesocosm experiments. These studies span the marine, freshwater and terrestrial realms, with most studies focusing on warming, CO_2 fertilisation and acidification, and precipitation. The authors also break these studies into population-, community- and ecosystem-level investigations, as well as considering both the temporal and spatial scale (in line with Cardinale et al., 2012). They find that idiosyncratic effects tend to dominate at the community level of biological organisation and below, but with more consistent effects emerging at the ecosystem level. For example, there appears to be functional redundancy in how different taxa alter process rates (with body size as the key driver), so process rates may be maintained even in the face of considerable species turnover. Systems also tend to move from transient dynamics to equilibrium conditions over longer timescales, yet most studies done to date are probably too short to reveal the latter, highlighting the context dependency of experimental duration (O'Connor and Crowe, 2005). This finding emphasises the need for longer-term experimental studies with multiple generations of the longest-lived organisms (see Cardinale et al., 2012; Raffaelli and White, 2013) if we are to detect true responses of ecosystems to the impacts of global change.

Ecology finally seems to be embarking on the research paths needed to address the grand challenge of understanding and predicting the impact of human and environmental modification of our ecosystems and environment. The limitations of past experimental approaches (Cardinale et al., 2012), the lack of interdisciplinary collaboration (Mace et al., 2012; Raffaelli and White, 2013) and the need for a more integrated approach to the problem (O'Gorman et al., 2012b; Stewart et al., 2013) are all now recognised as important issues to address. Shifting towards multidisciplinary international collaborations that combine larger-scale monitoring, manipulation and modelling may offer the best opportunity to fulfil that goal, as highlighted by the papers in this volume and its two predecessors in the series.

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