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Introduction

Climate change, biotic interactions and ecosystem services

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Climate change is real. The wrangling debates are over, and we now need to move onto a predictive ecology that will allow managers of landscapes and policy makers to adapt to the likely changes in biodiversity over the coming decades. There is ample evidence that ecological responses are already occurring at the individual species (population) level. The challenge is how to synthesize the growing list of such observations with a coherent body of theory that will enable us to predict where and when changes will occur, what the consequences might be for the conservation and sustainable use of biodiversity and what we might do practically in order to maintain those systems in as good condition as possible. It is thus necessary to investigate the effects of climate change at the ecosystem level and to consider novel emergent ecosystems composed of new species assemblages arising from differential rates of range shifts of species. Here, we present current knowledge on the effects of climate change on biotic interactions and ecosystem services supply, and summarize the papers included in this volume. We discuss how resilient ecosystems are in the face of the multiple components that characterize climate change, and suggest which current ecological theories may be used as a starting point to predict ecosystem-level effects of climate change.

Keywords: climate change; ecosystem services; biotic interactions; biodiversity; ecological networks; resilience

1. CLIMATE CHANGE IMPACTS BEYOND INDIVIDUAL SPECIES

Climate change is real. It is expected to be the major threat to biodiversity and one of the main factors affecting human health and well-being over the coming decades (Thomas *et al.* 2004; ME Assessment 2005; Schröter *et al.* 2005; Pimm 2009). Recent studies suggest CO_2 concentrations are over the safe boundary beyond which the risk of irreversible climate change is extremely high, such as the loss of major ice sheets, accelerated sea-level rise and abrupt changes in ecosystems, including agrosystems (Rockström *et al.* 2009). There is ample evidence that ecological responses are already occurring. First, data on many taxa in the Northern Hemisphere show a consistent trend of northward or westward expansion of species ranges and altitudinal shifts (Parmesan *et al.* 1999; Thomas *et al.* 2001; Walther *et al.* 2002; Walther 2010). Second, globally rising temperatures trigger spring advancement of phenology (Root *et al.* 2003; Edwards & Richardson 2004; Parmesan 2006). And third, reduction in body size owing to warming is generalized in aquatic systems (Daufresne *et al.* 2009; Moran *et al.* 2010).

At the individual species (population) level, much progress has been made in the area of range shifts and effects on population dynamics. But scaling from populations through to communities, let alone ecosystems, will be challenging (Kareiva *et al.* 1993; Schmitz *et al.* 2003; Tylianakis *et al.* 2008; Berg *et al.* 2010; Fenton & Spencer 2010). The population responses of many species to climate change are unlikely to be simply additive and their combinational dynamics are not likely to be linear, as reviewed by Walther (2010). All species are elements embedded in complex networks of interactions. Despite such complexity, several studies have shown universal patterns in the way species interact across different habitat types (Pimm 1991; Montoya *et al.* 2006; Bascompte 2009). For example, interaction networks are very heterogeneous—some species have a much larger number of interactions than expected by chance—and most interactions, among predators and their prey, for instance, tend to be weak (Wootton & Emmerson 2005; Montoya *et al.* 2006). These patterns determine the stability of populations to recover from perturbations, and the likely consequences of local species extinctions on the remaining species within the interaction network. How those network properties and the ecosystem services linked to them will be modified under climate change are poorly known (Berg *et al.* 2010; Walther 2010). Petchey *et al.* (2010) provide an intriguing example of how one of the fundamental food-web properties, connectance—the proportion of realized trophic interactions among the total number of potential interactions if all species were

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One contribution of 14 to a Theme Issue 'The effects of climate change on biotic interactions and ecosystem services'.

connected—may change with increasing temperatures. They develop a theoretical model based on assumptions from metabolic theory and foraging biology and show that increasing temperatures would have large effects on connectance, with further consequences for the stability of species populations and community dynamics.

2. EMERGENT ECOSYSTEMS: TEMPORAL AND SPATIAL DISLOCATIONS

However, the picture is more complex than a current assemblage adapting to local temperature changes. The issue is exacerbated by the differential rates of range shifts by species within ecosystems: present assemblages of interacting populations will not simply shift wholesale further north or to the west or to higher altitudes. Some species will move faster and further than others, and it is probable that spatial dislocations will occur, analogous to the temporal dislocations reviewed by Walther (2010). Short-lived species with high dispersal abilities will re-assemble differently to those which are long-lived and which have low dispersal potentials. Predictions on future species distributions need to consider changes in biotic interactions owing to those spatial mismatches (Araújo & Luoto 2007). Kissling *et al.* (2010) provide an illustrative example for bird assemblages and their associations with plants. Given the slow response time of woody plant distributions to climate change, they predict species losses of birds owing to climate change are significantly stronger when lagged response times of woody plants and their association with birds are modelled. They model generalized plant–animal associations, and they expect even stronger effects for more specialized associations.

Spatial dislocations are of particular concern for above-ground versus below-ground terrestrial assemblages, which though intimately linked, are characterized by quite different rate processes, and which could become dislocated as ranges shift through climate change. Van der Putten *et al.* (2010) investigate how these spatial dislocations may affect future plant distributions and diversity, explaining why some plants may while others may not become rare or abundant in their native or new range owing to climate change.

Future biodiversity landscapes are thus likely to look and behave quite different from those we see today. Future management practices need to consider biotic interactions in order to ameliorate the effects of climate change. A key question for management is whether we can make sufficiently confident predictions as to be able to anticipate ecosystem changes and bioengineer environments to accommodate the biodiversity changes when they arrive. Memmott *et al.* (2010) provide an example on how to manage farmland biodiversity sustainably in a changing world. They investigate changes in plant–pollinator interactions on field margins resulting from phenological changes in the flowering season. They conclude that extra plant species should be added in order to conserve bumble-bee diversity and the extension of their field season, and they suggest the plant species that could be used. Huxham *et al.* (2010) present an experiment which shows that biotic interactions between mangrove species may help guide mangrove management and restoration in the face of climate change. Mangroves provide a range of goods and services including coastal protection, fishery nursery habitat and carbon sequestration, yet they are particularly vulnerable to climate change. These authors show intra and interspecific facilitation that results from increasing species densities and richness, increased seedling survival and recruitment of different mangrove species, and also increased ecosystem resilience by enhancing sediment accretion and elevation.

Within these emergent ecosystems, novel species (invasives), which have previously been unable to sustain viable populations in ecosystems owing to physical environmental constraints, may flourish under climate change. Such species often lack natural competitors or consumers and when released from their climatic constraints can have runaway impacts on ecosystems (e.g. Japanese knotweed and the tree of heaven in the UK; Child & Wade 2000; Pyšek *et al.* 2009). There are important analogies, but also important differences, between introduced exotic species (invasives) and species that move into new ranges in response to warming. Van der Putten *et al.* (2010) discuss this topic for range-expanding plants. They suggest an important difference is enemy-release: while above-ground natural enemies can co-migrate with range-expanding plants, they do not tend to co-migrate with introduced exotic species.

3. PREDICTING CHANGES ON ECOSYSTEM SERVICE DELIVERY: AN EASIER TASK?

The dynamics of these novel, emergent ecosystems are difficult to predict with our current state of knowledge. Although extrapolating from population responses to ecosystem-level responses will be challenging, predicting the effects on ecosystem services delivery may be easier. This is because the same kind and level of ecosystem services can be derived (potentially) from different biodiversities. Thus, while there is compelling evidence from experimental and theoretical studies that ecosystem processes are different under varying amounts of biodiversity (e.g. Balvanera *et al.* 2006; Cardinale *et al.* 2006; Naeem *et al.* 2009; Reiss *et al.* 2009), the rate of ecosystem process change is much less pronounced across high levels of biodiversity, where there may be redundancy among species. This implies that ecosystems have at least some resilience, in terms of ecosystem processes impacts, in the face of biodiversity change. In addition, some services, like soil erosion prevention or flood risk alleviation or water purification, may be largely independent of the composition of the biodiversity: any plant may do.

However, if ecosystems are affected dramatically, as is already the case with widespread losses of biodiversity owing to overexploitation and habitat degradation, and numerous invasive plants and animals that have changed systems beyond recognition, the supply of ecosystem services from those systems is unlikely to be sustained. Also, ecosystems with high levels of abiotic stress (e.g. low precipitation, high radiation) might be more sensitive to climate change than systems under less biotic stress. Maestre *et al.* (2010) use a set of manipulative experiments from semiarid Mediterranean plant and biological soil crust communities to show that increasing abiotic stress associated with climate change does affect the delivery of ecosystem services like soil respiration, water-holding capacity, compaction and nutrient cycling. Their results contradict the expectation that, under increased abiotic stress, plant–plant biotic interactions would become more important in regulating these services. Instead, they show other community attributes, like species richness and cover, are responsible for regulating ecosystem service supply.

Two studies presented in this volume (Sarmento *et al.* 2010; Yvon-Durocher *et al.* 2010) suggest a different scenario. In them, ecosystem processes are affected by climate change independently of changes in biodiversity or biotic interactions. Both studies focus on how climatic warming affects the metabolic rate of organisms—the power required to sustain them—and how these changes in metabolism scale up to ecosystem processes. In both, they use the metabolic theory of ecology (*sensu* Brown *et al.* 2004) to predict changes in process rates with increasing temperatures.

Yvon-Durocher *et al.* focus on one of the most important services provided by ecosystems: the carbon cycle, which modulates climate change via the regulation of atmospheric CO_2. They investigate how climatic warming will affect the metabolic balance between the photosynthetic fixation and respiratory release of CO_2, using a combination of aquatic mesocosm manipulative experiments and theoretical predictions. Their experimental results agree qualitatively and quantitatively with their predictions: ecosystem respiration increased at a faster rate than primary production, and thus warming reduced carbon sequestration. This can be simply explained by differences in the sensitivity of both processes to temperature changes, independently of changes in other ecosystem attributes like standing biomass, community composition or trophic interactions.

Sarmento *et al.* (2010) also use the metabolic theory of ecology, in this case to predict changes in marine microbial food-web processes. They test several theoretical predictions with evidence from laboratory experiments, space-for-time substitutions and long-term data from microbial observatories. These authors show that changes in ecosystem processes can be predicted: bacterial respiration and production increased, and the biomass flux between bacteria and their grazers also increased. The rates of ecosystem process changes vary depending on the spatio-temporal scale of observation and the complexity of the system under study, suggesting that caution must be exercised when we extrapolate from controlled experiments to the more complex real world.

4. ECOSYSTEM RESILIENCE AND MULTIPLE STRESSORS

Of course, climate change is not simply about shifts in physical conditions that otherwise limit species distributions or the metabolism of organisms. Higher temperatures, changes in precipitation, increases in carbon dioxide levels, rising sea levels, more extreme weather events and human migrations will all impact on local ecosystem composition and dynamics. Species with small population sizes or which are highly specialized are likely to be most affected under these multiple stressors acting simultaneously. We need to move beyond investigations of the impacts of single factors, and Bulling *et al.* (2010) reveal how this can be addressed experimentally. These authors examine the roles of temperature and concentration of atmospheric CO_2 on the relationship between invertebrate species richness and nutrient release in an estuarine system. They show how the more extreme temperature level and greater concentrations of atmospheric CO_2 had a negative impact on nutrient release. Both climatic variables interact in a non-trivial way, hence predicting that the effects of future climate change will not be straightforward as multiple drivers are unlikely to have purely additive effects.

Along the same lines, Woodward *et al.* (2010) review how different components of climate change—temperature, hydrology and concentration of atmospheric CO_2—affect different levels of biological organization in freshwaters, from the individual organism up to ecosystem processes. Among other things, they predict that increasing atmospheric CO_2 concentrations would alter nutrient stoichiometry (carbon, nitrogen and phosphorous ratios) at the base of the food web, triggering changes of elemental fluxes throughout the food web.

In some cases, the effects of climate change on ecosystem services can be weaker than those effects related to other global change drivers. Separating those effects is difficult, but necessary to forecast the real magnitude of climate change impacts. Lee *et al.* (2010) compiled data from global change driver manipulation experiments in grasslands and combined these with climate data to assess grassland biomass responses to CO_2 and nitrogen enrichment across a range of climates. They found that both CO_2 and N enrichment increased above-ground biomass, but effects of N enrichment were stronger than those of CO_2.

Nevertheless, many more of such studies are needed if we are to make progress on evaluating the interactions between multiple stressors associated with climate change. For example, loss of biodiversity can increase the vulnerability of terrestrial and aquatic ecosystems to changes in climate and ocean acidification, thus reducing the safe boundary levels of these processes (Rockström *et al.* 2009).

5. TOWARDS A PREDICTIVE SCIENCE OF CLIMATE CHANGE IMPACTS ON ECOSYSTEMS: AN INTEGRATIVE PERSPECTIVE

We have seen that the question of how climate change will affect biotic interactions and ecosystem services supply is far from being solved. The papers in the present volume attempt to wrestle with different aspects of these issues, taking experimental, empirical and theoretical approaches. There are examples from freshwater, marine and terrestrial systems; different types of interactions and services are analysed, over diverse spatio-temporal scales of observation, from local and short-term manipulative experiments to biogeographic projections of future species distributions considering biotic interactions. Also, though there is a bias towards the most noticeable aspect of climate change—warming—some papers focus on alternative aspects of this change, e.g. increased abiotic stress, drought, CO_2 enrichment.

The challenge is how to synthesize the growing list of such observations with a coherent body of theory that will enable us to predict where and when changes will occur, what the consequences might be for the conservation and sustainable use of biodiversity and what we should do practically in order to maintain those systems in as good a condition as possible. In agreement with some of the papers in this volume, we suggest three theoretical frameworks that can be used as a starting point to build this body of theory. We do not include here climatic/species envelope models. We consider them a prior step necessary to forecast future species distributions based on different climate change scenarios and, as exemplified by Kissling *et al.* (2010), they need to include biotic interactions (see also Araújo & Luoto 2007).

The first theoretical framework is metabolic scaling theory. This theory predicts that increasing temperatures will change processes at different levels of biological organization following the Arrhenius equation (West *et al.* 1997; Brown *et al.* 2004). Changes in ecosystem process rates ultimately depend upon changes in the metabolic demands of organisms. This theory can be used for predicting the effects of warming in ecosystems where species cannot modify their ranges. Or it can provide the baseline of process rates in more dynamic ecosystems, addressing how ecosystem processes would change owing to warming, other things being equal. Petchey *et al.* (2010), Woodward *et al.* (2010), Yvon-Durocher *et al.* (2010) and Sarmento *et al.* (2010) apply and extend this theory to predict changes in specific ecosystem processes. They show that it works in most cases and that it provides accurate quantitative predictions.

The second theoretical framework is food-web theory and, by extension, network theory. Species higher in the food web—top predators—tend to be more sensitive to temperature change (e.g. Petchey *et al.* 1999; Voigt *et al.* 2003). Species moving ranges would mean non-random biodiversity loss or gain in local food webs, and its consequences on population and community dynamics can be explored using food web theory. Top predators moving towards cooler climates, for example, may trigger trophic cascades and coextinctions may also occur (Schmitz *et al.* 2003). In addition, the strength of predator–prey interactions may change, as well as consumer diet breadth, even in the absence of new invaders. Van der Putten *et al.* (2010), Memmott *et al.* (2010), Petchey *et al.* (2010) and Woodward *et al.* (2010) are examples of how to integrate food web theory into climate change research. In addition, theories predicting changes in other non-trophic interactions can be very useful. Facilitation theory among plant species is particularly relevant here, and Maestre *et al.* (2010) and Huxham *et al.* (2010) provide examples on how to use and test this theory with experiments, and on how it can inform management practices to ameliorate climate change impacts.

The third theoretical framework is biodiversity–ecosystem functioning (B-EF) theory, which can be viewed as a particular aspect of the more general resilience theory (Scheffer 2010). B-EF theory tries to explain why, whether and how changes in biodiversity and in the strength of biotic interactions may result in changes in ecosystem processes (Naeem *et al.* 2009; Reiss *et al.* 2009). This theory could be easily expanded to include the loss and addition of species that result from range shifts, the reduction of species body mass as a consequence of warming or the effects of spatial and temporal dislocations discussed earlier. Multiple ecosystem processes/services should be explored in parallel, since some of them might be more sensitive than others to different components of climate change. Maestre *et al.* (2010) and Bulling *et al.* (2010), use this theoretical framework in their experiments. Of particular interest, and discussed by Walther (2010), is to explore alternative stable states in ecosystems and critical thresholds caused by warming in which ecosystem services are seriously compromised (Pimm 2009; Scheffer 2010). This is particularly relevant for management practices, because alternative stable states imply path dependency (hysteresis), in which returning to the previous condition (in this case, prior to climate change) is not sufficient to recover the previous ecosystem state and its associated services.

6. CONCLUSION

Climate change is affecting, and will affect over the coming decades, biotic interactions and the provision of ecosystem services. The pace and magnitude of these effects are largely unknown. New, emergent ecosystems will appear, and the provision of services would be mostly compromised in already degraded systems. Research on ecosystem-level impacts of climate change is still in its infancy, and in the present volume we have compiled papers that wrestle with different aspects of these issues, taking experimental, empirical and theoretical approaches. Our hope is that this volume will motivate further research on this fundamental topic.

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