

Review

Community and ecosystem responses to recent climate change

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There is ample evidence for ecological responses to recent climate change. Most studies to date have concentrated on the effects of climate change on individuals and species, with particular emphasis on the effects on phenology and physiology of organisms as well as changes in the distribution and range shifts of species. However, responses by individual species to climate change are not isolated; they are connected through interactions with others at the same or adjacent trophic levels. Also from this more complex perspective, recent case studies have emphasized evidence on the effects of climate change on biotic interactions and ecosystem services. This review highlights the ‘knowns’ but also ‘unknowns’ resulting from recent climate impact studies and reveals limitations of (linear) extrapolations from recent climate-induced responses of species to expected trends and magnitudes of future climate change. Hence, there is need not only to continue to focus on the impacts of climate change on the actors in ecological networks but also and more intensively to focus on the linkages between them, and to acknowledge that biotic interactions and feedback processes lead to highly complex, nonlinear and sometimes abrupt responses.

Keywords: global warming; phenology; range shift; ecology; global change

1. INTRODUCTION

Numerous studies provide evidence for the ecological responses to recent climate change (reviewed in Walther *et al.* 2002; Parmesan 2006; Rosenzweig *et al.* 2007). A great majority of these studies have concentrated on the effects of climate change at the level of individuals and species, in particular focusing on the effects on phenology and physiology of organisms as well as changes in the distribution and range shifts of species (Root *et al.* 2003; Walther 2004). However, responses by individual species to climate change are not isolated; they are connected through interactions with others at the same or adjacent trophic levels (Harrington *et al.* 1999; Voigt *et al.* 2003; Tylianakis *et al.* 2008; Van der Putten *et al.* 2010). Temporal and spatial overlap play important roles in biotic interactions, and both are highly influenced by climatic parameters. Hence, with climate change, a considerable impact not only on the actors themselves but also on the linkages within ecological networks is expected and may amplify the direct effects of climate change. In the following, temporal and spatial changes in the behaviour and distribution of species are outlined and highlighted with particular emphasis on their effects on species interactions and with respect to the limitations of extrapolations from single species’ responses to community and ecosystem effects and to future trends and the magnitude of climate change.

2. PHENOLOGICAL CHANGES AND ECOLOGICAL NETWORKS

The timing of life-history events particularly in temperate regions follows a seasonal pattern. Such phenological phases have been monitored for decades, and thus provide long-term data that can track changes in environmental conditions (Peñuelas & Filella 2001; Visser & Both 2005; Menzel *et al.* 2006; Bertin 2008). For example, recent anomalies in spring phenophases of plant and animal species correlate well with mean spring air temperature (Walther *et al.* 2002; Rosenzweig *et al.* 2007). A global meta-analysis revealed a mean advance of 2.3 days/decade among 677 species averaged over the last four decades (Parmesan & Yohe 2003), but not every species is equally responsive (Jensen 2003). Furthermore, a threshold in the response in spring phenology, e.g. for plants (Zheng *et al.* 2006), suggests that present trends of species responses to changes in climatic conditions should not be linearly extrapolated to future warming, but may level off at a certain point and effects other than those simply due to climate come into play. Hence, although there is ample evidence for phenological changes of plants and animals owing to recent climate change, species do not respond synchronously in time. They might respond not exclusively to climate, but also to other environmental factors, such as e.g. seasonal changes in photoperiod (Edwards & Richardson 2004). Even in cases where climate is considered the dominant trigger that drives the phenology of species, different species may respond to different climatic parameters (e.g. Visser & Holleman 2001). The consequences of such differential responsiveness are revealed in differences in the timing of species interactions within ecological

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networks, such as food webs, host–parasitoid webs and/or mutualistic webs (Ings *et al.* 2009).

In food webs, climate fluctuations influence the relative timing of food requirement and availability (Stenseth *et al.* 2002). For aquatic systems, Winder & Schindler (2004) showed that warming trends in spring water temperatures over the latter part of the twentieth century in Lake Washington (northwest USA) have produced a mismatch in the timing of favourable environmental conditions in algal–herbivore interactions. The timing of the phytoplankton bloom changed in accordance with earlier spring thermal stratification and advanced 27 days since 1962. Earlier timing of peak densities was also observed for the herbivorous rotifer *Keratella cochlearis* (Gosse), which advanced 21 days, but not for *Daphnia pulicaria* (Forbes). The growing mismatch between peak algal densities and *Daphnia* populations resulted in a long-term decline in *Daphnia* densities. Marine pelagic phenology across three trophic levels was investigated in the North Sea using five functional groups (diatoms and dinoflagellates as primary producers, copepods as secondary producers, non-copepod holozooplankton as secondary and tertiary producers and meroplankton including fish larvae also as secondary and tertiary producers) (Edwards & Richardson 2004). The change in timing of the seasonal peaks from 1958 to 2002 was analysed for a total of 66 plankton taxa and revealed differing levels of response throughout the community and the seasonal cycle. This leads to a change in synchrony of timing between primary, secondary and tertiary production, and, thus, a mismatch between successive trophic levels. Phenological changes across four trophic levels representing a (simplified) food chain in north-west European deciduous forests were analysed in a long-term study starting in the mid-1980s (Both *et al.* 2009). Tree budburst advanced only slightly (and not significantly) by 0.17 d yr^{-1} , while the next two trophic levels, the herbivores (represented by caterpillar biomass peaks, which changed by 0.75 d yr^{-1}) and insectivorous birds (represented by the hatching date of four passerine species, changing between 0.36 and 0.50 d yr^{-1}), have advanced, but not the representative of the fourth trophic level, the hatching date of sparrowhawks, *Accipiter nisus* (L.), which showed no trend. Again, different trophic levels shifted their phenology to different magnitudes, revealing asynchronies in timing within the ecological network.

Also in host–parasitoid webs, species of the higher trophic level (parasitoids) may be affected by both the climatic variability itself and indirectly by the amplified variance in host dynamics in response to climate (Stireman *et al.* 2005). In order to relate parasitism frequency to climatic variability, an indirect approach was applied comparing parasitism frequencies of caterpillars across geographical localities that differ in their climatic predictability. This approach revealed a negative association between parasitism frequency and climatic (especially precipitation) variability and was interpreted as the result of increased lags and disconnections between herbivores and their enemy populations that occur as climatic

variability increases. Hence, climatic fluctuations may be responsible for increasing the risk of host outbreaks through disruption of synchronization in host–parasitoid systems (Hance *et al.* 2007).

In mutualistic webs, positive, non-trophic interactions occur, as in the case of, for example, plant–pollinator interactions. Hegland *et al.* (2009) reviewed current phenological responses to rising temperatures and how these changes influence the interactions among plants and pollinators. Although a linear relationship has been observed between climate warming and appearance dates in pollinators and plants, the authors emphasize that such linear responses cannot continue perpetually, but the few studies dealing with phenological decoupling (e.g. Kudo *et al.* 2004; Gordo & Sanz 2005) revealed varying responses among species and regions.

In consequence, the above examples show that the timing and synchrony is influenced by climatic factors, but that not all the individual actors involved in the various trophic levels are equally responsive (see also Voigt *et al.* 2003) and/or respond to the same environmental parameter.

3. SPECIES RANGE SHIFTS AND COMMUNITY COMPOSITION

Whereas the previous section focused on interactions among species occurring in the same localities, range shifts imply that species might be forced to interact with those from which they were formerly spatially separated. Climate-induced species' range shifts have been reported along altitudinal (e.g. Beever *et al.* 2003; Walther *et al.* 2005a; Cannone *et al.* 2007; Pauli *et al.* 2007; Holzinger *et al.* 2008) and latitudinal gradients (e.g. Parmesan *et al.* 1999; Lesica & McCune 2004; Walther *et al.* 2005b; Lemoine *et al.* 2007). However, again not all the species seem equally responsive. In French temperate and Mediterranean mountain forests, mountainous species experienced larger shifts in optimum elevation compared with ubiquitous species (Lenoir *et al.* 2008), whereas on the sub-Antarctic Marion Island, habitat generalists responded faster and with larger upslope expansions than habitat specialists (Le Roux & McGeoch 2008). Similar to the observed shift in species optimum elevation (Lenoir *et al.* 2008), Kelly & Goulden (2008) observed a change from a symmetrical, i.e. bell-shaped curve, to an upwardly skewed species' distribution along an elevation gradient in southern California's Santa Rosa Mountains. This upslope movement has been interpreted as a result of shifting dominance within existing communities, rather than the expansion of ranges to new elevations. Hence, based on the findings from field studies, Breshears *et al.* (2008) identified at least three different types of distributional change for species on elevational (the same may also apply for latitudinal) gradients: (i) 'march', with the simplified assumption of parallel shifts of leading and trailing edge of species' ranges, where the entire distribution and its ranges moves upslope, (ii) 'lean', where the absolute limits of the existing range remain constant but the central tendency shifts (see above), and (iii) 'crash',

where mortality is widespread throughout the existing range.

Hence, in analogy to temporal changes in species behaviour, there is also ample evidence for distributional changes of plants and animals owing to recent climate change, but species do not respond synchronously in space. This will result in shifting dominances of species within communities, but also to the formation of non-analogue communities, where existing species will co-occur, but in new combinations (Huntley 1991; Walther 2004; Kullmann 2006). For example, the present species' composition of communities at higher altitudes on sub-Antarctic Marion Island is not simply an analogue of past community composition of the native vascular flora at lower altitudes, but rather constitutes a new combination of extant species (Le Roux & McGeoch 2008). Likewise for marine biodiversity, European rocky shore species are showing changing abundance and geographical range in response to climatic warming in the NE Atlantic (Hawkins *et al.* 2008). At present, more advances of southern species (e.g. *Chthamalus* spp.) have been recorded than retreats of northern species (e.g. *Semibalanus balanoides* L.). Nonetheless, secondary production is expected to be reduced as a consequence of changing grazing pressure as species' identities change owing to subtle differences in their behaviour or physiology, with *Chthamalus* spp. growing much more slowly than *S. balanoides*.

Thus, changes in species ranges and resulting community reorganizations have considerable impacts on the way species interact, and, through trophic interactions, imply consequences for the functioning of ecosystems.

4. COMMUNITY REORGANIZATION AND ECOSYSTEM RESPONSES

The previous two sections have shown that temporal and spatial changes in species behaviour and distribution are not isolated processes; they are connected through interactions with other species at the same or adjacent trophic levels, and beyond, through indirect effects of trophic cascades. Hence, changes at lower trophic levels may induce bottom-up effects through ecological networks and may induce feedback processes.

In a Californian grassland experiment, it was shown that early responses to the altered rainfall regime may be reserved through species interactions and feedback processes across trophic levels (Suttle *et al.* 2007). Initially increased diversity and production in the grassland ecosystem was followed by a simplification of the food web and reductions in consumer abundance in the latter period of a 5-year experiment. On the other hand, a similar manipulative experiment in unproductive, grazed grassland in northern England revealed a highly resistant vegetation to climate shifts that was maintained over more than a decade (Grime *et al.* 2008). Furthermore, top-down effects may also occur and strongly influence and modify community responses. In a warming experiment, the response of the plant community was highly dependent on the presence or absence of herbivores (Post &

Pedersen 2008). Without herbivores, the warmed plant community shifted from graminoid-dominated to dwarf birch-dominated, suggesting that the control over primary productivity and plant community composition is mainly environmental. However, when natural herbivory by muskoxen and caribou was allowed, warmed plant community composition did not differ after 5 years from unwarmed reference plots, in this case suggesting a stronger biological than environmental control. In addition, density effects may also play a crucial role (e.g. Brathen *et al.* 2007; Forchhammer *et al.* 2008) and lead to ecological thresholds separating two different ecosystem configurations as shown for the Baltic Sea, with critical planktivore abundance separating states where zooplankton dynamics are either driven by biological (predation pressure) or environmental (hydroclimate) factors (Casini *et al.* 2009; cf. also Litzow & Ciannelli 2007; Beaugrand *et al.* 2008). These examples show that changes in species evenness may have important consequences for ecosystems (Chapin *et al.* 2000) and, thus, earlier than do changes in species richness, and before a species is threatened with extinction (Foden *et al.* 2008).

Threshold change in ecosystem becomes increasingly evident in ecosystems as different as tropical coral reefs, with bleaching when exposed to severe and prolonged thermal stress (Hughes *et al.* 2003), and terrestrial forest ecosystems, with, for example, widespread increase in tree mortality rates in the western USA. In the case of the latter, the climatic signal may act either directly, with warmer temperatures and consequent increases in water deficits (Van Mantgem *et al.* 2009), and/or indirectly, inducing massive outbreaks of, for example, insects (Kurz *et al.* 2008) and converting ecosystem functioning in a way that forest changes from a previous carbon sink to a net carbon source owing to widespread tree mortality.

Furthermore, climate change influences community composition and ecosystem processes not in isolation, but in concert with other drivers of global change (Dukes & Mooney 1999; Travis 2003; Walther *et al.* 2009; Schweiger *et al.* in press). For example, species' introductions, global warming and sea level rise are expected to interact with regional drivers such as nutrient supply, and thus affect food webs and the entire shallow-water ecosystem of the Wadden Sea (Reise & van Beusekom 2008). The combined impact of warming and biological invasions (see Walther *et al.* 2009 for a review) allowed the establishment of a mixed community of native and alien evergreen broad-leaved species in former deciduous lowland forests south of the Alps (Walther 2004), with likely implications for seasonal carbon and water balances of the entire forest ecosystems. Hence, community reorganization will not only lead to a reshuffling of existing species; in times of global exchange of organisms and goods also 'new' species will arrive, mix in and compose novel assemblages (Walther 2004; Williams & Jackson 2007; Hobbs *et al.* 2009), and thus contribute to modified ecological networks and alter ecosystem processes (Dukes & Mooney 2004).

5. INCREASING COMPLEXITY THROUGH BIOTIC INTERACTIONS AND FEEDBACK PROCESSES

Recent research has revealed an ever increasing number of ‘fingerprints’ of climate change (Walther *et al.* 2001; Parmesan & Yohe 2003; Root *et al.* 2003; Rosenzweig *et al.* 2007), and it is becoming increasingly apparent that many species respond to altered climatic conditions with cascading effects through ecological networks such as food webs. This increases uncertainty as, for instance, it is less clear whether or to what degree the climate signals initiating regime shifts work their way up through entire food chains and/or whether they act independently on each trophic level (Alheit 2009). Another source of uncertainty is the possibility that species may evolve tolerance to environmental change. Harmon *et al.* (2009) showed how the presence of different predator species affected the potential for rapid evolution in their prey, owing to the different strengths of predator–prey interactions. Furthermore, ecological complexity from biotic interactions and evolutionary complexity from evolution of tolerance to environmental change may influence each other (de Mazancourt *et al.* 2008), rendering it necessary to consider both in climate change impact assessments. Such interactions are usually non-additive (Chapin *et al.* 2000; Cohen *et al.* 2009) and include feedback processes that make them difficult to predict (Reise & van Beusekom 2008; Kissling *et al.* 2010). Likewise, ecosystems and thus also altered ecosystem processes influence climate through multiple pathways, e.g. by changing energy, water and carbon balances of the atmosphere (Field *et al.* 2007; Luo 2007; Chapin *et al.* 2008). There is evidence that these combinations of intrinsic and extrinsic processes result in non-linearities (Stenseth *et al.* 2002; Wall 2007), and there is certainly a clear need to intensify efforts to identify the causes of these phenomena and consider sensitive thresholds in the response of ecological communities and ecosystem processes (Lovejoy 2008; Rustad 2008). These are important properties of complex nonlinear dynamics (Gassmann *et al.* 2000, 2005) that range from sensitivities towards initial conditions (e.g. Körner *et al.* 2008) to limited predictability (e.g. Benincà *et al.* 2008; Sarewitz 2010), and pose obvious limitations to simple and linear extrapolations of recent responses to longer time scales, larger spatial scales and future warming rates and the magnitude of climate change (Lewis 2006; Shindell 2007).

6. CONCLUSION

The warming we have experienced so far is only minor compared with what is expected by the end of the century, but nonetheless the ecological impacts are already evident. For a better understanding of the mechanisms and processes behind the observed responses of species, the focus of climate impact research should not only focus on the actors (i.e. individuals, species) in ecological systems, but also intensify efforts to understand the dependencies and strengths of the linkages between them, addressing dynamic aspects and complex interactions. Nonlinear dynamics in complex systems, including abrupt changes owing to thresholds and feedback processes,

should caution against extrapolating ecological responses at the early stage of warming to future trends and magnitude of climate change.

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