

EDITORIAL

Ecophysiological forecasting for environmental change adaptation

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In its World Energy Outlook 2012; the International Energy Agency forecast more than a 30% growth in global energy demand over the next few decades (World Energy Outlook 2012). The energy mix to meet this demand will come largely from fossil fuels that, in 2011, were supported by \$ 523 billion in subsidies, six times more than the subsidies directed to renewables. The current trajectory for CO₂ emissions, which is at the high end of the IPCC scenarios (Peters *et al.* 2013), therefore seems set to continue. The implications for temperature trends are clear – average annual temperatures will continue rising, as they have been doing for several decades, in keeping with the IPCC projections (Rahmstorf, Foster & Cazanave 2012). Likewise, high-temperature anomalies will grow in spatial extent and severity, with a new category of extremely hot summer anomalies appearing (Hansen, Sato & Ruedy 2012). The latter were recognized widely by the global media when, in early 2013, Australia's Bureau of Meteorology added two new colours to its Interactive Weather Forecast Map scale to represent temperatures above 50 °C (see <http://www.bom.gov.au/australia/charts/index.shtml>). Accompanying rising temperatures are other climate change-related phenomena, such as increasing global aridity and droughts (Dai 2013), Arctic amplification and its mid-latitudinal consequences (Francis & Vavrus 2012), and rapid warming of the Antarctic Peninsula (Turner *et al.* 2009).

Environmental change of other forms is likewise persistent. Habitat alteration continues in many areas, and includes widespread forest conversion (Hansen, Stehman & Potapov 2010) and the more insidious change to global ocean pH (Hönisch *et al.* 2012). Overexploitation remains significant both in terrestrial and marine ecosystems (Ceballos & Ehrlich 2002; Chown 2012). Biological invasions, following the introduction of non-indigenous species, are increasing in rate and impact (e.g. McGeoch *et al.* 2010; Pyšek *et al.* 2012), with new areas becoming vulnerable as climate change and human activity increase (Chown *et al.* 2012).

Biodiversity impacts into the future

The biodiversity outcomes of these environmental changes are, in their broadest form, clear (Butchart *et al.* 2010).

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Abundances of many taxa, including those once common, are declining (Jackson 2010; Sinervo *et al.* 2010; Gaston 2011), with widespread ecosystem consequences (Estes *et al.* 2011; Anderegg, Kane & Anderegg 2013). Ranges are likewise showing substantial change, as are the timing of key life history and ecological events, and average body sizes in many groups (Gardner *et al.* 2011; Hoffmann & Sgrò 2011; Worm & Tittensor 2011; Sunday, Bates & Dulvy 2012). Large-bodied taxa and individuals are also disappearing from both terrestrial and marine systems (Chown 2012; Lindenmayer, Laurence & Franklin 2012) while, on the other end of the size scale, keystone taxa in marine systems are experiencing both temperature and acidification impacts (e.g. Bednaršek *et al.* 2012; Frieler *et al.* 2012). Weedy, often invasive, species are also starting to dominate many environments (Piola & Johnston 2008; Woodward & Kelly 2008).

Much as these impacts are being widely documented and novel approaches are being developed for incorporating them into policy-relevant assessments (Pereira *et al.* 2013), there are substantial challenges for developing area- and taxon-specific strategies that will enhance environmental change adaptation into the future. The successful management of biodiversity for conservation, agriculture, or human health-related purposes will depend on improvements to both the accuracy and precision of local-scale ecological forecasting (Lafferty 2009; Chown *et al.* 2010). Managers need to know what will happen to specific taxa and areas, and over what timescale, rather than what might be expected more generally (e.g. Dunlop *et al.* 2012). Providing such information is clearly non-trivial (Williams *et al.* 2008; Sgrò, Lowe & Hoffmann 2011; Bellard *et al.* 2012). However, the understanding, approaches and tools needed to make available such spatially and taxonomically explicit ecological forecasting are developing rapidly (e.g. Chown & Gaston 2008; Dawson *et al.* 2011; Hoffmann & Sgrò 2011; Chown 2012; Wisz *et al.* 2013).

Ecophysiological forecasting

In this issue of *Functional Ecology*, four papers present recent developments in this area, illustrating the importance

of what can be termed an ecophysiological forecasting approach.

The first of these papers, by Hoffmann, Chown & Clusella-Trullas (2013), asks the beguilingly simple question of whether upper thermal limits are constrained in ectotherms. The complexity underlying this apparently simple question arises in several ways. First is the need to understand the degree to which upper thermal tolerance traits (such as upper lethal temperature and critical thermal maximum) are both phylogenetically and spatially variable. If they are constrained, then tropical organisms, which are likely to experience, or are perhaps already experiencing, substantial fitness reductions because temperature extremes are exceeding or close to exceeding tolerance limits (Deutsch *et al.* 2008), may have little scope for adaptation and face considerable further extinction risk. It appears that subtropical organisms may face similar challenges. The risks to both groups of organisms may be exacerbated by changing precipitation regimes, which in turn are affected by landscape alteration (Ellison, Fitter & Bishop 2012). Second, is the need to determine whether, under substantial selection, metazoans may be able to escape extinction (or population decline) through the evolution of their upper lethal temperatures. Upper lethal temperatures appear to show limited variation, but evolution of that upper limit does appear to have taken place in a few remarkable metazoan taxa that are highly heat tolerant (e.g. some desert ants, some bruchid beetles). Finally, the complexity arises from the need to forecast how interactions among the rates of climate change and adaptation to climate change may play out into the future among populations in different areas and in marine and terrestrial systems. Local populations are in many ways the cornerstone of biodiversity (Ricklefs 2008), and evidence is growing that marine and terrestrial taxa may differ fundamentally in their responses and how these vary among populations. What this investigation does not address is whether seemingly general constraints to upper limits, by comparison with lower limits, are also found in plants and endotherms, although increasingly it appears that this may also be the case (Araújo *et al.*, ms. in review).

The second paper in the series, by Kearney *et al.* (2013), introduces a thermodynamic niche framework for understanding species' responses to environmental change. The approach builds on an integration of previous mechanistic models, the geometric framework of nutrition and dynamic energy budget theory. It recognizes that temperature, water and nutrition interact in fundamental ways to influence the response of organisms to the environment. In essence, population dynamics, and hence local abundance, are influenced by thermoregulation, hydoregulation and regulation of nutrition. These form the stage on which other evolutionary and ecological interactions play out. Importantly, the authors provide a worked model for a terrestrial ectotherm, showing how first-principle estimates of fluxes can be integrated with environmental information

to forecast the outcomes of organism–environment interactions, complementing previous demonstrations for marine systems (Lika *et al.* 2011). This ecophysiological forecasting approach forms a significant development in the field of metabolic ecology with the synthesis of dynamic energy budget theory and the geometric framework (see also Kearney & White 2012). To date, metabolic ecology has largely been influenced by the more specific metabolic theory of ecology, which is also growing in its ability to accommodate a range of biological scenarios (e.g. Price *et al.* 2012).

The third paper by Chevin, Collins & Lefèvre (2013), reviews models that consider the impact of phenotypic plasticity on climate change adaptation. Plastic responses are expected to be critical for many organisms adapting to climate change because rates of evolution will often be too slow to keep up with rapid environmental changes, particularly in species with long generation times. However, plastic responses can also reduce the likelihood of populations persisting if environments are unpredictable (Reed *et al.* 2010). Models that incorporate plasticity can test conditions under which populations might persist and also consider whether plastic responses will ultimately enhance or retard further evolutionary change (Chevin, Lande & Mace 2010). However, models have rarely been applied to understanding changes within natural populations, and the authors consider some of the complications involved in making such assessments. For instance, models usually assume that there is an optimum phenotype, but this can be difficult to define under changing environments and selection pressures. In addition, the plastic responses themselves can evolve, but this will depend on the nature of any costs associated with plastic responses, and other interactions among traits. Chevin *et al.* indicate how such issues may be overcome by detailed studies of specific systems, but also discuss the substantial challenges associated with such an effort. They then highlight how some progress has been made in investigating the plastic response of trees to drought and temperature stress, and in the response of marine phytoplankton to elevated CO₂ levels. However, they note that a large gap remains in our current understanding of whether plasticity might limit or promote further change, which in turn limits robust forecasting about individual species let alone entire communities.

Finally, Kelly & Hofmann (2013) consider the threats posed by ocean acidification, which may rival the challenges associated with temperature increases in marine ecosystems. The authors emphasize that assessments of these threats have mostly failed to take into account acclimation and evolutionary adaptation, although there is currently limited evidence on either of these issues, and the available evidence is mostly confined to experimental studies of algae (Lohbeck, Riebesell & Reusch 2012). Selection for adaptation to different pH conditions seems unlikely along latitudinal gradients, which do not vary for pH, but might occur locally where sharp changes in pH are possible. This contrasts with changes in temperature, where organisms

may become adapted along latitudinal gradients, providing predictable patterns of movement of species, but also potential sources of adaptive variation. The authors also highlight how modern –omics tools, in combination with quantitative genetic approaches, can enhance our ability to forecast adaptive shifts, and the extent to which adaptive responses might be constrained through interactions among traits and the presence of selection pressures in addition to ocean acidification.

Science and society

The collection of papers presented here highlights ecophysiological forecasting as a means to improve substantially our current ability to make taxon and area-specific forecasts, especially given brisk developments in understanding of the ways in which ecological interactions can be incorporated into similar approaches (Wisz *et al.* 2013). These papers also emphasize the rapidly growing importance of being able to integrate large environmental, trait-based and genomic datasets (Gaston *et al.* 2009). Indeed, future forecasting in biology will clearly benefit from the synthesis of more traditional bioinformatics and what is now largely considered ecoinformatics (Michener & Jones 2012).

What this collection of papers does not address, however, is the requirements for behavioural adjustment in almost every aspect of society to mitigate prospects for further environmental change (see e.g. Smith *et al.* 2011). Much of this kind of work is beyond the scope of our research and that published by *Functional Ecology*. However, we recognize that for adaptation to succeed, both in human society and on the part of other organisms, reductions in the rates of change are a pressing need. Without them, the optimism of the heart and pessimism of the intellect attributed by Rigby (2002) to many in the environmental field may well both wane – replaced by widespread acceptance and then neglect of the problems, to the detriment of biodiversity and society.

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