

Macrophysiology for a changing world

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Abstract

The Millennium Ecosystem Assessment (MA) has identified climate change, habitat destruction, invasive species, overexploitation and pollution as the major drivers of biodiversity loss and sources of concern for human well-being. Understanding how these drivers operate and interact and how they might be mitigated are among the most pressing questions facing humanity. Here, we show how macrophysiology—the investigation of variation in physiological traits over large geographical, temporal and phylogenetic scales—can contribute significantly to answering these questions.

We do so by demonstrating, for each of the MA drivers, how a macrophysiological approach can or has helped elucidate the impacts of these drivers and their interactions. Moreover, we illustrate that a large-scale physiological perspective can provide insights into previously unrecognized threats to diversity, such as the erosion of physiological variation and stress tolerance, which are a consequence of the removal of large species and individuals from the biosphere. In so doing we demonstrate that environmental physiologists have much to offer the scientific quest to resolve major environmental problems.

Keywords: Biological invasions, Conservation biology, Evolutionary physiology, Global climate change, Macroecology.

Introduction

In 1950, Aldous Huxley wrote ‘The human race is passing through a time of crisis, and that crisis exists, so to speak, on two levels—an upper level of political and economic crisis and a lower level of demographic and ecological crisis’. His words are prescient of the conclusions reached by the Millennium Ecosystem Assessment (MA; 2005). The MA identified five major drivers of biodiversity loss and, in consequence, sources of concern for human livelihoods via their implications for and effects on ecosystem services: habitat alteration, climate change, invasive species, overexploitation, and pollution. Understanding how these drivers have led to biodiversity loss, how they will continue doing so and what actions need to be taken to mitigate and adapt to their effects are among the most significant questions facing humanity.

That ecologists should address these questions is self-evident. What is less clear is that the *scope* of ecological research is perhaps not as well equipped to undertake this task now than it may have been in the early 1900s when there was little that distinguished ecology from physiology. However, developments in both fields led to their subsequent virtual separation. By the latter part of the last century, the barrier between the two was, if not impermeable, certainly crossed with a much lower frequency than that had been previously the case. Ecology’s gaze became fixed on population regulation and species interactions, while that of physiology turned to mechanisms at lower levels in the physiological hierarchy as new tools became accessible (Huey 1991; Spicer & Gaston 1999).

Although it is axiomatic that knowledge of physiological variation is required to understand organismal responses to and influences on environmental change (Kareiva *et al.* 1993; Hoffmann *et al.* 2003; Kearney & Porter 2004; Helmuth *et al.* 2005; Austin 2007), physiologists are increasingly being exhorted to focus on model organisms and dissect the genomic basis of functional traits (Dow 2007). In consequence, the physiological information required to address environmental change issues is either not available (Anon. 2007) or not given the priority it deserves. Such a situation can prove only to restrict rather than to catalyse solutions to these questions.

Here, to promote further consideration of the ways in which whole-organism physiology can provide insights into the mechanisms underlying and consequences of environmental change, we examine, in a macrophysiological context, the five main drivers of environmental change identified by the MA. Macrophysiology is 'the investigation of variation in physiological traits over large geographical and temporal scales and the ecological implications of this variation' (Chown *et al.* 2004a). Although its focus is largely on the ecological implications of physiological variation, explanations for this variation and the ways in which it might evolve form significant parts thereof (Osovitz & Hofmann 2007).

Macrophysiology has deep historical roots (Chown *et al.* 2004a). Large-scale comparative and cross-taxonomic physiological approaches were pioneered by several authors (e.g. Scholander *et al.* 1953; Janzen 1967; Bradshaw 1972; Rubinstein 1992), and the broad-scale integrative focus has since been explored in a variety of ways. These range from bottom-up model building of species responses to environmental change, to landscape-scale considerations of how the abiotic environment and physiological responses might interact to determine species abundances and distributions (Kareiva *et al.* 1993; Huey *et al.* 2002; Porter *et al.* 2002; Ghalambor *et al.* 2006).

Many of these studies have drawn attention to the importance of understanding physiological variation and its underlying mechanisms in research fields where they are often not explicitly considered, such as conservation biology (e.g. Parsons 1995; Tracy *et al.* 2006; Wikelski & Cooke 2006). Macrophysiology also has an ongoing dialogue with evolutionary physiology (Garland & Carter 1994), and recognizes the importance of understanding how processes at multiple scales interact and the significance of the mechanisms underlying physiological variation.

Habitat alteration

(a) Habitat alteration and changing climates

Habitat fragmentation and alteration are widely acknowledged as the most significant contributors to biodiversity change and loss. What are perhaps not so acutely appreciated are the positive feedbacks inherent in large-scale landscape conversion that might make our world substantially less habitable. At the regional scale, the effects of deforestation on moisture and temperature regimes are becoming more widely appreciated. For example, in tropical regions, forest removal has substantial impacts on moisture regimes of remnant patches, so altering the value of what might appear to be suitable habitat patches and thus changing species demographics and distributions (Webb *et al.* 2006).

Likewise, in temperate areas, the removal of forests promotes frost conditions and an increase in the frequency of freeze–thaw cycles (Bonan 1999). The latter have substantial impacts on organisms by either reducing growth rates (Sinclair & Chown 2006) or negatively affecting organismal energy balance during unexpectedly warm conditions, leading to mortality (Irwin & Lee 2003). However, what has only recently been recognized is that forest removal has wider impacts because the physiological actions of individual trees within large contiguous forests are required to draw in atmospheric water over continents for thousands of kilometres. Forests constitute a biotic pump,

moving atmospheric water into the interior of continental systems (Makarieva & Gorshkov 2007). In areas dominated by non-forested landscapes, ocean to land moisture transport ceases several hundred kilometres inland, which leads to a rapid decline in precipitation as a consequence of the absence of sufficient evaporative water loss.

By contrast, irrespective of the temperature of the region, where natural forests are supported, ocean to land transport of water, and hence precipitation, is sustained for thousands of kilometres inland. It is the concatenated evapotranspiration of water from many closely packed individual trees that gives rise to this biotic pump. Removal of the trees, especially along coastal fringes, shuts down the pump, and even in areas where rainfall is considerable it is predicted that deforestation will lead to a 10-fold reduction in mean continental precipitation and run-off (Makarieva & Gorshkov 2007).

This novel biologically based physical principle is perhaps one of the most significant discoveries for understanding the probable impacts of ongoing deforestation across the globe. It highlights the necessity for a rapid reduction in deforestation. Not only is biodiversity loss at stake, but the provision of freshwater via run-off is also in the balance.

(b) Species range modelling

At smaller scales, the designation and maintenance of protected areas have been widely encouraged to halt habitat conversion and thereby biodiversity loss: a strategy that requires the identification of priority areas for conservation activities (Sarkar *et al.* 2006). Although surrogates have been employed, this process is typically based on information on the spatial distribution (and abundance) of key species (Steinitz *et al.* 2005; Grenyer *et al.* 2006). For most groups and places adequate information is not available, and increasing reliance is being placed on modelling species distributions (Guisan & Thuiller 2005; Moisen *et al.* 2006): an approach that has been criticized on several grounds.

Concerns include among-model differences in outcomes and performance (Elith *et al.* 2006) that are often dependent on species characteristics (Thuiller *et al.* 2005), the absence from the models, at least explicitly, of the effects of biotic interactions and dispersal limitation (Araújo *et al.* 2005; Soberón 2007) and the poor performance of models constructed in one region when applied to another (Fitzpatrick *et al.* 2007). Much attention is now being given to identifying the best courses of action for resolving these questions. However, a further issue with modelling is the implicit assumptions made about the form of species, environmental responses (Austin 2007).

Many models assume that the response of species to variation in their environments takes either a linear, quadratic or exponential form. Discussions of some models, especially of plants, acknowledge that the environmental responses are typically Gaussian or asymmetric (Austin *et al.* 2006; figure 1) and incorporate these forms (or let them vary, see Thuiller *et al.* 2005). However, many animal models make no mention of the theoretical assumptions on which they are based (Austin 2007).

Moreover, the majority fail to acknowledge that model performance depends on the form of the environmental response, and whether environmental factors determine the probability of occurrence or abundance in an additive (deficiencies in one response can be compensated for by improvements in another) or multiplicative manner (no compensation is possible—often assumed as Liebig's law of the minimum). Likewise, inadequate distinctions between direct (e.g. temperature), indirect (e.g. altitude or aspect) and resource variables (e.g. food or space availability) can severely compromise model performance (Meynard & Quinn 2007). Macrophysiology can provide a solution.

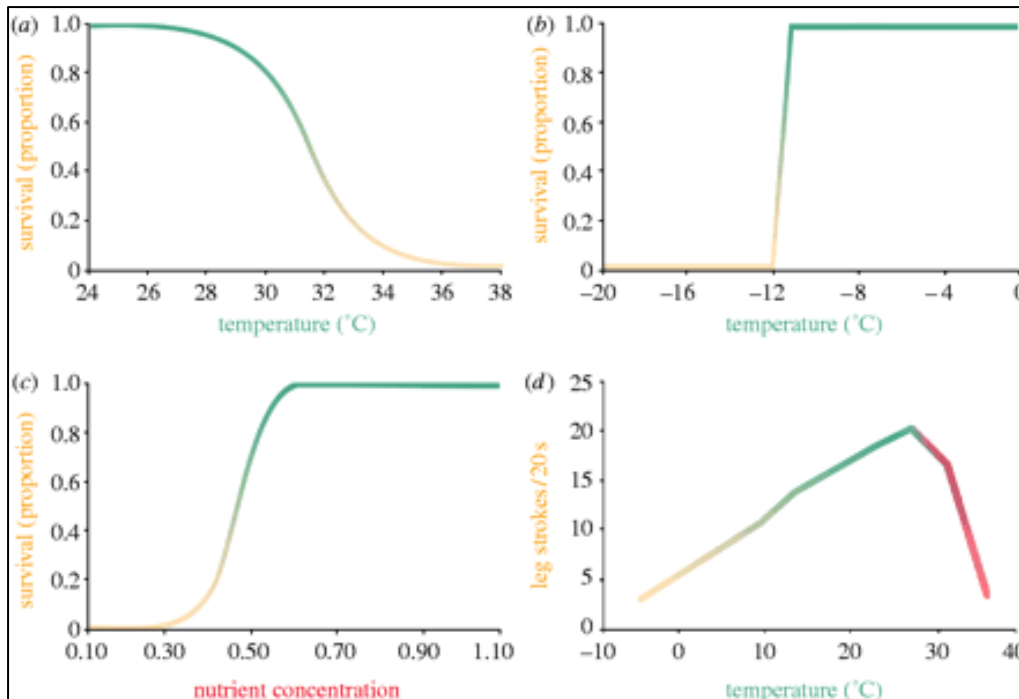


Figure 1

The form of responses populations show to varying environmental factors. These might be (a) logistic, as in this temperature response curve; (b) threshold, as in the survival response to low temperature in a species that can tolerate freezing up to -11°C ; or (c) asymptotic, as is frequently found in plants relative to a limiting nutrient. (d) Performance curve demonstrating a rate response to temperature. Note the asymmetry of the curve at the higher temperature end.

The forms of the response of populations to different components of the abiotic environment, their spatial and temporal variations and their interactions are part of macrophysiological research. For example, it is known that the relationship between survival and temperature is typically logistic (or Gaussian and platykurtic if the temperature extremes are considered simultaneously; e.g. Sinclair *et al.* 2006), whereas in those cases where animals encounter sub-zero temperatures, but cannot survive beyond their freezing point, a threshold response is more common (figure 1). While low temperature responses can change form between years, they are usually constant within a species (Bale 2002).

Thermal performance curves for fitness-determining traits (e.g. locomotion rate or feeding rate) tend to be asymmetric, with a slow increase from the low temperature end and a close coincidence of the optimum and inhibitory temperatures towards the upper end (Huey & Kingsolver 1993; figure 1). Responses to factors such as limiting nutrients or other resources tend to take a threshold or asymptotic form (Sternler & Elser 2002; figure 1), as is typical of plants. In all of these cases, abundant evidence exists that one or more of these variables can alter survival, reproductive output and/or other components of fitness in the laboratory and field.

Not only are large-scale species distribution modelling approaches available that might incorporate such theoretically plausible environmental response forms (e.g. Kareiva *et al.* 1993; Kearney & Porter 2004; Crozier & Dwyer 2006; Austin 2007), but considering their likelihood, and which factors may be of most biological relevance, can also substantially enhance the modelling process. Moreover, envelope models (also known as habitat models; see Kearney 2006), which constitute a 'top-down' approach, can be informed by alternative biophysical models that are built 'bottom-up' from knowledge of the mechanistic bases of species responses to the environment (Graham &

Hijmans 2006). Indeed, a two-pronged strategy incorporating both niche and habitat models can substantially improve the prediction of species distributions (Kearney 2006). While it has long been argued that mechanistic models are too complicated, several studies have demonstrated that realistic models may be built in a straightforward manner (Kearney & Porter 2004; Crozier & Dwyer 2006). Moreover, macrophysiological studies of the large-scale partitioning of physiological tolerances have demonstrated strong phylogenetic signal in traits in several groups (Chown *et al.* 2002; Blomberg *et al.* 2003). In consequence, the forms of environmental responses may need to be estimated only for representatives of many taxa, not for all species (i.e. several clear 'rules' may apply).

Climate change

Changes in the planet's abiotic environment have always had major effects on the form and distribution of biodiversity. Forecasts of the effects of climate change have focused on the way in which species' ranges will be altered and how extinction is affected by rapid change and habitat loss (Thomas *et al.* 2004). The human health consequences of changes in vector distributions have been an especially significant and controversial component of these forecasts (Rogers & Randolph 2000; Terblanche *et al.* 2006).

Much of the modelling work is based on habitat models that seek to understand the present correlations among environmental factors and species abundances or distributions. The environment is then altered according to changes in the means and/or extremes of one or more environmental variables and the species' abundances/distributions are projected into the future. The successes of such approaches and their theoretical and empirical challenges are the subject of a large and rapidly developing literature (e.g. Guisan & Thuiller 2005; Thuiller *et al.* 2005; Hijmans & Graham 2006; Soberón 2007).

(a) Modelling species responses

Incorporating the form of the environmental response can improve the realism of models that seek to understand the responses of species to a changing environment (Helmuth *et al.* 2005; Austin *et al.* 2006). Moreover, the ways in which environmental variation affects species distributions may be more complicated than simple models of changes in means and extremes suggest. For example, Helmuth *et al.* (2002) have shown that in Pacific intertidal mussels *Mytilus californianus*, tidal regime, wave height and local climate interact such that sites which might otherwise have been considered relatively temperate are associated with greater thermal stresses than apparently much warmer sites.

In tsetse, *Glossina morsitans* and *Glossina pallidipes*, population dynamic investigations have demonstrated that high temperatures substantially increase daily instantaneous mortality rates (Hargrove 2004). Recent macrophysiological work has shown that a combination of direct high-temperature effects on survival and indirect effects via an increase in foraging-associated risk precipitated by elevated resting metabolic costs at high (but sub-lethal) temperatures are probably the source of the change in mortality rates (Terblanche *et al.* 2006).

Differences in the predictability and frequency of freeze–thaw events may also account for substantial variation, between the hemispheres, in the kinds of cold-hardiness response shown by insects (Chown *et al.* 2004b). Thus, freeze–thaw events tend to be unpredictable in timing and occur year-round in high latitudes of the Southern Hemisphere, whereas in continental high-latitude areas of the Northern Hemisphere temperatures decline below zero in winter and remain so for long periods. In consequence, Southern Hemisphere insects tend to retain moderate freeze tolerance with little preparatory cost all year-round. By contrast, many Northern Hemisphere insects lose their

cold tolerance in summer, and in winter tend to either cool to low sub-zero temperatures without freezing or show exceptionally strong freeze tolerance, both of which require costly physiological change. Global changes in the predictability of threshold events, such as freeze–thaw cycles, will have very different consequences from those associated with changes along a smooth unvarying logistic curve.

(b) Phenotypic plasticity, evolution and responses to change

The effects of changes in climate will depend on the extent of phenotypic plasticity in the environmental responses of organisms, their rate of evolution and the nature and form of spatial variation (or, in geostatistical terms, the non-stationarity) of both (Janzen 1967; Ghalambor *et al.* 2007). The spatio-temporal dynamics of populations are often excluded from the models of the impacts of climate change on distributions, despite the fact that populations clearly evolve in response to changing environments. For example, Stillman (2003) demonstrated that species of *Petrolisthes* porcelain crabs from cooler environments have the greatest capacity to adjust to high-temperature stress over the short term (i.e. population responses, which lead to changes in geographical distributions, will differ substantially among regions).

These, and other results (e.g. Loeschcke & Hoffmann 2007), suggest that biological impacts of temperature changes may be most profound in tropical rather than in temperate areas despite predictions for much smaller thermal changes in the former. Macrophysiology is confirming this idea. Relative invariance in the upper thermal limits of ectotherms at global scales suggests that in regions where operative temperatures often approach upper limits, i.e. in the tropics, climate change impacts on these organisms will be most severe (Compton *et al.* 2007; Deutsch *et al.* in press). In temperate areas, while distributions and phenology will change (Parmesan 2006), extinctions as a consequence of climate change *per se* may not be as widespread as they might be in the tropics.

The extent of these impacts will also depend on the extent to which winter temperatures warm relative to summer ones. Low winter temperatures will limit poleward range extensions in tropical ectotherm species. A larger increase in winter than in summer temperatures might provide areas of respite for tropical terrestrial ectotherms, provided that they could overcome barriers caused by habitat alteration. However, such increases may also have negative impacts by altering species energy balances (Irwin & Lee 2003). By contrast, recent macrophysiological work has demonstrated that upper and lower thermal tolerance limits are likely to be coupled in marine invertebrates and fishes because aerobic performance capacity sets the limits (Pörtner 2001).

Changes in the thermal environment have led, via this mechanism, to large-scale changes in species distributions and in the replacement of closely related species in ecosystems owing to their different thermal tolerance limits (Pörtner & Knust 2006). Moreover, because upper and lower limits covary, large-scale range displacements, rather than simple expansions and contractions, are likely to be common in marine systems (Parmesan 2006). A further area in which macrophysiology illuminates understanding of climate change concerns the probable significance of evolutionary responses to such change. Investigations of clinal variation in physiological traits combined with laboratory selection experiments can reveal which traits respond to directional selection.

For example, despite clinal variation in desiccation resistance, *Drosophila birchii* showed limited responses to selection (Hoffmann *et al.* 2003). In consequence, drying trends will have a profound impact on this species. In other cases, evolutionary responses may be more rapid and substantial (Huey *et al.* 2005; Umina *et al.* 2005) especially where this evolution is effected by genetic accommodation of plastic phenotypes (Ghalambor *et al.* 2007).

For example, heat stressing larvae of the moth *Manduca sexta* revealed a hidden reaction norm in coloration. Selection for this colour change resulted in the evolution of a colour polyphenism (Suzuki & Nijhout 2006). At present, the relative significance of physiological evolution (in the broadest sense) and of movement across the landscape of unchanging phenotypes is not clear. However, this question goes to the heart of several deeper issues.

In particular, (i) does most trait evolution occur during speciation events or between them, (ii) is the form of this evolutionary pattern variable among traits and taxa and (iii) how do spatial patterning and small-scale evolutionary dynamics of traits interact ultimately to determine the probable response (and its rate) of a species to environmental change? Both adaptation at range edges and the extent of plasticity are affected substantially by dispersal and the level of autocorrelation in environmental variability (Chown & Terblanche 2007).

In consequence, it is clear that dispersal ability (and its lability) will affect responses to changing environments not only by enabling or preventing animals from tracking changes therein (Hill *et al.* 1999), but also by altering the extent and rate of their short- and long-term responses to local change.

Invasive species

Among the most significant synergistic interactions driving biodiversity loss are those between habitat alteration and climate change, and climate change and species invasions (MA 2005). An increasing number of studies are concerned with the ways in which habitat fragmentation and alteration affect species' responses to climate change (e.g. Hill *et al.* 1999). By contrast, investigations of the interactions between climate change and invasion are less common, despite concerns that in many instances climate change might facilitate invasion and increase the impacts of invasive species (Hobbs & Mooney 2005). The latter concerns make one or both of two key assumptions.

First, invasive alien species have characteristics that set them apart from non-invaders so making them more responsive to warming and, in some regions, to the warming and drying characteristic of global change-type drought. Second, climate change might alter the balance of interactions among species such that invasion is facilitated (e.g. an increase in fire frequency and/or intensity) or particular invasive species come to dominate the functioning of a given system.

Baker (1965) suggested that invasive species show greater phenotypic plasticity and, in plants, are capable of autonomous self-fertilization when compared with non-invaders. Recent broad-scale macrophysiological assessments of performance in plants have failed to provide evidence for consistent differences in some traits, but have identified important differences in others. Pairwise performance comparisons of indigenous and invasive alien species revealed that the latter have lower tissue construction costs, higher leaf area and greater phenotypic plasticity than indigenous species (Daehler 2003), while they did not differ in growth rates, fecundity and competitive ability.

By contrast, comparison of the traits of South African irises that have naturalized elsewhere with congeners that have not naturalized revealed a higher probability of autonomous self-fertilization, lower levels of pollen limitation of seed set and faster germination rates in the former species (van Kleunen *et al.* 2008). The situation is more complex in animals (Agrawal 2001). One study concluded that introduced ascidians typically grew faster than indigenous ones at maximum summer temperatures.

Moreover, the introduced species showed earlier and more substantial recruitment with warm winter temperatures, while the indigenous species showed lower recruitment following warm winters and a recruitment date unaffected by temperature variation (Stachowicz *et al.* 2002). Another study demonstrated that warmer temperatures typically suppressed the abundances of indigenous alpine zooplankton, but had little effect on invading species from lower elevation sites (Holzapfel & Vinebrooke 2005). Although phenotypic plasticity may mediate the success of animals in new environments (Ghalambor *et al.* 2007), the outcome is often less straightforward.

For example, on sub-Antarctic Marion Island, indigenous and invasive springtails did not differ in the extent of their plasticity, but exposure to warmer temperatures promoted greater resistance to desiccation in the invasive species and precisely the opposite in the indigenous ones. This resulted in a significant negative response of indigenous species to warming and drying in the field, but no negative effects on the invasive species (Chown *et al.* 2007). In other species, it is not so much phenotypic plasticity that mediates the response to new environments, but rather strong selection for new specialized phenotypes (Huey *et al.* 2005).

Despite these examples, it is not clear whether invasive alien species and indigenous species show consistent performance differences. The scale of comparisons has, to date, been too narrow. The role of plasticity as a facilitator of evolutionary change (Ghalambor *et al.* 2007) is, however, significant because the very conditions that influence the likelihood of plasticity are those that have an influence on the extent of change that can be expected in marginal populations or those that find themselves in novel environments (Chown & Terblanche 2007). By explicitly focusing on large-scale comparisons within a phylogeographic context, macrophysiology can determine the probable significance of interactions between climate change and biological invasions at the species and population levels.

Overexploitation

One of the most significant developments in macrophysiology has been the debate about the mechanistic underpinnings of the scaling of life-history and physiological attributes and its implications for understanding the diversity of life across a range of hierarchical levels (Brown *et al.* 2004; Makarieva *et al.* 2005). This issue has revitalized an interest in how and why physiological and life-history traits are related to body size and temperature. It is these strong relationships, especially within higher taxa, which reveal profound, but neglected, macrophysiological impacts of overexploitation: the erosion of large areas of physiological phenotypic space.

At both the inter- and intraspecific levels, overexploitation has resulted in a reduction in the size of the targeted organisms. Perhaps the most widely recognized of humankind's effects on diversity has been the removal of large-bodied species from the terrestrial landscape: as a consequence of overexploitation most continents no longer house the very large grazers and predators they once did (Jablonski 2007). Where very large animal species still occur, such as in Africa, their abundance is much reduced (Skead 2007), and they are frequently restricted to relatively small managed areas.

Moreover, in human-dominated systems, even comparatively small, large-bodied species are no longer present. In marine systems, large whale, fish and turtle species are in decline as ever lower levels in the marine food web are targeted to satisfy human resource demands. The resulting environmental problems are often not recognized as originating from the removal of large-bodied species (Jackson *et al.* 2001). At the intraspecific level, similar targeting of large individuals has been common. In many commercially exploited fish species, mean body size has declined dramatically over the past several decades (Sibert *et al.* 2006; Olden *et al.* 2007).

Similar declines in the mean body size of mammal species have been recorded, and especially of the horn-bearing males that are of most interest to trophy hunters (Coltman *et al.* 2003). Large trees have also been targeted, and it is common now to find particular individuals known and protected simply for their large size and antiquity (The Tree Register 2006, <http://www.treeregister.org/index.html>).

By removing large species and individuals, and by reducing their abundances, overexploitation has substantially reduced the range of physiological phenotype space once covered and has selected for a radically different suite of life histories (Kuparinen & Merilä 2007). In consequence, unique physiologies typical of larger species and individuals are threatened. These include regional heterothermy as found in fish species such as tuna (although apparently not all tuna populations are overexploited; Sibert *et al.* 2006), the capacity for the use of low-quality plant material such as in large herbivorous mammals and the resilience to overcome prolonged periods of resource deprivation that is a characteristic of the larger individuals of many species (because storage capacity rises more steeply with mass than maintenance metabolism).

The latter change makes clear that the erosion of physiological phenotypic space is not only intrinsically worrying, but will also have profound consequences for the ways in which plants and animals respond to other forms of environmental change over the short and long term. Increases in the variability of climatic conditions are forecast under most global climate change scenarios (Easterling *et al.* 2000). In many taxa, strong relationships exist between the tolerance of stressful conditions and body size. Likewise, large active dispersing organisms tend to have greater dispersal capacities than do smaller ones, whereas for passive dispersing organisms no clear relationship with mass exists (Jenkins *et al.* 2007).

Dispersal is not only a key factor determining survival of habitat fragmentation, but also plays a significant role in influencing adaptation to new environments and the likelihood and extent of plasticity (Chown & Terblanche 2007). In consequence, the loss of large-bodied individuals and species will reduce tolerance to variable environments and result in a loss in the capacity of systems to recover from or resist perturbation via either fragmentation or increases in temporal variability of abiotic conditions.

Large and small individuals also play different functional roles in food webs (Cohen *et al.* 2005), suggesting that the removal of the large-bodied will lead to trophic restructuring, even though the species may not have been removed from the system. It is by understanding the interactions between body size, life history and functioning over large spatial and temporal scales that macrophysiology can help assess the impacts of overexploitation and complement other investigations of the same issue, as well as draw attention to its significance even where extinction is not an outcome.

Pollution

(a) Pollutants

Organic and heavy metal pollutants impact biodiversity. Comparisons across many taxa and environments led to an early appreciation that persistent organic pollutants (POPs) are especially damaging. While not recognized as such, these studies were clearly macrophysiological in their approach. Although the global effects of POPs and heavy metal contamination are being documented (Finizio *et al.* 1998), it is less clear what their effects are at broad spatial and temporal scales.

Valuable as they are, smaller scale studies could usefully be complemented by investigations of larger scale variation in impacts and synergies with other global change drivers. For example, a tension exists between the pollutant effects of anti-fouling treatments and the likelihood of marine invasions via hull fouling (Minchin & Gollasch 2003), especially where that fouling takes place in recessed areas (such as ship's sea chests) that are conducive to organism survival and reproduction.

Clearly, ships move invasive species around, and innovative large-scale investigations are needed to inform changes in anti-fouling regimes. Similarly, broad-scale tolerance studies are beginning to show that invasive marine species, such as bryozoans, demonstrate resistance to anti-fouling treatments, even to chronic exposure to these pollutants, so increasing the likelihood of unintentional dispersal (Piola & Johnston 2006). Finally, the global relationships between endocrine disrupting compounds, other pollutants and changes in food webs remain unclear despite their obvious significance (Guillette 2005). Macrophysiology has much to offer owing to its explicit large-scale comparative approach.

(b) Nutrient enrichment and elemental ratios

Global-scale investigations of elemental ratios in the environment and within organisms have a long pedigree and can be considered among the earliest macrophysiological studies (e.g. Redfield 1958). Human perturbations of these stoichiometric relationships are having profound effects on biodiversity. Changes in carbon availability have enjoyed most attention because carbon dioxide is one of the most profound drivers of anthropogenic climate change. However, increasing carbon levels will also have less obvious effects, and the increases in N and P as a consequence of fertilizer production are already having major impacts (Sterner & Elser 2002). In marine systems, for example, declining pH as a consequence of increasing atmospheric CO₂ is predicted to cause major change across many levels in the biological hierarchy.

How organisms respond, especially to reduce impairment of calcification or dissolution, how such responses vary over large scales (Orr *et al.* 2005) and how this variation will influence the impacts of ocean acidification are unanswered macrophysiological questions. In terms of C:N:P ratios, human activities have altered not only the absolute availability of P and N but have also increased their abundance relative to C. Moreover, they have differentially accelerated global cycles in all of the most significant biological macroelements (Falkowski *et al.* 2000). The broad-scale effects of these changes are likely to be profound and difficult to predict (see Karnosky *et al.* (2003) and Cassar *et al.* (2007) for examples). Nonetheless, it is clear that if the influences of pollution on biodiversity are to be comprehended, then dedicated investigations of stoichiometric variation at broad spatial scales will be required (Sterner & Elser 2002, p. 364; Phoenix *et al.* 2006).

Conclusions and challenges

Ehrlich (1997) made it clear that ecologists cannot afford to devote their time only to the questions that pique their intellectual curiosity. He argued that they should also be concerned with work that will mitigate the profound effects that humans have on the living world, and with educating society about the need for environmental conservation. The same message applies to physiologists. Here, we have demonstrated that macrophysiology not only can make substantive contributions to the understanding of and the prospects for mitigating the effects of global environmental change on biodiversity, but also that much remains to be done.

Nonetheless, macrophysiology faces several challenges. For example, how multiple changing abiotic factors interact to limit responses to change is far from clear. Typically, studies are concerned with phenotypic plasticity or rates of evolutionary change in one physiological variable, while investigations of the genetic architecture of life-history variation have shown how constrained the evolution of particular traits can be. Likewise, for no single species is there yet a comprehensive understanding of what limits its geographical range (rather than what influences a single border of the range; Gaston 2003). By overcoming these problems and addressing questions of the kinds we have outlined, physiologists can meet some of humankind's most pressing challenges. It is here that macrophysiology will have its most important role.

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