Macrophysiology – progress and prospects

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Summary

1. Macrophysiology is the investigation of variation in physiological traits over large geographic and temporal scales and the ecological implications of this variation. It has now been undertaken, as a defined field, for a decade.

2. Here we overview its conceptual foundations, methodological approaches and insights, together with challenges the field is facing currently.

3. Macrophysiology builds on approaches that investigate the ecological and evolutionary significance of physiological trait variation and feedbacks in these processes. One of its key strengths is its ability to provide a basis for examining interactions among the intraspecific, interspecific and assemblage levels.

4. Macrophysiology is distinct from and typically concerns larger spatial and temporal scales than conservation physiology, whereas it is in several respects similar to, but antecedes functional biogeography. Contrary to some claims, macrophysiology is not concerned only with the implications for geographic ranges of physiological trait variation.

5. Several insights, which would not otherwise have been achieved, have arisen from the field, notably the understanding of variation in global patterns of upper and lower lethal temperature limits and organism performance, which have important implications for forecasting the impacts of climate change.

6. Ten major challenges are identified for the field of macroecology, including better integration of approaches and information for plants and animals. Nonetheless, the prospects for macrophysiology as a significant way to understand our world remain bright.
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Introduction and context

August Krogh’s (1929) seminal work on the progress of physiology is best known for a single sentence. ‘For a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied.’ The original idea was narrowed and enshrined as the August Krogh principle by Krebs (1975). This has since fostered much discussion (Jørgensen 2001; Sanford, Lutterschmidt & Hutchison 2002), some of it contracting Krogh’s views even further (Feder & Watt 1992; Strange 2007). Less widely appreciated is the paragraph preceding Krogh’s now famous remarks. Here he wrote ‘…I want to emphasize that the route by which we can strive toward the ideal is by a study of the vital functions in all their aspects throughout the myriad of organisms’. The general view that comparative physiology is insightful certainly inspired much research (e.g. Prosser 1955, 1991; Hochachka & Somero 2002), and continues to do so, despite an influential proposal in the late 1980s that it should not (Feder 1987). The benefits of this endeavour shine through in expanding knowledge of physiological diversity, its mechanistic basis, evolutionary dynamics and ecological importance.

Nonetheless, for a variety of widely discussed reasons (Huey 1991; Spicer & Gaston 1999; Gaston et al. 2009), the kinds of multi-population and multi-species physiological assessments common in early comparative physiology were eclipsed by other pursuits. Although physiological ecology (or comparative physiology or ecological physiology) continued to be undertaken by many research groups, with several enduring insights (e.g. Janzen 1967; Brattstrom 1968; Calow 1977; McNab 1980; Huey & Hertz 1984; Huey & Kingsolver 1993), broad-scale comparisons became less common. This was in keeping perhaps also with a smaller scale ecological focus that was common throughout the 1960s to 1980s (Lawton 2000).
The situation changed markedly in the last decades of the 20th Century for several reasons. New approaches to understanding the evolution of physiological diversity, in part stimulated by critical assessments of the field (Feder et al. 1987; Lawton 1991), were encouraging renewed interest in comparisons of multiple species and populations (Garland & Adolph 1991; Spicer & Gaston 1999; Porter et al. 2000). Appreciation of scaling effects in ecology (Ricklefs 1987; Wiens 1989) and the establishment of macroecology (Brown & Maurer 1989; Gaston & Blackburn 2000) also had a significant influence. Early in the development of macroecology it became clear that several of its main ideas rested on assumptions about the nature of physiological variation, be they about spatial variation in physiological tolerances or rates, or about interactions between body size, physiological rates, and abundance (see Brown & Maurer 1989: 1146; Stevens 1989 for examples). Growing availability of information technology, such as database and geographic information systems, along with global digital datasets on the abiotic environment (e.g. on climate variables and productivity), also meant that physiological information could more easily be compiled and analysed in a broad-scale environmental context (Addo-Bediako, Chown & Gaston 2000; Chown, Addo-Bediako & Gaston 2002).

In 2004 we published an extended editorial in *Functional Ecology* (Chown, Gaston & Robinson 2004), which argued that much common ground existed between several areas of investigation concerned with large-scale physiological variation and its implications, and which at the time were all gaining momentum. These included the physiological mechanisms underpinning macroecological patterns, the partitioning among species and populations of physiological trait variation both in assemblages and phylogenetically, the allometric scaling of various physiological attributes, and the investigation of variation in traits over large spatial and long temporal scales to understand the mechanisms underlying physiological diversity. We considered the underlying conceptual foundations and empirical approaches in
these areas sufficiently related to each other, and distinct from other areas of biology, that
they should be identified as part of an integrated field we named ‘macrophysiology’. We
defined the field as ‘the investigation of variation in physiological traits over large
geographic and temporal scales and the ecological implications of this variation’.
Macrophysiology has subsequently gained substantial traction, with several works
demonstrating how it provides insights that would otherwise not have been achievable
(Osovitz & Hofmann 2007; White et al. 2007; Cooke & Suski 2008; Huey et al. 2009;
Bozinovic, Calosi & Spicer 2011; Ellis, McWhorter & Maron 2011; Sanford & Kelly 2011;
Sunday, Bates & Dulvy 2011; Tuck & Romanuk 2012; White, Alton & Frappell 2012; Clarke
& O’Connor 2014; Khaliq et al. 2014). As part of its growth we showed how
macrophysiology can contribute to understanding and mitigation of the biodiversity impacts
of several major drivers of global environmental change (Chown & Gaston 2008) and, along
with many colleagues, highlighted how a range of key questions in ecology and physiological
ecology could be addressed in fresh ways by adopting the perspectives inherent to the field
(Gaston et al. 2009; Chown et al. 2010).

In the decade that has passed since we set out our original views, much progress has
been made in many of the areas encompassed by macrophysiology. An urgent focus on
understanding and mitigating the biodiversity impacts of environmental change, especially
from anthropogenic modification of the planet’s climate, has been one of the major factors
giving impetus to the field. Rapid developments in phenotyping and ecoinformatics
(Michener & Jones 2012), the growing availability and quality of global scale data on present
and past climate (e.g. Hijmans et al. 2005; Sandel et al. 2011; Kearney et al. 2014; Wang &
Dillon 2014), rapidly expanding compilations of physiological and other trait data from a
range of organisms and ecosystems (Clusella-Trullas, Blackburn & Chown 2011; Sunday,
Bates & Dulvy 2012; Yvon-Durocher et al. 2014; Atkin et al. 2015), and to a lesser, but
nonetheless important, extent genomics (e.g. Peck 2011; Chen et al. 2012; Porcelli et al. 2015), have similarly helped to promote progress in the area. Metabolic ecology and debates about the various approaches that are best suited to its understanding (Brown et al. 2004; White & Kearney 2014) have in some ways grown alongside macrophysiology. Their paths have crossed repeatedly, but perhaps not consolidating in ways we initially envisaged, given our view that metabolic ecology is about physiological variation and its ecological implications. Several alternative perspectives on physiological trait variation and its implications have also been offered, with the view by some that they encompass macrophysiology so rendering it a small part of a larger whole (e.g. Violle et al. 2014). Here we therefore provide an overview of the current status of macrophysiology, highlight several of the significant insights it has delivered, identify where progress has been slow, and set out what we think is its future and the challenges it faces.

**Conceptual and methodological developments**

Macrophysiology encompasses both a conceptual foundation and a suite of empirical approaches for understanding the ecological implications of physiological trait variation. Conceptually, it recognizes that the state of any given trait in a specific population depends on the shorter and longer term nature of environmental variation experienced by the population, the nature of the trait and its genetic context, and the extent to which migration and other factors, such as interspecific interactions, might affect trait variation (Chown & Terblanche 2007) (Fig. 1). Thus, it relies on, and can contribute to, those aspects of evolutionary biology which seek to understand the evolution of trait variation and its plasticity, and the demographic consequences thereof (e.g. Levins 1974; Kingsolver & Gomulkiewicz 2003; DeWitt & Scheiner 2004; Angilletta 2009; Latimer et al. 2014).

Macrophysiology explicitly requires the simultaneous consideration of multiple populations,
and in this sense remains somewhat underexplored because of the constraints of so doing (see discussions in Chevin, Lande & Mace 2010; Chevin, Collins & Lefèvre, 2013; Aguirre et al. 2014; but see also the reviews by Sanford & Kelly 2011 and Sinclair, Williams & Terblanche 2012).

The field also builds on evolutionary understanding of trait variation among species (reviews in Garland & Carter 1994; Feder, Bennett & Huey 2000), and in particular how such variation arises due both to macroevolutionary and macroecological processes (Gaston et al. 2009), reflecting interest in the decomposition of trait variation into its spatial and phylogenetic components (e.g. Kellermann et al. 2012a,b). Somewhat unusually, for physiology at least, its conceptual foundations are also concerned with the processes that give rise to the variation associated with the composition of species assemblages (Gaston et al. 2009). Here it is most allied to considerations of the ecological significance and origins of trait variation in assemblages, a feature identified in the original discussion of the field (Chown et al. 2004). However, much of the progress in this area has not explicitly been associated with macrophysiology (Shipley, Vile & Garnier 2006; Ackerley & Cornwell 2007; Webb et al. 2010; Reich 2014), perhaps reflecting also a long-standing, and periodically lamented (Rubinstein 1992; Huey et al. 2002; van Kleunen 2014), lack of coherence in the literatures on trait variation in plants and animals.

The empirical approaches adopted in macrophysiology arise from these foundations, providing spatially, temporally, and phylogenetically explicit ways to explore the field’s major questions. A key strength of macrophysiology is its ability to provide a basis for examining interactions among the intraspecific, interspecific and assemblage levels (Fig. 2), and for teasing apart what could be called, at the macroecological level, entry rules, exit rules, and rules of transformation (Gaston et al. 2009). These are, respectively, biases in the processes that determine which individuals or species join a population or assemblage
through immigration or speciation; biases in the processes that determine which leave a population or assemblage through emigration or extinction; and changes caused by environmentally induced or genetically based processes, such as shifts in resource profiles, behaviour or tolerance, that act on individuals or species when they are members of a particular population or assemblage. The spatially explicit nature of macrophysiology means that it can inform several other approaches, including mechanistic niche modelling (Kearney & Porter 2009) and spatially explicit population dynamic models (see discussion in Chown 2012). It is also closely allied to other perspectives, such as solutions to what has been termed the fourth corner problem in ecology (Dray & Legendre 2008; Brown et al. 2014) (Fig. 2).

Although investigations in some of these areas seem almost routine now, as do manipulations of various kinds of data matrices, such as species by species phylogenetic or interaction matrices (Ulrich, Almeida-Neto & Gotelli 2009; Jetz et al. 2012; Rudolf et al. 2014), species by trait matrices (Dray & Legendre 2008), and matrices of species occurrence (Bell 2003; Gaston & He 2010; Hui & McGeoch 2014), a key early innovation of macrophysiology was the recognition that much understanding would come from examination of physiological traits in the explicit Species X Sites approach previously applied typically to ecological questions (Gaston, Chown & Evans 2008; Gaston et al. 2009). This has certainly proven to be the case as we demonstrate below, though a recent example illustrates the point succinctly. Valladares et al. (2014) explored the way in which explicit examination of intraspecific variation in phenotypic plasticity and the thermal niche can be used to improve forecasts of species responses to environmental change. They used both theoretical and empirical approaches in a spatially explicit context to reveal the importance of considering intraspecific variation for forecast models.

Several recent studies have, by contrast, either suggested that macrophysiology can be subsumed within a broader area or have sought substantially to narrow its scope. To some
extent, the former will always remain true – macrophysiology is clearly a subset of biology, in turn a subset of science, and in turn again a subset of the ways in which we derive reliable knowledge (Ziman 1978). But the rise of conservation physiology (reviewed in Cooke et al. 2013), with a dedicated journal, and of functional biogeography (Violle et al. 2014), which is a much more recent idea, both deserve explicit attention.

Conservation physiology was originally defined as ‘the study of physiological responses of organisms to human alteration of the environment that might cause or contribute to population declines’ (Wikelski & Cooke 2006), and later broadened by Cooke et al. (2013) to ‘an integrative scientific discipline applying physiological concepts, tools, and knowledge to characterizing biological diversity and its ecological implications; understanding and predicting how organisms, populations, and ecosystems respond to environmental change and stressors; and solving conservation problems across the broad range of taxa (i.e. including microbes, plants, and animals’)’. What the expanded definition of conservation physiology has done is more explicitly outline many of the questions with which comparative physiology has long been concerned (e.g. Feder et al. 1987), but now broadens its remit to ecosystems and solving conservation problems, in line with the original thinking. Nonetheless, in practice, much of the focus has remained on vertebrates and on stress responses (often to do with glucocorticoids). Research on plants and invertebrates has contributed less than 20% of papers, in each case, according to a recent analysis (Lennox & Cooke 2014), and little work has been done on plants in particular (van Kleunen 2014). Clearly, the approaches of macrophysiology can be applied to conservation questions (Chown & Gaston 2008; Chown 2012), and a variety of approaches can be adopted to understand physiological diversity, but the key difference between conservation physiology and macrophysiology is the explicit large-scale, long-term foundation of the latter. Indeed, these differences are recognized by a
recent work recognizing the benefits to be had from combining the approaches (Ellis et al. 2012).

Functional biogeography is defined as ‘the analysis of the patterns, causes, and consequences of the geographic distribution of the diversity of form and function—namely, trait diversity’ (Violle et al. 2014). The proponents of the idea explicitly acknowledge that describing and accounting for large-scale variation in form and function has long been a scientific endeavour, with macrophysiology being key to doing so. They argue that functional biogeography pursues exactly the same goal, linking large-scale patterns in trait diversity to biogeographical patterns of species diversity, ecosystem functioning and ecosystem services (particularly given current global conservation concerns). In several ways (see specifically the definition in Violle et al. 2014: Fig. 1), functional biogeography is a junior synonym of macrophysiology. Indeed, Violle et al.’s (2014) Figure 3 is conceptually very similar to those produced in previous macrophysiological works (e.g. Chown et al. 2010; Chown 2012). The key difference between the two approaches, as revealed by Violle et al.’s (2014) Figure 1, is, however, the inclusion within the ambit of functional biogeography of most other aspects of biology. The three tenets of the field, set out in the work’s Figure 2, are also not unique to it, but are characteristic of all fields of science (‘describe, explain, predict’; we assume that experimental approaches to description are implied).

Conversely, restriction of the scope of macrophysiology has largely come from recent characterizations of the field by Gouveia et al. (2014). They set out by redefining macrophysiology as ‘a field that aims to describe the general properties between individuals’ endurance of environmental conditions and the geographical patterns of distribution of their species’. Subsequently they also suggest that a ‘holy grail’ of macrophysiology has been the extent to which physiological tolerance limits describe geographic range limits and vice versa. Both cases, but especially the former, are fallacies of composition. Several studies
have indeed sought to explain these relationships, and can rightly be considered macrophysiological (e.g. Gaston 2003; Lee et al. 2009; Calosi et al. 2010; also Bozinovic et al. 2011), but they form a subset of the much broader field that is macrophysiology (see above and Chown et al. 2004; Gaston et al. 2009). More difficult to interpret is Gouveia et al.’s (2014) aim to demonstrate the misleading nature of the idea that ‘macrophysiology is an effective measure of physiological tolerance’. The difficulty arises from an ontological category error (Ryle 1949). Macrophysiology belongs to a category of human approaches to understand the world, whereas physiological tolerance belongs to a category of physical properties of a given individual, population, species or larger grouping of organisms.

Gains in understanding

One of the most significant achievements in macrophysiology has been to reveal a range of patterns of physiological traits, their likely underpinnings and the implications of this variation. Our aim here is not to catalogue all of these discoveries, but to draw attention to the diversity of areas in which these gains in understanding, and indeed in forecasting, have been made.

In the case of body temperature, for example, Clarke & O’Connor (2014) demonstrated significant differences between diet groups for mammals, and a curious triangular relationship between body temperature and environmental temperature (Fig. 3A).

In further exploring the situation among other vertebrates, they concluded that evidence for an overall association between herbivory and high body temperature in vertebrates is strong enough for it to be regarded as a useful macrophysiological generalization. Staying with mammals and aspects of nutrition, Naya, Bozinovic & Karasov (2008) demonstrated increasing phenotypic plasticity in the length of the small intestine of rodents with latitude (Fig. 3B), arguing that it may well be a consequence of greater climatic variability at higher
latitudes. Similar evidence for latitudinal variation in phenotypic plasticity was found for fat body seasonal size differences (Fig. 3C) across 59 species of reptiles (Aguilar-Kirigin & Naya 2013).

Perhaps the most extensive investigation of global variation in plasticity, a frequently significant component of organismal responses to temperature change, has come from an assessment of changes in the Q_{10} (or change in rate with a 10°C change in temperature) of various rates in marine, freshwater and terrestrial groups (Seebacher, White & Franklin 2015) (Fig. 3D). The outcome supported previous, smaller-scale findings that phenotypic plasticity tends to be reduced in stable marine environments compared to more variable ones (Pörtner 2002), and that in terrestrial species, animals from warm environments are less sensitive to longer-term temperature change than those in cooler ones. The study has important implications, especially since it bears out the findings of an earlier investigation of terrestrial ectotherms demonstrating that climate change has significantly increased metabolic costs, as a consequence of acute rate-temperature relationships, particularly in tropical and Arctic species (Dillon, Wang & Huey 2010).

In their study, Dillon et al. (2010) also demonstrated significant differences in changes to ectotherm metabolic rates for the south temperate and north temperate regions, owing to differences in the way changes in ambient temperature had proceeded since 1980. These physical differences have long been known to be a consequence of the arrangements and proportion of land in the two hemispheres. What macrophysiology has revealed is that these physical differences have led to pronounced differences in physiological responses across the hemispheres, including a steeper relationship between latitude and the metabolic rate-temperature relationship of insects in the northern than in southern hemispheres (Irlich et al. 2009); a preponderance of moderate freeze tolerance in southern high latitude insect species, and of freeze avoidance in northern high latitude species (Sinclair, Addo-Bediako &
Chown 2003); and differences in the cold tolerance and proportions of winter deciduous species among plants (Woodward 1987; Magarey, Borchert & Schlegel 2008). These differences in spatial patterns among traits, or their proportions in given areas, extend to life history characteristics and to broader ecological patterns, such as the relationships between species richness and available energy, and the extent of cooperative breeding in birds (Chown et al. 2004; Jetz, Sekercioglu & Böhning-Gaese 2008; Jetz & Rubenstein 2011). In part they may be driven by the specific circumstances of particular continental regions (such as Australia, see e.g. Orians & Milewski 2007). Nonetheless, many broad-scale investigations do not seek to determine whether patterns to the north and south of the tropics either differ or are similar.

Much effort in the field has been expended on understanding large-scale variation in the parameters of what might broadly be termed thermal performance curves (Angilletta 2006), though the nature of the relationship between temperature and performance varies widely among plants, animal ectotherms and endotherms (Berry & Björkman 1980; McNab 2002; Angilletta 2009; Way & Yamori 2014; Atkin et al. 2015). Investigations pre-dating the development of the field had suggested several patterns might be general (summarized in Gaston et al. 2009: Table 1), including two on which we focus here. These are less geographic variation in upper than lower thermal limits (Brett 1956), and an increase in thermal tolerance range with latitude, but not in marine groups (Janzen 1967; Prosser 1986). Several studies have now shown that upper thermal tolerance limits, measured either as lethal temperatures or as critical thermal limits to activity, vary less, geographically, than do lower ones, in a wide variety of plants and ectotherms (Gaston & Chown 1999; Addo-Bediako et al. 2000; Clusella-Trullas et al. 2011; Sunday et al. 2011; Buckley, Hurlbert & Jetz 2012; Araújo et al. 2013; Hoffmann, Chown & Clusella-Trullas 2013), though the extent to which these differences are realized varies among sexes, species, higher taxa and among
environments (Hoffmann, Sørensen, & Loeschcke 2003; Calosi, Bilton & Spicer 2007; Kellermann et al. 2012a,b). In marine environments, upper and lower limits are more closely coupled than in terrestrial ones (Sunday et al. 2011), even though the extent to which this difference is realized varies among groups (Hoffmann et al. 2013). Strong phylogenetic signal is typically present where it is sought, and several studies are now starting to partition the relative contributions of phylogenetic and geographic signal to trait variation (Kellermann et al. 2012a,b; Grigg & Buckley 2013). At least some of the differences among traits and their geographic variation may be attributable to the measurement and analytical approaches used for collecting and comparing the data. These are the subject of much present discussion (Terblanche et al. 2007, 2011; Chown et al. 2009; Rezende, Tejedo & Santos 2011; Santos, Castañeda & Rezende et al. 2011; Rezende & Santos 2012; Allen, Clusella-Trullas & Chown 2012; Overgaard, Kristensen & Sørensen 2012; Rezende, Castañeda & Santos 2014; van Heerwaarden & Sgrò 2014), a point to which we return. In endotherms, similar patterns of limited variation in upper compared with lower limits have been found (with a less pronounced pattern for mammals) (Araújo et al. 2013; Khaliq et al. 2014), but these have been estimated using the upper and lower critical temperatures of the thermoneutral zone derived from measurements of metabolic rate across a variety of temperatures (see e.g. Rick & Geiser 2013). In consequence, they differ substantially from the critical thermal limits typically measured in ectotherms (Angilletta 2009 provides a recent review of these).

Strong relationships between upper critical temperatures and optimum temperature (or the temperature at which a given rate is maximized) have long been known (Huey & Kingsolver 1993). Several recent works have also demonstrated, however, that much variation exists in how these traits are related to the environment, and how maximum rate of performance varies with the temperature at which that rate is maximized. In the first case, for example, across reptiles globally, critical thermal maximum is most strongly related to
diurnal temperature range, while optimum temperature (in this case measured as preferred
temperature – the two are often, but not always, closely related) is most strongly related to
precipitation (Clusella-Trullas et al. 2011). Subsequent work has revealed that upper critical
temperatures are also related to precipitation in Drosophila (Kellermann et al. 2012b). In the
second case, several investigations have revealed a positive relationship between the
maximum value of a given rate function at its optimum (such as running speed, metabolic
rate or growth rate) and the temperature of that optimum (Frazier, Huey & Berrigan 2006;
Angilletta, Huey & Frazier 2010). In consequence, while ectothermic animals show some
ability to compensate for reduced temperatures, that compensation is incomplete and comes
at a cost, which is reduced performance at the lower temperatures. This so-called
thermodynamic effect also shows up in variation among C3, C4 and CAM photosynthetic
pathways (Yamori, Hikosaka & Way 2014) (Fig. 4A).

Several key lessons have emerged from these findings, some of which have been
taken up in global conservation policy such as the assessment reports of the
Intergovernmental Panel on Climate Change (IPCC 2014). Most prominent among these is
the suggestion that tropical species may be at more risk from global temperature change than
those in temperate regions owing to a reduced warming tolerance (the difference between
critical thermal maximum and habitat temperature) and reduced thermal safety margin (the
difference between the optimum temperature and habitat temperature) (Deutsch et al. 2008;
Huey et al. 2009). Subsequent works have suggested that subtropical species may be equally
at risk or perhaps more so (Clusella-Trullas et al. 2011; Hoffmann et al. 2013), while others
have suggested that owing to the specifics of the taxon concerned, species from temperate
areas may also be at risk (Hoffmann 2010; Overgaard, Kearney & Hoffmann 2014). Much
attention is now being focussed on these findings, with new assessments suggesting that
because thermal safety margins are already negligible or have been exceeded in many
tropical species, behavioural regulation must play an important role in mediating these effects (Sunday et al. 2014). Likewise renewed focus is being given to the significance of microclimate variation and how this may change estimates of safety margins and the demographic consequences of changing environmental conditions (Woods, Dillon & Pincebourde 2015). Other work has suggested that owing to a closer fit between thermal tolerance and latitudinal range in marine than in terrestrial ectotherms, range shifts in marine species will be more predictable and coherent than those of terrestrial ectotherms (Sunday et al. 2012). Such a finding has pronounced implications for environmental change forecasts, though the extent to which this coherence is realized for marine species is now under scrutiny (Faulkner et al. 2014). As a final example, Araújo et al. (2013) showed that differences between the actual physiological limits and those estimated from species range data and associated spatially explicit climatic variables can lead to substantial biases when predicting climate change impacts on species, inferring rates of niche evolution, or assessing invasion risk.

Further key findings include the significance of changes in winter temperatures for organismal responses to climate change (Williams, Henry & Sinclair, 2015). Warming winter temperatures may have profound fitness costs for organisms owing to elevated temperatures, which raise metabolic rates and thus deplete reserves (see also Williams, Shorthouse & Lee 2003). A similar outcome may be found in urban heat island environments (Chown & Duffy 2015). By contrast, in some regions, changing weather system patterns are increasing the frequency of cold exposures, over the short term anyway (e.g. Lee et al. 2009; Crimp et al. 2014). In turn this may likewise affect populations, and economic benefits derived from them (Zheng et al. 2015), though plastic and adaptive responses to low temperature tend to be less constrained than those to higher temperature.
The value of macrophysiological insights with respect to organismal responses to climate change seems more an indication of the potential of the field than something particular about this anthropogenic environmental pressure, other than its pressing significance. With appropriately focussed research, it is not difficult to envisage helpful contributions on a similar scale also being made in the context of other environmental change challenges, such as ocean acidification, overexploitation and invasive species (Chown & Gaston 2008; Godblod & Calosi 2013). Indeed, it is instructive that the recent mainstream recognition of the global significance of the environmental impacts of artificial nighttime lighting (including, but not exclusively, from street lighting), has led rapidly to the conclusion that the establishment of some key macrophysiological patterns is essential to rapid progress in understanding (Gaston et al. 2013, 2014). This includes the need to determine the responses of a wide diversity of species to nighttime lighting of different intensity and spectra, and how these responses might change spatially and temporally (Davies et al. 2013; Gaston et al. 2015).

**Challenges**

Reliable knowledge proceeds from science in several ways. A repeated process of conjecture and refutation is important among them (Medawar 1982). In consequence, controversy about key macrophysiological ideas is a healthy sign that the field is developing. It also reveals those areas where critical challenges lie (Table 1).

Perhaps one of the most significant of these is also that with the longest history – how much might be relied on the signal from large-scale comparisons of data originally collected to serve one, usually smaller-scale, purpose and now being put to a very different use? In other words, can small-scale physiological data often used to investigate the responses of one or a few populations or species to the environment, and collected in sometimes very different
ways, be drawn together to unveil new patterns which are reliable? The point was raised in
perhaps the most substantial detail by Hodkinson (2003) in response to work on latitudinal
variation in metabolic rates and their sensitivity to temperature (Addo-Bediako, Chown &
Gaston 2002). His comments would strike a chord with many today: ‘Their particular meta-
analysis requires huge simplification and extrapolation from limited data sets, which
undermines the veracity of their conclusions. It is based on a restricted knowledge of the
organisms involved and of the limitations of the data sets used. Furthermore, the
appropriateness of the comparative procedures employed is questionable. Metabolic
processes in cold-adapted species are not simple and often, when studied in detail, prove
highly subtle and species specific. This subtlety makes realistic comparison of different
species across latitudinal or altitudinal thermal gradients difficult. Are we truly comparing
like with like?’

At the time we responded to all of these questions, and to the specifics of the critique
(Chown, Addo-Bediako & Gaston 2003). The key question is whether, as we noted, there are
‘…patterns that will be revealed by averaging out the details in a broad-scale analysis.’ Much
of the work we have described in preceding sections suggests this is the case, and in
particular studies which bear out some of what we have called macrophysiology’s ‘rules’
(Gaston et al. 2009). The ways in which such matters of scaling can be addressed through the
integration of fine filter and coarse filter approaches have also been cogently laid out in the
context of the application of physiology to conservation challenges (Cooke & O’Connor
2010). Nonetheless, Hodkinson (2003) raised several points which are the subject of growing
discussion. The importance of microclimate and the nature of the climate variables used in
any analysis is a notable example (e.g. Storlie et al. 2014; Woods et al. 2015). It is
unsurprising that climate variables typically obtained directly or indirectly from a standard
weather station (including temperature recorded in a Stevenson Screen), do not tell the full
picture for a 25 g bird (such as a house sparrow), let alone an 18 μg soil-dwelling springtail. Standard weather stations were initially designed by and for the conditions likely to be experienced by a ca. 70 kg mammal. Indeed, biophysics had long been concerned with how to make measurements of animal or plant temperatures at the relevant scales (see reviews in Campbell & Norman 1988; Bonan 2002).

For macrophysiology, the problem originally was that the information required for such detailed analysis was not available for most species, nor indeed, were any comparative climate parameters at the microclimate level. Analyses were undertaken with the available data and, in many cases, this is still being done (reflected by the popularity of Hijman et al.’s (2005) data set in many investigations across ecology and physiology). Only now are microclimate data becoming available at global scales (Dillon et al. 2010; Kearney et al. 2014) that enable exploration of many of the nuances that may be important, such as the roles of behaviour and changes in daytime versus nighttime temperatures, or those among seasons (Sunday et al. 2014; Wang & Dillon 2014; Zhao et al. 2014). These data are revealing that some generalizations may need to be further considered (such as thermal safety margins in the tropics), and this is exactly the kind of progress the field should experience.

Nonetheless, what will remain a significant challenge are the kinds of data that will show how individual species might respond to an extremely variable microenvironment (Woods et al. 2015). Various models are becoming available that enable this to be estimated (Kearney et al. 2013), but at the moment their application is to a narrow range of taxa. Indeed, even narrower than those for which we have some measure of performance, tolerance or their variation (see Chown et al. 2013; Seebacher et al. 2015; also Fig. 4B). And even these measures may themselves be a source of controversy. For example, Rezende et al. (2014) have drawn attention to the long-standing knowledge (reviewed in Cossins & Bowler 1987) that both duration and temperature of exposure are important for understanding thermal
tolerance. Of course they are correct. Just as it is important to understand whether in thermal
tolerance experiments these variables affect tolerance estimates for reasons other than
artefact, and if so why this happens and what rates of experimental change might then be
most environmentally relevant (Peck et al. 2009; Rezende et al. 2011; Terblanche et al. 2011;
Richard et al. 2012). How the outcomes of laboratory studies then relate to fitness in the field
is an additional important area in need of further enquiry.

The question then becomes whether, given all of these potential sources of noise, no
reliable signal might ever be discerned. If this is the case, this particular approach to
macrophysiology should be reconsidered. Some other way should then be sought to
understand the ecological implications of physiological variation, and to respond to an urgent
stated need to determine how we might mitigate and assist organisms to adapt to the many
effects of global environmental change, and forecast what the outcomes might be (IPCC
2014). The alternative is to admit that much of what has been found is holding up to further
detailed scrutiny, but that some macrophysiological knowledge is tentative, and will change
subject to further investigation, much as is the case throughout science.

In doing so, what would then be most significant is to understand how some of the
important challenges raised (Table 1) might best be addressed. For example, rates of
temperature change might differ substantially across the world, as temperature means and
extremes do (Addo-Bediako et al. 2000; Bonan 2002), and perhaps these empirically-derived
rates might provide the most appropriate context for determining how best to understand
critical limits to activity (Terblanche et al. 2011). Likewise, while microclimate variation
plays an important role in determining environmental responses, how do the extremes of this
variation themselves vary geographically and how much difference would that make to
currently accepted macrophysiological outcomes? Perhaps as importantly, if we remain
convinced that methodological variation in compiled data may be biasing the signal, rather
than simply adding noise, the addition of new, more comparable data sets, focussing on experimental methods and analyses that take these concerns into account, are clearly needed. Here, the power of integrating newly developed phenotyping approaches, clear thought about macrophysiology’s various empirical and analytical challenges, such as the interrelationships between intraspecific, interspecific and assemblage variation, and new information and models on climate and organismal responses to it, might best be realized.

Several other significant challenges remain for the field (Table 1). Explicit investigation of the impacts of multiple interacting environmental drivers under realistic conditions is one of these. Investigating the way responses of non-indigenous species change or evolve through time (e.g. Hill, Chown & Hoffmann 2013), or what may be termed the ‘macrophysiology of invasion’, is one way to do so. Others include greater use of transplant and common garden experiments for investigations of organismal responses (Gaston 2003, 2009; De Frenne *et al.* 2013; Vergeer & Kunin 2013).

Null models built from first principles of hierarchical patch dynamics have also proven capable of accurately predicting many facets of the structure of species distributions and their aggregate properties (such as frequency distributions of species abundances and occupancies, and species-area relationships; Storch *et al.* 2008). Likewise, the spatial scaling of occupancy has been used to predict the abundance of populations (Hui *et al.* 2009). Much scope exists for the synthesis of these approaches with the methods of macrophysiology (Fig. 1).

Similar benefits may be derived from the use of integral projection models to investigate the demographic consequences of spatially explicit physiological trait variation. These models are being used increasingly to understand how continuous traits impact ecological and evolutionary processes (Coulson 2012; Merow *et al.* 2014; Rees, Childs & Ellner 2014), but are rarely applied in a macrophysiological context. Although initial
approaches for some groups may require mesocosm or microcosm investigations (Ozgul et al. 2012), which themselves have been criticized for various reasons (e.g. Skelly 2002), knowledge of how to overcome some of the problems associated with them is developing rapidly (Schmitz 2007; Wernberg, Smale & Thomsen 2012). Moreover, in many instances alternative options may not be practicable.

Finally, explicit consideration of the ecological consequences of physiological variation provides a means of understanding how that variation is translated into ecosystem scale patterns, that is to date underexplored for several groups. The approach is perhaps best developed for plants (Helliker & Richter 2008; Michaletz et al. 2014), and advances in similar work for soils and soil organisms are also being made (Pey et al. 2014; Yvon-Durocher et al. 2014).

Prospects

Macrophysiology has generated a suite of insights which would not have emerged using any other approach. Clearly it has much future scope to do so too. In particular, as the tools available to and costs of genomics decline, so the need to understand trait variation and its ecological consequences will continue to increase (Travisano & Shaw 2012; Chown et al. 2015), with phenotyping and modelling methods, and the growing availability of other data, providing much future potential for extending macrophysiology’s contributions.

How macrophysiology relates to other areas in biology will continue to change too. For example, metabolic ecology has expanded substantially in scope to become one of the main areas for investigating the consequences of metabolic variation for organisms and ecosystems (e.g. Brown et al. 2004; White & Kearney 2015). Other approaches, such as conservation physiology (Cooke et al. 2013), are also becoming prevalent. Although fragmentation of endeavour, especially if it is along taxonomic lines, will no doubt restrict
generality of insights, diversity in thinking is beneficial to the extent that it delivers new insights. Macrophysiology has certainly provided many fresh and important new perspectives and findings, and we look forward to the growth of a field that has significant scope to provide insight into the ecological and evolutionary consequences of physiological variation. Doing so is especially important as we reach a crisis in biodiversity loss and management. While there’s much to be negative about (Butchart et al. 2010; Tittensor et al. 2014), there are conservation endeavours that are succeeding (Coetzee, Gaston & Chown 2014) and macrophysiology will play a key role in further extending these successes.

Acknowledgements

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Table 1. Ten challenges for macrophysiology.

<table>
<thead>
<tr>
<th>No.</th>
<th>Description</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Comprehensive comparison of the similarities and differences in plant and animal responses to environments over large-scales (see also Fig. 4).</td>
<td>Huey <em>et al.</em> 2002; Atkin &amp; Tjoelker 2003; Clarke 2003; Koski &amp; Ashman 2015</td>
</tr>
<tr>
<td>2.</td>
<td>Improving the geographic coverage of physiological data for making key inferences.</td>
<td>Chown <em>et al.</em> 2003; White <em>et al.</em> 2015</td>
</tr>
<tr>
<td>5.</td>
<td>Understanding large-scale variation in rates of change of environments, and the relationships between these rates, mean temperatures and extremes, and their changing global form.</td>
<td>Peck <em>et al.</em> 2009; Terblanche <em>et al.</em> 2011; Wang &amp; Dillon 2014; Zhao <em>et al.</em> 2014</td>
</tr>
<tr>
<td>6.</td>
<td>Investigation of the outcomes of multiple interacting abiotic environmental factors on fitness variation over large scales.</td>
<td>Gaston <em>et al.</em> 2009; Bonebrake &amp; Mastrandrea 2010</td>
</tr>
<tr>
<td>7.</td>
<td>Using transplant and common garden experiments to understand significance of plasticity, adaptation and responses to environmental change under realistic</td>
<td>Gaston 2009; Chevin <em>et al.</em> 2013; De Frenne <em>et al.</em> 2013</td>
</tr>
</tbody>
</table>
8. Understanding the extent to which evolutionary rescue, or Chevin et al. 2010; evolution in ecological time, is likely to alter Hoffmann & Sgrò 2011 macrophysiological patterns and inferences drawn from them.

9. Implementing methods such as integral projection Ozgul et al. 2012; Rees modelling to investigate explicitly the relationships et al. 2014 between physiological variation and fitness.

10. Using macrophysiology to further understand the Evans 2010; Chown & ecological implications of massive landscape Duffy 2015; Gaston et transformation through urbanization and agriculture. al. 2015
Figure legends

Fig. 1. Macrophysiology as an integrated approach to understanding the ecological implications of physiological variation, and its relationships with other approaches. For example, bioclimatic models start with data from (1) and (5) or (6) and fit some function between them. Mechanistic models start with (1) and a trait function (3) to predict (5) or (6). Downscaling models use (7) to forecast (5) or (6). Some biodiversity modelling (of species richness, for example) estimates a relationship between (1) and (9). Macrophysiology provides conceptual and methodological links between all of these areas.

Fig. 2. The macrophysiological approach. A. Variation within a species (orange), among species (green), and among assemblages (blue) can be integrated, here for thermal minima. B. The relationship with various modelling approaches is readily discerned. C. Interactions among species, environments, and traits can be disaggregated. The environment-by-trait matrix is often estimated using the “fourth corner” method.

Fig. 3. Examples of progress in understanding of large-scale physiological variation. A. The relationship between ambient temperature and body temperature in mammal species from various trophic groups (white circles: herbivores; black symbols: carnivores; grey symbols: omnivores) (redrawn from Clarke & O’Connor 2014). B. Latitudinal variation in phenotypic plasticity of small intestine length in rodents (redrawn from Naya et al. 2008). d is a measure of plasticity. C. The relationship between latitude and seasonal variation in fat body size in reptiles (redrawn from Aguilar-Kirigin & Naya 2013). d is a measure of plasticity. D. Latitudinal variation in post-acclimation Q_{10} in marine, freshwater and terrestrial species (redrawn from Seebacher et al. 2015).
**Fig. 4.** Macrophysiological patterns in plants. 

A. Temperature responses of photosynthesis in CAM, C3 and C4 plants indicating the rates at the optimal temperatures and the breadth of optimal temperatures (redrawn from Yamori *et al.* 2014). 

B. Climatic space (MI is moisture index, T is ambient temperature) with vegetation (shown in grey hexagons) and coverage of data from the Stomatal Behaviour Synthesis Database (redrawn from Lin *et al.* 2015). 

C. Increase in dark pigmentation with latitude in *Argentina anserina* (Rosaceae) (red circles: New Zealand; black circles: Pacific Coast; white circles: Great Lakes; blue circles: Rocky Mountains), demonstrating a case of Gloger’s rule (redrawn from Koski & Ashman 2015). 

D. Latitudinal variation in predicted mass-based dark respiration rates at temperature of the warmest quarter of a location (solid and dashed lines indicated regression data and prediction intervals; red lines and circles: south; blue lines and circles: north) (Redrawn from Atkin *et al.* 2015).
Fig. 1
Fig. 2

A) Table showing species sites and temperatures:

<table>
<thead>
<tr>
<th>Species/Sites</th>
<th>Site A</th>
<th>Site B</th>
<th>Site C</th>
<th>Site D</th>
<th>Species mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>4.3°C</td>
<td>6.1°C</td>
<td>7.4°C</td>
<td>8.0°C</td>
<td>6.5°C</td>
</tr>
<tr>
<td>Species 2</td>
<td>3.7°C</td>
<td>4.4°C</td>
<td>5.5°C</td>
<td>4.5°C</td>
<td>4.5°C</td>
</tr>
<tr>
<td>Species 3</td>
<td>2.4°C</td>
<td>3.6°C</td>
<td>3.0°C</td>
<td>3.0°C</td>
<td>3.0°C</td>
</tr>
<tr>
<td>Species 4</td>
<td>1.9°C</td>
<td>1.9°C</td>
<td></td>
<td></td>
<td>1.9°C</td>
</tr>
<tr>
<td>Assemblage</td>
<td>3.1°C</td>
<td>4.7°C</td>
<td>6.5°C</td>
<td>8.0°C</td>
<td>6.5°C</td>
</tr>
</tbody>
</table>

B) Diagram showing abundance and performance over different environments.

C) Grids illustrating species, sites, environment, traits, and their interactions.
Fig. 3

A. Body temperature (°C) vs. Environmental temperature (°C)

B. Small intestine length flexibility vs. Absolute latitude (°)

C. Fat body size flexibility (d) vs. Latitude (°)

D. Post-acclimation Q₁₀ vs. Absolute latitude (°)