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Population responses within a landscape matrix: a macrophysiological approach to understanding climate change impacts

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Abstract Global environmental change (GEC) is a significant concern. However, forecasting the outcomes of this change for species and ecosystems remains a major challenge. In particular, predicting specific changes in systems where initial conditions, instabilities, and model errors have large impacts on the outcome is problematic. Indeed, predictive community ecology has been deemed unworthy of pursuit or an unreachable goal. However, new developments in large-scale biology provide ways of thinking that might substantially improve forecasts of local and regional impacts of climate change. Most notably, these are the explicit recognition of the regional and landscape contexts within which populations reside, the matrix approach that can be used to investigate the consequences of population variation across space and within assemblages, and the development of macrophysiology, which explicitly seeks to understand the ecological implications of physiological variation across large spatial and temporal scales. Here we explore how a combination of these approaches might promote further understanding and forecasting of the effects of global climate change and perhaps other GEC drivers on biodiversity. We focus on the population level, examining the ways in which environmental variation might be translated through performance and its plasticity to variation in demography.

Keywords Bioclimatic modelling · Mechanistic models · Performance curves · Phenotypic plasticity · $r \times c$ matrices

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Introduction

Anthropogenic environmental change now numbers among the world's most pressing political and economic concerns. Whilst the likelihood and impacts of the major drivers of global environmental change (GEC) have long been the subject of disquiet (Arrhenius 1896; Huxley 1950; Hardin 1968), the direct implications for human welfare, and their indirect effects through alterations to biodiversity and ecosystem services have only recently risen to substantial political prominence (Gore 2006; Stern 2007). In all of these arenas it is not only the impacts of the GEC drivers that are of concern, but also the extent to which they are likely to be additive and, more importantly, synergistic (Brook 2008; Brook et al. 2008; Tylianakis et al. 2008). Climate change is of particular significance in this respect because it is likely to interact with all of the other GEC drivers.

Much research has now documented how climate change has acted either alone or in concert with other GEC drivers to affect biodiversity, and an increasing component of the field is concerned with predicting future impacts (reviews in Walther et al. 2002, 2005; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006). Key messages from documented and forecast changes are that population extirpation will be ongoing, further species extinction is likely, and geographic ranges will continue to shift substantially and to be fragmented (see also Thomas et al. 2004, 2006; Pimm et al. 2006; Pounds et al. 2006). Moreover, the likelihood of particular outcomes will be contingent on the major climatic region being investigated, the extent of landscape fragmentation, and the life histories of the species concerned (Thomas et al. 2001, 2008; Stachowicz et al. 2002; Chown et al. 2007; Pörtner and Knust 2007; Theoharides and Dukes 2007; Deutsch et al. 2008).

In part, the challenge for biologists arises because it is exceptionally difficult to make predictions about the details of systems where initial conditions, instabilities, and model errors have large impacts on the outcome. The analogy may be drawn with predicting weather rather than climate, as made clear by Mahlman (1998: 91) in his pinball machine thought experiment. In this game, the path of the ball is unpredictable after a few collisions with the bumpers in the machine, although it is clear that at some point the ball will end in the gutter. However, the odds of the ball ending in the gutter can be altered dramatically by changing the slope of the playing field. In this latter scenario, the trajectory of the ball remains as unpredictable as before the change in slope, but the delay in the time to the ball reaching the gutter is predictable. So whilst the 'climate' has changed predictably, the 'weather' has remained as unpredictable as before (Mahlman 1998). In a similar vein, it has recently been shown that the context of change is likely to alter the direction and magnitude of global change effects on interactions among species (Tylianakis et al. 2008), so making precise ecological forecasting problematic. Nonetheless, broader forecasts of changes in geographic range limits and phenology are supported by current data (Parmesan 2006; Rosenzweig et al. 2008).

Part of the challenge is also associated with inadequacies of some the major methods currently used to investigate the forecast impacts of climate change, such as bioclimatic modelling. Both the utility of and problems associated with these models, and alternatives to them, are now being widely explored (e.g. Araújo et al. 2005; Elith et al. 2006; Austin et al. 2006; Austin 2007; Soberón 2007; Beale et al. 2008; Thuiller et al. 2008; Kearney and Porter 2009).

Fully addressing the forecasting challenge would appear almost to be arguing for the establishment of a predictive community ecology, a goal which seems either unworthy of pursuit at the community level (Ricklefs 2008) or simply unreachable (see discussion in Lawton 1999; Simberloff 2004). However, several recent advances in the field provide

ways of thinking that might substantially improve forecasts of local and regional impacts of climate change and its interactions with other GEC drivers. Most notably, these are the explicit recognition of the regional and landscape contexts within which populations reside (Gaston and Blackburn 2000; Hubbell 2001; Leibold et al. 2004; Chase 2005; Ricklefs 2008), a matrix approach that can be used to investigate the consequences of population variation across space and within assemblages (Gaston 2002; Bell 2003; Gaston et al. 2008), and the development of macrophysiology, which explicitly seeks to understand the ecological implications of physiological variation across large spatial and temporal scales (Chown et al. 2004a; Osovitz and Hoffman 2007; Chown and Gaston 2008; Gaston et al. 2009). Here we explore how a combination of these approaches might promote further understanding and forecasting of the effects of global climate change and perhaps other GEC drivers on biodiversity. Before doing so, we briefly draw attention to the significance of forecast changes in water availability, and changes in the variation and predictability of particular climate variables, which may be as important as, or indeed in some cases more significant than, changes in mean temperature.

The nature and form of change

Although much of the focus on the impacts of climate change has been with changing temperature regimes and the seasonality of these changes (Harvell et al. 2002; Hansen et al. 2006; Parmesan 2006), for large areas of the globe changes in precipitation regimes and water stress will also be significant. What the ecological consequences will be more generally of precipitation change, such as the global change-type drought expected over many temperate to sub-tropical areas (Easterling et al. 2000; Breshears et al. 2005; Overpeck and Cole 2006; Stige et al. 2006), has not been extensively investigated, but they are likely to be significant (Tauber et al. 1998; Ciais et al. 2005; McGeoch et al. 2006; Staley et al. 2006; Chase 2007; Engelbrecht et al. 2007; Franks et al. 2007). For example, although the ultimate causes of amphibian declines in tropical Central America remain the subject of debate (e.g. Pounds et al. 1999, 2006; Rohr et al. 2008), changes in water availability owing to global temperature change and local habitat destruction are important (Rovito et al. 2009). In many areas of the world, species richness variation is strongly related to water availability (Hawkins et al. 2003; Chown et al. 2004b), suggesting that substantial declines in the numbers of species will accompany dwindling precipitation, though the identity of the species that remain behind may be affected by other factors (Algar et al. 2009). More subtle effects may also be associated with a change in the timing and predictability of rainfall (Lima et al. 1999; Holmgren et al. 2006; Foden et al. 2007; Tolley et al. 2008). Even changing wind regimes, as are being documented across large sectors of the Southern Ocean (Le Roux and McGeoch 2008; Turner et al. 2007), may affect the distributions and richness of species dependent on wind as an energy source, such as procellariiform seabirds (Jouventin and Weimerskirch 1990; Hashmi and Causey 2008; Davies et al. 2009).

From a population perspective, perhaps just as important as identifying the constituents of climate that are changing, is the fact that it is not only mean conditions that are involved, but also the frequency of extremes, the predictability and nature of more usual, and extreme, variation, and interactions among abiotic drivers (Gaines and Denny 1993; Gilchrist 1995; Brown and Brown 2000; Easterling et al. 2000; Helmuth et al. 2006; Chown and Terblanche 2007; Pulido 2007; Jentsch and Beierkuhnlein 2008; Parker et al. 2008; Welbergen et al. 2008; Pelini et al. 2009). The predictability of conditions (i.e. cue

reliability) over various temporal and spatial scales is a key element determining whether phenotypic plasticity, one of two initial responses to environmental change (behavioural avoidance can be considered the other) is likely to be present or evolve in a population (Moran 1992; Tufto 2000; Sultan and Spencer 2002; Hazel et al. 2004; Gabriel 2005; Leimar 2009).

The response to change in a focal population

Within any given population, an environmental change might have a range of demographic effects. One particularly noteworthy, but relatively poorly addressed question is the magnitude of a change that is likely to trigger both a physiological effect and one that ultimately has a demographic outcome (Dunham et al. 1989; Porter 1989; Dillon et al. 2007). An alternative way of posing this question is to ask what the term 'given environment' means in the context, *inter alia*, of definitions such as that of beneficial acclimation (a form of plasticity), where acclimation to a given environment results in a performance advantage in that environment (Marais and Chown 2008), and under what conditions does acclimation affect individual performance in the field (Loeschcke and Hoffmann 2007; Kristensen et al. 2008). In other words, how large does a temperature change, for example, have to be to result in physiological and demographic responses. Nonetheless, assuming that an environmental change has effects that translate to a demographic level, these might result in emigration, decline (possibly to extinction), growth, or possibly a change in the dynamics of the population given that alterations in the intrinsic rate of increase can profoundly alter dynamics (May 1986; Gaston 2009).

The circumstances under which dispersal is selected for or against are the subject of a large literature and will not be examined in detail here (see McPeek and Holt 1992; Parvinen et al. 2003; Heinz et al. 2009). It is worth noting though that changes in dispersal ability and propensity can evolve rapidly (Cody and Overton 1996; Simmons and Thomas 2004), and may be more subtle than the presence of the physiological/morphological capability for dispersal might suggest (Moyle et al. 2009). Moreover, dispersal ability in a meta-population context has a considerable influence on the extent to which phenotypic plasticity, or alternatively ecotypes, might be expected in a local population (see below) so affecting short- and longer-term responses to change (Sultan and Spencer 2002).

At their most basic, changes in abundance reflect the ways in which alterations to environmental conditions are translated through individual responses, so altering survival probability and growth rate in the juvenile stage prior to reproduction, the probability and extent of reproduction, and, in iteroparous species, the timing of and survival between reproductive bouts (Sibly and Calow 1986; see also Dunham et al. 1989; Huey and Kingsolver 1989; Gilchrist 1995; Gaston 2009). One of the most straightforward ways to consider this translation of environmental conditions to alterations in survival or growth rates is in terms of response curves or performance curves (Huey and Kingsolver 1993; Chown and Gaston 2008). The variety in form of response curves is relatively small (Fig. 1), and they provide a clear illustration of the mechanistic relationship between the environment and some demographic parameter (or a trait closely related to such a parameter), which can be readily described mathematically (see e.g. Huey and Kingsolver 1989; David et al. 1997; de Jong 2005; Izem and Kingsolver 2005; Angilletta 2006). Although performance curves may legitimately be thought of as reaction norms (Angilletta et al. 2003), it is practically useful to consider them as the function linking one or more environmental variables to one or more demographic parameters; a function which in turn
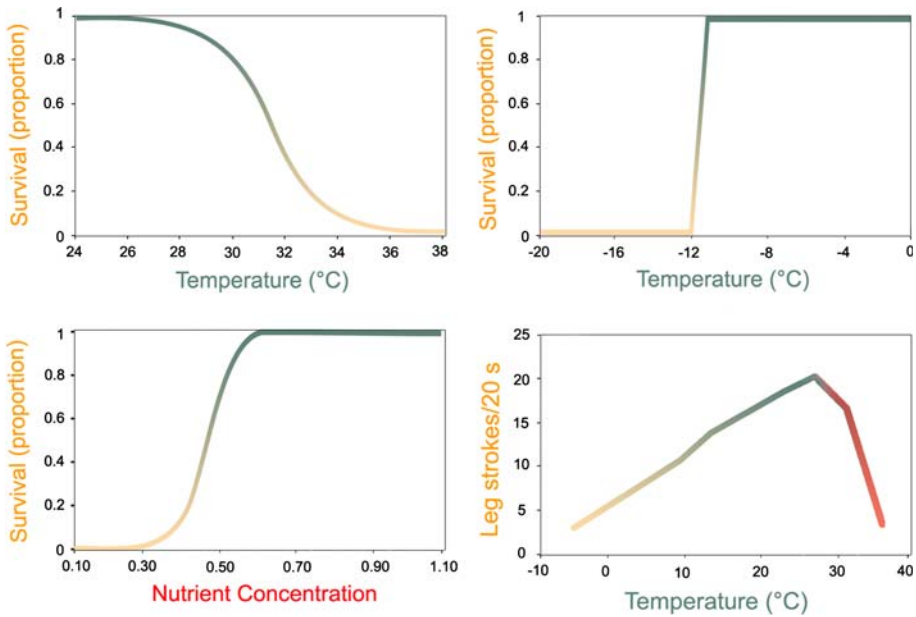
Fig. 1 The form of responses populations show to varying environmental factors. These might be (*top left*) logistic as in this temperature response curve; (*top right*) threshold, as in the survival response to low temperature in a species that can tolerate freezing up to −11°C; or (*bottom left*) asymptotic, as is frequently found in plants relative to a limiting nutrient. In (*bottom right*) a performance curve is shown. Redrawn from Chown and Gaston (2008)

may be fixed or phenotypically plastic, and may be subject to selection for changes in mean and variance (or the extent of plasticity; see also Lynch and Gabriel 1987; Gilchrist 1995; de Jong 2005; Ghalambor et al. 2007; Chown et al. 2008; Angilletta 2009).

Using a typical performance curve relating temperature and population growth rate, a response to change can readily be illustrated. If the optimum is relatively broad, and the environmental change small, little to no demographic effect is likely. The form of the curve itself is a function of both within and among generation variation in environmental conditions (Gilchrist 1995), so illustrating why changes in variance and their predictability are important. If the curve has a steeper form (see Angilletta 2009 for discussion of the evolution of shallow and steep response curves) and is fixed within a population (the latter might be the outcome either of environmental predictability or extreme unpredictability, see de Jong 2005; Deere and Chown 2006), then a relatively small increase in temperature might lead to a substantial decline in performance. Indeed, this is precisely the small thermal safety margin effect predicted for tropical ectotherms by Deutsch et al. (2008) owing to the asymmetric nature of performance curves, and the generally limited temperature acclimation capacity of tropical species compared to temperate ones. Many bioclimatic models assume such fixed response curves too, although rarely do they explore complex response curves (see discussion in Austin 2007; Chown and Gaston 2008). Curiously, few models also explore the longer-term population dynamic outcomes of changes in the intrinsic rate of increase, but simply assume that a change in climate translates directly into a change in presence/absence, and sometimes in abundance (but see Crozier and Dwyer 2006; Régnìere and Bentz 2007; Buckley 2008; Keith et al. 2008; Anderson et al. 2009).

Alternatively, if the individuals within a population show phenotypic plasticity, and the environmental change is relatively slow, predictable, and long-lasting (by comparison with longevity of individuals, and in multi-stage species, one or more of their stages), then some form of short-term demographic response might take place. The timing of avian migration to a site provides an appropriate example (Gienapp et al. 2008). The plasticity that is characteristic of individuals within a population can take on several forms (Huey et al. 1999; Deere and Chown 2006; Angilletta 2009), though they do constitute something of a continuum, and will depend also on the trait in question (see e.g. Liefting et al. 2009), life stage and its duration, and the behavioural flexibility of the species. For example, in the sub-Antarctic kelp fly *Paractora dreuxi*, upper and lower lethal limits show no significant phenotypic plasticity in adults and larvae (Marais et al. 2009). By contrast, chill coma recovery shows beneficial acclimation in larvae, whereas adults perform best after being exposed to low temperatures (Marais and Chown 2008). Nonetheless, the relationship between phenotypic changes in populations (for examples of population variation in plasticity see e.g. Liefting and Ellers 2008; Liefting et al. 2009; Orizaola and Laurila 2009), which may be rapid under anthropogenic environmental change, and alterations in the probability of persistence or establishment remain poorly investigated (see Hendry et al. 2008).

If an alteration in performance curve does take place, then it may well be that little demographic effect is realized, or that it is exacerbated relative to the situation of no change. Moreover, some acclimation responses have substantial physiological penalties such that although one trait (e.g. survival) may show no change, another (such as performance) might be markedly affected (see discussion in Hoffmann 1995; Feder and Hofmann 1999). Although the costs of plasticity form an important component of models for understanding the conditions under which plasticity might evolve (van Tienderen 1991; Sultan and Spencer 2002; Masel et al. 2007), studies thereof are only now starting to accumulate (Relyea 2002; van Kleunen and Fischer 2005, 2007; Kristensen et al. 2008).

Over several generations, selection for changes in the mean trait values or their plasticity may also take place (see discussion in Gilchrist 1995). Recent work has shown that genetic changes in populations are taking place in response to climate change. In many species these have to do with shifts in phenology (Bradshaw and Holzapfel 2006, 2008), and evolutionary change in response to climate fluctuations may be rapid (Pulido and Berthold 2004; Franks et al. 2007), though apparently not always fast enough to keep up with the rate of climate change (Etterson and Shaw 2001). Nonetheless, much of the phenotypic change that has been documented as a response to anthropogenic change may be due more to phenotypic plasticity than to evolutionary changes of trait means (Gienapp et al. 2007, 2008; Pulido 2007; Hendry et al. 2008).

Populations in a regional context

Although the extent of plasticity, its form and its demographic effects may seem, from the above discussion, to be entirely contingent, several, relatively consistent, broader patterns have long been noted, and increasingly the evidence seems to support them. For example, physiological plasticity is likely to be reduced in the presence of behavioural flexibility (Marais and Chown 2008; see also Huey et al. 2003), tropical species tend to show reduced plasticity by comparison with their temperate counterparts (Ghalambor et al. 2006), tropical and marine polar stenotherms show much less plasticity than do temperate eurytherms (Pörtner 2002), and species with considerable basal tolerance may have reduced plasticity (Gause 1942; Stillman 2003).

At a more local level, the extent of plasticity, and the likelihood that this may change through time, depends on the regional context of the population, and notably the extent of dispersal among patches differing in quality (Sultan and Spencer 2002; Hazel et al. 2004; Leimar 2009). This local dependency on regional circumstances is well reflected in Ricklefs' (2008: 746) remark that the '*presence and relative abundance of a species at a particular point might depend on interactions with populations that do not occur there*'. Perhaps unsurprisingly, the extent of dispersal among patches also plays a role in determining the likelihood that a population will evolve to overcome a particular environmental constraint (Kirkpatrick and Barton 1997; Holt and Keitt 2005; Alleaume-Benharira et al. 2006; Goldberg and Lande 2007). Interactions among metapopulations may promote or retard adaptation to a given environment, influenced also by the temporal autocorrelation structure of the environmental change (Holt et al. 2004).

In the context of climate change, the obvious question is the extent to which phenotypic plasticity might promote or retard changes in geographic ranges associated with changing local conditions (Chown and Terblanche 2007; see also Gienapp et al. 2007, 2008; Hendry et al. 2008). At least part of the answer to this question depends on the way in which phenotypic plasticity is viewed in the context of evolutionary change (discussed at length in de Jong 2005). Nonetheless, a range of outcomes is possible, and these have been most recently, and clearly, set out by Ghalambor et al. (2007). First, adaptive plasticity might produce a phenotype that is close to optimal under the new environmental conditions. In this case, little demographic change in the population would take place, and the population would not evolve owing to the absence of directional selection. Second, adaptive plasticity might produce a phenotype that goes some way towards reaching the local optimum, but will be sufficiently distant for strong directional selection to take place. Initially, a demographic change will occur, but this may be reversed following several generations of selection. Third, plasticity might be non-adaptive, and carry a phenotype away from the local optimum. Here extinction is very likely and such non-adaptive plasticity is likely to be common (van Kleunen and Fischer 2005). Finally, environmental stress might increase trait variance to such an extent that some variant is able to cross an adaptive valley and find a new local optimum. In the first two cases the least alteration in range sizes and positions is expected with climate change, whereas in the latter cases substantial range shifts might be expected. Of course, the nature of the change is dependent also on how plasticity arose in the past in a given population, and the extent to which it is constrained by dispersal from other populations. Intermediate levels of dispersal may well facilitate crossing to a new local optimum by promoting plasticity, but may also leave scope for directional selection (see related discussion in de Jong 2005; Ghalambor et al. 2007: 402). However, further to complicate matters, the extent to which phenotypic change is possible is likely to be limited by the presence of other species (de Mazancourt et al. 2008). This idea has so far been explored only for evolutionary change in trait means among patches and not for how plasticity might influence this evolution or how species and patch diversity might influence plasticity. Nonetheless, an important conclusion of de Mazancourt et al.'s (2008) study is that under many circumstances phenotypes are less likely to change than are abundances.

Scaling up

Local population responses, though potentially complex, can readily be scaled up by considering them in the context of species by sites (rows by columns, $r \times c$) matrices (Fig. 2a). Indeed, such matrices, which can be further resolved into several spatial
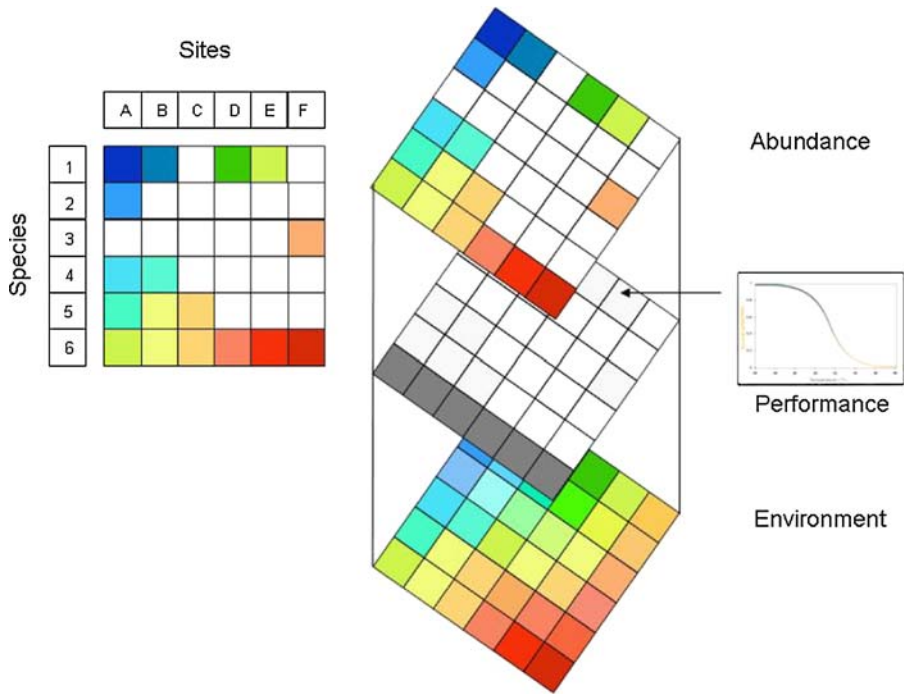
Fig. 2 *Left*: A typical $r \times c$, species x sites matrix. The *colours* can be interpreted as variation in any characteristics, such as abundance, body size, birth rate, desiccation resistance, lower lethal temperature or development rate. *White squares* indicate that the species does not occur at that site. *Right*: The matrix can be thought of either exactly as in the *left-hand panel*, with environmental variation giving rise, through either a spatially stable or spatially variable performance curve, to variation in a characteristic such as abundance. Alternatively, the matrix can be seen as a spatially expanded one. The x and y coordinates provide the explicit spatial position in the landscape, again with the environment being translated by the organism into some form of variation in other traits, although responses might also reduce the extent to which environmental variation is realized in some characteristic. In models of the kind being developed by Kearney and Porter (2009) several parameters are included in the intermediate layers. The mean trait value and mean spatial position then serve as inputs to the $r \times c$ matrix. Formal statistics for relating such matrices are also provided by Dray and Legendre (2008)

dimensions (Fig. 2b), may be the key to relating local population mechanisms and patterns to those that emerge at the interspecific and assemblage levels (Dray and Legendre 2008; Gaston et al. 2008). Traditionally, cells of such a matrix would comprise the presences/absences of species or their respective abundances at a series of sites (e.g. Gaston 2002; Bell 2003). However, the matrix can be populated with virtually any parameter (e.g. Fig. 3), such as the resting metabolic rate or critical thermal minimum of a series of populations (see e.g. Klok and Chown 2003; Wikelski et al. 2003 for these kinds of data). Moreover, in the spatially explicit form, spatial variation in an environmental parameter (e.g. mean growing season temperature) might form the first matrix, and, with an appropriate function relating the environmental parameter to survival of growth rate, this might be translated into predicted abundance. The function matrix could be considered invariant across space, time and/or taxonomy (niche conservatism—see Wiens and Graham 2005), or some form of nonstationarity (used in the geostatistical sense, see Foody 2004) could be introduced. The spatial variation might reflect realized or predicted phenotypic plasticity,

i Species / j Sites	Site A (40°S)	Site B (38°S)	Site C (35°S)	Site D (30°S)	Mean CTmin (°C)	Mean latitude (°S)
Sp. 1	4.0	5.0	6.0	8.0	5.8	35.8
Sp. 2	3.0	4.0	7.0		4.7	37.7
Sp. 3	3.0	4.0			3.5	39.0
Sp. 4	2.0				2.0	40.0
Mean CTmin (°C)	3.0	4.3	6.5	8.0		
Variance	0.7	0.3				

Fig. 3 A matrix of species (*i*) by sites (*j*) indicating how physiological variables may be included in such a matrix and can provide insight into intraspecific, interspecific and assemblage-level variation. The variable is critical thermal minimum (CTmin, see Chown and Terblanche 2007). The red rectangle indicates intraspecific variation across space. Interspecific variation (*green*) is calculated as a mean value for the species at the centre of their latitudinal range, whilst assemblage characteristics are the mean and variance a trait across all species at a given site (*blue*; redrawn from Chown & McGeoch, in review) (Color figure online)

or ecotypic variation, in turn associated with a matrix containing realized or predicted connection strength (dispersal) among populations. Likewise, a realized abundance matrix could be subject to the effects of interactions with other species based on what might be expected from interaction strengths or other food web parameters (see e.g. Berlow et al. 2004), or to the effects of a regional source pool. Formal mathematical approaches for investigating the relationships among matrices and for testing the significance of the parameters of the associations are available (see. Legendre et al. 1997; Dray and Legendre 2008). Likewise, characteristics of matrices, such as nestedness, can be analyzed to assess the roles various factors play in structuring assemblages (e.g. Azeria and Kolasa 2008; see also Chown 1993; Worthen et al. 1998 for examples of how desiccation resistance might influence assemblage structure).

At their most straightforward, a spatially explicit set of matrices amount to bottom-up modelling of the kind increasingly being used to understand the ways in which environmental variation translates into abundance/distribution (Kearney 2006; Kearney and Porter 2009). Such approaches have long been used to investigate crop plant performance (see e.g. Whisler et al. 1986; Brisson et al. 1992), and indeed have been scaled up to higher levels to understand richness variation and biome distributions across the planet (Kleidon and Mooney 2000; Bond et al. 2005). More recently, they have also started to be used to explore habitat preferences and abundances at a variety of spatial scales in animals (Kearney and Porter 2004; Helmuth et al. 2005, 2006; Crozier and Dwyer 2006; Buckley 2008; Kearney et al. 2008), and to understand the link between species traits and environments (Legendre et al. 1997; Dray and Legendre 2008). Not only can they incorporate subtle variation in the environment (such as changes in the predictability of conditions; Porter et al. 2000), but they can also include spatially varying physiological responses, and responses to other species. Moreover, these responses can be allowed to vary in ways that might be predicted by within- and between generation responses to various forms of environmental change, so allowing evolutionary dynamics to be included into the models (Kearney et al. 2009).

Bioclimatic approaches adopt various methods to resolve the function relating abundance or presence/absence to several environmental matrices, often neglecting the physiological, dispersal, evolutionary, and biotic interaction components of the function. As Kearney (2006) has noted, combining top–down and bottom–up approaches improves

understanding of the likelihood to which either historical factors or biotic interactions might be responsible for present distributions. Moreover, environmental matrices can also be used to predict species richness, either by using empirically derived relationships (O'Brien et al. 2000; Kalmar and Currie 2007) or theoretical expectations (Allen et al. 2002). Concatenation of the spatially explicit population-level matrices can be compared with the predicted matrices to provide further insight into how climate change might actually translate into assemblage level change. Indeed, a variation of such an approach has been used to understand how spatial variation in common species might be responsible for much of the variation seen in species richness at large spatial scales (Šizling et al. 2009). Alternatively, both sets of data can be re-expressed more simply as $r \times c$ matrices to provide insights into likely morphological and functional change (Gaston et al. 2008, submitted manuscript).

Conclusions

Forecasts of the effects of climate change and other GEC drivers on biodiversity are likely to be most significant at two levels. First, the fates of individual species are likely to remain a concern for both conservation and control reasons, and will encompass the likelihood of these species shifting along the rare-common axis (both in abundance and range; see Gaston 1999). Second, maintaining the efficacy of large areas for ecosystem service delivery is growing as a conservation priority (Millennium Ecosystem Assessment 2005). In both cases, effective empirical and theoretical means for understanding GEC impacts are being developed. The $r \times c$ matrices discussed here are especially noteworthy because they provide a way of moving between all levels in the biological hierarchy, recognizing that the higher ones are emergent from the population level, but also feed back to influence it. They do not resolve the difficulty of understanding and predicting complex systems where initial conditions, instabilities in the system, and model errors have large impacts on the outcome. Nonetheless, they do suggest that ways may be found to couple broad-brush generalizations with the specifics of particular populations. For example, a growing number of modelling studies are demonstrating that assemblage level characteristics can be derived from patterns of aggregation at multiple spatial scales (e.g. Hui et al. 2006; Storch et al. 2008). At several of these scales, aggregation is dependent on the autocorrelation structure of the environment and the way in which this translates through individual responses to aggregation—or the spatial autocorrelation—of abundance.

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