



Extending spatial modelling of climate change responses beyond the realized niche: estimating, and accommodating, physiological limits and adaptive evolution

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ABSTRACT

Aim Spatial models of the impacts of climate change generally assume that species are restricted to their realized niche, and will persist only if that niche remains accessible through time. However, species often have physiological limits beyond the range of environmental conditions experienced in their present realized niche, and these limits may also be extended further through evolution in response to the selection pressure provided by climate change. Our aim was to develop a general framework for incorporating key parameters relating to physiological limits and adaptive evolution into models of the impact of climate change.

Location Global.

Methods Four types of parameter are defined in our framework: the realized limit, the current physiological limit, the evolutionary physiological limit and the rate of adaptive evolution. These parameters can be estimated or predicted using a variety of information sources, and can be applied to a diverse range of modelling approaches.

Results We illustrate the utility of this approach by describing how parameters can be measured directly for model species, and by exploring how minimal information on phylogeny and distribution might enable parameter estimation for less well-studied species. We outline a general strategy for deriving these parameters from ongoing research, involving a cascading hierarchy of information ranging from direct observations of traits closely linked to the parameters of interest (e.g. from physiological or evolutionary experimentation) through to more distal indicators (e.g. ecological traits such as niche position or range size).

Main conclusions The incorporation of adaptive capacity into spatial modelling of biological responses to climate change is now eminently achievable. Significant sources of data are available that can be used as predictors or indicators of physiological limits and the capacity for adaptive evolution in non-model organisms. These data offer a common currency for addressing one of the most important limitations of current efforts to model the impacts of climate change on biological distributions.

Keywords

Adaptive capacity, biodiversity, ecosystems, evolutionary adaptation, physiological limits, resilience.

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INTRODUCTION

Local climates are changing as a result of human-induced changes in global climate (IPCC, 2013). A growing number of studies have therefore used various forms of modelling to assess the potential impact that climate change might have on the persistence and distribution of individual species (e.g. Thomas *et al.*, 2004; La Sorte & Jetz, 2012; Warren *et al.*, 2013). Most of this modelling relies on the assumption that any given species is restricted to that portion of environmental space in which it is currently known to occur, often referred to as the 'realized niche'. Assessments of the potential for persistence therefore focus largely on the extent to which species will have continued accessibility to their realized niche through time. This approach assumes that the primary impact of climate change will involve shifts in the geographical distribution of

species, tracking changes in the distribution of their realized niches (Fig. 1a,b; Corlett, 2011; Bellard *et al.*, 2012). This same assumption applies to approaches that model the potential impacts of climate change on whole assemblages of species within broader ecosystem types (e.g. Williams *et al.*, 2003; Dullinger *et al.*, 2012) or to those that model changes in community composition using macroecological modelling techniques (e.g. Ferrier & Guisan, 2006; Ferrier *et al.*, 2007). The assumption is also implicit within approaches that predict impacts from analyses of environmental change alone, without any involvement of biological data, for example analyses of the velocity of climate change (Loarie *et al.*, 2009; Ackerly *et al.*, 2010), in which the rate of displacement of climatic conditions across space and time is interpreted as the rate at which species will need to move to track these changes.

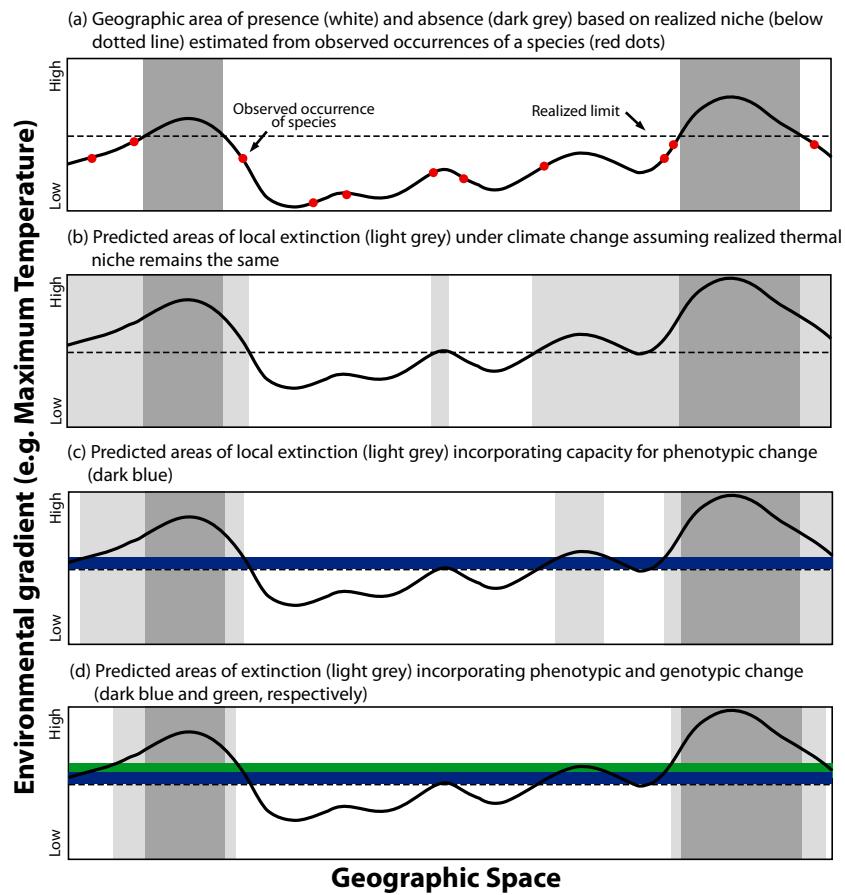


Figure 1 Adaptive capacity complicates predictions of persistence under climate change. In (a) we show the current distribution of maximum temperature (curved bold line) across a hypothetical geographic space that is partially occupied by a species. The observations of this species (red dots) indicate that it has a realized thermal limit (straight dotted line). Dark grey areas depict geographic regions unoccupied by the species under current environmental conditions. If climate change increases the thermal profile of the landscape (b, where the bold line representing the thermal profile has risen), and the species can tolerate only the realized thermal limit, we would expect local extinction across extensive geographic areas (light grey). However, species can often tolerate temperatures beyond those experienced in their realized niche (c). If the species illustrated here can persist up to the physiological limit depicted in dark blue we would see a reduction in the projected extent of local extinctions (reduced light grey between parts b and c). Climate change is also likely to place strong selection pressure on organisms, resulting in the evolution of traits associated with persistence of climate change (d, green) and thereby further reducing the extent of local extinctions (reduced light grey between c and d).

There are important reasons why the assumption that species will need to track changes in the geographical distribution of their realized niche could be violated (Fig. 1). Species often have physiological limits beyond the range of environmental conditions experienced in their present realized niche (Fig. 1c); for example traits that are important to the persistence of species in novel climates, such as thermal tolerance, may exceed the conditions currently experienced (Clusella-Trullas *et al.*, 2011; Sunday *et al.*, 2012; Early & Sax, 2014; Overgaard *et al.*, 2014). Phenotypic plasticity, the ability for a genotype to produce multiple phenotypes in response to environmental conditions, also makes an important contribution to higher fitness within variable environments (reviewed in Hoffmann & Sgrò, 2011). Evolutionary processes including genetic adaptation are also likely to affect organismal responses to climate change, and therefore the capacity of species to accommodate conditions beyond their present realized niche (Fig. 1d). Genetic adaptation to climatic change has been demonstrated in plants (Linhart & Grant, 1996; Etterson & Willis, 2004) and animals (Kolbe *et al.*, 2012). Over the past decade, these data have led to numerous calls for the incorporation of information on physiological limits, phenotypic plasticity and evolutionary adaptive potential into models of the impact of climate change (Pearson & Dawson, 2003; Williams *et al.*, 2008; Hoffmann & Sgrò, 2011; McMahon *et al.*, 2011; Moritz & Agudo, 2013).

To help promote a broader consideration of physiological limits, plasticity and genetic adaptation in modelling biological responses to climate change, we propose here a simple framework of parameters for factoring these phenomena into a wide range of models. This set of parameters is sufficiently generic to be applicable to both single-species and community-level modelling, and to both correlative and mechanistic modelling paradigms. The framework is also designed to allow values for these parameters to be estimated, or predicted, from a wide variety of information sources or lines of evidence, as we demonstrate here using hypothetical examples. We describe and discuss the framework largely in relation to thermal gradients. However, our framework is equally applicable to gradients in other environmental attributes (e.g. aridity, seasonality) that determine the climate space occupied by species.

The parameters defined in our framework offer a ‘common currency’ for linking estimates of adaptive capacity with spatially explicit projections of rates of climate change, thereby addressing a major challenge in the spatial modelling of biological responses (Hoffmann & Sgrò, 2011; Moritz & Agudo, 2013). Our hope is that this framework will facilitate consideration of physiological limits and genetic adaptation in modelling for a much wider array of organisms – including what we call here ‘non-model organisms’ – than has been possible previously. We use hypothetical examples to illustrate ways in which this broadening of application might best be achieved in the future, and outline a number of promising methods for incorporating these parameter values into estimates of the impact of climate change for non-model organisms and ecosystems. We also discuss where further research is needed to inform broad-scale estimation of our parameters, and how we

see this framework affecting biodiversity assessment and conservation planning.

FRAMEWORK OF PARAMETERS FOR INCORPORATING ADAPTIVE CAPACITY INTO MODELLING

The IPCC (2013) defines adaptive capacity as the ‘ability of systems, institutions, humans, and other organisms to adjust to potential damage, to take advantage of opportunities, or respond to consequences’. Here we further define adaptive capacity in the ecological sense as *the ability of a species, or an assemblage of species, to persist in novel or changing environments through phenotypic capacity (i.e. physiological tolerances or phenotypic plasticity) or changes in genotype (i.e. adaptive evolution)*. We propose a simple framework of parameters to enable the incorporation of the best available estimates, or predictions, of physiological limits and adaptive evolution into spatial modelling of the impacts of climate change on biological distributions (Fig. 2a). The framework is general enough to be applied to any environmental variable or set of variables. Four key parameters are defined at both the upper and lower ends of tolerance to a given environmental variable. Including both the maximum and minimum value in this perspective recognizes that some environmental variables (e.g. moisture-related variables) are expected to change in different directions in different parts of the world under climate change, even though most attention is likely to focus understandably on the upper end of tolerance for temperature.

Initially we describe the four parameters depicted in Fig. 2(a) as applying to a single species of interest. However, our framework offers sufficient generality to be applied to multiple populations within a species (exhibiting variation in physiological limits or capacity for adaptive evolution) or to be used to describe the expected mean, and/or frequency distribution, of the parameters for a whole guild or assemblage of species (Fig. 2b).

Parameter 1: Realized limit

The first parameter is simply the observed, or realized, limit of a species relative to an environmental variable of interest. This limit is a property of the environmental space currently occupied by a species, resulting from a wide range of biotic and abiotic interactions, past and present. It therefore equates directly to the concept of the realized niche, as invoked in correlative species distribution modelling (Araújo & Peterson, 2012). Within our framework this parameter is viewed as a soft limit on the current distribution of species, with tolerance of novel extremes determined by the remaining parameters introduced below.

Parameter 2: Current physiological limit

The distribution of a species is often limited by interactions that may have little to do with its physiology (Early & Sax, 2014; Warren *et al.*, 2014), which means that changes in environment,

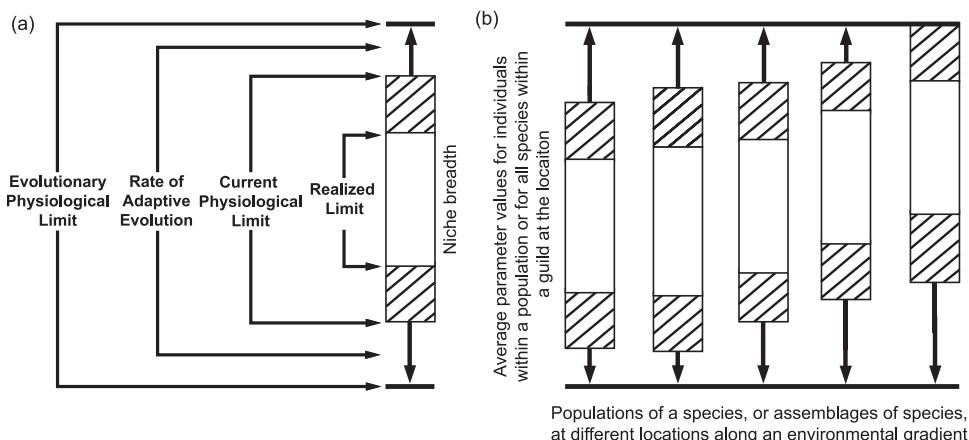


Figure 2 The parameters of adaptive capacity employed in our framework (a). Realized limits represent the niche space currently occupied by a species (or population) in relation to a specific trait, for example maximum thermal tolerance or minimum rainfall. Current physiological limits are the maximum or minimum values of an environmental variable that a species can tolerate through physiological adaptation if all other environmental conditions are met. The rate of adaptive evolution is the rate at which the current physiological limit can evolve through genetic change. Evolutionary physiological limits represent the maximum or minimum value that a trait can attain through evolution. Adaptive capacity can vary spatially (b) between populations within a given species, or between assemblages of species within a given guild, across an environmental gradient. The five populations, or assemblages, depicted here vary in the niche space they occupy (their realized limits). Each of the five can also tolerate different amounts of environmental change through physiological means alone (current physiological limits). Given the spatial variation in current physiological limits, they vary in the amount that genetic change (adaptive evolution) can contribute to persistence in a particular location before reaching an evolutionary physiological limit. Linking this spatial variation in adaptive capacity to spatial variation in rates of climate change could enable more accurate assessment of areas where species or assemblages are at risk of local extinction under climate change.

such as increases in temperature, may be well within the limits a species can tolerate and therefore little distributional change would be expected. To accommodate this, the second parameter is the current physiological limit, which represents the highest (e.g. for temperature) or lowest (e.g. for precipitation) level of an environmental variable that a species can tolerate through changes in phenotype (Turcotte *et al.*, 2012), and includes plastic phenotypic changes. This definition is analogous to the concept of the fundamental niche as defined by Hutchinson (1957). In our framework, the current physiological limit is viewed as an absolute constraint on survival within a single generation. Given that the difference between the fundamental and realized niche is driven by factors such as dispersal ability, the presence of adequate food and the absence of predators or competitors, this parameter is then interpreted as the amount of climatic change a species can accommodate without any corresponding change in distribution or abundance. This limit therefore also accounts for any effects of phenotypic plasticity on environmental tolerance.

Parameter 3: Evolutionary physiological limit

The third parameter is the evolutionary physiological limit; this functions as an absolute constraint on the value that a species' physiological limit can reach through evolutionary adaptation over time frames relevant to adaptation to climate change (versus the current physiological limit, which refers to the physiological capacity of a single generation). Phylogenetic

studies often show clear limitations to the evolution of traits such as thermal tolerance (Kellermann *et al.*, 2009, 2012a; Clusella-Trullas *et al.*, 2011; Grigg & Buckley, 2013), especially those related to heat tolerance (Kellermann *et al.*, 2012b). These plateaus are often explained through the limiting requirement of substantial molecular changes, or 'key innovations', required to alter upper thermal limits (Bettencourt *et al.*, 2008). Key innovations occur rarely and usually require substantial ecological opportunity, i.e. little or no competition for accessible resources (Rabosky *et al.*, 2007; Patarnello *et al.*, 2011).

Parameter 4: Rate of adaptive evolution

The fourth parameter is the rate of evolutionary adaptation, defined as the maximum rate (expressed per generation, or per unit time) at which the current physiological limit can evolve, each generation/time step, towards the evolutionary physiological limit. This equates to what Williams *et al.* (2008) referred to as the 'intrinsic capacity to adapt to changing conditions'. This parameter allows us to represent the fact that evolutionary change can be rapid, at least in some species, and may provide a method for organisms to swiftly counter climate change (Franks *et al.*, 2014; Schilthuizen & Kellermann, 2014).

QUANTIFYING ADAPTIVE CAPACITY PARAMETERS

Values for the parameters defined in our framework can be observed, or measured in a relatively direct manner, for only a

small proportion of species – so-called ‘model organisms’. For example, in work we are currently undertaking with *Drosophila*, we are utilizing measured trait values for physiological limits, such as the critical upper thermal limits (CTmax; Kellermann *et al.*, 2012b). These values represent the current physiological limit – the threshold value that would determine extinction at a given location when exceeded in a generation. The evolutionary physiological limit for individual species is estimated as the maximum value for the clade of the target species, given patterns of trait evolution across the phylogeny. For example, in *Drosophila*, the highest CTmax in the *Drosophila ananassae* clade is 39.1 °C, while the highest CTmax in the *Drosophila repleta* clade is 43.0 °C. These differing values can set the evolutionary physiological limit for individual species in the target clade. For many species of *Drosophila*, the narrow-sense heritability (h^2), mean, and variance (V_p) for CTmax are known. With these data, the rate of adaptive evolution can be determined by using the breeder’s equation to calculate the change in mean CTmax for each generation (as per Kearney *et al.*, 2009), where climate change sets the intensity of selection. Using these explicit values, the modelling approach developed by Kearney *et al.* (2009) can be extended to incorporate all the parameters defined in our framework (Kellermann *et al.*, 2012b; R.A.C., unpublished data).

However, the vast majority of species on the planet are ‘non-model organisms’ for which most, if not all, of the parameters defined in our framework are not readily quantifiable through direct observation. The only exception here are realized limits, which can be estimated directly for a sizeable proportion of species using distributional records, optionally combined with correlative species distribution modelling (Foden *et al.*, 2013). For the remaining parameters – current physiological limits, evolutionary physiological limits, and rates of adaptive evolution – quantification will need to rely either on linking indicators of adaptive capacity to proximal (i.e. directly relevant and measured) and distal (i.e. correlated with adaptive capacity across taxonomic groups) traits of organisms, or estimating parameter values from evolutionary and ecological information for related species. In other words ‘the best interim solution will be to make informed estimates based on the best available ecological knowledge of closely related species . . .’ (Williams *et al.*, 2008). In many cases this will provide only an approximate estimate for these parameters. However, any approximation of parameter values is still likely to improve the accuracy of predictions from spatial models, and is therefore better than none.

In determining which traits and environmental attributes should be assessed, consideration needs to be given to the likelihood that assessment of a particular attribute will result in a significant change in model output. For some species, increases in temperature may be the biggest threat, so assessment of parameters relevant to thermal traits would be most important in this case. In regions with large predicted changes in precipitation, parameters most related to desiccation tolerance may be most important. Further, consideration must be given to the spatial scale of the assessment. Divergence in traits, for instance soil type, during sympatric speciation is often undetectable using current environmental layers. This would lead to the

interpretation that important traits are conserved when they are actually potentially labile.

Promising types of information for estimating, or predicting, values for the parameters in our framework are described in Tables 1 & 2 (with full references provided in Tables S1 & S2 in Supporting Information). In addition to data derived from direct physiological measurement, various sources of ecological, demographic, genetic and phylogenetic information have considerable potential to assist the estimation, or prediction, of parameter values, as discussed later. To help illustrate the envisaged method of estimating parameter values from information on closely related species, we present a hypothetical example (in Box 1 and below) that employs relatively sparse data combined with well-established concepts in evolutionary biology.

For the eight species depicted in Box 1 we assume knowledge only of the current geographical distribution of each species, and of the phylogeny linking these species. The difference between the realized and current physiological limit, such as the thermal limit, represents the amount of environmental change an organism can tolerate before distributional changes occur, given that all other interactions remain the same – as is currently assumed in most other modelling approaches. This difference is often referred to as the existing thermal tolerance (ETT), warming tolerance, or thermal safety margin (Kellermann *et al.*, 2012b). Variation in realized niche between closely related species is often the outcome of allopatric diversification and range shift in a spatially autocorrelated environment (Warren *et al.*, 2014). If the pattern suggests that vicariance has driven diversification between sister pairs, and also implies competitive exclusion, as illustrated in Box 1, we can use this information to reconstruct maximum thermal limits across a phylogeny.

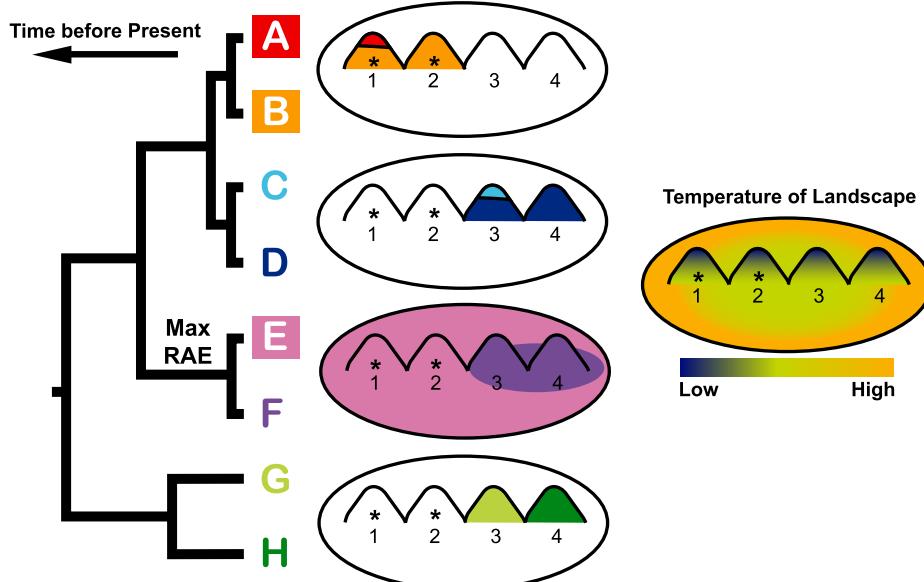
A practical approach to estimating evolutionary physiological limits is based on the hypothesis that although current trait limits may vary between species, clades of species often have firm limits beyond which acquisition of a novel trait, or key innovations, is required (Losos, 2010), as demonstrated in the literature (Rabosky *et al.*, 2007; Matschiner *et al.*, 2011; Blount *et al.*, 2012). In our example (Box 1), the concept that closely related species have a shared physiological machinery, and therefore physiological limits, can be applied by utilizing the maximum realized thermal limit within closely related species.

A broad range of evolutionary, ecological and life-history factors determine the rate of adaptive evolution, defined as changes in genotype in response to selection. These factors can be directly related to evolutionary estimation, such as the heritability of key traits. However, for most non-model organisms we need to employ evolutionary and ecological correlates as proxies for the potential rate of adaptive evolution (Table 2), including utilizing maximum rates of trait evolution as in Box 1. In many cases these estimations of the evolutionary history of the niche could be tested empirically using ancestral state reconstructions (e.g. Kellermann *et al.*, 2012a) and related statistical tests.

The example in Box 1 illustrates how the current physiological limit, the evolutionary physiological limit and the rate of adaptive evolution might be estimated for modelling. Where we know very little about the physiology of species we can

Box 1.

Hypothetical example of how current physiological limits and evolutionary limits might be estimated from distributional data. The figure indicates the phylogenetic relationship between eight species and their distribution across four mountains, with the main interest being predictions of changing distributions of species on two mountains (marked with an asterisk). The species occupying the target region are represented by letters in boxes and distributions are colour coded. The table outlines how the different parameters for the species were identified. The landscape on the right indicates the temperature profile.



Parameter:	Species A	Species B	Species E
Current Physiological Limit (CPL)	The ability of B to occupy similar climate space on mountain 2 as Species A on mountain 1, and the replicated distribution of sister clade (C,D) on mountains 3 & 4 suggest A and C are limited primarily by competitive interactions. Therefore the CPL of A is probably the maximum extent of B and D.	All species within the clade have the same realized thermal limit (except E & F, which are sympatric and therefore not competitively excluding other species from the plain). Therefore, the realized thermal limit of B, which is the same as D, G, & H, is the CPL of B.	Limited by current thermal environment, the CPL likely is realized thermal limit of E.
Evolutionary Physiological Limit (EPL)	All species within the clade, except E and F, have similar realized thermal limits. This suggests that the maximum extent of the EPL is that of E, and applies to all other species in the clade.	All species within the clade, except E and F, have similar realized thermal limits. This suggests that the maximum extent of the EPL is that of E, and applies to all other species in the clade.	As E has the highest known realized thermal limit, we cannot assume that further evolution is possible, and the EPL is the same as the realized thermal limit.
Rate of Adaptive Evolution (RAE)	The RAE, in units of time, is the rate of niche change on the branch marked Max RAE on the phylogeny. Because E & F are parapatric, suggesting competitive exclusion, the rate is only estimated to the ancestral node of E & F.	The RAE, in units of time, is the rate of niche change on the branch marked Max RAE on the phylogeny. Because E & F are parapatric, suggesting competitive exclusion, the rate is only estimated to the ancestral node of E & F.	Species E is at the EPL, therefore adaptive evolution is unlikely.
Modelling Implications:	Accurate modelling of A requires existing thermal tolerances to be incorporated into models because it is likely to tolerate a higher level of change prior to changes in distribution. Evolution is likely to contribute to persistence, but in the future.	Accurate modelling of B requires adaptive evolution to be incorporated into models, as evolution is likely to contribute to persistence in the near term.	Current modelling methodology adequate as species likely fills fundamental thermal niche and has little capacity for adaptive evolution.

approximate the current and evolutionary physiological limits of each species based on phylogenetic relationships and distributional data, and the rate of adaptive evolution based on rates of niche evolution estimated across a phylogeny. A key factor in the phylogenetic approach is that it is dependent upon statistical non-independence due to phylogenetic relatedness or phylogenetic signal (Losos, 2008). Once phylogenetic signal for the target trait becomes small between the outgroup and target group, this approach is likely to become less useful for parameter estimation, as shared evolutionary history no longer provides information on trait evolution in the target clade.

OPPORTUNITIES FOR INCORPORATING PARAMETERS INTO MODELLING

Our framework is not intended to replace, nor compete with, the many existing species- and community-level approaches to the spatial modelling of biological responses to climate change, but rather to provide a simple means of extending these approaches to consider the potential effects of adaptive capacity.

Species-level mechanistic modelling has already taken some steps towards incorporating a few, or occasionally all, of the parameters defined in our framework (Kearney *et al.*, 2009;

Table 1 Types of information likely to be of value in estimating or predicting realized limits, current physiological limits, or evolutionary physiological limits.

Information type	Contribution to parameter estimation
<i>Realized limit</i>	
Distribution data	Species presence data, where well-sampled, provides explicit information on environmental tolerances of a species
Expert opinion	Spatial polygons created by experts on the target taxa can give a basis for estimating environmental tolerances
Species distribution models	Carefully considered models utilizing less dense distribution data can give a probability of presence in an area, which can then be used to estimate the environmental niche a species is likely to occupy
<i>Current physiological limit</i>	
Physiological measurements (e.g. thermal maxima)	Provide explicit information on the physiological limits of a species
Common garden experiments	Provide explicit information on the ability of organisms to survive in different environmental profiles; tests the innate variation in species tolerances
Prediction from climatic variables	Climatic variability, extremes and precipitation are linked to physiological limits, with species experiencing greater climatic variability or higher extremes having greater physiological limits
Niche position	Niche position in multivariate hyperspace is correlated with physiological limits – species in more extreme niche have higher fundamental limits
Range size	Species with narrow ranges fill less of the fundamental niche
Phylogenetic trait prediction	Missing trait information (e.g. CTMax) can be predicted from phylogeny and environment for single species
<i>Evolutionary physiological limit</i>	
Cladistic limits	Strong phylogenetic signal in traits such as upper thermal limits suggests limited potential for evolutionary change
Trait data from related species in a similar environment	Ecosystems with similar climatic history are likely to contain organisms with similar thermal traits, and data on species separated through vicariant events may provide information on similar species in allopatric but similar environments

Full references available in Table S1.

Huey *et al.*, 2012; Kearney, 2012). There is also considerable potential to incorporate these parameters into correlative species distribution modelling (e.g. Maxent; Elith & Leathwick, 2009), not by changing the model-fitting process itself but rather by extending post-hoc analyses employing these models in projecting distributional shifts under climate change. By clearly interpreting the output of correlative models as the ‘realized niche’, analysis of predicted distributional changes in light of the estimated current physiological limit becomes possible. Then the estimated rate of adaptive evolution could be used to shift this physiological limit progressively over the time-scale of the projection. For example, in projections of distributional shifts in *Eucalyptus* species through future climate change (Butt *et al.*, 2013), the current physiological limit could be incorporated through cladistic assessments as per the hypothetical example in Box 1. In long-lived trees such as eucalypts, the rate of adaptive evolution is likely to be low due to long generation times, high genetic admixture through to pollen dispersal, and age-related fecundity (Kuparinen *et al.*, 2010; Table 2), thus the rate of adaptive evolution would be extremely low, possibly undetectable in a 100-year time frame. Given the prevalence of projections based on correlative species distribution modelling (Elith & Leathwick, 2009), incorporating estimated parameters from our framework

offers a significant opportunity to better address adaptive capacity in such work.

Similar opportunities exist for incorporating estimates of these parameters into community-level modelling of the impacts of climate change on community composition, or turnover, employing either correlative (e.g. Ferrier *et al.*, 2007) or semi-mechanistic (e.g. Mokany *et al.*, 2012) approaches. As depicted in Fig. 2(b), species in different assemblages within a guild spread along an environmental gradient are likely, on average, to not only occupy different realized portions of environmental space but may also exhibit different current physiological limits. The challenge in defining such parameters for community-level modelling is to identify patterns of adaptive capacity correlated with trait distribution and the evolutionary processes that determine the evolution of such traits. For example, studies on birds have identified that species occupying extreme niche space and with a small population size have poorer responses to habitat loss (Lavergne *et al.*, 2013), while studies on reptiles have found that existing thermal tolerance varies by continent (Grigg & Buckley, 2013). Building spatial community assemblage databases on the basis of findings such as these provides a significant opportunity to expand community-based modelling to represent the fundamental versus realized niche, and improve our predictions of turnover under climate change.

Table 2 Non-exhaustive list of research areas, and types of information, likely to be of value in estimating or predicting potential rates of adaptive evolution.

Research area	Effect	Biological explanation for adaptive evolutionary effect
<i>Population genetics</i>		
Heritability and phenotypic variance	+	Allows better phenotypic matches to changing or heterogeneous environment
Standing genotypic variation	+	Increases likelihood of suitable alleles being present in the population
Hybridization (intraspecific)	+/-	Determined by extent of local adaptation, may suppress adaptation, or generate novel phenotypes
Hybridization (interspecific)	+/-	Likely to be negative, but may be positive if novel phenotypes can be generated
<i>Patterns of genetic variation</i>		
Areas of high neutral diversity	+	Areas with higher diversity have greater capacity for evolutionary response
Adaptive loci on ecological gradients	+	Organisms with adaptive loci are likely to possess variations more suited to future ecosystems
<i>Genomics</i>		
DNA decay	-	Loss of gene function probably indicates specialization
Presence of candidate genes	+	Species with genes that are associated with specific stress tolerance phenotypes provide capacity to tolerate extremes
Gene duplication	+	Multiplication of genes associated with stress may improve adaptive responses
Inversion frequency	+	Increasing inversion frequency may indicate blocks of genes are under adaptive selection
<i>Population dynamics</i>		
Population size	+	Larger populations have greater likelihood of recovery from a similar proportional decline than a smaller population, and will lose less genetic diversity in bottlenecks
Generation time	-	Longer generation times increase lag behind the selective optimum
Overlapping generations and low mortality	-	Greater overlap and low adult mortality increases lag behind the selective optimum
Age-related fecundity	-	Increasing fecundity with age increases lag behind the selective optimum
Density dependence	-	Increasing density dependence reduces the chance of recovery from demographic decline
Fluctuating population size	-	Changes in population size (boom/bust cycles) reduce long-term effectiveness of selection
Interspecific competition	+/-	Level of overlap influences rates of adaptation through competitive exclusion
Dispersal distance	+/-	Distance interacts with ecological gradients to impact adaptation
<i>Ecosystem and niche information</i>		
Niche breadth/clinal variation	+	Species with a larger niche breadth are likely to have more variation suitable for changing climates and greater standing genetic variation
Relative niche position	+/-	Species at extreme positions in niche space are likely to have a lower ability to adapt to further extremes
Environmental predictability	+	Greater predictability allows closer match through plasticity, and more effective selection pressure
Climatic stress history	+	History of climatic stress linked to an increased rate of adaptation
Rate of niche evolution	+/-	Historical changes in niche within clades may indicate underlying niche lability

'Effect' refers to whether the factor concerned increases (+) or decreases (-) capacity to have an evolutionary response.

Full references are available in the Table S2.

REFOCUSING ADAPTATION RESEARCH

Many areas of research of possible relevance to estimating the parameters defined in our framework have already made, or are making, progress in identifying species traits that have the potential to serve as indicators of adaptive capacity. Approaches involving in-depth consideration of relevant processes, such as that illustrated in Box 1, are likely to be most effective for modelling small numbers of species within better-known taxa. However, application of our framework to modelling larger numbers of species, including through the use of community-level modelling, will often require the use of simpler correlative approaches. Our intention is not to evaluate the science behind each area of research, but to illustrate the types of data and methodologies that may prove relevant to future estimations of

species vulnerability. Yet numerous areas of research exist that provide information relevant to parameter estimation. As shown in Table 1 and Box 1, reasonable estimations of the realized limit, current physiological limit and evolutionary physiological limit can be generated using data ranging from climate and niche information, to phylogenetic data and physiological measurements, or from comparisons between closely related species. The types of data informing the capacity for adaptive evolution (Table 2) are more varied, and targeted research into quantifying the rate of adaptive evolution, as a parameter of adaptive capacity, is needed.

The challenge ahead is to move from qualitative to quantitative descriptions of the expected relationships between candidate indicators and actual values for the parameters we have defined. The overall strategy that we envisage for addressing this

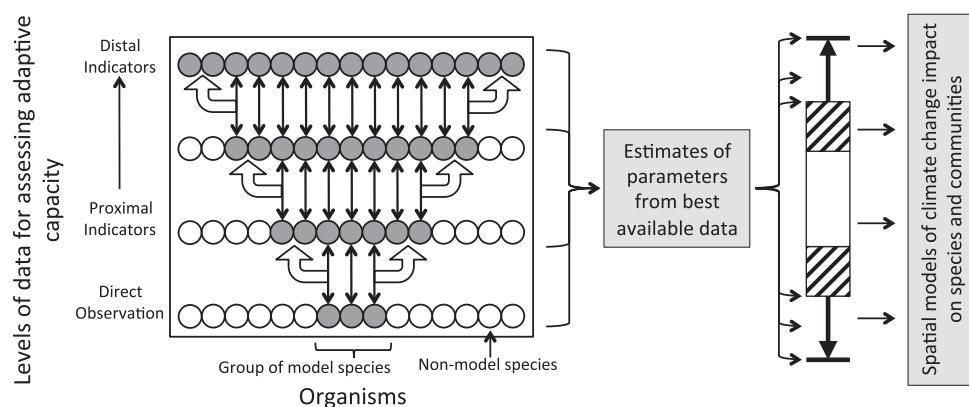


Figure 3 To apply our framework universally across both model organisms (dark circles) and non-model organisms (light circles), research must first investigate correlations (bottom row of black arrows) between proximal indicators, and direct observations, of adaptive capacity in model species. Once such correlations are established for more proximal indicators these can be used to estimate adaptive capacity across an increasingly broad set of species (white arrows) thereby enabling, in turn, the exploration of correlations with more distal indicators (middle and top rows of black arrows), and eventually culminating in prediction of adaptive capacity across any species of interest based on best-available indicators.

challenge is depicted in Fig. 3. This involves a cascading hierarchy of levels of information for estimating adaptive capacity, ranging from direct observations (e.g. from physiological or evolutionary experimentation) based on traits closely linked to the parameters of interest, through proximal to distal indicators based on traits less directly linked to these parameters. Of particular interest is the use of growing numbers of observational data for model organisms to develop straightforward methods for assessing adaptive capacity, which can then be used to test and calibrate ecological and/or phylogenetic proxies for rapid assessment of non-model organisms (Fig. 3).

The mechanistic modelling of adaptive evolution in dengue mosquitoes by Kearney *et al.* (2009), which incorporated empirical measures of physiological tolerance and modelled trait evolution in response to climate change, serves as an example of what can be gained by extending spatial modelling in this direction. Detailed studies of this type, using model organisms, are showing considerable potential to identify ecological and evolutionary traits that are correlated with adaptive capacity – including many of the individual-, population- and environmental-level traits reviewed in Tables 1 & 2 – and to quantitatively calibrate these relationships. As depicted in Fig. 3, correlations established between proximal indicators and direct observations of adaptive capacity for model species can be used to estimate adaptive capacity across a broader set of species (e.g. species lacking direct observations, but with data on proximal indicators). This, in turn, enables the exploration of correlations with more distal indicators. This strategy, taken to its logical conclusion, offers a means of estimating, or at least predicting, adaptive capacity across any species of interest based on the best available indicators.

Further, the big data sets being assembled across a range of disciplines offer considerable potential to develop broadly applicable indicators of adaptive capacity. For example, a recent study of European plants now naturalized in the USA found that species that natively occupy narrow ranges or marginal niche

positions colonize further outside their native climate conditions than those with wider, or closer to average, niches (Early & Sax, 2014), suggesting a plausible path to estimating necessary parameters from distribution data. A study of range shifts found that changes in the distribution of marine organisms more closely match thermal tolerances than did the distributional shifts of terrestrial organisms (Sunday *et al.*, 2012). The expansion of these types of studies, and validation of their results across taxonomic groups (e.g. that species with narrow ranges have significant ETT across taxa, or that marine species are more susceptible to thermal shifts), opens up considerable opportunities to improve assessments of adaptive capacity for climate change research and mitigation planning.

CONCLUSION

The parameter framework we have described offers a relatively simple and generic foundation for incorporating a consideration of physiological limits and the capacity for evolutionary adaptation into spatially explicit modelling of biological responses to climate change. We see considerable potential for the parameters that we have defined to play an important role in integrating on-going research exploring indicators of adaptive capacity with on-going development of modelling approaches, by effectively providing a ‘common currency’ linking these two vital domains.

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- Additional references pertaining to the data sources used in this study can be found in the Supporting Information after Table S2.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1 References for Table 1.

Table S2 References for Table 2.

BIOSKETCHES

Renee A. Catullo investigates how biological information can improve spatial models of climate change impact on biodiversity.

Simon Ferrier develops macroecological modelling approaches to assessing and projecting impacts of global change on biodiversity.

The research of **Ary A. Hoffmann** addresses the way organisms evolve to deal with environmental stresses.

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