REVIEW AND SYNTHESIS

Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges

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Abstract

Species distribution models (SDMs) use spatial environmental data to make inferences on species' range limits and habitat suitability. Conceptually, these models aim to determine and map components of a species' ecological niche through space and time, and they have become important tools in pure and applied ecology and evolutionary biology. Most approaches are correlative in that they statistically link spatial data to species distribution records. An alternative strategy is to explicitly incorporate the mechanistic links between the functional traits of organisms and their environments into SDMs. Here, we review how the principles of biophysical ecology can be used to link spatial data to the physiological responses and constraints of organisms. This provides a mechanistic view of the fundamental niche which can then be mapped to the landscape to infer range constraints. We show how physiologically based SDMs can be developed for different organisms in different environmental contexts. Mechanistic SDMs have different strengths and weaknesses to correlative approaches, and there are many exciting and unexplored prospects for integrating the two approaches. As physiological knowledge becomes better integrated into SDMs, we will make more robust predictions of range shifts in novel or non-equilibrium contexts such as invasions, translocations, climate change and evolutionary shifts.

INTRODUCTION

An understanding of the constraints on the distribution and abundance of species has long stood as a primary goal in ecology (Andrewartha & Birch 1954). To even the casual observer of nature, there are clear correlations between where different animals and plants thrive and coarse environmental variables such as climate, soil, terrain and vegetation. The advent of geographical information systems (GIS) and fine-resolution digital maps of terrain and climate have allowed ecologists to develop powerful and sophisticated means to study these associations, giving rise to the field of species distribution modelling. In particular, there has been major progress in the development of species distribution models (SDMs) that can link species distribution records or abundances to environmental data (reviewed in Guisan & Zimmerman 2000; Guisan & Thuiller 2005; Elith *et al.* 2006). These correlative SDMs require little knowledge of the mechanistic links between organisms and their environments, which is often an advantage for poorly studied taxa. In many circumstances, however, it is desirable to explicitly incorporate potentially range-limiting processes. For instance, a mechanistic SDM can provide deep understanding of the proximate constraints limiting distribution and abundance, and may be more robust in contexts of environmental change that require extrapolation of correlative SDMs (Davis *et al.* 1998; Dormann 2007).

The most basic and fundamental constraints on the distribution and abundance of organisms are their physiological limitations and in this review, we focus particularly

on how physiological knowledge can be directly incorporated into SDMs. The field of physiological ecology has developed over many decades leading to a wealth of knowledge about physiological constraints on organisms (Helmuth *et al.* 2005; Chown & Gaston 2008). However, a major barrier to the development of physiologically grounded SDMs has been in linking data on the limiting behavioural, morphological and physiological traits of organisms with GIS datasets on climate and terrain. In this paper, we discuss how the techniques of biophysical ecology (Gates 1980) provide the tools to make such links and therefore provide a basis for developing mechanistic SDMs. We review the current state of this newly emerging field, discuss its utility in both theoretical and applied contexts in comparison with correlative approaches, and suggest future directions in which mechanistic SDMs may be taken.

SPECIES DISTRIBUTION MODELS AND THE NICHE CONCEPT

The ecological niche has become a central theme in species distribution modelling (Kearney 2006; Soberon 2007; Pearman *et al.* 2008). The niche concept has been used and defined in a bewildering number of ways (Chase & Leibold 2003), but in the context of SDMs it is considered in the Hutchinsonian manner as a hypervolume in multivariate environmental space that depicts a species' environmental limitations. The development of a SDM can be conceived of as first constructing an ecological niche model, and then projecting it onto space to infer a species' potential distribution.

There are many ecological and evolutionary processes that influence a species' distribution and abundance, including but not limited to aspects of a species' niche (Fig. 1). At one level, these include the interactions between the functional traits of the organism and its habitat as it attempts to obtain sufficient conditions and resources to maintain homeostasis, develop and reproduce. For example a frog will behaviourally exploit its microhabitat to find environments where it can maintain positive water balance, achieve suitable body temperatures for capturing and digesting prey, and, at some stage, lay its eggs. Where this interaction permits the completion of the life cycle and sufficient births to compensate deaths, population growth remains non-negative and the site (habitat) is suitable. Such a site may be described as providing environments within the organism's fundamental niche (Hutchinson 1957). At a second level, interactions between the focal species and
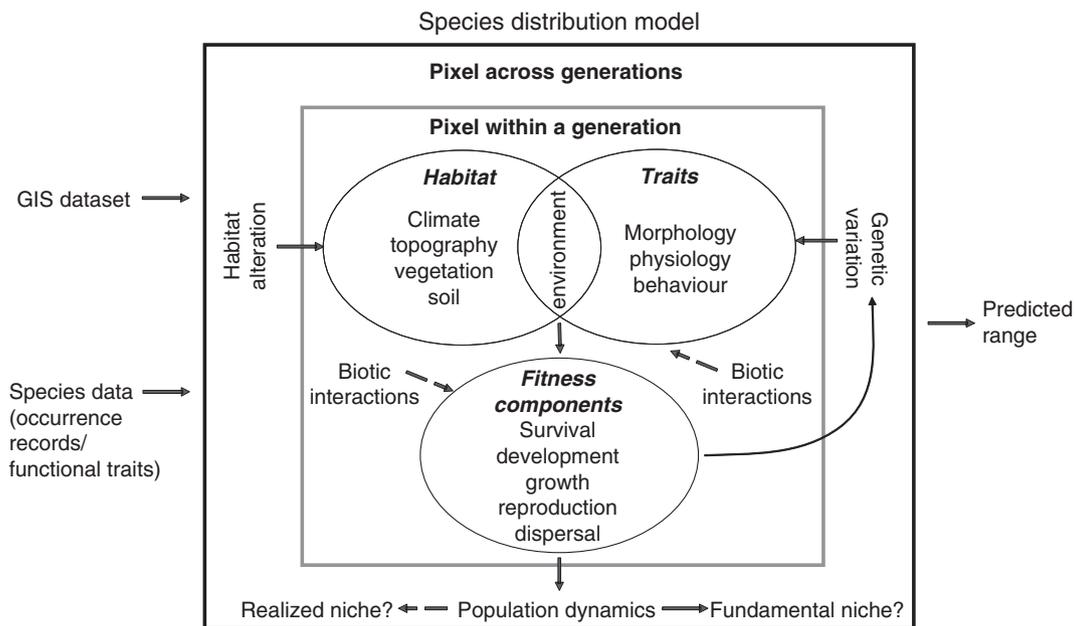
Figure 1 Major ecological processes captured by a species distribution model (SDM). In a correlative approach, species occurrence data are linked to geographical information systems (GIS) data through a statistical description that implicitly captures these processes to the extent that they are statistically associated with the predictor variables. In a mechanistic approach, functional trait data are linked to GIS data through a model that explicitly captures the key processes by which traits and habitat features interact to determine the species' environment. The outcome of that environment for individual fitness (survival and reproduction) and ultimately population dynamics is then mapped to the landscape. These processes may or may not include biotic interactions (realized niche vs. fundamental niche). Intergenerational changes in habitat characteristics (environmental change) and functional traits (evolutionary change) can be incorporated to produce dynamic models.

other non-prey species, i.e. competition, predation and disease, will act as constraints that further limit the environmental conditions where survival and reproduction is possible. If non-negative population growth is possible in the face of these biotic interactions, a site may be considered as providing environments within the organism's realized niche. Finally, movement patterns at the landscape scale, as dictated by dispersal behaviours and constraints, will affect metapopulation dynamics and thus the long-term persistence of the population at that site. This can lead to species being present in habitats outside its niche (population sinks), or absent from areas within its niche (Pulliam 2000).

Ecological niche models are developed very differently for correlative and mechanistic SDMs (Table 1, Fig. 2). Correlative SDMs begin with geo-referenced locality records for a species. A presence (or high abundance) record suggests that, at some stage, individuals of that species were able to develop, survive to the adult stage and successfully reproduce in that location (but see Pulliam 2000). Spatial conditions also geo-referenced to that site, such as climate or soil, are then inferred to be within that species' tolerance range. This alters model parameters or coefficients such that other sites with similar conditions are weighted in favour of a prediction of presence (Fig. 2a), ultimately defining a multivariate space of suitable environmental conditions (Fig. 2b) [we prefer to consider this as a description of an organism's habitat rather than its niche (Kearney 2006)]. Implicit in these parameters are many of the ecological processes and interactions that lead to successful persistence at that site, to the extent that they are statistically associated with the chosen predictor variables (Fig. 1). This is the great strength and advantage of correlative approaches. However, it is not clear whether a given response represents a direct causal relationship with that variable, an indirect effect mediated by a biotic interaction, or a direct response to another collinear variable absent from the model (Mac Nally 2000). Thus correlative SDMs do not necessarily reflect a mapping of the fundamental niche to the landscape (Pearson & Dawson 2003; Kearney 2006).

If a species' niche is to be modelled mechanistically to make inference on its potential range, the organism must not enter the model as a point on a map but rather as a set of behavioural, morphological and physiological traits. For instance, the thermal niche of an organism reflects a physiological response to its body temperature (Fig. 2c). Body temperature in turn reflects an interaction between local environmental variables such as air temperature, wind speed and radiation as well as characteristics of the animal such as body shape and size, solar reflectivity and its behavioural choice of microclimatic environment (Fig. 2d). The challenge is to link key functional traits to the spatial habitat data through a mechanistic model that captures the processes in Fig. 1, translating the interaction of the organism with its environment into key fitness components. This represents a mechanistic model of a species' fundamental niche (Fig. 2d), which can then be mapped to the landscape to infer its potential distribution.

BIOPHYSICAL ECOLOGY: BRIDGING THE GAP BETWEEN FUNCTIONAL TRAITS AND CLIMATE

Climate is a principle driver in most species distribution models and we focus on climatic factors in this review, although other physical factors such as soil types and water chemistry could be substituted. Organisms are most intimately connected to climatic conditions through exchanges of energy and mass. The field of biophysical ecology applies the principles of thermodynamics to organisms to derive mechanistic models of these processes and their physiological consequences (Porter & Gates 1969; Gates 1980). This field had its origins in the work on lizards (reviewed in Tracy 1982; Porter et al. 2000) and has since been applied to a variety of different organisms and environmental contexts. As we will illustrate, these procedures are now being used in conjunction with GIS data on climate and terrain to make inference on species distributions (Porter et al. 2000; Kearney & Porter 2004; Buckley 2008).

Biophysical ecology is specifically concerned with transport phenomena: heat transfer, mass transfer and, less commonly, momentum transfer (or fluid dynamics) (Bird et al. 2002). These phenomena often occur simultaneously, are highly analogous, and are mathematically characterized by balance equations which can be solved on the basis of the conservation laws of thermodynamics. Energy balances depend on the exchange of heat through the processes of conduction, convection, radiation and evaporation. Mass balances depend on exchanges of gases through the respiratory surfaces, food (dry matter) through the intestinal tract, and water through the gut, respiratory surfaces and excretory organs. Solving the energy balance equation for an ectotherm (Fig. 3) provides an estimate of the core body temperature given a set of environmental conditions, a critical variable with regard to physiological function and survival. For an endotherm, solving the same equation provides an estimate of the metabolic rate or evaporative heat loss required to maintain a stable core temperature, depending on whether the organism is above or below its thermal neutral zone. The energy balance equation is coupled with the mass balance equations describing food, gas and water exchange through the metabolism and evaporation terms (Fig. 3). Thus one can determine the energy and mass balance of an organism under a single mechanistic framework.

Clearly, an organism cannot survive long in locations where it would be in negative energy or mass balance, and

Table 1 A comparison of mechanistic and correlative approaches to species distribution modelling

	Mechanistic (physiological) approches	Correlative (statistical) approches	Advantages of mechanistic approches	Advantages of correlative approches
Conceptualization				
Theoretical basis	Energy/mass balance, 'climate space', mechanistic conceptualization of the Hutchinsonian niche	Probability, statistical theory, pattern recognition, often considered in the context of the Hutchinsonian niche or habitat concepts	Grounded in physico-chemical principles, provides mechanistic understanding of underlying processes	Can implicitly incorporate any process, biotic or abiotic, statistically associated with the independent variables, can be used to develop hypotheses about underlying processes
Model selection	Prescribed (variants of an energy balance equation)	Flexible (numerous algorithms and variable selection procedures, e.g. regression, maximum entropy, polynomial/linear terms)	Energy/mass balance equation provides a common frame of reference	Can be more easily tailored to fit available data
Generality (transferability) and precision	High generality across environments but potentially low precision	Local analysis often with high precision, although choice of variables and fitting strategy can be tailored for emphasizing generality or precision	Scope of applications extends to non-equilibrium/novel circumstances	More likely to capture a limiting processes, less likely to overestimate potential range
Data requirements				
Species data	Functional traits, (morphology physiological and behavioural responses)	Occurrence data (presence only, presence/absence or abundance records)	Directly applies physiological understanding to range prediction. Can be applied when occurrence data is limited or in non-equilibrium/novel circumstances	Exploits a more commonly available data source
Spatial data	Prescribed – energy balance equations demand specific independent variables	Flexible	Less subjectivity in variable selection	While directly related (proximal) environmental variables are preferable, can exploit a wider range of proxy spatial data types
Scale	Prescribed – highly proximal (scale of an individual organism)	Flexible	Less subjectivity in variable selection	Can use data sets of a wider range of scales, can capture processes at different scales within a single model
Model fitting				
Parameters	Trait values, energy/mass transfer coefficients, physiological response curves (may themselves be parameterized statistically)	Dimensionless coefficients	Robust because parameters are estimated independently of the (geographical range/abundance) data	Pragmatic because parameters are estimated from a single dataset within a single analytical framework

Table 1 Continued

	Mechanistic (physiological) approches	Correlative (statistical) approches	Advantages of mechanistic approaches	Advantages of correlative approaches
Geographical variation (plastic and genetic)	Explicit	Implicit	Permits assessments of the degree of geographical variation and inference on its adaptive significance	Easier to incorporate geographical variation because it is indirectly represented in the occurrence data
Evolutionary change	Explicit	Implicit	Permits explicit consideration of evolution, avoids confounding with other processes that may alter environmental associations through time	Can exploit readily available datasets to set up testable hypotheses about the past evolution of traits
Inference				
Output	Fitness components (survival, performance, development, growth and reproductive capacity)	Dimensionless habitat suitability indices or estimates of probability of occurrence or abundance	Highly interpretable ecologically, may serve as input into other process models (e.g. dispersal)	Provides a simple output indirectly representing many different processes
Validation and evaluation	Validation through independent empirical studies (field and laboratory), e.g. of behaviour, body temperature, energy and water turnover, evaluation against independently observed occurrence	Fit evaluated against original occurrence input data, subsets of original data left aside for validation, or (rarely) independent data on distribution and abundance	Biologically grounded and independent of the data used to derive the model	Often easier because model construction and validation/evaluation uses a single, readily available dataset and analytical framework

its reproductive capacity will be closely tied to 'profits' in these currencies. Thus, an analysis of the energy and mass balance of an organism as a function of climate provides information on basic biological processes required for survival and reproduction, i.e. the fundamental niche. For the remainder of this section, we provide a very brief synopsis of how the techniques of biophysical ecology can be applied to different organisms, pointing the interested reader to key literature for further details.

Small dry-skinned ectotherms

The core temperature of many reptiles, insects and other invertebrates can be adequately modelled using steady state energy balance equations assuming little or no cutaneous water loss. By steady state, it is meant that the organism has stabilized at the core temperature it would attain if placed indefinitely in the environment of interest, i.e. there is no heat storage. This is also known as the 'operative environmental temperature' and can be determined empirically with physical models of low heat capacity that capture the thermal properties of the organism in question (e.g. Porter

et al. 1973b). For mathematical models of heat transfer of such organisms, the dominating energy fluxes to be included are thus radiation, convection and, in some cases, conduction. Key challenges in determining these fluxes involve empirical measurement of solar reflectivity, surface areas involved in radiative convective, and conductive exchange, and convection coefficients (Porter et al. 1973b; Kingsolver & Moffat 1982).

Small wet-skinned ectotherms

While evaporative heat exchange is of minor significance to the core body temperatures of small, dry-skinned ectotherms, it is of great significance to their mass balances. Moreover, many taxa including amphibians and molluscs have very wet integuments across which considerable amounts of heat (and water) are exchanged. Procedures for calculating these exchanges to both the air and substrate have been detailed for frogs (Tracy 1976), and these procedures are readily generalized to other wet-skinned taxa. Methods exist for partitioning cutaneous and respiratory water loss to calculate the fraction of the total surface area
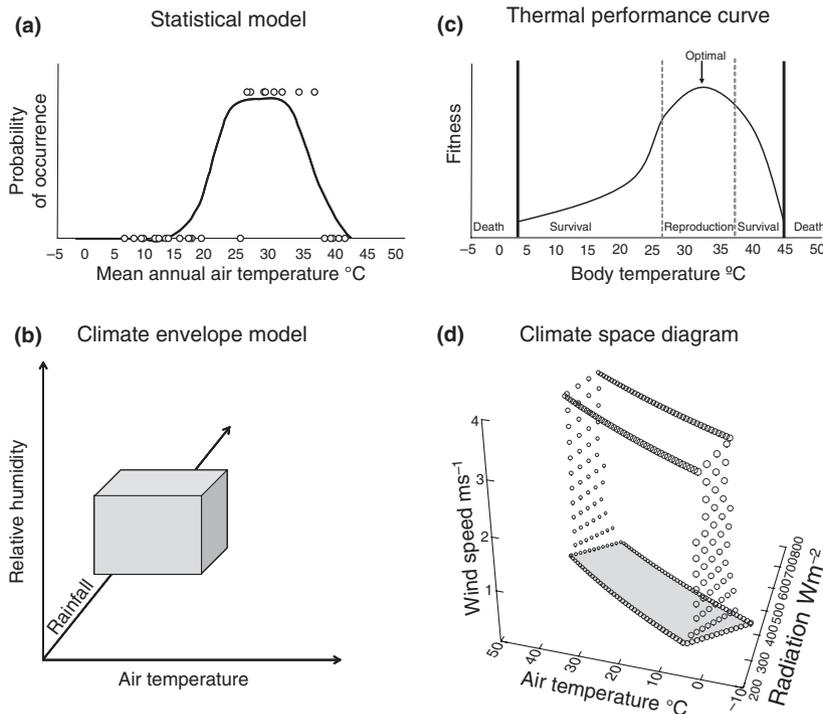
Figure 2 Ecological niche concepts used in developing species distribution models. For correlative models, species occurrence data (e.g. presence/absence or abundance) is modelled as a function of spatial data such as air temperature (a), ultimately describing a hypervolume in multivariate space within which the organism has been observed (b). This may be a simple box-shaped space as depicted in this figure (representing, e.g. a Bioclim analysis), or a more complex space defined by non-linear responses and interaction terms. This niche is then mapped to the landscape to infer the potential distribution. In contrast, mechanistic species distribution models can be derived through knowledge of physiological processes. For instance, a thermal performance curve (c) represents a fitness component (e.g. survival, growth, development, reproduction, movement potential) as a function of body temperature. The principles of biophysical ecology can be used to translate multivariate environmental space into a set of body temperatures as a function of key traits (e.g. size, solar reflectivity and metabolic rate), and the performance curve can then be invoked to describe the 'climate space' within which the performance curve constrains survival and reproduction (d). This represents a mechanistic depiction of a species' fundamental niche which can then be used to infer distribution limits.

acting as a free-water exchanger (Appendix D of Kearney & Porter 2004). This is a key trait allowing one to generalize from measurements of water loss rates under particular combinations of wind speed, air temperature, relative humidity and body size to any other combination.

Endotherms

In some organisms, sufficient metabolic heat is produced that it significantly affects core body temperature. These include birds and mammals, some insects, and even some plants. Where homeothermy is maintained, one can solve for the unique metabolic rate that satisfies the energy balance equation (Porter & Gates 1969; Porter et al. 1994; Porter et al. 2000; Porter & Mitchell 2006). As heat load on an endotherm rises, the metabolic rate eventually reaches a lower limit (basal metabolic rate) and in response many endotherms then alter their evaporative heat loss and hence

their mass balance. Animal geometry and posture are key variables affecting metabolic heating, as is the insulation (fur, feathers and setae) if present, and general solutions have been provided for calculating their influence on energy balances (Porter et al. 1994; Porter et al. 2000; Porter & Mitchell 2006).

Large organisms

As body size increases, an organism's capacity for heat storage increases and its temperature changes more slowly. If the environmental conditions change faster than the temperature of the organism, it is no longer in steady state but instead lagging behind. Such a state is referred to as 'transient' and becomes important in modelling large organisms or when working on very fine time-scales, where heat storage capacity acts to dampen temperature fluctuations relative to steady-state conditions. This is

Figure 3 Coupled energy (Q) and mass (m) balance equations can be developed for organisms and their habitats (from Porter and Tracy 1983). Energy is exchanged in the form of heat (diagonal equation) through the processes of conduction, convection, radiation, evaporation and metabolism. The heat energy balance equation is intersected by two mass balance equations at the metabolism term – the mass balance for dry food (horizontal equation) and the mass balance for respiratory gases (vertical equation). The heat balance equation is also intersected by the mass balance for water at the evaporation term. Food ingested minus that defecated is equal to food absorbed, which is available as energy for metabolism. Energy not used for maintenance or activity (discretionary energy) may be allocated to growth, reproduction or storage. The mass of oxygen plus the mass of oxidizable substrate equals the mass of carbon dioxide produced, by-products of nitrogen-containing waste products from protein metabolism as well as water. Water produced by metabolic reactions is an input into the water balance. Water ingested minus water lost by defecation is the absorbed mass of water plus metabolic water. A fraction of this water may be evaporated or lost in urine, and the remaining (discretionary) water may be allocated to growth, reproduction or storage.

computationally more challenging and various solutions have been proposed (e.g. Spotila *et al.* 1973; Stevenson 1985; Seebacher *et al.* 1999; Christian *et al.* 2006).

Aquatic organisms

Some aquatic organisms periodically experience areal conditions and detailed biophysical models have been developed for intertidal organisms, especially mussels (Helmuth 1998; Gilman *et al.* 2006). Most aquatic organisms are permanently under water where heat exchange is dominated by convection, and they assume the temperature of the surrounding water. Only those organisms capable of some degree of endothermy can maintain core body temperature above water temperature, and energy balances for such organisms can be solved using the principles for endotherms described above.

Momentum balances become very important for the energy and mass requirements of organisms that swim or must maintain position in water currents (Prange 1976), or under conditions of wave splash (Helmuth & Denny 2003), and also affect patterns of growth in organisms like corals and sponges (Sebens *et al.* 2003). Momentum balances for swimming can dictate most of an animal's energy and mass requirements because locomotion is much more costly in an aquatic medium. This is especially so for large animals, such

as sea turtles, penguins, seals and cetaceans, and recent developments in numerical methods allow accurate estimates of these costs (e.g. Borazjani & Sotiropoulos 2008). Chemical energy used in locomotion results in heat energy release that tends to raise body temperature, and this internal heat production must be dissipated to appropriate water temperatures. Thus, the temporal and spatial distribution of species living in aquatic media can be directly constrained by the water temperatures available to them and by their own properties, especially body size.

Plants

Literature in the nominal field of biophysical ecology has been focused on animals. Yet, as is often the case, a rich and equivalent literature on plants has developed in parallel and quite independently under different banners (e.g. Gates 1980; Jones 1992; Campbell & Norman 1998). Only rarely has the literature on the biophysical ecology of plants and animals been integrated (Gates 1980; Campbell & Norman 1998) and the field would clearly benefit from greater interaction across the plant/animal divide. Biophysical responses of vegetation have major impacts on climate, hydrology and animal distributions at both small and large spatial scales through the processes of transpiration, sap flow, shading, nutrient content and water content.

Mechanistic models of plant mass and energy transport processes have been developed and tests of them are changing some basic assumptions about how plants may work (e.g. Daley & Phillips 2006).

In summary, biophysical models can be, and have been, developed for a wide range of organisms and can be very species-specific (and hence precise) depending on how finely the relevant traits are specified. For example, when modelling convection, one may use 'recipes' for convection coefficients derived for simple shapes like spheres, ellipses and cylinders, or one may empirically derive coefficients more specific to the organisms' shape (e.g. Porter *et al.* 1973b). The degree of precision required will depend on the particular application or question being asked. If such biophysical models of organisms are to be applied, however, one must also know the environment that the organism experiences.

RECONSTRUCTING ENVIRONMENTS AS ORGANISMS SEE THEM

Organisms do not passively experience their environments but actively construct or select them (Lewontin 2000; Oldling-Smee *et al.* 2003). For example, diurnal and nocturnal animals in the same habitat experience very different radiation environments, while plant root systems alter the structure of the surrounding soil, and body size and shape alters the depth of boundary layers of air adhering to the surface of an organism. Any mechanistic model of organism and environment must capture this two-way interaction in a realistic way. While there have been some attempts to incorporate physiological processes into species distribution models in both the plant (Sykes *et al.* 1996; Hijmans & Graham 2006) and animal (Sutherst *et al.* 1996) literature, typically they have not accounted for this dynamic interaction between organism and environment. Organisms do not, of course, experience the climatic conditions measured by weather stations but instead seek out microclimates that are in part the result of their own behaviour, morphology and physiology. A major challenge in modelling species distributions mechanistically as a function of their physiological constraints is thus to translate climate layers derived from weather station data into biologically relevant microclimates. This may involve developing general models of microclimatic conditions as a function of habitat, as well as specific models for microhabitat features used for shelter or oviposition. Such microclimatic estimates may also be of great value as more proximal variables for use in correlative modelling approaches (Austin 2002).

Modelling microclimates

Microclimatic conditions are strongly influenced by the interaction between climate, local topography, vegetation and soil (Oke 1992; Geiger *et al.* 2003). The key microclimatic variables required for solving energy and mass balances of organisms are: direct and diffuse solar radiation, infra-red radiation, air (or water) temperature, surface temperature, wind speed and relative humidity. A wide variety of microclimates are available to terrestrial organisms, contingent on their body size and behavioural repertoire. A suitable microclimate model will provide the ranges of these variables available to organisms in different parts of their habitat.

The energy, mass and momentum balance calculations described above for organisms can be applied to their habitats. This allows a mechanistic derivation of microclimatic conditions available to organisms as a function of macroclimatic (weather station) data as well as information on location, local terrain and vegetation characteristics. One such model (Porter *et al.* 1973b; Porter & Mitchell 2006) incorporates a first-principles solar radiation subroutine, a transient soil energy balance and micrometeorological equations for air temperature and velocity profiles with height above ground. It was developed for deserts but has since been applied in a wide range of contexts (Kearney & Porter 2004; Porter *et al.* 2006; Natori & Porter 2007; Kearney *et al.* 2008; Mitchell *et al.* 2008). A coarser model relying more on remote-sensing data was recently developed by Buckley (2008) using the equations presented in Campbell and Norman (1998). Microclimate models for intertidal organisms have also been developed that account for shifts between aerial and aquatic conditions on periodicities asynchronous with the daily cycle, as well as high energy wave environments and the influence of wave splash (Helmuth 1998; Helmuth & Denny 2003; Gilman *et al.* 2006).

Variable selection and scale are major issues for any kind of species distribution modelling (Guisan & Zimmermann 2000; Mac Nally 2000; Austin 2002; Guisan & Thuiller 2005; Austin 2007), and there are unique issues for modelling microclimates. First, mechanistic SDMs require more specific spatial datasets as inputs than do correlative SDMs, both in terms of variables and the spatio-temporal scale (Table 1). Correlative SDMs can take advantage of the statistical association between proximal variables directly affecting organisms and the more easily accessible 'distal' variables such as standard air-temperature and rainfall-related metrics, elevation and geographical location (Austin 2002). In contrast, many of the variables required for reconstructing microclimates, such as surface albedo, soil thermal properties, wind speed, cloud and canopy cover, are presently difficult to obtain or unavailable for many regions. Nonetheless, advances in remote-sensing and GIS technology are continuing to provide a wealth of resources useful for determining microclimatic conditions, including fine-scale topography and vegetation metrics (e.g. LIDAR,

NDVI, leaf area indices, high-resolution spectroscopy and subtle gravitation effects on satellite orbits that reveal subterranean water). For some applications, effects of slope and aspect on soil energy budgets are relevant and these variables can be easily derived from digital elevation models of the appropriate resolution. It is also possible to calculate hill-shade effects on radiation balances for regions of complex terrain (e.g. Dozier & Frew 1990). For some applications, mean monthly maximum and minimum values of macroclimatic conditions may provide suitable input, but for others, especially where extreme weather events are important, finer temporal scales may be more suitable.

Modelling microhabitats and incorporating behaviour

Animals often seek out or construct complex structures for shelter, oviposition, and other activities, and in some cases it may be necessary to separately model such features within the general microclimate at a location. For instance, Kingsolver (1979) modelled the environment inside pitcher plants to determine larval development in mosquitoes, Huey et al. (1989) considered rocky retreat sites of snakes and Kearney et al. (2008) modelled ponds used for spawning by toads. Many endotherms use tree hollows and other cavities as retreat sites with the complication that they significantly alter environmental conditions through their metabolism. In the case of parasites, it is necessary to develop a model of the host to determine available microclimates.

Once microclimatic conditions have been constructed, behavioural subroutines are required to assess the biophysical consequences of an organism using different parts of the available microclimatic space. For example, an animal's activity period may be nocturnal, diurnal or crepuscular, it may be terrestrial or arboreal, it may thermoregulate by seeking shade, retreating underground, climbing bushes, or through subtle alterations of posture/leaf angle or solar reflectance, etc (e.g. Porter et al. 1973a). In most cases, these responses will ideally be assessed on an hourly timescale or shorter, thus the microclimatic estimates must also be provided at this temporal scale. This can be achieved through a knowledge of maximum and minimum daily or monthly values by assuming sinusoidal changes in variables through time (Porter et al. 1973b; Campbell & Norman 1998). A flow diagram of the overall process is depicted in Fig. 4.

MAPPING THE NICHE TO THE LANDSCAPE

The output of correlative SDMs typically involve dimensionless indices of habitat suitability or estimates of probability of occurrence, and a variety of approaches are used to assess the threshold at which the distribution limit should be placed (Liu et al. 2005). In contrast, for
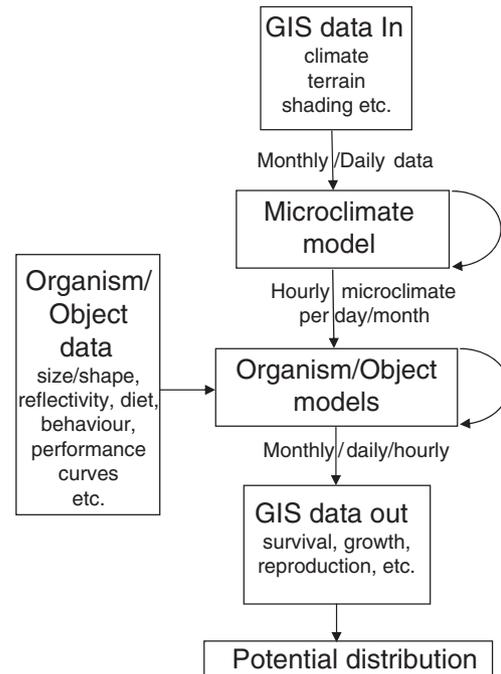
Figure 4 Flow diagram illustrating an approach to mechanistic species distribution modelling whereby GIS data on macroclimate, terrain and vegetation are used to reconstruct microclimates on an appropriate timescale. An organism/object model then determines the particular environments that are experienced within the constraints set by the microclimate model, given the functional traits of the system in question, and outputs geo-referenced data on key fitness components.

mechanistic SDMs of the type described here, the output relates to key fitness components such as survival, performance, development, growth, or, ultimately, reproductive capacity (Table 1). The potential distribution is then determined through a process of elimination whereby regions that can be identified as outside the organism's niche are progressively excluded from the final distribution. This can be done at various levels depending on the available information on the physiological responses and tolerances of the study organism and its interaction with other species.

Climate space

At the coarsest level, one can map out regions that are within the 'climate space' of an organism. Climate space is a (typically) four-dimensional hypervolume described by the axes of radiation, air temperature, wind speed and humidity, which encloses the combinations of these variables on earth that result in survivable body temperatures (Fig. 2d) (Porter & Gates 1969). An organism's climate space is defined by its traits and can be conceived of as the organism's

fundamental niche in the broadest sense (Kearney & Porter 2004; Kearney 2006). Organisms with the same body temperature limits for survival may withstand very different combinations of environmental conditions depending on their morphology (e.g. size, reflectivity) and physiology (e.g. endothermy). Moreover, behavioural constraints (e.g. obligate nocturnality or arboreality) and morphological constraints (e.g. size) may limit a species' access to suitable climate space within its habitat. Energy balance equations can be solved pixel by pixel across a landscape for an organism with defined biophysical characteristics and behavioural repertoire to assess whether it could find a microclimate within its climate space (Fig. 4). This results in a prediction of potential distribution as constrained by thermal limits to survival. For most species, this distribution will be much broader than their actual distribution.

Constraints on thermal performance

The potential distribution can be further constrained from a thermal perspective by integrating biophysical models with thermal performance curves for vital activities such as locomotion and feeding. Thermal performance curves express key physiological processes as a function of temperature. For many species, such curves rise slowly from a lower critical temperature up to an optimum value of maximum rate, and then rapidly decline towards the upper critical temperature (Fig. 2c) (Huey & Stevenson 1979). The critical temperatures may reflect absolute survival limits, as defining the climate space described above, or they may reflect temperatures where survival is possible but a key physiological process (e.g. movement) is halted. Thus, through a summation of total performance for a given physiological process as a function of biophysically calculated body temperature (e.g. distance moved), one can produce a map of habitat suitability for that process which may further constrain the potential range. For example, while the body temperature limits to survival of the cane toad *Bufo marinus* ranges from *c.* 5 to 42 °C, locomotion is constrained to a range of 13.7–37.4 °C with an optimum at around 30 °C (Kearney *et al.* 2008). Implementation of this locomotor performance curve in a biophysical model of the potential range of the cane toad in Australia indicated that much of the south of the continent was unsuitable for toads (Kearney *et al.* 2008) (Fig. 5a). Similarly, the thermal dependence of egg development rates and growth can also be an important constraint on species' ranges. For example, biophysical models of the degree days available for egg
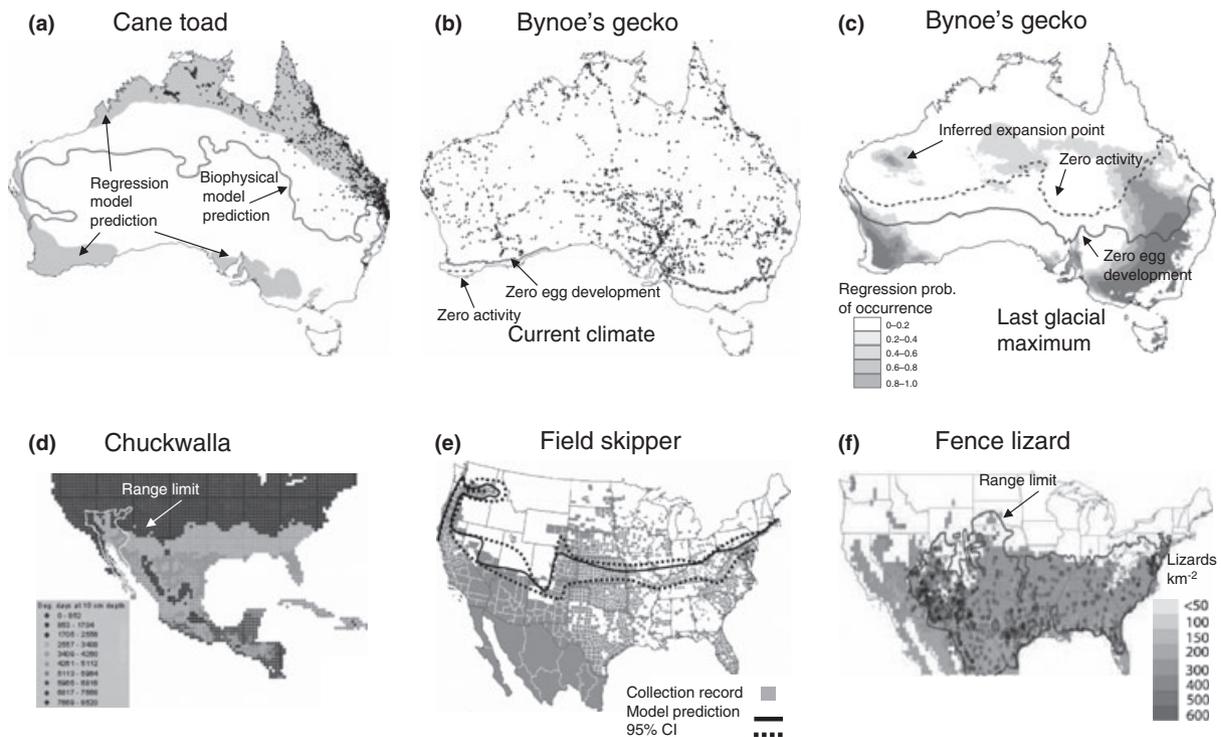
Figure 5 Mapping the niche to the landscape – examples from the literature of range predictions using mechanistic (and correlative) models. The cane toad predictions (a) are from Kearney et al. (2008) and Urban *et al.* (2007). The Bynoe's gecko predictions are from Kearney and Porter (2004) (b) and Strasburg et al. (2007) (c). The chuckwalla prediction (d) is from Porter et al. (2002), the field skipper prediction (e) is from Crozier and Dwyer (2006) and the fence lizard prediction (f) is from Buckley (2008).

development have been shown to correspond with the range limits of lizards (Porter *et al.* 2002; Kearney & Porter 2004) (Fig. 5b–d). More subtle developmental influences of temperature, such as phenology and sex ratio, can be determined biophysically and used to determine distribution limits (Mitchell *et al.* 2008).

Energy, water and nutrient balance

To persist at a given location, organisms must not only maintain physiologically suitable body temperatures but must also acquire sufficient energy, water and nutrients to maintain the soma, grow and reproduce. Biophysical models of the energy and mass balance of organisms can provide estimates of the climatic cost to an organism of living in a given location with respect to energy and water. Absolute maintenance energy costs for ectotherms increase with body size and temperature according to well-described empirical relationships (Gillooly *et al.* 2001). Thus, biophysical estimates of core body temperature summed over a relevant time period, together with knowledge of the organism's size, allow very good estimates of maintenance energy requirements imposed by climate at a given location. The same relationships between basal maintenance energy requirements, body size and temperature also hold for endotherms. However, endotherms typically maintain constant and high core body temperatures in cool environments by increasing metabolic rate above basal levels, and energy balance models can be solved to estimate this thermoregulatory cost. Water expenditure as a function of climate is in part determined by metabolic rates and the resultant respiratory water exchange, but is also influenced by evaporation from the integument and thermoregulatory demand. Coupled energy and mass balance models can therefore account for much of an organism's water expenditure.

If it is also possible to determine intake and assimilation efficiencies of energy and water, an estimate can be made of the 'discretionary' energy and water available to an organism for growth, reproduction or storage. Mass balances related to nutrients such as protein and mineral salts may also be determined. The profits an animal makes in these currencies can then be converted into a single currency strongly linked to fitness, e.g. growth, eggs, milk or live young, according to the most limiting factor. An inference of 'discretionary' resources not only requires considerable knowledge of the digestive physiology of the organism and the energy, water and nutrient content of the food, but also of the availability of food within the habitat in question. Determining the latter will be most straightforward in organisms feeding on high density, persistently available food types like perennial plants. Obtaining good estimates of food availability for use in SDMs will be more challenging for organisms such as carnivores that feed on low-density, patchy or ephemeral

resources, but it has been attempted with lizards (Buckley 2008). In the absence of good data on food availability, one can still determine the required rate of feeding or drinking to maintain energy and water balance at a given location as a function of climatically imposed activity and prey capture/handling constraints (Kearney & Porter 2004). Locations can then be deemed as unsuitable if such rates are unlikely to be achieved in given location (e.g. if required rates are in excess of gut or handling capacity).

Population dynamics

The persistence of a population at a given location depends on the balance between births and deaths as well as migration. Consequently, the mapping of a species' niche to the landscape involves inference at the population level. Work has begun to integrate population dynamics into SDMs (e.g. Keith *et al.* 2008). Biophysical calculations can provide key input data for models of population dynamics including climate-dependent mortality, development and growth rates (Adolph & Porter 1993, 1996), movement potential (i.e. dispersal), sex ratios, and rates of reproduction as a function of discretionary energy, water and nutrients. While this is largely unexplored territory, two studies have used ecophysiologically informed population dynamics models to predict species range limits as a function of climate. Crozier and Dwyer (2006) used field and lab data on the relationships between air temperatures, winter survival and summer recruitment in a North American butterfly to model its northern range limit under different climate scenarios (Fig. 5e). This study did not explicitly link interactions between the butterflies and their microhabitats but it could easily be tailored to include the techniques of biophysical ecology. Buckley (2008) integrated an optimal foraging model incorporating density dependence with biophysical calculations of body temperature to predict the carrying capacity and growth rates of lizards and to thereby infer potential distributions (Fig. 5f). There is clearly much more that can be done to couple population dynamics models and climate via biophysical models, and this is a promising area for future research.

Biotic interactions

One of the greatest challenges in modelling species distributions is accounting for biotic interactions such as predation and competition into range predictions, i.e. to model and map the realized niche. The lack of explicit biotic interactions in SDMs has been a particular source of criticism in the context of predicting climate change impacts (Davis *et al.* 1998; Dormann 2007). There is also strong interest in revitalizing the niche concept from a mechanistic perspective to tackle questions about biotic interactions in

community ecology (Chase & Leibold 2003; McGill *et al.* 2006). Approaches are currently being developed to include biotic interactions in correlative SDMs, e.g. through including the presence/absence of host plants explicitly in the model (Araújo & Luoto 2007).

We see two possible ways to apply biophysical ecology in context of biotic interactions. For simple systems where there are strong interactions between small numbers of species, the fundamental niches of all species could be modelled to determine the extent that the overlap in their climatic niches translates to overlap in the uses of space and resources through time. This, together with knowledge of the strength and direction of the interactions, and potentially their thermal dependence, could enable spatially explicit quantification of the interaction outcomes. For example, if a pathogen of a focal species is known to exert a particular energetic demand on the host, and that pathogen's fundamental niche is determined so that areas of overlap are noted, one could adjust the energy balance of the focal species accordingly where the ranges intersect. The link between thermal requirements and their constraints on the use of space through time has long been appreciated (Magnuson *et al.* 1979; Roughgarden *et al.* 1981; Tracy & Christian 1986). Attempts at biophysical modelling of biotic interactions include both predation (Porter *et al.* 1973b; Porter *et al.* 2002) and resource partitioning (Roughgarden *et al.* 1981). Such analyses are yet to be extended to consider constraints on species distributions but it in principle this is possible. An alternative pathway is required for the perhaps more typical scenario of diffuse interactions among a large number of species. In such cases, one might consider the biotic interactions as a background 'milieu' defined by the distributions of functional traits of the interacting species (McGill *et al.* 2006), that acts to impose additional costs to the energy or mass balance (Parsons 1996). For instance, the energy balance of a focal species may be limited by shade from other species as a function of plant height distributions (McGill *et al.* 2006). Many biotic interactions will, however, be local and idiosyncratic, potentially posing major challenges for SDMs of any kind.

Incorporating trait variability and evolutionary change

Finally, the functional traits of organisms are not fixed parameters but may change through time and space both as plastic and genetic responses to environmental change (Levins 1968) (Fig. 1). The problem of species distribution limits is thus an evolutionary one as much as it is an ecological one (Hoffmann & Blows 1994), and this poses an important issue for SDMs, particularly in the context of novel environmental change.

As trait values are explicitly stated in mechanistic niche models, it is possible to allow these values to change according to independently assessed geographical variation and reaction norms. This is both a blessing and a curse for mechanistic models; while the ability to include spatial variation in traits provides the opportunity to study the adaptive significance of geographical variation, if a mechanistic model is not parameterized appropriately with respect to this variation it will be of reduced accuracy. In contrast, correlative models implicitly include geographical trait variation, whether it is of a plastic or genetic nature (Table 1). For example, if a species can alter its low temperature tolerance across its range via acclimation, this is reflected directly in the occurrence data used to build correlative models. Mechanistic models should ideally be parameterized based on a representative sample of populations across the focal species' range, or on populations near the range limits, and the reaction norm of the limiting traits must be described.

Examples of the incorporation of trait variation in mechanistic models include analysis of the plastic response of sex ratio to egg incubation environment in species with temperature-dependent sex determination (Mitchell *et al.* 2008), 'virtual reciprocal transplants' of trait values to different geographical locations to quantify the fitness consequences of acclimation responses in cane toads (J.J. Kolbe, M. Kearney & R. Shine, unpublished data), and assessments of the influence of geographical trait variation on the distribution of lizards (Buckley 2008). Such mechanistic analyses of functional trait variation hold great promise for addressing topics such as niche conservatism, which at present are being explored using correlative models that consider the habitats of organisms as if they were traits (Wiens & Graham 2005; Kozak *et al.* 2008).

Traits may also change through time via evolutionary processes, posing difficulties for correlative and mechanistic models alike (Table 1). While there have been attempts to include evolutionary change in correlative models by considering sequential time-slices of distribution records (Urban *et al.* 2007), this may be confounded by other processes that alter environmental associations through time such as range expansion during invasion (Kearney *et al.* 2008). A trait-based approach is thus necessary if the influence of evolution is to be incorporated into a species distribution model. Genetic shifts in quantitative traits depend on both trait heritability as well as selection intensity. Trait heritability must be measured empirically and this has been achieved for numerous climate-sensitive traits (e.g. Hoffmann *et al.* 2003). Selection intensity, however, depends on the interaction between organism and environment. If mechanistic niche models can link key fitness components such as mortality and reproductive output to trait values and selection intensity, the resultant evolutionary change can be determined in a spatially explicit context (Kearney *et al.*, in press). Our ability to incorporate

evolutionary change into species distribution models will be crucial for understanding the responses of many organisms to novel environmental change.

WHEN ARE MECHANISTIC SPECIES DISTRIBUTION MODELS MOST USEFUL?

A major disadvantage of mechanistic models in comparison to correlative models is that they often require more time, effort, resources and data to construct and validate (Table 1). There are many important circumstances, however, where mechanistic approaches are preferable and therefore worth the investment of time and resources. These circumstances either require an understanding of the underlying causal processes, e.g. in some management contexts, or they require violation of the assumptions of correlative models, such as extrapolative prediction and the modelling of species with non-equilibrium distributions. Moreover, there are a number of ways in which correlative and mechanistic approaches to modelling species distributions can be integrated. For the remainder of this section, we discuss some applications where mechanistic SDMs are particularly useful, using examples from the literature wherever possible.

Developing hypotheses about species distribution limits

A basic aim in many modelling procedures is to construct hypotheses about the underlying causes of a phenomenon. Whatever the main impetus for developing a SDM, it will inevitably lead to explicit hypotheses about the factors limiting a species' distribution that can be tested empirically. While correlative SDMs are also very useful for developing hypotheses about range constraints, mechanistic SDMs will often provide more focused and detailed hypotheses through explicitly identifying a limiting process. Mechanistic SDMs are thus useful tools for investigating a fundamental and rarely answered question in ecology and evolution – what limits a species' range? For example, a mechanistic SDM of a widespread nocturnal lizard *Heteronotia binoei* from Australia indicated that thermal constraints on activity time and/or on egg development rates might influence its southern range limit (Kearney & Porter 2004). There were also some regions (i.e. the southeast) where the correspondence between the inferred southern limit and the actual limit was poor, suggesting the operation of different constraints (Fig. 5b).

Predicting past and future species distributions

One of the major applications of SDMs in the future will be to anticipate range shifts and contractions as a function of human-induced climate change (Thomas *et al.* 2004). There

is also increasing interest in using SDMs to explore the impact of past climates on species distributions, particularly as an independent means of assessing phylogeographic patterns inferred with molecular data such as refugial zones (Hugall *et al.* 2002; Peterson & Nyari 2008). Mechanistic SDMs of organisms' fundamental niches can provide robust answers to these questions by identifying changes in the major climatic constraints on the range – the stage on which the biotic interactions and other events are then played out. For example, the mechanistic SDM of a parthenogenetic lineage of the gecko *H. binoei* described above was applied to approximate climatic conditions at the last glacial maximum, predicting considerable northward shift in the southern range border (Strasburg *et al.* 2007). In contrast, a correlative model inferred a southward shift into regions that even under present conditions are too cold for survival (Fig. 5c). The latter inference was a reflection of how that particular correlative model extrapolated into cold desert conditions, for which there are no present day analogues (Strasburg *et al.* 2007).

Modelling invasive species and other non-equilibrium situations

Predicting the potential range of invasive species represents another important application of SDMs (Peterson 2003). Present strategies involve building correlative SDMs based on the native range and projecting them to potential introduction sites (Sutherst *et al.* 1996; Fitzpatrick *et al.* 2007), as well as building correlative SDMs based on snapshots of the introduced range as the species expands (Urban *et al.* 2007). The former strategy of using the native range may require extrapolation of the model to novel combinations of environmental conditions and unique biotic interactions. The latter strategy of using snapshots of the range expansion through time violates the assumption of equilibrium in correlative SDMs because the invading species is shifting its range. Both strategies have been applied to predict the final range extent of the cane toad in Australia, with conflicting predictions about the suitability of southern Australia (Sutherst *et al.* 1996; Urban *et al.* 2007). However, a mechanistic SDM showed that much of southern Australia can be ascribed as outside this species' fundamental niche because it is too cold for the toads to forage (Kearney *et al.* 2008) (Fig 5a).

Developing management strategies

There are often cases where it is necessary to alter a species range through some kind of intervention. In conservation biology, e.g. translocations might be necessary for a species' survival (e.g. Hoegh-Guldberg *et al.* 2008). Mitchell et al. (2008) used biophysical models to assess thermal habitat

quality of an endangered reptile vulnerable to sex-ratio biases under global warming. This approach will be useful in assessing the suitability of translocation sites if this becomes necessary in the future. Manipulations may also be necessary to control the range of an invasive or pest species. While correlative SDMs can be useful in developing hypotheses about potential variables to manipulate in developing management strategies, a strategy emphasizing mechanisms is most desirable. For example, Kearney *et al.* (in press) used a biophysical approach to model range constraints on the dengue mosquito *Aedes aegypti* in Australia as a function of oviposition sites. These mosquitoes only breed in artificial containers and the model was able to determine the regions of Australia that are vulnerable to mosquito spread if insufficient precautions are taken with water storage practices.

Combining mechanistic and correlative models

There are a number of ways that correlative and mechanistic approaches could be combined in a species distribution modelling strategy. Most obviously, a comparison of their outputs for the same species may either provide greater confidence in the predictions made if they concur, or generate interesting hypotheses if they do not (Hijmans & Graham 2006). In the case described above, where the distribution of the gecko *H. binoei* during the last glacial maximum was predicted using a correlative and a mechanistic model (Strasburg *et al.* 2007), there was one region where both models agreed the species could have been (Fig. 5c). This region was also independently identified, through molecular analyses, as the place from which the species had expanded (Strasburg *et al.* 2007).

Another way of combining the two approaches is to use mechanistic SDMs to develop highly 'proximal' spatial layers on which to base correlative predictions (Austin 2002, 2007). A biophysically based SDM can translate daily and seasonal fluctuations in variables such as air temperature, radiation, wind, humidity and soil temperatures into composite variables, filtered through the organism's morphology, behaviour and physiology interacting with the surrounding terrain and vegetation. Examples of such surfaces include potential activity time, water loss, energy costs and development time. Such independent variables may provide better and more interpretable correlative SDMs.

Finally, a mechanistic model may also be useful in defining the geographical scope of a correlative model. For instance, if certain regions on a landscape can be clearly identified as being outside an organism's fundamental niche with a mechanistic SDM, the correlative SDM can be more tightly focused by placing absence points in such areas or by excluding them from the analysis.

CONCLUSION

Our aim in this review has been to highlight the potential for applying the principles of biophysical ecology to develop mechanistic models of species distributions that directly incorporate known physiological processes. Biophysical principles provide a means to capture the interaction between key functional traits of an organism and its physical environment to infer the consequences for key states such as body temperature, energy balance and water balance. This in turn provides a means to incorporate knowledge of physiological constraints on survival and reproduction, and therefore to derive a mechanistic formulation of a species fundamental niche. This niche can be mapped to the landscape by reconstructing microclimatic conditions from spatial data on climate and terrain. While we have focused on the application of biophysical ecology, we note that there are other mechanistic frameworks of energy and mass balance, as well as nutrition, that could be applied independently or in combination with biophysical approaches (Kooijman 2000; Raubenheimer & Simpson 2004; Kearney & Porter 2006).

There are many practical advantages to a mechanistic strategy in terms of understanding the underlying processes limiting species' ranges and in making predictions in non-equilibrium or novel circumstances. However, mechanistic SDMs are not necessarily an alternative to correlative SDMs and are usually more difficult to construct (Table 1). This is in part because mechanistic SDMs require the collection of very specific data on an organism's traits and its environmental context, and also because they require extensive field and laboratory validation. To the extent that the key limiting traits exhibit geographical variation, whether due to genetic adaptation or phenotypic plasticity, model parameterization may prove challenging. This is in contrast to correlative SDMs which require only one type of observational data (occurrence records) and are very flexible about the independent variables to be used. Moreover, validation procedures can be implemented as part of the correlative modelling procedure by using observational data set aside for this purpose. A correlative strategy is therefore most prudent when the main aim is interpolative prediction (Mac Nally 2000; Austin 2002; Dormann 2007). In many cases, a strategy involving both correlative and mechanistic approaches may provide very robust predictions of species potential ranges.

We hope this review encourages ecologists to bring the great wealth of knowledge about distribution constraints that exists within the field of physiological ecology more directly into models of species distributions. In doing so, we will make more robust and confident predictions of species ranges under the environmental changes to come. We will

simultaneously enrich our understanding of the ecological and evolutionary limits to species distributions.

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