# How to understand species' niches and range dynamics: a demographic research agenda for biogeography

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## ABSTRACT

Range dynamics causes mismatches between a species' geographical distribution and the set of suitable environments in which population growth is positive (the Hutchinsonian niche). This is because source–sink population dynamics cause species to occupy unsuitable environments, and because environmental change creates non-equilibrium situations in which species may be absent from suitable environments (due to migration limitation) or present in unsuitable environments that were previously suitable (due to time-delayed extinction). Because correlative species distribution models do not account for these processes, they are likely to produce biased niche estimates and biased forecasts of future range dynamics. Recently developed dynamic range models (DRMs) overcome this problem: they statistically estimate both range dynamics and the underlying environmental response of demographic rates from species distribution data. This process-based statistical approach qualitatively advances biogeographical analyses. Yet, the application of DRMs to a broad range of species and study systems requires substantial research efforts in statistical modelling, empirical data collection and ecological theory. Here we review current and potential contributions of these fields to a demographic understanding of niches and range dynamics. Our review serves to formulate a demographic research agenda that entails: (1) advances in incorporating process-based models of demographic responses and range dynamics into a statistical framework, (2) systematic collection of data on temporal changes in distribution and abundance and on the response of demographic rates to environmental variation, and (3) improved theoretical understanding of the scaling of demographic rates and the dynamics of spatially coupled populations. This demographic research agenda is challenging but necessary for improved comprehension and quantification of niches and range dynamics. It also forms the basis for understanding how niches and range dynamics are shaped by evolutionary dynamics and biotic interactions. Ultimately, the demographic research agenda should lead to deeper integration of biogeography with empirical and theoretical ecology.

## Keywords
Biodiversity monitoring, climate change, ecological forecasts, ecological niche modelling, ecological theory, geographical range shifts, global environmental change, mechanistic models, migration, process-based statistics.

## THE DEMOGRAPHIC BASIS OF NICHES AND RANGE DYNAMICS

The niche concept is central to ecology (Hutchinson, 1957; Holt, 2009). It is widely used to characterize requirements and impacts of species (Chase & Leibold, 2003), to study community dynamics, and to predict ecological and evolutionary responses of species to environmental change (Wiens & Graham, 2005; Lavergne *et al.*, 2010). In particular, the niche concept is invoked in a plethora of recent studies that attempt to forecast future range dynamics of species under environmental change (Elith & Leathwick, 2009). Such range forecasts are widely used to assess the impacts of environmental change on biodiversity (Pereira *et al.*, 2010; Dawson *et al.*, 2011) and increasingly serve as the basis for systematic conservation planning (Pressey *et al.*, 2007).

While the ecological literature abounds with various definitions of the niche (Chase & Leibold, 2003), the most influential quantitative definition is arguably that of G. Evelyn Hutchinson (Hutchinson, 1957, 1978). The Hutchinsonian niche is defined as the set of environmental conditions under which a species can 'exist indefinitely' (Hutchinson, 1957). In the absence of dispersal and environmental variability, the persistence of a species in a given location depends on its population growth rate. As this is the difference between per-capita birth and death rates, the Hutchinsonian niche can be expressed in demographic terms (Maguire, 1973; Hutchinson, 1978). Fundamentally, a species' niche consists of those environments for which the intrinsic population growth rate $r$ (the population growth rate at low population density) is positive (Maguire, 1973; Hutchinson, 1978). In the case of complex population dynamics, this simple demographic niche definition has to be refined somewhat (Holt, 2009). Importantly, however, all of these refinements of the Hutchinsonian niche can be derived from 'demographic response functions' (Pulliam, 2000) that describe how birth and death rates vary with environmental conditions (Maguire, 1973; Hutchinson, 1978; Holt, 2009).

Furthermore, demographic responses link Hutchinsonian niches to range dynamics (Pulliam, 2000; Fig. 1). This is because demographic response functions translate spatio-temporal variation in environmental variables into variation of the three fundamental demographic rates of birth, death and dispersal (with the former two determining local population growth and the niche). Range dynamics then arise from the dynamics of many local populations that are founded and connected by dispersal, with range size changes depending on how many sites
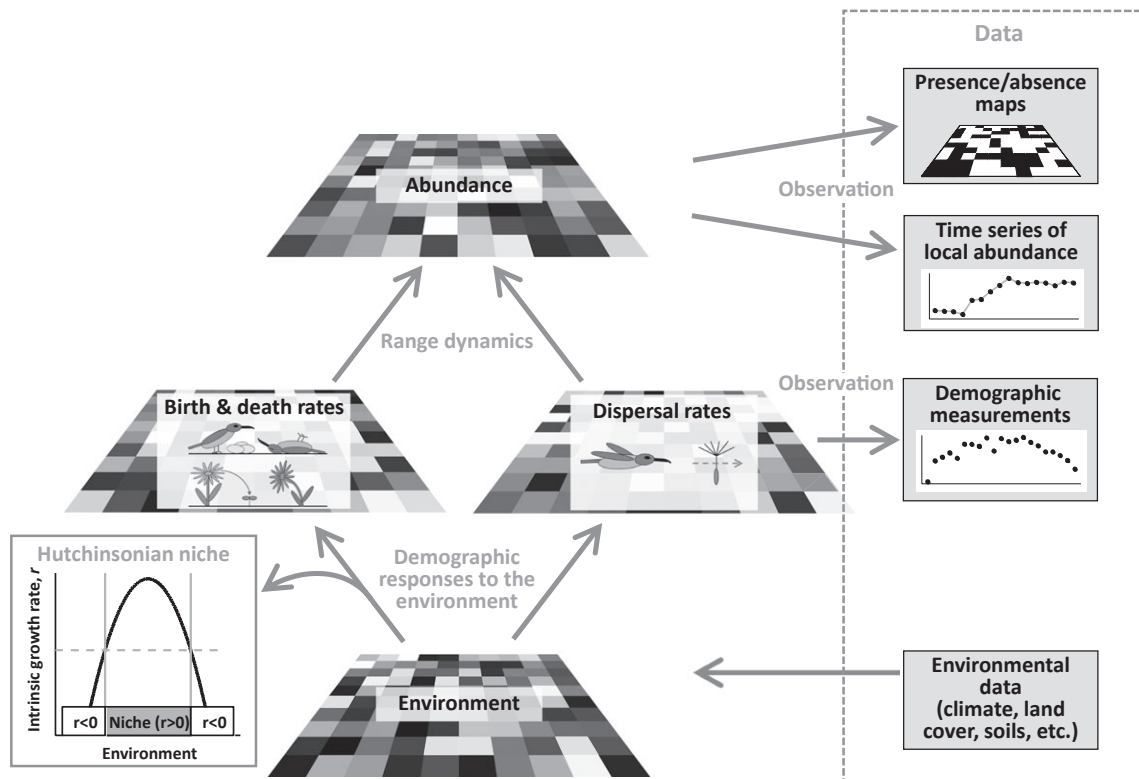


**Figure 1** The demographic basis of Hutchinsonian niches, range dynamics and biogeographical data. Demographic response functions translate spatio-temporal variation of the environment into variation of the fundamental demographic rates of birth, death and dispersal. In particular, the demographic response of birth and death determines variation in local population dynamics and defines the Hutchinsonian niche as the set of environments for which population growth is positive. Range dynamics then result from the dynamics of local populations that are coupled by dispersal. Data useful for the estimation of niches and range dynamics are collected by observing spatio-temporal variation in distribution, local abundance, demographic rates and environmental conditions. However, these observations are subject to observation errors and they typically represent only a subsample of the entire variation present.

are newly colonized and how many are vacated by population extinction (Fig. 1; Pulliam, 2000; Holt & Keitt, 2005).

The central importance of demographic responses (and the Hutchinsonian niches that they lead to) has led ecologists to develop various methods for quantifying and predicting them (see Holt, 2009). The most direct way of quantifying demographic response functions and species' niches is to measure rates of birth, death and dispersal in experimentally manipulated environments. This approach has been taken in laboratory experiments with animals (Birch, 1953; Hooper *et al.*, 2008) and in field transplant experiments with plants (e.g. Latimer *et al.*, 2009; Moore, 2009). So far, however, such direct demographic measurements are scarce, mostly restricted to small and short-lived organisms, often do not cover all three fundamental demographic rates, and typically do not span the full range of environmental variation relevant at biogeographical scales (Gaston, 2009; Holt, 2009). A promising alternative to such direct measurements are mechanistic niche models that describe how physiology, phenology, environmental conditions and functional traits determine the birth and death of individuals and how this demographic performance translates into population dynamics (Buckley, 2008; Chuine, 2010; Bykova *et al.*, 2012; Kearney, 2012). Yet, these mechanistic models require substantial knowledge about the biology of the study organism and their parameterization for specific environments is typically labour-intensive (Holt, 2009). The large efforts required for the direct measurement of demographic responses and the development of mechanistic niche models thus currently preclude the application of these methods to large numbers of species.

The predominant method for quantifying niches and range dynamics are hence statistical analyses that link the geographical distribution of species to large-scale environmental variation. Typically, environmental information available at large spatial scales does not directly quantify the resources for which species compete, but describes non-interactive ('scenopoetic') variables (Soberón & Nakamura, 2009). Consequently, large-scale niche analyses cannot explicitly resolve biotic interactions between species (Kissling *et al.*, 2012) or impacts of species on their environment (Linder *et al.*, 2012). At best, such large-scale analyses can thus characterize Hutchinson's realized niche (the set of environments in which a species can persist in the presence of interacting species, Hutchinson, 1957).

## THE GORDIAN KNOT OF BIOGEOGRAPHY: ESTIMATING NICHES AND RANGE DYNAMICS

Currently, the statistical estimation of species' niches and the prediction of range dynamics under environmental change rest almost entirely on correlative species distribution models (SDMs, also termed habitat models, environmental niche models or bioclimate envelope models). SDMs link geographical patterns of observed presences and absences with environmental data to estimate a correlation between distribution and environment (Guisan & Thuiller, 2005). While these distribution–environment correlations are often assumed to reflect species' niches, they can in fact deviate strongly from a species'

Hutchinsonian niche (Pulliam, 2000). These deviations arise because range dynamics cause mismatches between a species' Hutchinsonian niche and its geographical distribution (Holt, 2009; Fig. 2). Source–sink dynamics can lead to the export of individuals from high-quality habitats to adjacent low-quality habitats (Fig. 2a). This leads to the presence of species in environments in which their intrinsic population growth rate is negative (Pulliam, 2000) and causes correlative SDMs to overestimate the niche extent (Holt, 2009). Such source–sink dynamics will bias correlative niche estimates even if a species is in dynamic equilibrium with its environment (Pagel & Schurr, 2012). Two further sources of bias occur in non-equilibrium situations that may arise when species are exposed to environmental change. First, limited dispersal and migration can cause a species to be absent from geographical regions and from parts of the niche space in which it could in principle show positive population growth (Fig. 2b). As correlative SDMs do not explicitly describe this effect, they tend to underestimate the niche extent of migration-limited species (e.g. Guisan & Thuiller, 2005; Pagel & Schurr, 2012). Second, environmental change can also cause correlative SDMs to overestimate niche extents: a species may be present in unsuitable environments because environmental deterioration occurred recently and local populations have not yet gone extinct from areas that recently turned unsuitable (e.g. Thuiller *et al.*, 2008; Fig. 2c).

Correlative analyses of species distribution data thus cannot provide unbiased estimates of niches and range dynamics. This is problematic for fundamental research in biogeography, ecology and evolutionary biology, which increasingly uses correlative niche estimates (e.g. Wiens & Graham, 2005; Elith & Leathwick, 2009). Moreover, biased niche estimates will cause biased forecasts of range dynamics under environmental change. This is a problem not only for the direct extrapolation of correlative SDMs to future conditions (e.g. Thomas *et al.*, 2004) but also for more recently developed hybrid models that combine niche estimates of correlative SDMs with process-based models of spatial population dynamics (e.g. Keith *et al.*, 2008; Midgley *et al.*, 2010; Meier *et al.*, 2012): such hybrid models may under- or overestimate future range sizes depending on whether the underlying correlative niche model under- or overestimates the niche.

Biogeography, macroecology and evolutionary biology are thus faced with a dilemma: to obtain unbiased niche estimates one has to quantify range dynamics, but this requires knowledge of how demographic rates respond to environmental variation – and thus knowledge of the niche. We argue that this apparent Gordian knot can be undone by pursuing a demographic research agenda. The central point of this agenda is to replace correlative models with process-based dynamic range models (DRMs) that: (1) describe both demographic response functions and range dynamics, and (2) can be statistically estimated from data on species distributions and variation in demographic rates. In the following, we summarize first steps of this demographic agenda that have been taken recently. Subsequently, we point out key aspects in the fields of statistical modelling, data collection, and ecological theory that
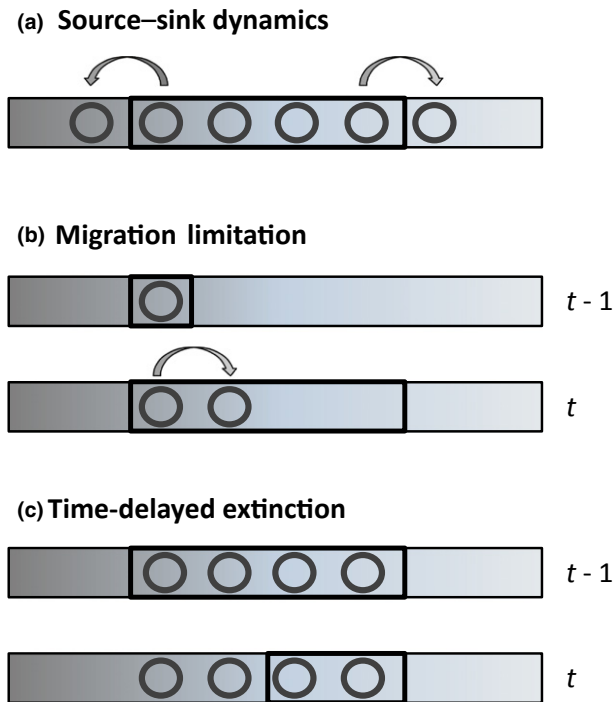
### (a) Source–sink dynamics

### (b) Migration limitation

$t - 1$

$t$

### (c) Time-delayed extinction

$t - 1$

$t$

**Figure 2** Three mechanisms by which demographic processes and the resulting range dynamics can cause mismatches between the geographical distribution of a species (circles) and the Hutchinsonian niche (the set of environments in which intrinsic population growth rate is positive, black box). (a) Source–sink dynamics act irrespective of whether geographical distributions are in equilibrium with the environment or not. In contrast, (b) migration limitation and (c) time-delayed extinction are relevant in non-equilibrium situations.

need to be addressed to implement the agenda for a wide range of species and study systems. We end by briefly outlining why this demographic agenda also has considerable potential for understanding how interspecific interactions and microevolution shape niches and range dynamics.

## PROCESS-BASED STATISTICAL ESTIMATION OF NICHES AND RANGE DYNAMICS

How can one jointly estimate Hutchinsonian niches and range dynamics from distribution data? The first step is to formulate a DRM that describes the link between environmental variation and biogeographical data (Fig. 1) in three submodels: (1) a *demographic response model* describes how spatio-temporal variation in the environment translates into spatio-temporal variation in birth, death and dispersal (with the former two determining the niche), (2) a *range dynamics model* describes how spatio-temporal variation in population growth and dispersal determine the spatio-temporal distribution of local population size, and (3) an *observation model* describes how the variation in population size and demographic rates is sampled to obtain the available data (e.g. presence/absence maps or time series of local abundance). These three submodels form a hierarchy in the sense that the

predictions of the demographic response model are input for the range dynamics model, whose output is in turn input for the observation model.

An example of a DRM is a statistical model developed by Hooten & Wikle (2008) to analyse spatio-temporal abundance data documenting the invasion of the Eurasian collared-dove (*Streptopelia decaocto*) in North America. In this model, the environment (human population density) affects dispersal but not population growth rate. While this model thus predicts range dynamics, it cannot be used to estimate Hutchinsonian niches (and the same is true for several other recent statistical models for the spatio-temporal dynamics of species; Cook *et al.*, 2007; Purves *et al.*, 2007; Hooten & Wikle, 2010). In Box 1 and Fig. 3, we therefore illustrate the functioning of a DRM with a statistical model that jointly estimates Hutchinsonian niches and range dynamics (Pagel & Schurr, 2012). We emphasize that the DRM framework is flexible and can integrate a wide range of alternative submodels for range dynamics and environmental effects on demographic rates (see 'The statistical modelling agenda' below). Moreover, by adjusting the observation model one can link DRMs to different types of data (see 'The empirical agenda' below).

The parameters of the three hierarchical DRM submodels can be estimated from data using hierarchical Bayesian methods (Clark, 2005; Hooten & Wikle, 2008; Marion *et al.*, 2012; Pagel & Schurr, 2012). In Bayesian terminology, parameter estimation amounts to determining the posterior probability distribution of the model parameters given the data. In the case of a DRM, the posterior probability of a set of parameter values is calculated from the product of three conditional probabilities (defined by the three submodels) and of the prior probability of the parameter values (see Box 1). The prior probability distribution of a parameter can represent existing knowledge on which parameter values are likely (e.g. from detailed mechanistic models or from studies on how population growth rate varies across environments), or it can be 'non-informative' (reflecting ignorance about the parameter, Hartig *et al.*, 2012). The posterior probability distribution of DRM parameters typically cannot be calculated analytically, but numerical methods enable one to sample parameter values from this distribution (Box 1; Marion *et al.*, 2012; Pagel & Schurr, 2012). This sample from the posterior can then be used to calculate niche estimates (Fig. 3b), to forecast range dynamics (Fig. 3a), and to quantify the uncertainty in these forecasts (Fig. 3c).

Because they integrate the quantification of range dynamics and demographic response functions in a single statistical framework, DRMs have several advantages over alternative methods for estimating niches and forecasting range shifts: (1) they can statistically synthesize different types of biogeographical and demographic data, (2) they can infer spatio-temporal range dynamics in equilibrium and non-equilibrium conditions, (3) they provide estimates of a species' realized Hutchinsonian niche that are founded in ecological theory, and (4) they yield fully probabilistic forecasts of future range dynamics under environmental change that transparently quantify the involved uncertainty. Currently, however, such
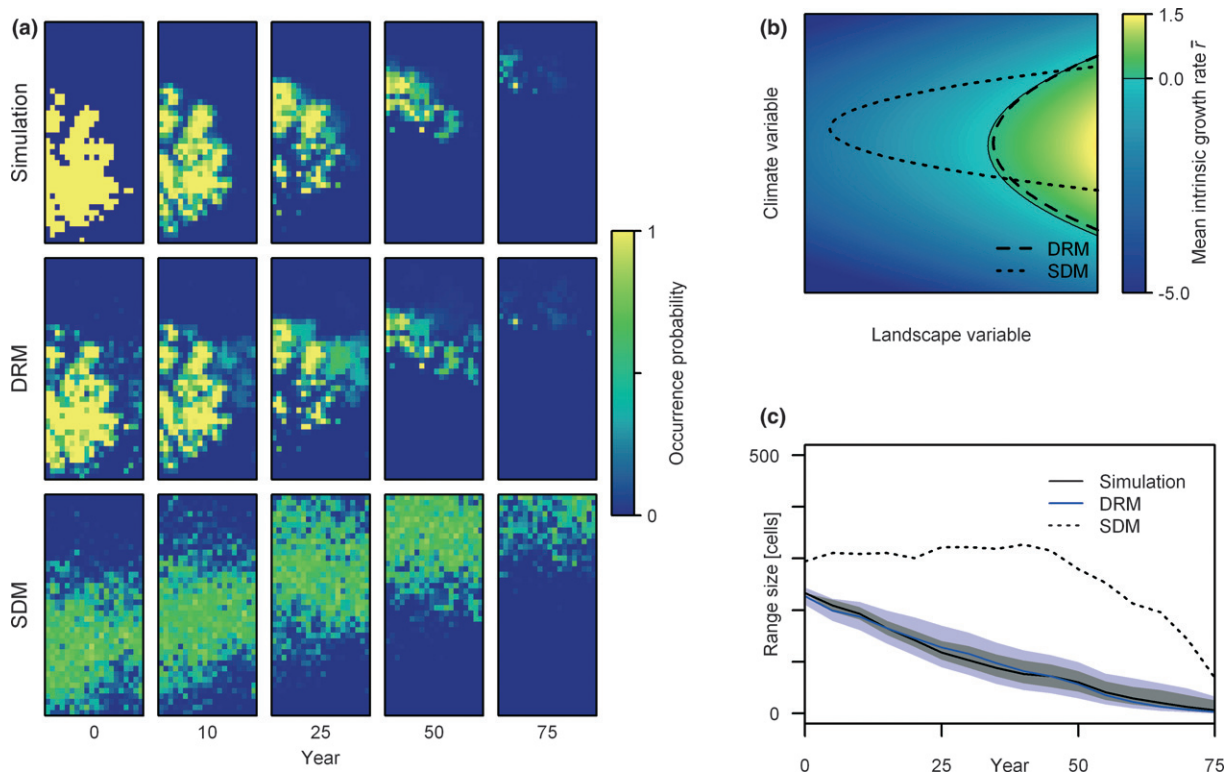
**Figure 3** An example analysis demonstrating how dynamic range models (DRMs) can be used to estimate Hutchinsonian niches and to forecast range dynamics (modified from Pagel & Schurr, 2012). (a) 'True' (simulated) versus predicted range dynamics of a hypothetical study species during 75 years of climate change. The top row shows the spatio-temporal dynamics of occurrence probabilities for replicate simulations of the true model. The lower two rows show the corresponding predictions of the DRM and a correlative species distribution model (SDM, in this case a logistic regression) that were estimated from data collected in the first 10 years. (b) Estimates of the species' Hutchinsonian niche. Colours indicate the expected intrinsic population growth rate $\bar{r}$ as a function of a climate and a landscape variable, with the limit between green and blue denoting the niche boundary where $\bar{r} = 0$. The hatched and dotted lines indicate the niche boundaries estimated by the DRM and the correlative SDM, respectively. (c) Dynamics of future range size for replicate simulations of the true model versus the corresponding forecasts of the DRM and SDM. Shaded areas indicated the central 95% of future range size values that reflect variation between replicate simulations of the true model and uncertainty in DRM forecasts, respectively. For further details see Pagel & Schurr (2012).

process-based statistical analyses are only applicable to species with simple life cycles for which sufficient data exist. The application of this approach to a broader range of study species and study systems requires substantial efforts in demographical research. In the following, we outline this demographic research agenda, which includes advances in the fields of statistical modelling, data collection and ecological theory.

## THE STATISTICAL MODELLING AGENDA

When selecting submodels of demographic responses and range dynamics for a DRM analysis, one can choose from a large number of existing models. In the following, we review these models to identify the ones most promising for the statistical estimation of niches and range dynamics in a DRM framework.

Ecological theory has produced a bewildering number of population dynamics models that could be integrated into a submodel for range dynamics (e.g. Bellows, 1981). Four criteria can help to choose a population model suitable for DRM analysis. First, models of local population dynamics have to include immigration and emigration terms that describe

dispersal between populations (Fig. 1). Second, population models should include stochastic elements that account for the effect of processes that are not modelled explicitly (Clark & Gelfand, 2006; see Box 1). Third, the quantification and forecasting of range dynamics requires an adequate description of the dynamics of populations that were recently founded and/or are threatened by local extinction. Because these populations typically have low densities, models describing their dynamics should account for the fact that organisms come in discrete entities (individuals or ramets) that cannot be infinitely subdivided. Fourth, data on spatio-temporal variation of environmental conditions are typically available on spatially discrete grids and for temporally discrete time steps. Hence, temporally and spatially discrete population models may be more relevant for use in DRMs than their continuous counterparts (although continuous models can be linked to discrete data through interpolation in space or time).

Within these general constraints, the choice of a specific population model will depend on the life history of the target species and the ecological processes considered important for its range dynamics. In the following, we indicate ways in which

## BOX 1: BUILDING A DYNAMIC RANGE MODEL (DRM)

We illustrate the functioning of DRMs with a statistical model that estimates niches and range dynamics of annual species with non-overlapping generations from presence/absence maps and time series of local abundance (Pagel & Schurr, 2012). In the following, we briefly describe the three submodels of this DRM. Note that the general DRM framework is not restricted to this illustrative example: alternative formulations of the demographic response and range dynamics model can describe organisms with different properties (see 'The statistical modelling agenda'), alternative observation models can integrate different data types (see 'The empirical agenda'), and alternative error distributions in each submodel can represent different effects of processes that are not modelled explicitly.

### Demographic response model

The intrinsic population growth rate $r$ is assumed to change linearly with two spatially heterogeneous 'landscape' variables ($X$ and $Z$) and to show linear and quadratic responses to a spatio-temporally variable climate measure $C$ (so that $r$ can have a climatic optimum). The probability of $r$ across sites $i$ and years $t$ is thus given by a multiple linear regression

$$p(\mathbf{r}|\beta, \sigma_r) = \text{Normal}\left(\mathbf{r}|\mu, \sigma_r^2\right) \ \text{ with } \ \mu_{i,t} = \beta_0 + \beta_1 X_i + \beta_2 Z_i + \beta_3 C_{i,t} + \beta_4 C_{i,t}{}^2,$$

where the normally distributed errors (with variance $\sigma_r^2$) describe processes not explicitly resolved in the demographic response model, such as effects of further environmental variables or interspecific interactions (Kissling *et al.*, 2012) on $r$. The carrying capacity $K$ is assumed to be proportional to $r$ ($K = r/h$, where $h$ describes a constant intensity of intraspecific competition in all environments). Moreover, dispersal is assumed to be independent of the environment (which is why the demographic response model was termed the *niche model* in Pagel & Schurr, 2012).

### Range dynamics model

Local population dynamics are described by a stochastic Ricker model with Poisson error $N_t \sim \text{Poisson}(N_{t-1} \cdot \exp(r - h\,N_{t-1}))$. The probability of dispersal from cell $j$ to cell $i$ is given by a spatially discrete kernel $P_{j \to i}(f_{\text{LDD}}, \alpha)$ that describes the fraction $f_{\text{LDD}}$ of individuals dispersed beyond cell $j$ as well as a negative exponential distribution of dispersal distance for these individuals. Given parameters of the population model ($\mathbf{r}$, $h$), dispersal parameters ($f_{\text{LDD}}$, $\alpha$) and initial population sizes $\mathbf{N^0}$, the probability of population sizes $\mathbf{N}$ across sites and years is then

$$p\left(\mathbf{N}|\mathbf{N^0}, \mathbf{r}, h, f_{\text{LDD}}, \alpha, \sigma_P\right) = \prod_t \prod_i \text{Poisson}\left(N_{i,t}|\tilde{N}_{i,t-1} \exp\left(r_{i,t-1} - h\tilde{N}_{i,t-1} + \varepsilon_{i,t-1}\right)\right)$$

with post-dispersal abundances $\tilde{N}_{i,t} = \sum_j P_{j \to i}(f_{\text{LDD}}, \alpha) \cdot N_{j,t}$. Again, normal errors $\varepsilon$ with variance $\sigma_P^2$ account for processes that are not explicitly represented in the range dynamics model.

### Observation model

We assume that individuals are observed independent of each other and that the per-individual observation probability is $\pi_A$ for an abundance census and $\pi_P$ during presence/absence mapping. Hence, the likelihood of recording $A$ individuals in an abundance census is given by a binomial distribution and the likelihood of a presence record is the probability to observe at least one out of $N$ individuals (which is $\psi = 1 - (1 - \pi_P)^N$ and defines the success probability of a Bernoulli distribution). If $\Theta$ and $\Omega$ denote the subset of sites and years for which we have abundance data $\mathbf{A}$ and presence/absence records $\mathbf{P}$, respectively, the likelihood of these data given the population sizes $\mathbf{N}$ is

$$p(\mathbf{A}, \mathbf{P}|\mathbf{N}, \pi_A, \pi_P) = \prod_\Theta \text{Binomial}\left(A_{i,t}|N_{i,t}, \pi_A\right) \ \times \prod_\Omega \text{Bernoulli}\left(P_{i,t}|\psi_{i,t}\right).$$

simple population models (like the Ricker model used in Box 1) can be modified to represent further aspects of population dynamics and more complex life histories (Table 1).

The population model can be modified to represent the way in which individuals compete for resources as well as their small-scale spatial clustering (e.g. Brännström & Sumpter, 2005). While the Ricker model describes scramble competition (in which the limiting resource is divided equally among competing individuals, Nicholson, 1954), equally simple alternatives like the Beverton–Holt model describe contest competition (in which resources are divided unequally, Nicholson, 1954), whereas slightly more complex models (e.g. Maynard-Smith & Slatkin, 1973) can describe gradual variation between pure contest and pure scramble competition. Such differences in resource competition are relevant for DRM analyses as they can affect large-scale abundance dynamics (Münkemüller & Johst, 2007; Cabral & Schurr, 2010). Yet, even more important than these differences between different types of negative density-dependence could be positive density-dependence of population growth at low densities (so-called Allee effects). Allee effects can be caused by various ways in which conspecifics facilitate each other at low population densities: for instance, conspecifics may ensure successful reproduction in sexual species, act as cooperation partners in social animals, or provide protection against predators (Courchamp *et al.*, 2008). Because Allee effects strongly alter the dynamics of small populations, they can have profound consequences for range dynamics and range limits

(Keitt *et al.*, 2001; Holt, 2009; Cabral & Schurr, 2010). Moreover, Holt (2009) recently showed that in the presence of Allee effects, one has to distinguish two variants of the Hutchinsonian niche: the population establishment niche (in which a species can establish a population when starting from low densities) and the population persistence niche (in which populations above some threshold density can persist). Both niche variants could be estimated by incorporating population models with Allee effects (Courchamp *et al.*, 2008) into DRM analyses.

To apply the DRM framework to a wider range of study species, it seems particularly important to expand it to iteroparous species with overlapping generations. If rates of reproduction and mortality are equal for all individuals, this can be done easily by adding a simple survival term to the abovementioned population models for non-overlapping generations [as done in the analysis of Hooten & Wikle (2008) for the iteroparous Eurasian collared-dove]. However, in many iteroparous species these rates vary systematically with the age, size or some other state of individuals. The dynamics of such structured populations can be described with matrix models that distinguish discrete classes of individuals (Caswell, 2001) or with integral projection models that represent continuous variation between individuals (e.g. Rees & Ellner, 2009). Of these two modelling frameworks, integral projection models tend to have fewer parameters and can more easily be estimated from demographic data (Rees & Ellner, 2009).

In addition to describing local population dynamics, the submodel for range dynamics has to describe dispersal between

**Table 1** Population models and data types that are, or might become, useful for statistically estimating demographic response functions and spatial dynamics with dynamic range models (DRMs). References listed in the future directions section indicate examples of methodological achievements that could be integrated into future extensions of DRMs.

| Properties of study organisms | Properties of model | Informative data* |
|---|---|---|
| *State of the art*[1,2] | | |
| Unstructured populations | Unstructured models of local dynamics and dispersal | Presence/absence maps |
| Intraspecific competition at all population densities | Negative density-dependence of population growth | Time series of local abundance |
| Scramble competition | Over-compensatory dynamics | Population growth rate ~ environment + population density |
| Environment affects population growth or dispersal | Response functions for dispersal[1] | Dispersal ~ environment + population density |
| | or intrinsic population growth rate[2] | Spatio-temporal variation in environment |
| *Future directions: expanding dynamical behaviour* | | |
| Other forms of competition | Variation in compensation strength[3,4] | Reproduction/mortality ~ density + environment |
| Spatial clustering of individuals | | |
| Intraspecific facilitation at low population density (Allee effects)[5] | Positive density-dependence of reproduction or survival[5] | Reproduction/mortality ~ density + environment[5] |
| Any | Dynamics of neutral loci[6] | Spatial or spatio-temporal variation in neutral molecular markers |
| *Future directions: extension to other life histories* | | |
| Perennial | Matrix models[7] or integral projection models[8] | Reproduction/mortality/growth ~ environment + individual age/size/state[8,9] |
| Populations age-, size- or state-structured | | |
| Iteroparous | Dispersal age-, status- or stage-structured[9,10] | Dispersal ~ age/stage (e.g. capture–mark–recapture data) |
| Individual state affects dispersal (e.g. breeding versus natal dispersal) | | |

[1]Hooten & Wikle, 2008; [2]Pagel & Schurr, 2012; [3]Maynard-Smith & Slatkin, 1973; [4]Brännström & Sumpter, 2005; [5]Courchamp *et al.*, 2008; [6]Kuparinen & Schurr, 2007; [7]Caswell, 2001; [8]Rees & Ellner, 2009; [9]Patterson *et al.*, 2008; [10]Schurr *et al.*, 2008.

*The '~' notation describes informative datasets as response variable ~ explanatory variable A + explanatory variable B.

populations. Simple alternatives to the exponential distribution of dispersal distance used in Box 1 are distributions with fatter or thinner tails that predict higher or lower rates of long-distance dispersal, respectively (Nathan & Muller-Landau, 2000). More complex dispersal functions arise from mechanistic dispersal models (Nathan *et al.*, 2008) or from statistical models that quantify effects of spatial heterogeneity on dispersal (Schurr *et al.*, 2008). Moreover, when considering structured population models, one should be aware that population structure may not only affect reproduction and mortality, but can also affect dispersal (Bowler & Benton, 2005). This is particularly relevant for many vertebrates in which the breeding dispersal of adults differs from the natal dispersal of juveniles in both frequency and spatial scale. DRM analyses could represent this by including a structured dispersal model that distinguishes between juveniles and adults.

The choice of a suitable niche model (describing the environmental response of population growth or its component birth and death rates) is as important for DRM analysis as the choice of an appropriate model for range dynamics. Formulation of the niche model has to answer the following three questions. (1) Which parameters of the population dynamic model respond to environmental variation? (2) To which environmental factors do they respond? (3) What is the functional form of this response? For a simple population model (Box 1), the answer to the first question could essentially be intrinsic growth rate $r$, carrying capacity $K$ and/or competition intensity $h$ (note that any of these three parameters can be calculated from the other two so that no more than two parameters can show independent environmental responses). While niche theory has largely focused on the environmental response of intrinsic growth rate (Maguire, 1973; Chase & Leibold, 2003), the other two parameters may also respond to certain environmental variables (e.g. carrying capacity may vary with the proportion of available habitat or competition intensity may depend on the amount of resources). When addressing the second and third question, one should bear in mind that the niche model can integrate more than just the current value of an environmental variable. For example, demographic performance could show a unimodal response to the difference between the current value and the long-term average at each site. If performance is optimal when this difference is zero, the niche model describes intraspecific niche differentiation resulting from local adaptation in stable ranges (Holt, 2009). While long-term adaptive niche differentiation across species ranges can thus be integrated rather easily, the description of rapid niche evolution under environmental change requires further extensions of the DRM framework (see below 'Towards a demographic understanding of how evolution and interspecific interactions shape niches and ranges').

The relevant environmental variables and the functional form of their effect can be inferred from demographic and distribution data by describing demographic responses with flexible models such as multiple regression (see Box 1). However, DRMs could also integrate a more mechanistic

understanding of organismic responses to the environment. A prominent example is the metabolic theory of ecology, which predicts the functional form in which intrinsic growth rate should increase and carrying capacity should decrease with temperature (Brown *et al.*, 2004). Beyond the very simple and general niche models predicted by the metabolic theory, more refined mechanistic niche models have been developed based on information about the metabolism, energetics and behaviour of specific animal species (e.g. Buckley, 2008; Kearney *et al.*, 2008, 2009; Kearney, 2012) or the physiology and phenology of plant species (Chuine & Beaubien, 2001; Bykova *et al.*, 2012; Higgins *et al.*, 2012). For plants, we also have increasing mechanistic understanding of how long-distance seed and pollen dispersal responds to environmental variability and global change (Nathan *et al.*, 2008, 2011; Schurr *et al.*, 2008, 2009; Kuparinen *et al.*, 2009). These mechanistic models can thus be used to formulate submodels for the environmental response of dispersal. Yet, mechanistic models of demographic quantities are often computationally demanding, which means that they might have to be simplified in order to be suitable for statistical estimation in a DRM framework (for an example see Higgins *et al.*, 2012).

The above overview of potential submodels for DRM analyses should not convey the impression that DRMs can easily be estimated for arbitrary species and situations. While DRMs can be statistically estimated in relatively simple cases (Pagel & Schurr, 2012), the efficient estimation of DRMs in a wider range of situations still poses challenges for statistical research. One of these challenges arises if the study region does not cover the entire geographical range of a species. In this case, dynamics within the study region may be affected by dispersal across the region's boundaries. Research is needed to quantify the importance of such edge effects and to find efficient ways of statistically accounting for them.

A second, more general challenge arises in the statistical estimation of complex population dynamics. While the DRM framework can, in principle, incorporate models of arbitrary complexity, extensions like the inclusion of Allee effects or population structure introduce new process parameters which may respond to the environment, thereby adding additional hierarchical levels to the model. Additionally, stage-structured submodels can substantially extend the state space because local populations are characterized by a frequency distribution of different stages rather than a single abundance value (integral projection models are one solution to this problem as they can reduce the state space to a manageable size). For population models that cannot be formulated as state-transition probabilities and thus cannot be estimated with hierarchical Bayesian methods, simulation-based methods such as approximate Bayesian computation (ABC) may potentially provide solutions (e.g. Hartig *et al.*, 2011). Further issues that deserve consideration include parameter identifiability: complex models may include parameters whose effects are difficult to disentangle. For instance, population size and per-capita detection probability cannot be independently estimated from a single abundance observation. The resulting strong correlations in the

posterior distributions of parameters can slow down Markov chain Monte Carlo (MCMC) sampling algorithms and require specialized sampling techniques (Haario *et al.*, 2006). For an extensive discussion of computational challenges in estimating dynamic state-space models for species distributions see Marion *et al.* (2012). Yet, it is important to note that more complex DRMs do not only pose challenges. By describing processes in greater detail, they can also be linked to a wider range of empirical data (see next section), which should generally facilitate model estimation (Clark, 2005). Moreover, because complex Bayesian models quantify the full posterior distribution of parameters and forecasts, they are not as sensitive to parameter uncertainty as complex models in classical statistics (Clark, 2005). Due to their process-based and Bayesian nature, DRMs thus need not be subject to the bias-variance trade-off known from classical statistics.

## THE EMPIRICAL AGENDA

It is likely that the geographical distributions of many species are in disequilibrium with their environment. Unbiased estimation of niches and range dynamics in such non-equilibrium situations requires more than presence/absence data for a single point in time (the standard data type used in correlative SDM analyses). DRMs may provide a way out of this dilemma as they can integrate a much broader range of data types than SDMs: they can be estimated from data on: (1) large-scale distributions and dynamics of species (presence/absence or abundance), (2) dynamics of local populations, (3) variation in demographic rates, and (4) environmental variation at spatial and temporal scales matching those of the other data types. As stated above, the more processes DRMs represent, the greater the variety of data types they can incorporate.

Minimum requirements for the estimation of DRMs in non-equilibrium conditions seem to be either data on the spatio-temporal dynamics of environmental variables and species (e.g. presence/absence maps for several time points or abundance time series for several populations, Pagel & Schurr, 2012), or the combination of demography–environment relationships with large-scale distribution and environmental data for at least one time point. Below we discuss the availability of different data types useful for DRM estimation and the effort required to collect informative new data.

Large-scale presence/absence data for a single time period are available for many organisms. These data are often presented as having no temporal dimension. Yet, presence/absence data frequently summarize records collected over a long period and we may know when each record was taken. Hence, such 'single time-slice' data can have a hidden temporal dimension that could be useful for the estimation of DRMs. Incorporating this temporal aspect may also render presence-only data useful for DRM estimation. For species with a potentially wide distribution, the collection of new presence/absence data that are informative for DRMs requires substantial efforts and will typically only be manageable in a coordinated research project.

Citizen science projects seem highly valuable for taxa that are relatively easy to find and identify (Devictor *et al.*, 2010).

Presence/absence maps for multiple time periods are currently available only for a relatively small set of organisms (prime examples include several datasets on birds and invasive species as well as data on British butterflies and plants). But where presence/absence data have already been collected at some time in the past, it may be relatively easy to motivate and manage the collection of new data (because such projects can build on experience, networks and results from previous campaigns). Nevertheless, given the substantial effort required for an atlas survey the question is, how long should the time lag be between two surveys to avoid redundancy? This obviously depends on the life history of the study organisms: the shorter their generation time and the more mobile they are, the shorter the time lag between two informative campaigns can be. In short-lived, mobile organisms, such as butterflies, substantial range shifts have been observed at a time-scale of decades (Parmesan *et al.*, 1999).

When combined with presence/absence data for multiple time periods, population genetic data can help improve DRM fits because they can simplify the inverse problem of where the founders of a population came from (e.g. Estoup & Guille-maud, 2010; Lachmuth *et al.*, 2010). Moreover, if DRMs can be extended to represent large-scale genetic dynamics, they could integrate molecular data on large-scale genetic structure and dynamics (see Csillery *et al.*, 2010 for related developments in phylogeography).

Comprehensive data on large-scale variation in local abundance are rare. An example of such data is the Protea Atlas Database (Rebelo, 2001), in which local abundance was recorded (in broad categories) across the global geographical range of *c.* 330 species of African Proteaceae. Even such rough estimates of local abundance may contain substantial information on spatio-temporal dynamics (Cabral & Schurr, 2010) and can often be collected relatively easily. They should thus be routinely included in future atlas projects whenever feasible.

Data on local population dynamics have been collected in many studies (some of them are summarized in the Global Population Dynamics Database; NERC, 2010). However, to inform the estimation of DRMs, we need to replicate population time series that are collected over a range of environmental conditions using a standardized methodology. Such data are currently available only for a limited set of species. A prime example is the North American Breeding Bird Survey (parts of which were used in the analysis of Hooten & Wikle, 2008). Initiated in 1966, this massive monitoring programme records abundance proxies for more than 420 bird species along 4100 survey routes located across North America. Such extensive monitoring programmes obviously require large efforts, but reasonable DRM estimates can be obtained from abundance data of far more modest extent: simulations of Pagel & Schurr (2012) showed for annual species that abundance time series collected over 10 years in 30 populations can substantially improve DRM estimates. This spatial and temporal extent of sampling seems manageable for small-scale research projects (even though the temporal extent clearly exceeds the horizon of

most funding schemes). However, the necessary temporal extent of abundance monitoring will increase with the generation time of the study species. For organisms with long generations times (such as trees), we cannot hope to collect informative abundance time series within a decade.

When considering data on demographic responses, it seems sensible to distinguish between birth and death on the one hand and dispersal on the other. As outlined above, the environmental response of birth and death rates determines the Hutchinsonian niche, whereas dispersal plays a crucial role for range dynamics and for the mismatch between the niche and distribution of species (Pulliam, 2000; Fig. 2).

Data on birth and death rates (or components of these fundamental demographic rates) are available for many organisms. For some organisms, such data are collected over large spatial extents according to a standardized protocol (e.g. forest inventory data for trees, Kunstler *et al.*, 2011). In other species, data on large-scale variation have been assembled from the literature (e.g. data on large-scale variation in the breeding success of seabirds; Sandvik *et al.*, 2008). For most organisms, however, there are no data on large-scale variation in demography. Moreover, existing data on large-scale demographic variation are often restricted to a single demographic quantity (Gaston, 2009). However, for many species it may be feasible to collect informative demographic data within a relatively short time frame. Particularly promising for the estimation of DRMs are transplant experiments beyond the current range boundaries of study species. Such experiments are still rare (Geber, 2008; Stone, 2010) but should yield a more complete description of Hutchinsonian niches (that is not restricted to the niche space currently occupied by a species). Moreover, such experiments may help to assess risks associated with assisted migration (e.g. Stone, 2010).

Collecting demographic data on birth and death seems particularly important for long-lived organisms for which the collection of informative abundance time series takes too long (see above). Such data can be obtained from plot-based studies of sessile species or from mark–recapture studies of mobile species (O'Hara *et al.*, 2009). Clearly, in extremely long-lived organisms, it is often difficult to measure birth and death rates directly (Cody, 2000). However, if DRMs contain refined models of population dynamics (e.g. matrix or integral projection models, Table 1), they can integrate data on measurable components of birth and death rates (e.g. on transition rates between sizes or stages). The decomposition of birth and death rates into quantifiable and unquantifiable components should also enable the estimation of DRMs for the large number of species in which environmental responses are known only for some demographic quantities (Gaston, 2009). Furthermore, physiological and phenological research has led to a mechanistic understanding of how some key components of birth and death rates respond to environmental variation (Cleland *et al.*, 2007; Kearney & Porter, 2009; Bykova *et al.*, 2012; Higgins *et al.*, 2012). Such knowledge can help to constrain the functional form of demographic response functions in DRMs.

For many organisms we have limited quantitative data on dispersal in general and long-distance dispersal in particular. European bird species form an exception, as extensive capture–mark–recapture and band recovery studies yielded large datasets on distances of breeding and natal dispersal (Paradis *et al.*, 1998). However, even for such intensely studied organisms we currently have limited information on how long-distance dispersal varies with environmental conditions. While data on long-distance dispersal are still relatively scarce, they can be collected with a variety of methods (e.g. Nathan *et al.*, 2003). For instance, quantitative data on long-distance dispersal can be gathered through population genetic or capture–mark–recapture methods. Furthermore, novel technologies enable the direct tracking of dispersing animals over large spatial extents: for example, micro radio telemetry and harmonic radar were used to track insect movements at the landscape scale (Ovaskainen *et al.*, 2008; Hagen *et al.*, 2011) and satellites might in the future be used to track small vertebrates and large insects at global scales (Pennisi, 2011). Such direct tracking still seems impossible for most plant propagules. However, mechanistic models can be used to predict plant dispersal at scales relevant for range dynamics from measurements of dispersal traits and dispersal environments (Schurr *et al.*, 2007; Nathan *et al.*, 2008).

Datasets on spatial and temporal variation in important environmental variables can generally be obtained more easily than reliable data on the distribution, dynamics and demography of individual species. For many regions, environmental data already exist at high spatial and temporal resolution and they are further improved and extended through co-ordinated measurement campaigns, remote sensing, and mechanistic modelling. Climatic data of sufficient spatial and temporal resolution can be obtained by interpolation of global long-term datasets (e.g. Hijmans *et al.*, 2005; Di Luzio *et al.*, 2008) or from statistical downscaling of coarse resolution temporal climate time series of the recent past in combination with high-resolution climate normals maps (e.g. Engler *et al.*, 2011). Land cover dynamics can be quantified by remote sensing (e.g. Homer *et al.*, 2007; Vierling *et al.*, 2008) or from historical information (e.g. Steyaert & Knox, 2008). Edaphic and topographic information are additional useful sources that increasingly become available at high spatial resolution (e.g. Jarvis *et al.*, 2008). It should, however, be noted that existing environmental datasets mostly quantify non-interactive scenopoetic variables, whereas data on the spatio-temporal dynamics of resources are largely lacking (see above).

In summary, the monitoring of species distributions and abundances, observations of large-scale variation in key demographic rates, transplant experiments beyond range boundaries and various methods to estimate long-distance dispersal can provide data that are particularly useful to estimate species' niches and range dynamics. These data should thus receive particular attention in emerging biodiversity observation schemes such as the Group on Earth Observations Biodiversity Observation Network (GEO-BON, Scholes *et al.*, 2008).

## THE THEORETICAL AGENDA

The widespread application of DRMs is not just a matter of formulating appropriate models and collecting informative data – it also poses questions to ecological theory. Here, we first discuss two of these issues: the identification of scaling relationships for demographic rates and the theoretical analysis of spatially coupled population dynamics. Subsequently, we highlight the potential of the demographic research agenda for testing and developing theory.

Grid-based DRMs cannot explicitly represent heterogeneous distributions of individuals and environments within grid cells. Yet, such within-cell heterogeneity will affect the way in which small-scale demographic measurements are linked to parameters describing grid-level population dynamics. As an extreme example consider a grid cell that is large enough to host an entire metapopulation. Abundance dynamics of the whole metapopulation may be well described by a simple population model with parameters for intrinsic growth rate and carrying capacity (Hanski, 1999). However, the values of these metapopulation-level parameters may have little to do with values of the corresponding parameters measured in single populations. This is because 'intrinsic growth rates' at the metapopulation-level do not just depend on local population growth but also on the species' ability to colonize new patches in an empty habitat network (Hanski, 1999). Similarly, the metapopulation-level 'carrying capacity' need not be closely related to local carrying capacity as it strongly depends on the dynamic balance between patch colonization and population extinction (Hanski, 1999). While in this example the spatial scaling of demographic rates is well understood, similar challenges arise if within-cell environmental heterogeneity has nonlinear effects on population dynamics or when describing continuous population spread across spatially discrete grids. In general, the scaling challenge becomes smaller as one refines the grid resolution (Lischke *et al.*, 2007). However, use of a finer resolution also increases the computer time for DRM estimation and may not be feasible when environmental and/or distribution data are only available on coarse grids. In such cases, one can resort to existing analytical or simulation-based techniques for scaling up ecological dynamics (reviewed by Lischke *et al.*, 2007). Nevertheless, there is a need for further theoretical research that derives general scaling relationships for demographic rates and identifies cases in which the grid-based discretization of range dynamics will fail.

A second challenge for ecological theory results from the potentially complex behaviour of the spatially coupled population models contained in DRMs. For example, a species' range that is made up of coupled populations with temporally variable growth rates might persist even though the average growth rate of each population is negative (Roy *et al.*, 2005). Hence, a DRM for a species with stable range size might predict that there is no site where the considered environmental variables have values inside the estimated niche. This apparent paradox can, however, be resolved when one

acknowledges that the temporal variability of population growth in this DRM arises from the stochastic error term of the niche model (Box 1). This stochastic term describes, inter alia, the effects of additional environmental variables that are not considered explicitly (Box 1). A more complex DRM that explicitly includes such additional variables should thus identify the environmental conditions under which any given site supports positive population growth and is inside the niche. Further complexity of spatially coupled population dynamics may arise from over-compensatory density-dependence (Hastings, 1993; Holt, 1993; Münkemüller & Johst, 2007), from different types of temporal variability in the environment (Schwager *et al.*, 2006), or from the exploitation of species (e.g. Sinha & Parthasarathy, 1996; Cabral *et al.*, 2011). Better understanding of these complex dynamics will help to interpret DRM estimates and the resulting range dynamics forecasts.

While ecological theory thus contributes important elements to the demographic research agenda, the wider application of DRM analyses in turn provides opportunities for testing and developing theory. In part, this is simply because DRMs yield better niche estimates than state-of-the-art correlative SDMs (Fig. 3). As an example, consider an introduced species that spreads on a new continent where it has not yet filled its entire niche space. In such non-equilibrium situations, DRMs provide less biased niche estimates that should enable more conclusive tests of whether a putative niche shift between the native and the invaded range (e.g. Broennimann *et al.*, 2007) reflects true niche differentiation.

Beyond producing better niche estimates, the demographic agenda can also paint a more nuanced picture of niches and range dynamics. DRMs estimate otherwise inaccessible niche characteristics, such as the maximum population growth rate and the associated environmental conditions (Fig. 3b). This provides novel opportunities for testing whether different niche characteristics are determined by different functional traits, whether their macroevolution proceeded at different rates, and whether their covariance can be explained by life history theory. For instance, it could be tested whether niches are shaped by a generalist–specialist trade-off between niche width and maximum population growth rate (MacArthur, 1972). Moreover, DRMs estimate dispersal rates and thus the spatial and temporal scales at which a species experiences environmental variation (cf. Holt, 2009). This will help to determine the temporal and spatial resolution at which niche axes should be assessed. This is not only relevant for developing niche theory but also for the empirical and statistical modelling aspects of the demographic agenda.

In general, because DRMs are rooted in demographic and niche theory, they offer new tools for testing theoretical findings against large-scale data. Statistical methods of model selection can be used to compare alternative DRMs representing competing theories. Moreover, DRM estimation can identify which parameter ranges of theoretical models are realistic and hence which dynamical behaviours of these models are relevant for real species. For instance, DRM

analyses could test the real-world relevance of the theoretically important distinction between the population establishment and the population persistence niche (Holt, 2009; see above).

## TOWARDS A DEMOGRAPHIC UNDERSTANDING OF HOW EVOLUTION AND INTERSPECIFIC INTERACTIONS SHAPE NICHES AND RANGES

The fundamental demographic rates of birth, death and dispersal not only determine niches and range dynamics but are also central to evolutionary and meta-community dynamics (e.g. Leibold *et al.*, 2004; Metcalf & Pavard, 2007; Holt, 2009). The quantification of large-scale variation in these demographic rates thus forms the basis for understanding how niches and range dynamics are shaped by evolution and interspecific interactions in a meta-community. The DRMs discussed so far do not explicitly describe these processes but subsume them in error terms (see Box 1). However, extended DRMs could build upon existing theoretical models for meta-communities (Leibold *et al.*, 2004) and eco-evolutionary range dynamics (Kirkpatrick & Barton, 1997; Holt, 2009). For instance, a multi-species DRM could describe interspecific interactions in a meta-community through coefficients that describe the interaction between each pair of species (as in classic Lotka–Volterra models) or by explicitly modelling the 'currencies' that mediate interactions (Kissling *et al.*, 2012). Rather than making the binary distinction between fundamental and realized niches (Hutchinson, 1957), this would promote a gradual view of how a species' niche responds to the abundance of interacting species (with the fundamental niche arising in the extreme case where all interacting species are absent). An eco-evolutionary DRM could describe how selection, gene flow, drift and mutation interact to determine demographic response functions and hence the dynamics of niches and dispersal across species ranges (Kirkpatrick & Barton, 1997; Travis & Dytham, 2002; Holt, 2009). This requires introducing additional state variables that describe the genetic composition of populations. Clearly, such possible extensions will substantially increase the computational and data demand of DRMs. Yet, they also highlight the potential of the proposed demographic research agenda for biogeography.

## CONCLUSIONS

A demographic research agenda for biogeography can markedly advance the quantitative understanding of how geographical ranges of species arise from the fundamental demographic processes of birth, death and dispersal. Such a bottom-up demographic understanding will improve the quantification of niches and the forecasting of range dynamics. However, the relevance of the demographic agenda may extend much further: understanding how niches and ranges arise from demographic rates is a prerequisite for understanding how they are shaped by evolutionary processes and interspecific interactions in meta-communities.

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## BIOSKETCH

The team of authors is interested in biogeography, population, community and evolutionary ecology, global change biology, ecophysiology, ecological and statistical modelling.

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