Title: Forecasting species range dynamics with process-explicit models: matching methods to applications

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Abstract

Knowing where species occur is fundamental to many ecological and environmental applications. Species distribution models (SDMs) are typically based on correlations between species occurrence data and environmental predictors, with ecological processes captured only implicitly. However, there is a growing interest in approaches that explicitly model processes such as physiology, dispersal, demography, and biotic interactions. These models are believed to offer more robust predictions, particularly when extrapolating to novel conditions. Many process-explicit approaches are now available, but it is not clear how we can best draw on this expanded modelling toolbox to address ecological problems and inform management decisions. Here, we review a range of process-explicit models to determine their strengths and limitations, as well as their current use. Focusing on four common applications of SDMs – regulatory planning, extinction risk, climate refugia and invasive species – we then explore which models best meet management needs. We identify barriers to more widespread and effective use of process-explicit models and outline how these might be

overcome. As well as technical and data challenges, there is a pressing need for more thorough evaluation of model predictions to guide investment in method development and ensure the promise of these new approaches is fully realised.

Introduction

Understanding and projecting species' distributions is central to ecology, evolution, and conservation science (Holt 2003; Guisan *et al.* 2013; Sutherland *et al.* 2013). The simplest way to infer where a species might be now or in the future is to correlate observed occurrences to variables that may limit or promote persistence (e.g., climate, resource availability). Predictions of how those variables are likely to change (e.g., under climate change, land use changes or the establishment of protected areas) are then used to predict future species' ranges (Araújo *et al.* 2005; Lütolf *et al.* 2008). These *correlative species distribution models* (SDMs) implicitly include the mechanisms that affect observations but do not explicitly model the processes that drive population dynamics or organismal responses to the environment (Elith & Leathwick 2009). While correlative models have been widely applied, there is growing recognition of their limitations, particularly when predicting to new environments (Box 1).

Ultimately, the presence or absence of a species at a given location and time is the consequence of demographic processes: births, deaths and migration, which emerge from the interaction between an organism's physiological, morphological and behavioural traits and its environment. In the last decade many have argued for explicit consideration of demographic and physiological processes when predicting species' ranges (Kearney & Porter 2009; Thuiller *et al.* 2013; Ehrlén & Morris 2015; Urban *et al.* 2016), resulting in a diverse range of approaches often called process-based models (hereafter, *process-explicit models*). These include occupancy dynamics models (Kéry *et al.* 2013), abundance dynamics models (Schurr *et al.* 2012), demographic distribution models (Merow *et al.* 2014), eco-physiological models (Kearney & Porter 2009), and coupled SDM-population approaches (Keith *et al.* 2008) (Fig. 1). By quantifying the biotic or abiotic mechanisms that drive populations, process-explicit models are, at least in principle, expected to forecast range dynamics (i.e. distribution and abundance across space and time) more accurately than correlative models (Evans *et al.* 2016). However, proposed process-explicit methods differ in their characterisations of species' demography and environmental effects, and all have identifiable limitations. Further, although process-explicit models are increasingly common, data needs and technical accessibility present substantial barriers. There is a need to identify the strengths and weaknesses of different approaches so that they can be used effectively in ecological and management applications in changing climatic and environmental conditions.

Here, we address two interrelated questions that hamper more effective use of process-explicit models for conservation and management. First, *how do we choose the most relevant modelling framework (see Fig. 1) and the most appropriate implementation, for a particular application?* For this, we compare different process-explicit models by focusing on four common objectives when predicting range dynamics: i) predicting ranges to inform planning and regulation, ii) predicting extinction risk to evaluate and prioritize conservation and recovery actions, iii) identifying climate refugia for threatened species, iv) determining the risk of invasive species establishing and spreading in novel environments. Second, we ask: *what are the key barriers that prevent wider use of process-explicit models of species' ranges, and how might these be overcome?* These two issues of promise and barriers are not independent: matching different modelling approaches to specific applications will help to identify and overcome barriers to use. Throughout, our discussion is underpinned by a quantitative literature review (See Appendix S1 in Supporting Information).

Types of process-explicit models and their application to predicting range dynamics

Most process-explicit models of range dynamics draw heavily on population modelling (Box 2). Typically, process-explicit modelling involves two steps: (1) characterising relevant processes, generally by estimating parameters from data, and (2) projecting or simulating species' range dynamics based on these characterised processes (Fig. 2). We focus on six key classes of process-explicit models and how they are used to predict individual species' range dynamics over relatively broad (regional to continental) spatial scales. These classes are defined based on the types of data used and how these data are combined to characterise key processes (Box 3). Methods differ in the processes included, how these depend on the environment, and the biological level (individual, population, or species) at which they are characterised (Fig. 1). Recognizing that this is an imperfect taxonomy, we describe exemplars of each model class, and use these to illustrate strengths and limitations of each class (Box 3; see Appendix S2 for additional descriptions of model classes).

In describing process-explicit methods, we focus on population models commonly used in each model class but acknowledge that alternatives exist (Box 2). We include one such alternative, individual-based models (IBMs), to highlight situations in which a focus on individuals is likely to be beneficial. In contrast to the other methods considered, we group IBMs based on how they simulate range dynamics (Fig. 2) rather than on how key processes are characterised (typical inputs, outputs and key steps: Fig. 1).

To identify current uses of process-explicit models of range dynamics we conducted a literature review using terms relating to each method class in combination with terms relating to range dynamics. We analysed a subset of the returned papers (n = 650) and used relevant papers (n = 121) to identify the ecological and management problems and taxonomic groups models have been applied to, and how they were parameterised and tested (Appendix S1). Key patterns in model use are highlighted in the model description sections, and results inform subsequent discussions.

Occupancy dynamics models (also known as species patch occupancy models; SPOMs): Despite frequent use at landscape scales and for inference, occupancy dynamics models have not been widely used to model range dynamics at broad (e.g. continental) spatial scales (although see Bled *et al.* 2011; Garcia-Valdes *et al.* 2013). In the studies we reviewed, occupancy dynamics models were most commonly applied to bird species (Fig. 3a), likely due to the availability of bird atlas data. Kéry and colleagues (2013) used the European crossbill in Switzerland to illustrate the value of occupancy dynamics models for predicting range dynamics. Detection/non-detection data from multiple sites in multiple years were used to model local extinction and colonisation probabilities as a function of environmental covariates, while repeat surveys within each season were used to model detection (i.e. the probability that the species was detected at a site when present). Accounting for imperfect detection (optional in these models) can improve the accuracy of range dynamics predictions (Kéry *et al.* 2013; Lahoz-Monfort *et al.* 2014) but requires data informative about the detection process (Guillera-Arroita 2017). Occupancy dynamics models can explicitly model colonisation and extinction probabilities as functions of environmental and spatial factors, accounting for spatial dependence in these processes. These models should therefore provide more reliable estimates of range dynamics (particularly for invasive or range-shifting species) than static correlative SDMs, which assume that species are at equilibrium and typically do not adequately account for dispersal constraints (Bled *et al.* 2011; Yackulic *et al.* 2015). However, occupancy dynamics models may be unreliable when relationships between colonisation, extinction and the environment are extrapolated to novel environmental conditions. They also do not model abundance, which is often of most interest to managers of threatened and invasive species.

Abundance dynamics models (including dynamic range models, DRM): Abundance dynamics models are yet to be widely applied to range dynamics (Fig. 3) but are included here due to their links to inverse models of demographic parameters, which allow estimates of demographic processes in the absence of individual-level demographic data, and show promise for simulating range dynamics (Schurr *et al.* 2012; González *et al.* 2016). Cabral and Schurr (2010) used this method to simulate local population dynamics, dispersal, and range dynamics from a time series of abundances of Proteaceae species of the South African Cape. Demographic and detection parameters were estimated via simulation, with parameter values selected based on the match between simulated abundances (accounting for imperfect detection) and observed abundances. Simulated dynamics were restricted to areas identified as suitable habitat in a correlative SDM. Although this example assumed demographic parameters were constant throughout species' potential ranges, Pagel and Schurr (2012) provided an expanded modelling framework ('dynamic range models') in which demographic rates can vary with the environment.

Challenges of abundance dynamics models include the appropriate selection of an underlying demographic model (although alternative model structures can be tested formally), as well as data availability and model identifiability (Schurr *et al.* 2012). Fitting these models may also be computationally challenging, depending on model complexity and temporal and spatial scale. Our review uncovered few examples of abundance dynamics models (n = 7). These were most commonly case studies using simulated species (Fig. 3a), where model structure (Pagel & Schurr 2012) or some parameters (dispersal, detection) are known perfectly (Zurell *et al.* 2016). It is therefore still unclear how readily abundance dynamics models can be applied to different sets of real data (Ehrlén & Morris 2015).

Coupled SDM-population models (also known as hybrid models or coupled niche-population models): Coupled SDM-population models have been used to predict responses of a wide range of species to environmental change (Fig. 3a, Pearson *et al.* 2014; Fordham *et al.* 2018). For example, Keith *et al.* (2008) used this approach to model the viability and spatial distribution of plant populations under climate change in South African fynbos.

Correlative SDMs were linked to spatially explicit stochastic population models by assuming carrying capacity scaled with predictions of species occurrence. If the population exceeded the predicted patch carrying capacity, the population's vital rates (i.e. survival and fecundity) were reduced until abundance fell below carrying capacity. Dynamics in new habitat patches were governed by the species' density-independent vital rates and seed dispersal. This hybrid approach can explicitly account for dispersal, species' life history traits, and processes such as Allee effects, and should therefore predict extinction risk more accurately than estimates based only on the amount of habitat (Fordham *et al.* 2012). It is also well-suited to examining the interacting effects of multiple processes (e.g. land-use change, climate change, overexploitation, fire regimes) and conservation actions on species' persistence (e.g. Wintle *et al.* 2005, Fordham *et al.* 2013a).

However, as correlative SDMs constrain predicted range shifts and carrying capacity, coupled SDM-population models face many of the same limitations highlighted in Box 1. For example, a species' absence due to dispersal constraints or historic disturbances can cause correlative SDMs to underestimate potential habitat or carrying capacities in some environments, reducing the accuracy of population projections. Predictions of potential habitat and carrying capacities from correlative SDMs may also be unreliable when models are extrapolating (Elith *et al.* 2010). Despite this, most of the studies we reviewed that used coupled SDM-population models predicted range dynamics under climate change (Fig. 3b), often in combination with other drivers (Appendix S1). As noted by Gallien *et al.* (2010), using occupancy data – itself the outcome of spatial population processes such as biotic interactions, disturbances and dispersal – to model habitat and carrying capacity, and then overlaying a model that explicitly accounts for these same processes may over-emphasize these processes by effectively double-counting them (see also Zurell 2017). How this affects model prediction accuracy is currently not well studied. While early studies adopting this approach often assumed that carrying capacity was proportional to predicted habitat suitability from the correlative SDM, the relationship between probability of occurrence, demographic parameters and carrying capacity varies (VanDerWal *et al.* 2009; Thuiller *et al.* 2014; Weber *et al.* 2017). Ideally, these potentially non-linear relationships should be estimated directly using empirical data, which is now more common (Fordham *et al.* 2013b).

Demographic distribution models (DDM): Most demographic distribution models we reviewed were applied to plants (Fig. 3a). For example, Merow *et al.* (2014) used individual-level data on survival, growth, fecundity and seedling recruitment of *Protea repens* across South Africa to build integral projection models that predicted range dynamics under climate change. Regression models were fitted to vital rates and environmental variables and the fitted models used to project asymptotic population growth rates (λ) across the region. Range dynamics were inferred by assuming the species could persist only where $\lambda > 1$. Strengths of this approach include the ability to capture variation among individuals within a cohort (e.g. population structure), and efficient use of available data using regression techniques, both of which facilitate interpolation within the population structure and across environments. However, as data are only collected from sites where the species occurs, regressions of demographic parameters on environment are not informed by data from unsuitable sites. Experimental translocations beyond the range can provide this information (Crozier 2004; Crozier & Dwyer 2006; Merow *et al.* 2017) and reduce the likelihood of extrapolation. But, translocations may not be practical or ethical for many species, including invasive or endangered species. The use of λ to infer occupancy is also problematic, as it only provides information about population trajectories (under somewhat unrealistic assumptions of density independence, no net migration and stationary environmental conditions), and therefore may not accurately predict occurrence (Ehrlén & Morris 2015; Csergo *et al.* 2017). Likewise, demographic compensation may mean that range limits inferred from mapped predictions of a single vital rate (e.g. without incorporating the full life cycle and its potential trade-offs) may be misleading (Villellas *et al.* 2015). Finally, in many systems, few extreme individuals may define the dynamics of a population (e.g., super-breeders, long-lived individuals) so care must be taken when parameterising demographic models that extrapolate from individuals to populations (Clark *et al.* 2011; Vindenes & Langangen 2015).

Eco-physiological models (also known as mechanistic niche models): Eco-physiological models have been applied to a range of taxa (Fig. 3a), but most commonly reptiles, amphibians and invertebrates, likely because data collection and modelling is often more straightforward for ectotherms. As predictions are based on mechanistic relationships, derived from experiments or first principles, and are closer to the idea of fundamental niche, they are expected to be more robust than correlative approaches when predicting range limits in new environments (Kearney & Porter 2009), provided key mechanisms are captured and climate is a key driver of range dynamics. Consistent with this, eco-physiological models have been widely used to model climate change impacts, as well as the potential range of invasive species (Fig. 3b). Range predictions are typically based on estimates of individual-level fitness components such as predicted survival of one or more life stages or reproductive output (Kearney *et al.* 2008, 2010), with these sometimes translated into metrics of population growth rate or relative abundances (Buckley & Roughgarden 2006; Levy *et al.* 2015; Gutierrez *et al.* 2016). These models typically do not account for spatial population processes or landscape configuration. Eco-physiological models can be computationally intensive and are prescriptive about required environmental and trait data, which limits their feasibility under many circumstances. In many species, traits also vary within and between individuals and populations in ways that may influence range dynamics (Buckley 2008; Kolbe *et al.* 2010; Briscoe *et al.* 2012; Dong *et al.* 2017). This must be accounted for explicitly in eco-physiological models, further increasing data requirements and model complexity. While the modelled relationships should clearly define climatically unsuitable areas, other important drivers of range dynamics including fine-scale landscape features, resources and biotic interactions are often not included (Appendix S1), which can limit their utility and predictive performance (Tingley *et al.* 2014; Briscoe *et al.* 2016).

Individual based models (IBMs, also called agent-based models): IBMs are particularly suited to understanding ecological dynamics in heterogeneous environments, where individual variation, local interactions or spatial processes such as dispersal are important (Cotto *et al.* 2017) and are commonly used to model invasive species spread (Fig. 3b). For example, Jordt *et al.* (2016) coupled a spatially explicit individual-based model with a correlative SDM that defined habitat to predict the potential expansion of wild boar across Denmark. IBMs based on virtual species are also commonly used to develop and test methods (Fig. 3), and explore mechanisms that drive species range dynamics, such as dispersal, evolution or biotic interactions (Bocedi *et al.* 2014; Henry *et al.* 2015; Mohd *et al.* 2016). Whether an IBM overcomes challenges related to biased or imperfectly observed data, species non-equilibrium and extrapolation depends on how they are parameterised. Due to limited data availability, a mix of approaches is often used, and data sourced from a range of populations (e.g. Murphy *et al.* 2017). Scaling-up high-resolution IBMs to explore range dynamics can present computational challenges, particularly for widespread species (Wang 2013; Liénard & Strigul 2016).

Matching promise to need

There are substantial challenges to using process-explicit methods for conservation and management questions. Model choice should therefore be driven by management needs to avoid investment in models that do not deliver. Relevant considerations include: the type of information required to make a good decision for the management objective, key processes that need to be captured, the risk of violating assumptions of the analytical approach, and data availability. As illustrated in Fig. 4, different models have different strengths; correlative SDMs can use widely available and easily collected data, coupled SDM-population and abundance models provide outputs of interest to managers (e.g. abundance, risk of extinction), and individual-based models readily capture processes such as dispersal and biotic interactions. Eco-physiological models are likely to provide more robust predictions in new environments or when species are not in equilibrium, demographic distribution models show promise for efficiently capturing individual variation, and occupancy dynamics models may effectively balance detailed dynamics and model complexity.

The performance of a particular method depends heavily on *how* models are built and parameterised (Fig. 4, Appendix 2). For example, bias and detection can be accounted for in some correlative SDMs (and coupled SDM-population models, which rely on these), but this is not common practice (Araújo *et al.* 2019). Similarly, while examples exist of coupled SDM-population, eco-physiological and demographic distribution models that explicitly model biotic interactions (e.g. Buckley & Roughgarden 2006; Fordham *et al.* 2013b; Peron *et al.* 2016), these are rare. Individual implementations of models tend to focus on particular processes – with other processes ignored or simplified – mostly because it is extremely challenging to obtain data on all relevant processes from across species' ranges.

Below we consider the promise of different process-explicit models for four major applications of modelled range dynamics.

Predicting ranges to inform planning and regulation

Information about the species likely to occur at a particular location can be used to inform planning and regulate development. This requires predictions of probability of occupancy, potentially for many species. In some cases, such as regulatory approvals of development applications, the focus is whether species are likely to currently occur at the proposed impact site, which may trigger additional surveys or conditions on the development. However, in a growing number of cases, often related to land-use or statutory planning, there is concern about where species might occur both now and in the future (Dunlop *et al.* 2012; Kujala *et al.* 2015), requiring models that better capture dynamic processes.

Which methods show promise?

When the regulatory process requires only contemporary predictions, process-explicit models might not provide greater utility than correlative SDMs, assuming the data used to build the correlative SDM are appropriate (e.g. not biased, adequately cover environmental conditions, detection is high and consistent or accounted for; Guillera-Arroita *et al.* 2015). Occurrence data required to build correlative SDMs are often available or can be collected relatively quickly or easily, meaning that a wider range of taxa can be modelled to inform development planning (Whitehead *et al.* 2017). Model comparisons suggest that correlative SDMs can perform as well or better than process-explicit modelling approaches when predicting species occurrence under current conditions (Buckley *et al.* 2010; Briscoe *et al.* 2016; Zurell *et al.* 2016), when the ability to identify and map a pattern is sufficient.

Accounting explicitly for dynamics may be important when predictions of future species' occurrences are required for planning. The ideal method of prediction will depend on the type of dynamics relevant to the species, landscape or time horizon over which the plan holds jurisdiction. Occupancy dynamics and coupled SDM-population models readily capture the likely impacts of changes in spatial configuration of habitat (e.g. Heard *et al.* 2013). When long-term forecasts under climate change are required for plan development, approaches that are more robust to extrapolation, such as eco-physiological models, should be considered (see below: Identify climate refugia).

Caveats

Correlative SDMs may overpredict the area currently occupied by a species if they inadequately capture dispersal constraints or biotic interactions that prevent species colonising suitable habitat (Uribe-Rivera *et al.* 2017). Occupancy dynamics or coupled SDM-population models that explicitly model dispersal processes may provide improved contemporary range predictions for dispersal-limited species in landscapes where range dynamics are strongly driven by periodic or stochastic disturbances, or species are unlikely to be in equilibrium with their environment (Bled *et al.* 2011). Coupled SDM-population models rely on correlative SDMs for input and are, therefore, impacted to some degree by errors in the SDMs.

Predicting extinction risk to evaluate and prioritize conservation and recovery actions

By identifying species most at risk of extinction and evaluating options for reducing extinction risk, conservation practitioners can prioritise allocation of conservation resources to reduce the chances of species loss. This requires that the biological and population processes and exogenous drivers of population decline are accurately characterised. Modelling challenges include the fact that populations may not be at equilibrium with their environment (e.g. lagged responses to historic habitat loss or rapid environmental change) and the characteristic lack of monitoring and distribution data for many threatened species (Legge *et al.* 2018).

Which methods show promise?

Coupled SDM-population models, abundance dynamics models, and many IBMs (e.g. Sun *et al.* 2016) provide predictions of population size through time, and explicitly account for dispersal and life history factors that may render species more vulnerable to extinction or responsive to conservation management (Keith *et al.* 2008; Cabral & Schurr 2010). To date, abundance dynamics models have primarily been fitted with simple population models (e.g. Ricker models) with relatively few covariates. Modelling complex life histories or environmental responses may be quite challenging, particularly if data are limited (Schurr *et al.* 2012). In contrast, coupled SDM-population models and IBMs can be parameterised using diverse sources, including previous studies of particular processes and expert knowledge (Penman *et al.* 2015; Sun *et al.* 2016), and hence show promise for this application. This flexibility also means that they are more commonly used to examine a suite of conservation actions or the interactive effects of multiple stressors, which may be critical for accurately forecasting extinction risk and identifying optimal management actions (Regan *et al.* 2003; Wintle *et al.* 2011; Fordham *et al.* 2013a). DDMs and eco-physiological models can provide predictions of population trajectories (and abundances if initial population sizes can be estimated). These methods are most likely to offer improved predictive capacity when vital rates are directly linked to the environment (Pomara *et al.* 2014). If intra or inter-specific interactions such as competition, predation or pathogens are thought to underpin fluctuations in population size or responses to conservation actions, then explicit incorporation of these in coupled SDM-population models (Fordham *et al.* 2013b) or IBMs may be a useful approach (Cramer & Portier 2001).

Occupancy dynamics models can estimate the probability of extinction (across the entire study region or select sites), including under different management scenarios, helping to set conservation priorities (Santika *et al.* 2014; Heard *et al.* 2018). These methods can also be used to estimate changes in the area of occupancy, which can inform assessments of extinction risk (IUCN Standards and Petitions Subcommittee 2017). Occupancy dynamics models may be more easily applied to threatened species than other process-explicit models because the required occupancy data are more often available or more readily collected (Fig. 4).

Caveats

The source and reliability of input data used to parameterise responses should be carefully considered. For example, projected species' trajectories may be inaccurate if vital rates estimated from historical data or individual populations do not capture the current causes of decline or are inferred from closely related species that may differ in important ways (Che-Castaldo *et al.* 2018). Similarly, potential habitat – an input to coupled SDM-population models and some IBMs – may not be estimated accurately from historical occurrence data (e.g. due to mismatch in time period, dispersal constraints, or lagged responses). Projected changes in the area of occupancy may not accurately reflect changes in population size or extinction risk, as these may not scale linearly (Lawton 1993; Fordham *et al.* 2012).

Identifying climate refugia for threatened species

Climate refugia are areas where species can persist (and potentially expand from) under climate change (Keppel *et al.* 2012). Thus, models are required to identify areas that will be environmentally suitable, occupied or reachable by the species, and allow populations to persist as surrounding areas are lost (i.e. source rather than sink habitat). Crucially, identifying climate refugia often requires predicting where species will occur under novel environmental conditions (Williams & Jackson 2007).

Which methods show promise?

The need to predict species responses in novel environmental conditions poses challenges for approaches that forecast species' responses from correlations between occurrence or demographic data and environmental predictors captured under current conditions. Extrapolation is of less concern for eco-physiological models that characterise limiting responses over the full expected range (e.g. thermal response curves spanning survival limits) or are based on established physical principles likely to hold under novel conditions (e.g. heat-transfer physics). These methods should perform similarly in current and future conditions, and model realism can be tested under current conditions (e.g. Kearney *et al.* 2018). To ensure that management effort is directed towards viable populations, models should capture the entire life cycle, including reproduction. Species' abilities to track shifts in the future locations of suitable conditions should also be explicitly modelled, unless translocation is involved (Mitchell *et al.* 2012). Linking eco-physiological models, which often ignore spatial population processes, with population models or IBMs that explicitly incorporate information about dispersal capabilities and habitat configuration as well as other interacting processes such as disturbances, habitat loss or disease, should provide more reliable predictions of accessible climate refugia likely to support long-term population persistence (Fordham *et al.* 2013c).

Approaches that fit separate response curves for processes such as survival and fecundity or colonisation and extinction (e.g. DDMs, occupancy dynamics models) can account for processes such as demographic compensation (Villellas *et al.* 2015) and, may therefore be more robust to changes in correlation structure of environmental variables in future conditions (Evans *et al.* 2016). This contention is not yet tested, however, and extrapolating to novel environmental and biotic conditions remains a challenge not fully addressed by these approaches. Experimental demographic data, such as those from warming experiments (Panetta *et al.* 2018), could be used in DDMs or coupled SDM-population models to capture responses over a broader range of environmental conditions, reducing the need for extrapolation.

Caveats

Eco-physiological models may not provide accurate forecasts of climate refugia if spatial and temporal variation (e.g. local adaptation, evolutionary responses) in traits that drive responses to the environment are not accounted for. These approaches can also predict poorly if modelled responses are not the key factors limiting species' range dynamics, such as when competitive interactions constrain range limits (McGill 2012). Modelling dispersal explicitly may be less important if species are likely to undergo range contractions rather than range shifts and if patterns of occupancy are not dynamic, but identifying such cases may be challenging. Similarly, a broader range of methods may be appropriate if climate change does not result in large changes in environmental conditions or inter-annual variation in long-term population or demographic data captures likely responses to future conditions.

Determining the risk of invasive species establishing and spreading in novel environments

Risk assessments for invasive species pose one of the most challenging applications of range dynamics models. Predicting invasive range dynamics of a species using information from its native range frequently involves extrapolation, often into environments with novel biotic interactions and abiotic conditions, or novel combinations of conditions (Broennimann & Guisan 2008). Conversely, the assumption that species are at equilibrium and occupy all potential suitable habitat is likely to be violated if using data from the invasive range (Elith *et al.* 2010). For invasive species there are two broad decision contexts (Elith 2017): (i) what is the potential invaded range (to inform pre-incursion risk assessments)? (ii) given an outbreak, how far and quickly could a species spread and what is its likely impact?

Which methods show promise?

As noted above, methods that model range dynamics based on biophysical constraints or experimental data (e.g. eco-physiological models, some IBMs, CLIMEX models if parameters are estimated from experimental data; Sutherst & Maywald 1985) can avoid issues of extrapolation. Eco-physiological models typically characterise the fundamental niche, so are less likely to underestimate the potential invasive range if biotic interactions constrain the species in its native range (Tingley *et al.* 2014). When predicting how far or how quickly a species could spread, the formal methods of invasion biology – reaction diffusion and integro-difference approaches – are powerful tools (Hastings 1996; Hastings *et al.* 2005), although these methods often assume homogeneous habitat. It is also apparent that spreading populations can experience rapid evolution causing invasions to accelerate (Phillips *et al.* 2010). While it is possible to capture such complexities in analytical models (Perkins & Nowak 2013), simulation is often necessary, and IBMs are the most flexible platform (Bocedi *et al.* 2014). By capturing dispersal constraints, simulation models can provide more realistic estimates of risk compared to mapping potential habitat, particularly if the location of the source population is known (Kearney *et al.* 2008; Prasad *et al.* 2010).

Caveats

When faced with an outbreak, rapid decisions require models that already exist or can be quickly implemented (e.g. using available or readily collected data; Fig. 4). Eco-physiological models may overestimate risk if biotic interactions or dispersal limitations constrain the invasive species, as these processes are typically not accounted for (although see Kearney *et al.* 2008; Gutierrez & Ponti 2014). Conversely, failure to account for evolution could lead models to underestimate the invasive range and the speed of the invasion (Kolbe *et al.* 2010).

Often dispersal is characterised statistically within process-explicit models, but these relationships may be context-specific and not apply under altered environmental conditions or different spatial configurations of habitat. Mechanistic dispersal models that account for abiotic and biotic drivers of dispersal (Travis *et al.* 2012; Trakhtenbrot *et al.* 2014) could provide more reliable forecasts, particularly under novel conditions.

Overcoming barriers to use

While process-explicit models show great promise for many applications, our collective experience using a range of modelling methods to inform conservation and management indicates there are two key barriers that currently restrict the use of these approaches: data availability and accessibility of methods.

Data availability

What is the problem?

Unlike correlative models, which use commonly available occurrence data, process-explicit models typically require detailed data on individuals or populations, often measured repeatedly through time and under multiple environmental conditions (Fig. 1). These data are typically lacking (Urban *et al.* 2016) and can be expensive and difficult to collect. For example, demographic distribution models require data on vital rates collected from populations that span key environmental gradients to adequately model range dynamics (Merow *et al.* 2014) – yet these are rare (Fig. 5). The estimation of demographic rates and population processes often requires long-term data collection: occupancy data used to parameterise models in the studies we reviewed used 14 years of data on average, and sometimes spanned > 50 years (van Strien *et al.* 2011). Abundance dynamics models fit by Zurrell *et al.* (2016) and Pagel and Schurr (2012) relied on 10–20 years of abundance data from 30–50 sites, as well as extensive presence-absence data. Given that long-term data collection efforts may exceed many research-funding cycles (Lindenmayer *et al.* 2012), it is unsurprising that the data required to parameterise process-explicit models are rare. The need for specialist skills and equipment for data collection (e.g. animal capture or laboratory experiments) can also make data collection challenging.

Correlative SDMs are often built using long-term averaged environmental data (e.g. mean annual temperature or rainfall) that are readily available at 1 km^2 resolution across the globe for past, present, and even future conditions (Hijmans *et al.* 2005; Fick & Hijmans 2017). However, accurate projection of eco-physiological and demographic processes will often require that environments are characterised at much finer temporal and spatial resolutions to match the resolution over which these processes occur (e.g., hourly, daily or weekly data at cm^2 or m^2). This is likely to be particularly important for species whose microclimates are decoupled from macroclimate – such as some intertidal species, or species whose survival is strongly influenced by the timing or duration of extremes (Helmuth *et al.* 2010; Levy *et al.* 2015; Maclean *et al.* 2017). Currently, these data are not readily available across large spatial extents (e.g., 100s km^2) or time periods (historic, current and future), which may limit the use of process-explicit models in many applications. There can also be substantial uncertainty in existing long-term environmental data layers, particularly in poorly sampled regions (Fick and Hijmans 2017), and this uncertainty is likely to be higher for data at finer spatial and temporal resolutions (Kearney *et al.* 2014).

Implications of poor data availability

The belief that process-explicit models will generate more reliable predictions than correlative methods is based partly on an assumption that these methods more accurately capture (and project) the fundamental processes that underpin species' range dynamics. However, without detailed observations of individual or population responses across the full range of environmental conditions (either in the lab or in the field), such processes may not be accurately captured. In these situations, generating predictions at large spatial extents will require extrapolation or interpolation. Given that the drivers of population dynamics and species traits can vary in space and time (Jongejans & Kroon 2005; Messier *et al.* 2010) and at different scales, process-explicit models that extrapolate or interpolate ecological processes might not support reliable predictions (Coutts *et al.* 2016). Similarly, reliable predictions will not be achieved if environmental data used to project process-explicit models do not accurately match those used to parameterise the model (e.g. local temperatures measured in the field or during laboratory experiments) – and lack of environmental data at appropriate scales may increase prediction uncertainty (Levy *et al.* 2015; Briscoe *et al.* 2016).

Cause for optimism

Relevant data are increasingly being collated in centralised databases (e.g. BAAD: Falster *et al.* 2015; GlobTherm: Bennett *et al.* 2018; AmP: Marques *et al.* 2018; Global Population Dynamics Database: NERC 2010; COMPADRE: Salguero-Gómez *et al.* 2015; COMADRE: Salguero-Gómez *et al.* 2016; see Fig. 5) and efforts are underway to enable large global biodiversity databases (e.g. GBIF https://www.gbif.org; BIEN http://biendata.org) to store new data types, including trait data, and repeat survey and count data that underpin many occupancy and abundance models. Citizen science projects, (e.g. eBird; Sullivan *et al.* 2014), and collaborations between NGOs, governments and individuals (e.g. MAPS; Saracco *et al.* 2008) are rapidly increasing the availability of occurrence, abundance and demographic data at fine spatial and temporal resolutions over large spatial extents. Similarly, high resolution satellite data and aerial survey techniques are improving our ability to regularly monitor changes in population abundance or occurrence over large or remote areas (Tredennick *et al.* 2016; Fretwell *et al.* 2017).

Alongside increases in species data availability, new methods are being developed to make better use of existing data, supporting parameter estimates in situations typically assumed to be data-limited. Recently developed statistical methods enable estimates of demographic parameters without requiring repeated surveys of marked individuals, drawing on non-traditional data types (e.g., growth nodes and rings, otoliths; Morrongiello *et al.* 2012; Cohn *et al.* 2013; Merow *et al.* 2014; paleoecological data; Fordham *et al.* 2016a) and readily available population data (e.g., inverse population models; Doak & Morris 1999; González *et al.* 2016). These methods are complemented by statistical tools suited to complex ecological models, including integrated models and simulation-based inference (Schaub & Abadi 2011; Hartig *et al.* 2011; Maunder & Punt 2013; Fithian *et al.* 2015).

Environmental data are also increasingly available. These include spatial predictions of microclimates at continental or global scales (Kearney *et al.* 2014; Levy *et al.* 2016), as well as computational tools for generating microclimate predictions from gridded weather data (e.g. Kearney & Porter 2017). High-resolution satellite data and new computational approaches are being used to obtain fine spatial (5–25 m) and temporal information on land cover, soil properties, vegetation structure, surface temperature and disturbance (Goodwin & Collett 2014; Midekisa *et al.* 2017), although it remains challenging to project models parameterised using these data to the future, and uncertainties in these data are often ignored.

Accessibility of methods

What is the problem?

Process-explicit models have emerged from different disciplines, each with their own terminology and technical methods. Many of these methods are yet to be applied widely to modelling range dynamics and, in some cases (e.g. complex eco-physiological models, IBMs or abundance dynamics models), their implementation can require substantial computing power, time and technical expertise (Zurell *et al.* 2016). As a result, many process-explicit models are not readily accessible, particularly compared to correlative SDMs. Free, open-source software is available (Lurgi *et al.* 2015), but only for a subset of methods and, where software does exist, a lack of technical knowledge can hamper potential applications.

Implications of poor method accessibility

Inaccessibility will limit the uptake of many process-explicit models, preventing their use for applications where they are likely to deliver substantial benefits over traditional correlative SDMs. A lack of accessible software and computational power makes it difficult to test the capability and limitations of process-explicit models through detailed sensitivity analyses. Thus many studies, particularly those using complex eco-physiological models or IBMs that involve detailed calculations (e.g. of microclimates and/or organism states) at fine time steps over broad spatial scales, do not comprehensively explore potential sources of uncertainty. Such tests have been critical to the uptake and implementation of correlative SDMs, identifying technical, practical, and conceptual limitations of these methods (Elith *et al.* 2006, 2010). Lastly, the technical complexity of many process-explicit models can discourage potential collaborations among disciplines, reducing opportunities to share knowledge and expertise that might otherwise overcome barriers to the implementation of process-explicit models.

Cause for optimism

Rapid increases in computing power are overcoming computational barriers associated with many process-explicit models (Grimm & Berger 2016). Increases in computing power are complemented by increased interest in explicitly modelling ecological processes, which has led more researchers to address the technical and computational barriers posed by these methods and make software more openly available (Nenzén *et al.* 2012; Metcalf *et al.* 2013; Kearney & Porter 2017; Leonard *et al.* 2017).

These advances will enable more applications of process-explicit models, and it is likely that detailed documentation of methods will accumulate alongside applications. Broader uptake of standard protocols for describing model implementations (e.g. ODD protocol; Grimm et al., 2010) will also increase model accessibility. There is growing interest in calibration, verification and sensitivity analysis for process-explicit models (Augusiak *et al.* 2014; van der Vaart *et al.* 2016). Methods for running sensitivity analyses and propagating key sources of uncertainty are now commonly applied to some model classes (e.g. coupled SDM-population models, Naujokaitis-Lewis & Curtis 2016; Fordham *et al.* 2016b), and increasingly being developed and applied to others (e.g. IBMs, van der Vaart *et al.* 2015, DDMs, Paniw *et al.* 2016).

Next steps

Although there is substantial cause for optimism, targeted efforts to increase the availability of data and the accessibility of methods will hasten progress towards reliable models of range dynamics. Active collaboration among disciplines and with research fields such as epidemiology or agriculture (e.g. Bradhurst *et al.* 2015), which face similar objectives and challenges, will foster the development of new process-explicit models, drawing on the complementary strengths of existing methods (Fig. 4). Collaborations among disciplines need to be supported by common goals. One possibility is to identify specific examples or case studies using simulated or real datasets that could be used to develop, demonstrate, and test multiple process-explicit models (Zurell *et al.* 2016; Fordham *et al.* 2018). Ideally input and test data would be made available so that models can be re-evaluated (or new models tested) as methods develop. Focusing on a common example would help standardise model outputs and testing, potentially removing linguistic or historical barriers among disciplines.

Validation of model predictions against independent data has been critical in identifying key limitations and developing methods to improve predictive performance of correlative SDMs (Elith *et al.* 2006; Uribe-Rivera *et al.* 2017), though admittedly there is still much progress to be made (Araujo *et al.* 2019). Process-explicit models make definitive statements about the processes driving range dynamics that can be tested against other sources of data including independent measurements of vital rates, dispersal, activity and genetic data (Cabral & Schurr 2010; Rossman *et al.* 2016; Kearney *et al.* 2018). Model output can also be tested against independent occurrence or abundance data (Merow *et al.* 2014; Briscoe *et al.* 2016; Fordham *et al.* 2018). Yet our review of process-explicit models found that model outputs were not commonly quantitatively evaluated against independent data (< 30% of studies). This is consistent with a recent review of correlative SDMs, which found that > 50% of studies did not evaluate model outputs against independent data (Araújo *et al*. 2019). This hampers our understanding of the transferability of models, and is particularly problematic when process-explicit models are used to forecast range dynamics in new times and places (Fig. 3). More consistent tests of process-explicit models, including hindcasting (Wethey & Woodin 2008; Fordham *et al.* 2018) and simulation studies (Zurell *et al.* 2016), are needed to help determine which conceptual and practical barriers are important to different applications, and test expectations about model performance (Fordham *et al.* 2016a). In addition, tests of model predictions could be used to assess how data availability and quality affect model performance (Pagel & Schurr 2012) and help target data collection towards particular data types and sampling regimes most expected to improve predictive performance.

Readily accessible software is crucial to the uptake and application of process-explicit models. Alongside the development of open-source software, detailed documentation, as well as non-technical guides and tutorials (e.g. Merow *et al.* 2014b; Railsback & Grimm 2019) should improve accessibility and implementation of process-explicit models. Perhaps most importantly, however, greater quantitative and computational training, and stronger collaborations between those with specialist modelling expertise and field ecologists, physiologists and land managers with detailed understanding of the study system, will improve the uptake and implementation of these methods.

Conclusion

Despite their differences (Fig. 1), process-explicit models are commonly perceived collectively as overcoming limitations of correlative SDMs. This can make it difficult for potential users to select the most appropriate method for their given application. Importantly, there is no silver bullet. None of the reviewed approaches overcome all the challenges associated with modelling range dynamics (Fig. 4). Their use should therefore be driven by careful consideration of the application and species: the types of information required to make a decision, key processes to be included, how these processes will be characterised and an understanding of underlying assumptions and data availability. Combining multiple approaches (e.g. using output from physiological models as input into an IBM or population model) could draw on the strengths of different approaches (Malishev *et al.* 2018; Thomas & Bacher 2018). However, more complex models can take longer to build, lack appropriate data to parameterise, and can also be more difficult to interpret and communicate to other researchers and decision-makers (Dormann *et al.* 2012).

In general, process-explicit methods are data hungry, and a lack of data increases the gap between theoretical potential and realised outcomes (Singer *et al.* 2016). For example, occupancy dynamics and abundance dynamics models can theoretically account for spatial dependence when simulating range dynamics, but this requires data at appropriate scales to estimate these relationships. Similarly, the detailed knowledge and data required to select appropriate physiological thresholds, reliably model microclimates or identify key processes, can make it difficult for eco-physiological models to achieve good predictive performance (Buckley *et al.* 2010). Two of the key studies that evaluate process-explicit SDMs have shown that more complex models that explicitly capture additional processes do not always provide more reliable predictions (Zurell *et al.* 2016; Fordham *et al.* 2018). Investment in the collection and collation of species and environmental data required for these methods is needed (Urban *et al.* 2016), but these efforts should be strategic and informed by explorations of how data availability and quality affect model performance for different taxonomic groups or applications (Buckley 2008; Pagel & Schurr 2012; Rossman *et al.* 2016). Critically, quantitative evaluation of whether process-explicit models capture important responses and sub-processes and accurately predict occurrence and abundance patterns needs to become standard practice.

In addition to improving forecasts of species range dynamics, process-explicit models have the potential to dramatically increase our understanding of the mechanisms that drive range dynamics. Such an understanding can help identify and evaluate potential management actions (Florance *et al.* 2011; Keith & Spring 2013; Penman *et al.* 2015; Merow *et al.* 2017). This ability to explicitly model the effect of relevant actions on conservation outcomes is appealing to managers and policy makers and might justify efforts to collect the species and environmental data required to capitalise on the promise of process-explicit approaches.

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Supporting Information

Appendix S1: Literature review methods and summary

Appendix S2: Details for rankings of process-explicit models in Figure 4

References

Adams, V.M., Petty, A.M., Douglas, M.M., Buckley, Y.M., Ferdinands, K.B., Okazaki, T., *et al.* (2015). Distribution, demography and dispersal model of spatial spread of invasive plant populations with limited data. *Methods Ecol. Evol.*, 6, 782–794.

Akçakaya, H.R. (2000). Viability analyses with habitat-based metapopulation models. *Popul. Ecol.*, 42, 45–53.

Altwegg, R., Wheeler, M. & Erni, B. (2008). Climate and the range dynamics of species with imperfect detection. *Biol. Lett.*, 4, 581–584.

Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, e*t al.*, (2019). Standards for distribution models in biodiversity assessments. *Sci. Adv*, 5, p.eaat4858.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Glob. Change Biol.*, 11, 1504–1513.

Augusiak, J., Van den Brink, P.J. & Grimm, V. (2014). Merging validation and evaluation of ecological models to 'evaludation': A review of terminology and a practical approach. *Ecol. Model*, 280, 117–128.

Bennett, J.M., Calosi, P., Clusella-Trullas, S., Martínez, B., Sunday, J., Algar, A.C., *et al.* (2018). GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci. Data*, 5, 180022.

Bled, F., Royle, J.A. & Cam, E. (2011). Hierarchical modeling of an invasive spread: the Eurasian Collared-Dove *Streptopelia decaocto* in the United States. *Ecol. Appl.*, 21, 290–302.

Bocedi, G., Zurell, D., Reineking, B. & Travis, J.M.J. (2014). Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. *Ecography*, 37, 1240–1253.

Bradhurst, R.A., Roche, S.E., East, I.J., Kwan, P. & Garner, M.G. (2015). A hybrid modeling approach to simulating foot-and-mouth disease outbreaks in Australian livestock. *Frontiers in Environmental Science*, 3, 17.

Briscoe, N.J., Kearney, M.R., Taylor, C.A. & Wintle, B.A. (2016). Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. *Glob. Change Biol.*, 22, 2425–2439.

Briscoe, N.J., Porter, W.P., Sunnucks, P. & Kearney, M.R. (2012). Stage-dependent physiological responses in a butterfly cause non-additive effects on phenology. *Oikos*, 121, 1464–1472.

Broennimann, O. & Guisan, A. (2008). Predicting current and future biological invasions: both native and invaded ranges matter. *Biol. Lett.*, 4, 585–589.

Buckley, L.B. (2008). Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Am. Nat.*, 171, E1–E19.

Buckley, L.B. & Roughgarden, J. (2006). Climate, competition, and the coexistence of island lizards. *Funct. Ecol.*, 20, 315–322.

Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010). Can mechanism inform species' distribution models? *Ecol. Lett.*, 13, 1041–1054.

Cabral, J.S. & Schurr, F.M. (2010). Estimating demographic models for the range dynamics of plant species. *Glob. Ecol. Biogeogr.*, 19, 85–97.

Caswell, H. (2001). *Matrix Population Models: Construction, analysis and interpretation*. 2nd Edition. Sinauer Associates, Inc. Publishers, Massachusetts.

Che-Castaldo, J., Che-Castaldo, C. & Neel, M.C. (2018). Predictability of demographic rates based on phylogeny and biological similarity. *Conserv. Biol.*32, 1290-1300.

Clark, J.S., Bell, D.M., Hersh, M.H., Kwit, M.C., Moran, E., Salk, C., *et al.* (2011). Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecol. Lett.*, 14, 1273–1287.

Cohn, J.S., Lunt, I.D., Bradstock, R.A., Hua, Q. & Mcdonald, S. (2013). Demographic patterns of a widespread long-lived tree are associated with rainfall and disturbances along rainfall gradients in SE Australia. *Ecol. Evol.*, 3, 2169–2182.

Colwell, R.K. & Rangel, T.F. (2009). Hutchinson's duality: The once and future niche. *Proc. Natl. Acad. Sci.*, 106, 19651–19658.

Cotto, O., Wessely, J., Georges, D., Klonner, G., Schmid, M., Dullinger, S., *et al.* (2017). A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nat. Commun.*, 8. 15399.

Coutts, S.R., Salguero-Gómez, R., Csergő, A.M. & Buckley, Y.M. (2016). Extrapolating demography with climate, proximity and phylogeny: approach with caution. *Ecol. Lett.*, 19, 1429–1438.

Cramer, P.C. & Portier, K.M. (2001). Modeling Florida panther movements in response to human attributes of the landscape and ecological settings. *Ecol. Model.*, 140, 51–80.

Crozier, L. & Dwyer, G. (2006). Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *Am. Nat.*, 167, 853–866.

Crozier, L.G. (2004). Field transplants reveal summer constraints on a butterfly range expansion. *Oecologia*, 141, 148–157.

Csergo, A.M., Salguero-Gomez, R., Broennimann, O., Coutts, S.R., Guisan, A., Angert, A.L., *et al.* (2017). Less favourable climates constrain demographic strategies in plants. *Ecol. Lett.*, 20, 969–980.

DeAngelis, D.L. & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000Prime Rep.*, 6, 39.

Doak, D.F. & Morris, W. (1999). Detecting population-level consequences of ongoing environmental change without long-term monitoring. *Ecology*, 80, 1537–1551.

Dong, Y.W., Li, X.X., Choi, F.M.P., Williams, G.A., Somero, G.N. & Helmuth, B. (2017). Untangling the roles of microclimate, behaviour and physiological polymorphism in governing vulnerability of intertidal snails to heat stress. *Proc. R. Soc. B Biol. Sci.*, 284, 20162367.

Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., *et al.* (2012). Correlation and process in species distribution models: Bridging a dichotomy. *J. Biogeogr.*, 39, 2119–2131.

Dunlop, M., Hilbert, D.W., Ferrier, S., House, A., Liedloff, A., Prober, S.M., *et al.* (2012). *The Implications of Climate Change for Biodiversity Conservation and the National Reserve System: Final Synthesis*. A report prepared for the Department of Sustainability, Environment, Water, Population and Communities, and the Department of Climate Change and Energy Efficiency. CSIRO Climate Adaptation Flagship, Canberra.

Ehrlén, J. & Morris, W.F. (2015). Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.*, 18, 303–314.

Elith, J. (2017). Predicting Distributions of Invasive Species. In: *Invasive Species: Risk Assessment and Management*. Cambridge University Press, pp. 94–129.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., *et al.* (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151.

Elith, J., Kearney, M. & Phillips, S. (2010). The art of modelling range-shifting species. *Methods Ecol. Evol.*, 1, 330–342.

Elith, J. & Leathwick, J.R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu. Rev. Ecol. Evol. Syst.*, 40, 677–697.

Ellner, S.P., Childs D.Z. & Rees, M. (2016). *Data-driven Modelling of Structured Populations: A Practical Guide to the Integral Projection Model*. Springer International Publishing. Switzerland.

Evans, M.E.K., Merow, C., Record, S., McMahon, S.M. & Enquist, B.J. (2016). Towards Process-based range modeling of many species. *Trends Ecol. Evol.*, 31, 860–871.

Falster, D.S., Duursma, R.A., Ishihara, M.I., Barneche, D.R., FitzJohn, R.G., Vårhammar, A., *et al.* (2015). BAAD: a Biomass and Allometry Database for woody plants. *Ecology*, 96, 1445–1445.

Feng, Z., Ji, R., Campbell, R.G., Ashjian, C.J. & Zhang, J. (2016). Early ice retreat and ocean warming may induce copepod biogeographic boundary shifts in the Arctic Ocean. *J. Geophys. Res. Oceans*, 121, 6137–6158.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.*, 37, 4302–4315.

Fithian, W., Elith, J., Hastie, T. & Keith, D.A. (2015). Bias correction in species distribution models: pooling survey and collection data for multiple species. *Methods Ecol. Evol.*, 6, 424–438.

Florance, D., Webb, J.K., Dempster, T., Kearney, M.R., Worthing, A. & Letnic, M. (2011). Excluding access to invasion hubs can contain the spread of an invasive vertebrate. *Proc. R. Soc. Lond. B Biol. Sci.*, 278, 2900–2908.

Fordham, D.A., Akçakaya, H.R., Alroy, J. Saltre, F., Brook, B.W. (2016a) Predicting and mitigating future biodiversity loss using long-term ecological proxies. *Nature Clim. Change.* 6 909-916.

Fordham, D.A., Akcakaya, H.R., Araujo, M.B., Elith, J., Keith, D.A., Pearson, R., *et al.* (2012). Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Glob. Change Biol.*, 18, 1357–1371.

Fordham, D. A., Akçakaya, H. R., Araújo, M. B., Keith, D. A. & Brook, B. W. (2013a), Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography*, 36, 956-964.

Fordham, D.A., Akçakaya, H.R., Brook, B.W., Rodríguez, A., Alves, P.C., Civantos, E., *et al.* (2013b). Adapted conservation measures are required to save the Iberian lynx in a changing climate. *Nat. Clim. Change*, 3, 899–903.

Fordham, D.A., Bertelsmeier, C., Brook, B.W., Early, R., Neto, D., Brown, S.C., *et al.* (2018). How complex should models be? Comparing correlative and mechanistic range dynamics models. *Glob. Change Biol.,* 24, 1357-1370.

Fordham, D.A., Haythorne, S. & Brook, B.W. (2016b). Sensitivity Analysis of Range Dynamics Models (SARDM): Quantifying the influence of parameter uncertainty on forecasts of extinction risk from global change. *Environ. Model. Softw.*, 83, 193–197.

Fordham, D.A., Mellin, C., Russell, B.D., Akcakaya, R.H., Bradshaw, C.J.A., Aiello-Lammens, M.E., *et al.* (2013c). Population dynamics can be more important than physiological limits for determining range shifts under climate change. *Glob. Change Biol.*, 19, 3224–3237.

Fretwell, P.T., Scofield, P. & Phillips, R.A. (2017). Using super-high resolution satellite imagery to census threatened albatrosses. *Ibis*, 159, 481–490.

Gallien, L., Münkemüller, T., Albert, C. H., Boulangeat, I. and Thuiller, W. (2010), Predicting potential distributions of invasive species: where to go from here? *Divers. Distrib.*, 16: 331-342.

García-Callejas, D., Molowny-Horas, R. & Retana, J. (2017). Projecting the distribution and abundance of Mediterranean tree species under climate change: a demographic approach. *J. Plant Ecol.*, 10, 731–743.

Garcia-Valdes, R., Zavala, M.A., Araujo, M.B. & Purves, D.W. (2013). Chasing a moving target: projecting climate change-induced shifts in non-equilibrial tree species distributions. *J. Ecol.*, 101, 441–453.

González, E.J., Martorell, C. & Bolker, B.M. (2016). Inverse estimation of integral projection model parameters using time series of population-level data. *Methods Ecol. Evol.*, 7, 147–156.

Goodwin, N.R. & Collett, L.J. (2014). Development of an automated method for mapping fire history captured in Landsat TM and ETM+ time series across Queensland, Australia. *Remote Sens. Environ.*, 148, 206–221.

Grimm, V. & Berger, U. (2016). Structural realism, emergence, and predictions in next-generation ecological modelling: Synthesis from a special issue. *Ecol. Model.*, Next generation ecological modelling, concepts, and theory: structural realism, emergence, and predictions, 326, 177–187.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F. (2010) The ODD protocol: A review and first update, *Ecol. Model.*, 221, 2760–2768

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography*, 40, 281–295.

Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., *et al.* (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.*, 24, 276–292.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., *et al.* (2013). Predicting species distributions for conservation decisions. *Ecol. Lett.*, 16, 1424–1435.

Gutierrez, A.P. & Ponti, L. (2014). Analysis of Invasive Insects: Links to Climate Change. In: *Invasive Species and Global Climate Change*, CABI Invasives Series (ed. Ziska, LH and Dukes, JS). pp. 45–61.

Gutierrez, A.P., Ponti, L. & Dalton, D.T. (2016). Analysis of the invasiveness of spotted wing Drosophila (*Drosophila suzukii*) in North America, Europe, and the Mediterranean Basin. *Biol. Invasions*, 18, 3647–3663.

Hartig, F., Calabrese, J. M., Reineking, B., Wiegand, T. & Huth, A. (2011), Statistical inference for stochastic simulation models – theory and application. *Ecol. Lett.*, 14, 816-827.

Hastings, A. (1996). Models of spatial spread: A synthesis. *Biol. Conserv.*, Invasion Biology, 78, 143–148.

Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., *et al.* (2005). The spatial spread of invasions: new developments in theory and evidence. *Ecol. Lett.*, 8, 91–101.

Heard, G.W., McCarthy, M.A., Scroggie, M.P., Baumgartner, J.B. & Parris, K.M. (2013). A Bayesian model of metapopulation viability, with application to an endangered amphibian. *Divers. Distrib.*, 19, 555–566.

Heard, G.W., Scroggie, M.P., Ramsey, D.S.L., Clemann, N., Hodgson, J.A. & Thomas, C.D. (2018). Can Habitat Management Mitigate Disease Impacts on Threatened Amphibians? *Conserv. Lett.*, 11, e12375.

Helmuth, B., Broitman, B.R., Yamane, L., Gilman, S.E., Mach, K., Mislan, K. a. S., *et al.* (2010). Organismal climatology: analyzing environmental variability at scales relevant to physiological stress. *J. Exp. Biol.*, 213, 995–1003.

Henry, R.C., Coulon, A. & Travis, J.M.J. (2015). Dispersal asymmetries and deleterious mutations influence metapopulation persistence and range dynamics. *Evol. Ecol.*, 29, 833–850.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25, 1965–1978.

Holt, R.D. (2003). On the evolutionary ecology of species' ranges. *Evol. Ecol. Res.*, 5, 159–178.

IUCN Standards and Petitions Subcommittee. (2017). *Guidelines for Using the IUCN Red List Categories and Criteria. Version 13.* Prepared by the Standards and Petitions Subcommittee. Downloadable from http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Jongejans, E. & Kroon, H.D. (2005). Space versus time variation in the population dynamics of three co-occurring perennial herbs. *J. Ecol.*, 93, 681–692.

Jordt, A.M., Lange, M., Kramer-Schadt, S., Nielsen, L.H., Nielsen, S.S., Thulke, H.-H., *et al.* (2016). Spatio-temporal modeling of the invasive potential of wild boar-a conflict-prone species-using multi-source citizen science data. *Prev. Vet. Med.*, 124, 34–44.

Kearney, M., Phillips, B.L., Tracy, C.R., Christian, K.A., Betts, G. & Porter, W.P. (2008). Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography*, 31, 423–434.

Kearney, M. & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecol. Lett.*, 12, 334–350.

Kearney, M.R., Munns, S.L., Moore, D., Malishev, M. & Bull, C.M. (2018). Field tests of a general ectotherm niche model show how water can limit lizard activity and distribution. *Ecol. Monogr.*, 88. 672-693.

Kearney, M.R. & Porter, W.P. (2017). NicheMapR – an R package for biophysical modelling: the microclimate model. *Ecography*, 40, 664–674.

Kearney, M.R., Shamakhy, A., Tingley, R., Karoly, D.J., Hoffmann, A.A., Briggs, P.R., *et al.* (2014). Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data. *Methods Ecol. Evol.*, 5, 273–286.

Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conserv. Lett.*, 3, 203–213.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., *et al.* (2008). Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.*, 4, 560–563.

Keith, J.M. & Spring, D. (2013). Agent-based Bayesian approach to monitoring the progress of invasive species eradication programs. *Proc. Natl. Acad. Sci.*, 110, 13428–13433.

Keppel, G., Niel, K.P.V., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., *et al.* (2012). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.*, 21, 393–404.

Kéry, M., Guillera-Arroita, G. & Lahoz-Monfort, J.J. (2013). Analysing and mapping species range dynamics using occupancy models. *J. Biogeogr.*, 40, 1463–1474.

Kolbe, J.J., Kearney, M. & Shine, R. (2010). Modeling the consequences of thermal trait variation for the cane toad invasion of Australia. *Ecol. Appl.*, 20, 2273–2285.

Kujala, H., Whitehead, A.L., Morris, W.K. & Wintle, B.A. (2015). Towards strategic offsetting of biodiversity loss using spatial prioritization concepts and tools: A case study on mining impacts in Australia. *Biol. Conserv.*, 192, 513–521.

Lahoz-Monfort, J.J., Guillera-Arroita, G. & Wintle, B.A. (2014). Imperfect detection impacts the performance of species distribution models. *Glob. Ecol. Biogeogr.*, 23, 504–515.

Lawton J. H. (1993) Range, population abundance and conservation. *Trends Ecol. Evol.* 8, 409–413.

Legge, S., Lindenmayer, David, Robinson, N., Scheele, B., Southwell, D. & Wintle, B. (2018). *Monitoring Threatened Species and Ecological Communities*. CSIRO Publishing.

Leonard, P.B., Duffy, E.B., Baldwin, R.F., McRae, B.H., Shah, V.B. & Mohapatra, T.K. (2017). gflow: software for modelling circuit theory-based connectivity at any scale. *Methods Ecol. Evol.*, 8, 519–526.

Levy, O., Buckley, L.B., Keitt, T.H. & Angilletta, M.J. (2016). A dynamically downscaled projection of past and future microclimates. *Ecology*, 97, 1888–1888.

Levy, O., Buckley, L.B., Keitt, T.H., Smith, C.D., Boateng, K.O., Kumar, D.S., *et al.* (2015). Resolving the life cycle alters expected impacts of climate change. *Proc R Soc B*, 282, 20150837.

Liénard, J. & Strigul, N. (2016). An individual-based forest model links canopy dynamics and shade tolerances along a soil moisture gradient. *R. Soc. Open Sci.*, 3, 150589.

Lindenmayer, D.B., Likens, G.E., Andersen, A., Bowman, D., Bull, C.M., Burns, E., *et al.* (2012). Value of long-term ecological studies. *Austral Ecol.*, 37, 745–757.

Lurgi, M., Brook, B.W., Saltré, F. & Fordham, D.A. (2015). Modelling range dynamics under global change: Which framework and why? *Methods Ecol. Evol.*, 6, 247–256.

Lütolf, M., Bolliger, J., Kienast, F. & Guisan, A. (2008). Scenario-based assessment of future land use change on butterfly species distributions. *Biodivers. Conserv.*, 18, 1329.

Maclean, I.M.D., Suggitt, A.J., Wilson, R.J., Duffy, J.P. & Bennie, J.J. (2017). Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Glob. Change Biol.*, 23, 256–268.

Malishev, M., Bull, C.M. & Kearney, M.R. (2018). An individual-based model of ectotherm movement integrating metabolic and microclimatic constraints. *Methods Ecol. Evol.*, 9, 472–489.

Marques, G.M., Augustine, S., Lika, K., Pecquerie, L., Domingos, T. & Kooijman, S.A.L.M. (2018). The AmP project: Comparing species on the basis of dynamic energy budget parameters. *PLOS Comput. Biol.*, 14, e1006100.

Maunder, M.N. & Punt, A.E. (2013). A review of integrated analysis in fisheries stock assessment. *Fish. Res.*, 142, 61–74.

McGill, B.J. (2012). Trees are rarely most abundant where they grow best. *J. Plant Ecol.,* 5, 46–51.

Merow, C., Bois, S.T., Allen, J.M., Xie, Y. & Silander, J.A., Jr. (2017). Climate change both facilitates and inhibits invasive plant ranges in New England. *Proc. Natl. Acad. Sci. U. S. A.*, 114, E3276–E3284.

Merow, C. , Dahlgren, J. P., Metcalf, C. J., Childs, D. Z., Evans, M. E., Jongejans, E. , Record, S. , Rees, M. , Salguero-Gómez, R. and McMahon, S. M. (2014b), Advancing population ecology with integral projection models: a practical guide. *Methods Ecol. Evol.*, 5: 99-110.

Merow, C., Latimer, A.M., Wilson, A.M., McMahon, S.M., Rebelo, A.G. & Silander, J.A., Jr. (2014). On using integral projection models to generate demographically driven predictions of species' distributions: development and validation using sparse data. *Ecography*, 37, 1167–1183.

Messier, J., McGill, B.J. & Lechowicz, M.J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecol. Lett.*, 13, 838–848.

Metcalf, C.J.E., McMahon, S.M., Salguero-Gómez, R. & Jongejans, E. (2013). IPMpack: an R package for integral projection models. *Methods Ecol. Evol.*, 4, 195–200.

Midekisa, A., Holl, F., Savory, D.J., Andrade-Pacheco, R., Gething, P.W., Bennett, A., *et al.* (2017). Mapping land cover change over continental Africa using Landsat and Google Earth Engine cloud computing. *PLOS ONE*, 12, e0184926.

Mitchell, N., Hipsey, M.R., Arnall, S., McGrath, G., Tareque, H.B., Kuchling, G., *et al.* (2012). Linking eco-energetics and eco-hydrology to select sites for the assisted colonization of Australia's rarest reptile. *Biology*, 2, 1–25.

Mohd, M.H., Murray, R., Plank, M.J. & Godsoe, W. (2016). Effects of dispersal and stochasticity on the presence–absence of multiple species. *Ecol. Model.*, 342, 49–59.

Morrongiello, J.R., Thresher, R.E. & Smith, D.C. (2012). Aquatic biochronologies and climate change. *Nat. Clim. Change*, 2, 849–857.

Murphy, J.T., Johnson, M.P. & Viard, F. (2017). A theoretical examination of environmental effects on the life cycle schedule and range limits of the invasive seaweed *Undaria pinnatifida*. *Biol. Invasions*, 19, 691–702.

Naujokaitis-Lewis, I. & Curtis, J.M.R. (2016). Advances in global sensitivity analyses of demographic-based species distribution models to address uncertainties in dynamic landscapes. *PeerJ*, 4, e2204.

Nenzén, H.K., Swab, R.M., Keith, D.A. & Araújo, M.B. (2012). demoniche – an R-package for simulating spatially-explicit population dynamics. *Ecography*, 35, 577–580.

NERC (2010) The global population dynamics database. Version 2. NERC (Natural Environment Research Council) Centre for Population Biology, Imperial College, London. Available at: https://www.imperial.ac.uk/cpb/gpdd2 (last accessed February 2019).

Pagel, J. & Schurr, F.M. (2012). Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Glob. Ecol. Biogeogr.*, 21, 293–304.

Panetta, A.M., Stanton, M.L. & Harte, J. (2018). Climate warming drives local extinction: Evidence from observation and experimentation. *Sci. Adv.*, 4, eaaq1819.

Paniw, M. , Quintana-Ascencio, P. F., Ojeda, F. & Salguero-Gómez, R. (2017), Accounting for uncertainty in dormant life stages in stochastic demographic models. *Oikos*, 126, 900-909.

Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., *et al.* (2014). Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim. Change*, 4, 217–221.

Penman, T.D., Keith, D.A., Elith, J., Mahony, M.J., Tingley, R., Baumgartner, J.B., *et al.* (2015). Interactive effects of climate change and fire on metapopulation viability of a forest-dependent frog in south-eastern Australia. *Biol. Conserv.*, 190, 142–153.

Perkins, L.B. & Nowak, R.S. (2013). Invasion syndromes: hypotheses on relationships among invasive species attributes and characteristics of invaded sites. *J. Arid Land*, 5, 275–283.

Peron, G., Altwegg, R., Jamie, G.A. & Spottiswoode, C.N. (2016). Coupled range dynamics of brood parasites and their hosts responding to climate and vegetation changes. *J. Anim. Ecol.*, 85, 1191–1199.

Phillips, B.L., Brown, G.P. & Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology*, 91, 1617–1627.

Pomara, L.Y., LeDee, O.E., Martin, K.J. & Zuckerberg, B. (2014). Demographic consequences of climate change and land cover help explain a history of extirpations and range contraction in a declining snake species. *Glob. Change Biol.*, 20, 2087–2099.

Prasad, A.M., Iverson, L.R., Peters, M.P., Bossenbroek, J.M., Matthews, S.N., Davis Sydnor, T., *et al.* (2010). Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. *Landsc. Ecol.*, 25, 353–369.

Railsback, S. F., Grimm, V. (2019) *Agent-Based and Individual-Based Modeling - A Practical Introduction*. 2nd Ed. Princeton University Press. Princeton, New Jersey

Regan, H.M., Auld, T.D., Keith, D.A. & Burgman, M.A. (2003). The effects of fire and predators on the long-term persistence of an endangered shrub, Grevillea caleyi. *Biol. Conserv.*, 109, 73-83.

Rossman, S., Yackulic, C.B., Saunders, S.P., Reid, J., Davis, R. & Zipkin, E.F. (2016). Dynamic N-occupancy models: Estimating demographic rates and local abundance from detection-nondetection data. *Ecology*, 97, 3300–3307.

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., Buhr, H. de, Farack, C., *et al.* (2016). COMADRE: a global data base of animal demography. *J. Anim. Ecol.*, 85, 371–384.

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Buckley, Y.M., Che-Castaldo, J., Caswell, H., *et al.* (2015). The compadre Plant Matrix Database: an open online repository for plant demography. *J. Ecol.*, 103, 202–218.

Santika, T., Mcalpine, C.A., Lunney, D., Wilson, K.A. & Rhodes, J.R. (2014). Modelling species distributional shifts across broad spatial extents by linking dynamic occupancy models with public-based surveys. *Divers. Distrib.*, 20, 786–796.

Saracco, J.F., Desante, D.F. & Kaschube, D.R. (2008). Assessing Landbird Monitoring Programs and Demographic Causes of Population Trends. *J. Wildl. Manag.*, 72, 1665–1673.

Schaub, M. & Abadi, F. (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.*, 152, 227–237.

Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O'Hara, R.B., *et al.* (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *J. Biogeogr.*, 39, 2146–2162.

Singer, A., Johst, K., Banitz, T., Fowler, M.S., Groeneveld, J., Gutierrez, A.G., *et al.* (2016). Community dynamics under environmental change: How can next generation mechanistic models improve projections of species distributions? *Ecol. Model.*, 326, 63–74.

Skellam, J. G. (1951). Random dispersal in theoretical populations. *Biometrika*, 38,196–218.

Suárez-Seoane, S., Álvarez-Martínez, J.M., Wintle, B.A., Palacín, C. & Alonso, J.C. (2017). Modelling the spatial variation of vital rates: An evaluation of the strengths and weaknesses of correlative species distribution models. *Divers. Distrib.*, 23, 841–853.

Sullivan, B.L., Aycrigg, J.L., Barry, J.H., Bonney, R.E., Bruns, N., Cooper, C.B., *et al.* (2014). The eBird enterprise: An integrated approach to development and application of citizen science. *Biol. Conserv.*, 169, 31–40.

Sun, Y., Wang, T., Skidmore, A.K., Palmer, S.C.F., Ye, X., Ding, C., *et al.* (2016). Predicting and understanding spatio-temporal dynamics of species recovery: implications for Asian crested ibis *Nipponia nippon* conservation in China. *Divers. Distrib.*, 22, 893–904.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., *et al.* (2013). Identification of 100 fundamental ecological questions. *J. Ecol.*, 101, 58–67.

Sutherst, R. W., & Maywald, G. F. (1985). A computerised system for matching climates in ecology. *Agric. Ecosyst. Environ.*, 13, 281–299.

Thomas, Y. & Bacher, C. (2018). Assessing the sensitivity of bivalve populations to global warming using an individual-based modelling approach. *Glob. Change Biol.*, 24, 4581–4597.

Thuiller, W., Münkemüller, T., Lavergne, S., Mouillot, D., Mouquet, N., Schiffers, K., *et al.* (2013). A road map for integrating eco-evolutionary processes into biodiversity models. *Ecol. Lett.*, 16, 94–105.

Thuiller, W., Münkemüller, T., Schiffers, K.H., Georges, D., Dullinger, S., Eckhart, V.M., *et al.* (2014). Does probability of occurrence relate to population dynamics? *Ecography*, 37, 1155–1166.

Tingley, R., Vallinoto, M., Sequeira, F. & Kearney, M.R. (2014). Realized niche shift during a global biological invasion. *Proc. Natl. Acad. Sci. U. S. A.*, 111, 10233–10238.

Trakhtenbrot, A., Katul, G.G. & Nathan, R. (2014). Mechanistic modeling of seed dispersal by wind over hilly terrain. *Ecol. Model.*, 274, 29–40.

Travis, J.M.J., Mustin, K., Bartoń, K.A., Benton, T.G., Clobert, J., Delgado, M.M., *et al.* (2012). Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods Ecol. Evol.*, 3, 628–641.

Tredennick, A.T., Hooten, M.B., Aldridge, C.L., Homer, C.G., Kleinhesselink, A.R. & Adler, P.B. (2016). Forecasting climate change impacts on plant populations over large spatial extents. *Ecosphere*, 7, 1–16.

Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.-B., Pe'er, G., Singer, A., *et al.* (2016). Improving the forecast for biodiversity under climate change. *Science*, 353, aad8466.

Uribe-Rivera, D.E., Soto-Azat, C., Valenzuela-Sánchez, A., Bizama, G., Simonetti, J.A. & Pliscoff, P. (2017). Dispersal and extrapolation on the accuracy of temporal predictions from distribution models for the Darwin's frog. *Ecol. Appl.*, 27, 1633–1645.

van Strien, A.J., van Swaay, C.A.M. & Kéry, M. (2011). Metapopulation dynamics in the butterfly *Hipparchia semele* changed decades before occupancy declined in The Netherlands. *Ecol. Appl.*, 21, 2510–2520.

van der Vaart E, Beaumont MA, Johnston ASA, Sibley RM (2015) Calibration and evaluation of individual-based models using Approximate Bayesian Computation. *Ecol. Model.*, 312, 182-190.

van der Vaart, E., Johnston, A.S.A. & Sibly, R.M. (2016). Predicting how many animals will be where: How to build, calibrate and evaluate individual-based models. *Ecol. Model.*, 326, 113–123.

VanDerWal, J., Shoo, L.P., Johnson, C.N. & Williams, S.E. (2009). Abundance and the environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance. *Am. Nat.*, 174, 282–291.

Villellas, J., Doak, D.F., García, M.B. & Morris, W.F. (2015). Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecol. Lett.*, 18, 1139–1152.

Vindenes, Y. & Langangen, Ø. (2015). Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecol. Lett.*, 18, 417–432.

Wang, M. (2013). From home range dynamics to population cycles: Validation and realism of a common vole population model for pesticide risk assessment. *Integr. Environ. Assess. Manag.*, 9, 294–307.

Weber, M.M., Stevens, R.D., Diniz-Filho, J.A.F. & Grelle, C.E.V. (2017). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography*, 40, 817–828.

Wethey, D.S. & Woodin, S.A. (2008). Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. In: *Challenges to Marine Ecosystems*, Developments in Hydrobiology (eds. Davenport, J., Burnell, G.M., Cross, T., Emmerson, M., McAllen, R., Ramsay, R., *et al.*). Springer Netherlands, pp. 139–151.

Whitehead, A.L., Kujala, H. & Wintle, B.A. (2017). Dealing with Cumulative Biodiversity Impacts in Strategic Environmental Assessment: A New Frontier for Conservation Planning. *Conserv. Lett.*, 10, 195–204.

Williams, J.W. & Jackson, S.T. (2007). Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.*, 5, 475–482.

Wintle, B.A., Bekessy, S.A., Keith, D.A., van Wilgen, B.W., Cabeza, M., Schröder, B., *et al.* (2011). Ecological–economic optimization of biodiversity conservation under climate change. *Nat. Clim. Change*, 1, 355–359.

Wintle, B.A., Bekessy, S.A., Venier, L.A., Pearce, J.L. & Chisholm, R.A. (2005). Utility of dynamic-landscape metapopulation models for sustainable forest management. *Conserv. Biol.* 19, 1930–1943.

Yackulic, C.B., Nichols, J.D., Reid, J. & Der, R. (2015). To predict the niche, model colonization and extinction. *Ecology*, 96, 16–23.

Zurell, D. (2017). Integrating demography, dispersal and interspecific interactions into bird distribution models. *J. Avian Biol*, 48, 1505–1516.

Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Münkemüller, T., Gravel, D., *et al.* (2016). Benchmarking novel approaches for modelling species range dynamics. *Glob. Change Biol.*, 22, 2651–2664.

Box 1. Correlative SDMs: key challenges and missing processes

A major challenge in using correlative SDMs for predicting range dynamics is defining the link between the modelled distribution and the species niche (Colwell & Rangel

2009). It is often impossible to disentangle the biological (e.g. dispersal limitation, biotic interactions) and observational processes (e.g. bias, imperfect detection) that influence where species are observed, and to characterise species' responses over relevant dimensions of environmental space. Models are likely an incomplete and potentially biased representation of the niche that may not extrapolate well to new conditions. Specific challenges include:

- ***Observation bias, including imperfect detection*** – observations of where species occur are often biased or incomplete due to uneven sampling or imperfect detection.
- ***Non-equilibrium/ Source-sink dynamics*** – the assumption that species fill their niche (i.e. where average fitness > 1) and do not occur elsewhere is often not true.
- ***Extrapolation*** – relationships fitted under current conditions may have to be projected beyond the range of the training data to predict to new conditions. This is problematic for correlative models. Moreover, they may no longer capture key limiting processes in new times or places (due to changes in correlation structure between environmental variables, biotic interactions, local adaptation, evolution).
- ***Dispersal*** – projections usually assume that species distributions are not affected by dispersal limitations (e.g. dispersal ability or physical barriers), but they often are.
- ***Biotic interactions*** – facilitation, competition and predation (including historic) can influence species' ranges but these effects are often incompletely captured by modelled relationships and likely to vary under novel conditions.

Box 2: Population models and process-explicit models

Population models capture fundamental demographic processes that underpin range dynamics and thus have played a central role in the development of process-explicit distribution models. Mathematically, population dynamics can be captured most succinctly with reaction-diffusion models or integro-difference models (Skellam 1951; Hastings *et al.* 2005), which combine a function for population growth with one for dispersal. Many process-explicit models of species' ranges can be seen as variations on this basic theme of combining descriptions of growth and dispersal. Both can be arbitrarily complex: population models might, for example, consist of matrix population models (Caswell 2001) or integral projection models (Ellner *et al.* 2016), which explicitly capture age or size-based differences in vital rates. Dispersal can, likewise, be modelled in different ways (Travis *et al.* 2012). At the most complex, individual-based models (IBMs) readily incorporate individual heterogeneity and context-dependent rates (DeAngelis & Grimm 2014). The challenge for applications of range dynamics models is to link population dynamics and dispersal or movement to the environment with enough detail to accurately predict species' abundances or occurrences through space and time.

Box 3: Different classes of process-explicit models

Occupancy dynamics models (also known as species patch occupancy models; SPOMs): species occurrence data across time are used to estimate probabilities of local extinction and colonisation. These probabilities can then be used to predict future range dynamics, including via stochastic simulation (Heard *et al.* 2013; Garcia-Valdes *et al.* 2013).

Abundance dynamics models (including dynamic range models, DRM): here defined as models where spatially replicated time series of species' abundances (possibly coupled with occurrence data) are used to estimate latent demographic properties such as population growth rate and dispersal within an integrated hierarchical model (Pagel & Schurr 2012). The resulting model can then be used to simulate future abundance.

Coupled SDM-population models (also referred to as hybrid models or coupled niche-population models): spatial predictions from a correlative SDM are used to define habitat patches, initial abundances and/or the carrying capacity of these patches through time. This habitat structure is combined with external information about vital rates and dispersal (e.g. a matrix population model (Caswell 2001) with a dispersal kernel), which may be constant across the landscape or vary with features of the environment estimated directly from spatially replicated field data or based on previous studies or expert opinion (Fordham *et al.* 2013a). The resulting spatial population model is used to predict future population abundances via stochastic simulation (Akçakaya 2000; Keith *et al.* 2008; Fordham *et al.* 2012).

Demographic distribution models (DDM): demographic rates (e.g. survival, development, fecundity) are estimated directly from individual demographic field data, and correlated with environmental predictors to make spatial predictions of these rates (Suárez-Seoane *et al.* 2017) or population metrics (e.g. population growth rate, Merow *et al.* 2014). Modelled demographic rates could also be combined with dispersal information in a spatial population model, although examples of this are rare (García-Callejas *et al.* 2017).

Eco-physiological models (also known as mechanistic niche models): measurements or calculations of physiological limitations of the environment on vital rates are used to define species' range limits. This is necessarily done at the scale of the individual and relies on an adequate characterisation of the environment experienced by individuals, as well as details on the species' physiology, morphology, behaviour and life history (Kearney & Porter 2004, 2009).

Individual based models (IBMs, also called agent-based models): simulated populations are composed of discrete individuals, each with a set of attributes and behaviours. These attributes and behaviours can vary among individuals and in response to environmental conditions, interactions with conspecifics or other species, and through time. Dynamics emerge from local interactions among individuals and their environment (DeAngelis & Grimm 2014). Parameters may be fitted using experimental or field data on individuals such as development times under different temperatures (Feng *et al.* 2016), or inversely fitted to observed occurrence or abundance data using a pattern-oriented modelling approach (Adams *et al.* 2015).

Figure legends

Figure 1 Characterisation of process-explicit distribution model classes (columns) with respect to typical inputs (*), key steps, and model outputs. Arrows indicate how input data are used to compute/estimate intermediate quantities and arrive to model outputs. Rows above 'Environmental Predictors' represent increasing levels of biological organisation (individuals, populations, species). Methods differ in terms of the processes they capture, the level at which these are characterised, and whether they are typically modelled as a function of environment predictors. Model outputs may be abundance (Abund), or occupancy (Occ). Processes captured at the population level include colonisation (Col), extinction (Ext), detection (Det), dispersal (Disp), population growth parameters (Pop Growth), and density dependence (via carrying capacity (K)). Individual trait and demographic data or vital rates are also used in some models. Double headed arrows indicate that process parameters are estimated based on matching emergent patterns of occurrence or abundance (e.g. in occupancy and abundance dynamics models), rather than these data being used to characterise processes separately (e.g. in coupled SDM-population models where past or current occurrence data are combined with environmental predictors in an SDM to describe carrying capacity, which is later used when simulating abundance). Dashed arrows indicate common alternative links (e.g. eco-physiological models can either model vital rates using species' traits and environmental data or estimate these using experimental demographic data measured under varying environmental conditions).

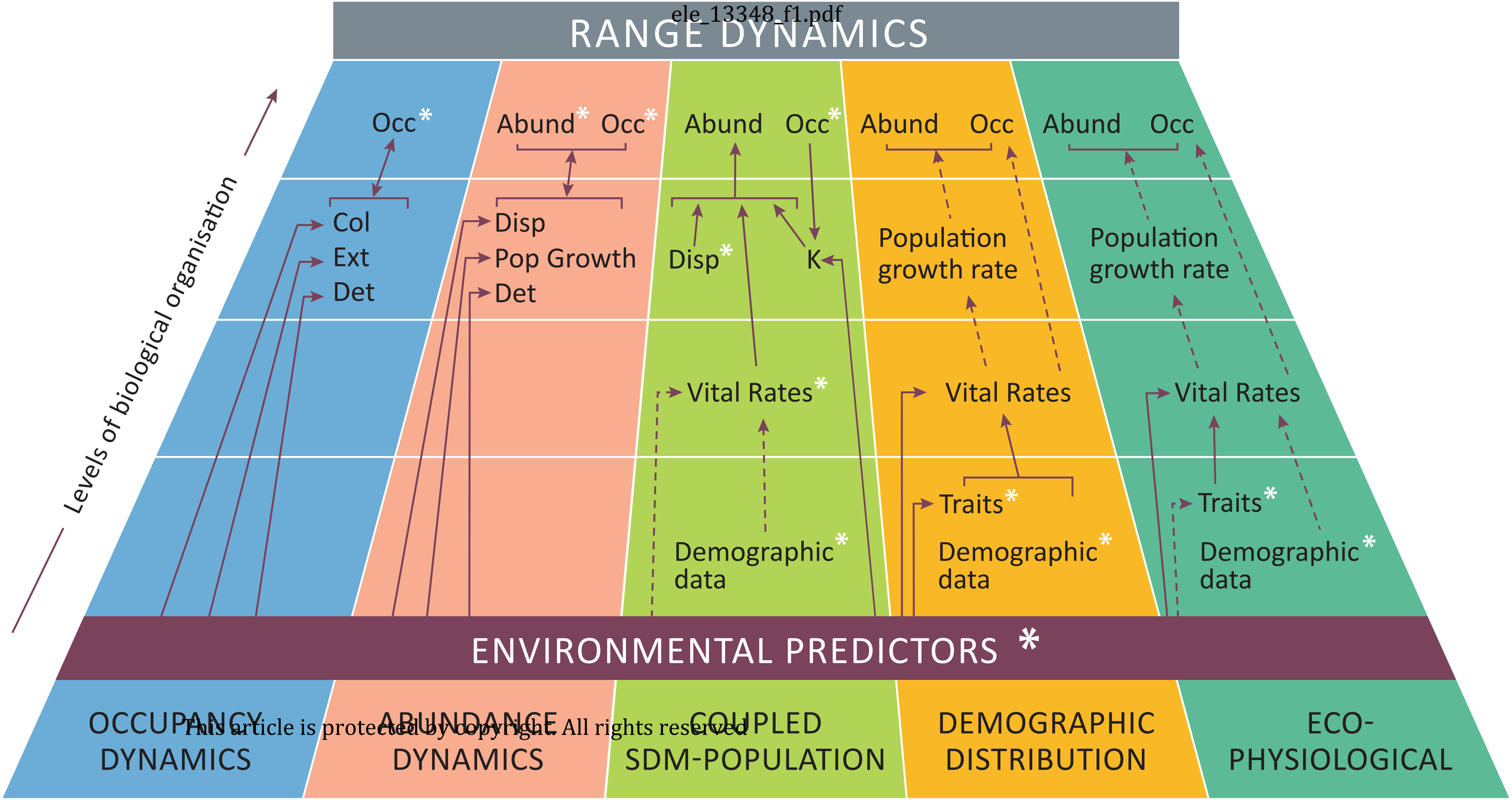
Figure 2. Predicting range dynamics involves characterising relevant processes (blue) and producing predictions based on the parameterised model (green). Sometimes this takes place simultaneously (i.e. the same model is fitted to data for estimation and used to project dynamics). Processes can be modelled from first principles based on biophysical constraints or estimated using experimental data. Processes can also be estimated from field data, either based on direct observations or by fitting statistical models to infer them from abundance and/or species occurrence data. Expert knowledge can also inform model structure and

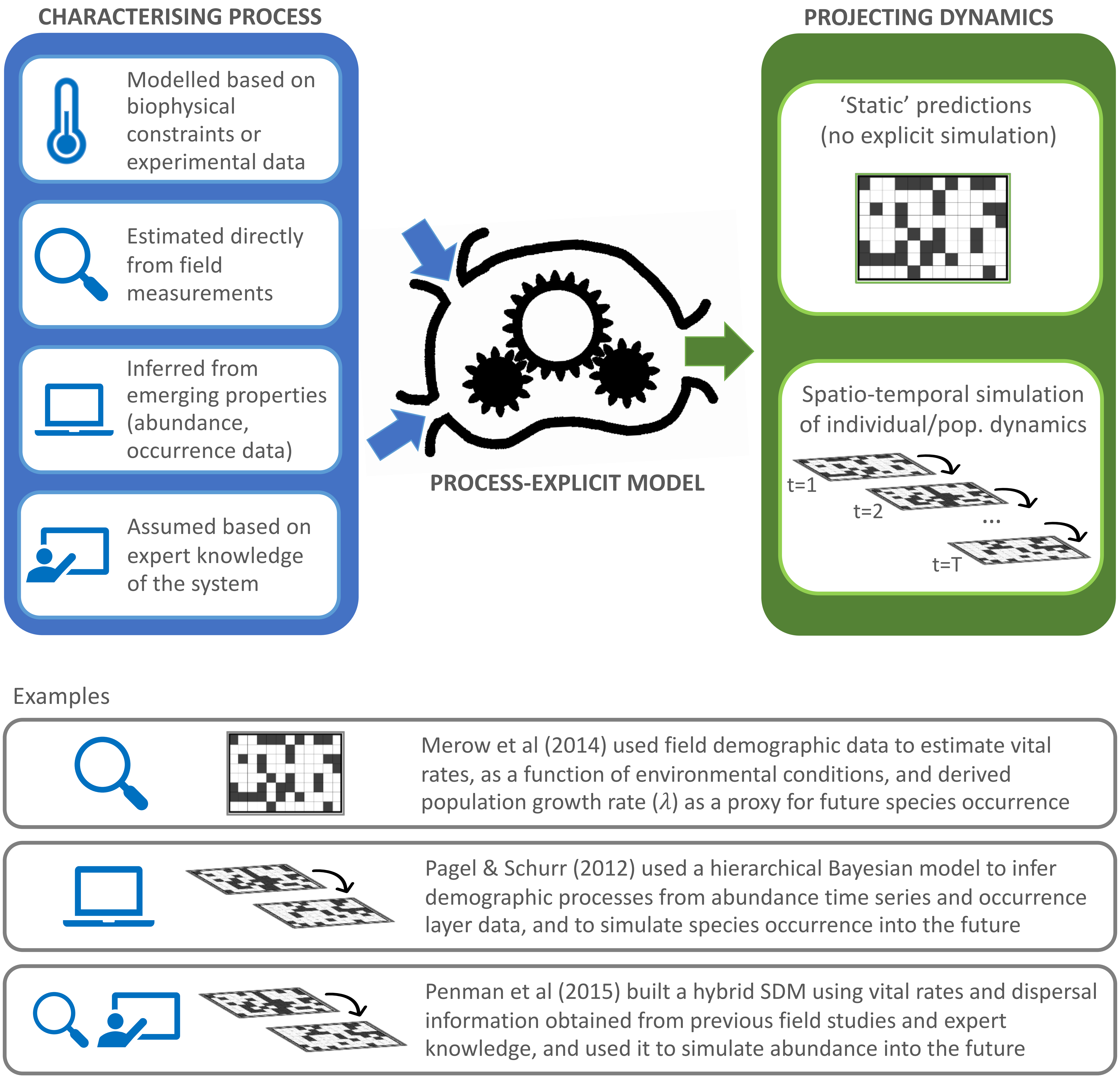
parameters. Range dynamics predictions can be produced by running simulations, where the status of a cell or individual at a time step is a function of the conditions in the previous time step (at that cell, and potentially at neighbouring cells). Alternatively, 'static' predictions may be produced, where a metric expected to reflect the outcome of range dynamics is obtained without modelling temporal dynamics.

Figure 3. Number of reviewed papers from each class of process-explicit models focused on particular (a) taxonomic groups and (b) applications/research areas. Research areas include demonstrating or refining a new method (Method dev); examining the impact of changes in key drivers: climate/weather (Climate change), land-use and landscape dynamics (LandscapeDyn); threatened species management (Extinction risk, Key habitat), and invasive species (Range invasives, Spread invasives). Separate literature searches were conducted for each model class and a subset of papers reviewed (n=75-125 in each class, total n= 650). Sample sizes represent the number of reviewed papers that actually used each approach, and hence differ between model classes. These are shown above bars in (a). Studies often addressed more than one application/research area and sometimes multiple taxonomic groups (see Appendix S1 for additional details).

Figure 4. Ability of different types of range models to provide particular types of information, capture key processes, as well as risk of violating key assumptions, and data availability. Colour/size indicate suitability (or ease or danger) for task (see Appendix S2 for justification of rankings).

Figure 5. Availability of demographic data (the number of replicate populations per study) in two global demographic databases Compadre (plants; Salguero-Gómez *et al.* 2015) and Comadre (animals; Salguero-Gómez *et al.* 2016).

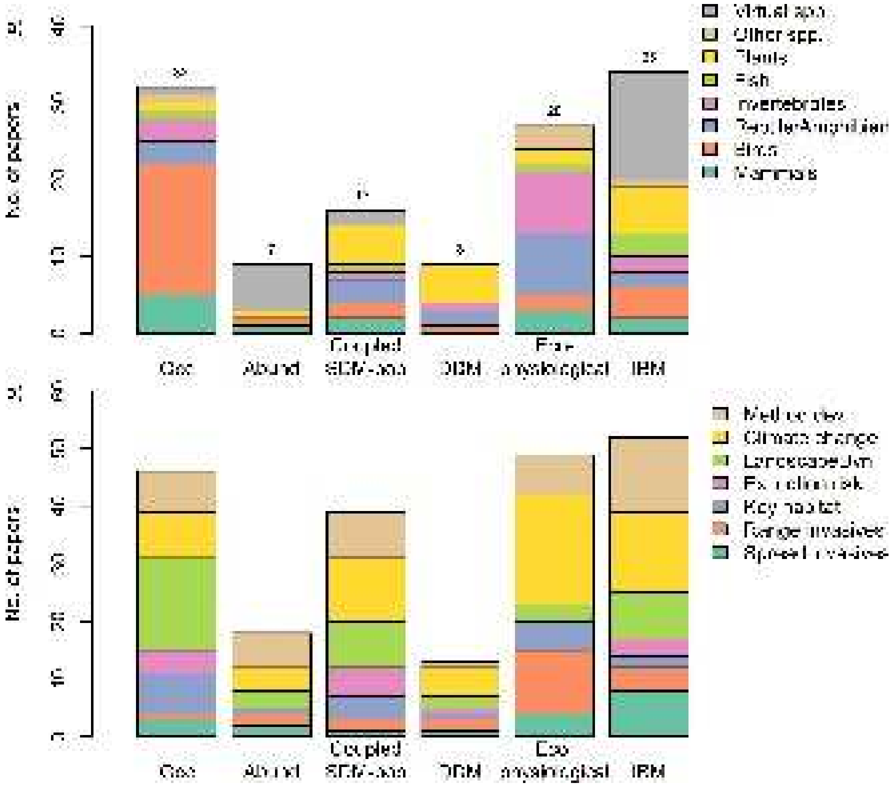

RANGE DYNAMICS
Levels of biological organisation
Occ*
Col
Ext
Det
Abund* Occ*
Disp
Pop Growth
Det
Abund Occ*
Disp*
K
Vital Rates*
Demographic* data
Abund Occ
Population growth rate
Vital Rates
Traits*
Demographic* data
Abund Occ
Population growth rate
Vital Rates
Traits*
Demographic* data
ENVIRONMENTAL PREDICTORS *
OCCUPANCY DYNAMICS
ABUNDANCE DYNAMICS
COUPLED SDM-POPULATION
DEMOGRAPHIC DISTRIBUTION
ECO-PHYSIOLOGICAL



Merow et al (2014) used field demographic data to estimate vital rates, as a function of environmental conditions, and derived population growth rate (λ) as a proxy for future species occurrence

Pagel & Schurr (2012) used a hierarchical Bayesian model to infer demographic processes from abundance time series and occurrence layer data, and to simulate species occurrence into the future

Penman et al (2015) built a hybrid SDM using vital rates and dispersal information obtained from previous field studies and expert knowledge, and used it to simulate abundance into the future



ele_13348_f3.tif

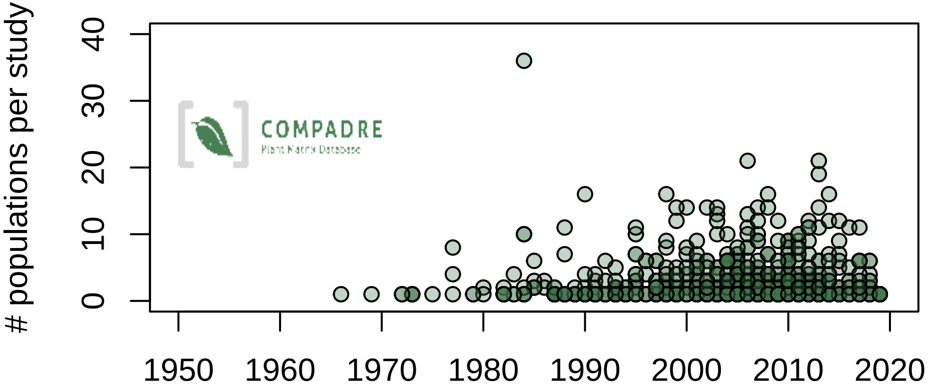
Method	Output provided			Ability to handle/ Susceptibility					Input data	
	Prob. Occ	Extinct. risk	Pop size	Detect. & bias	Sp. not at equilib.	Extrap.	Dispersal	Biotic int.	Avail.	Ease/ time to collect
Correlative SDM	🟡	🟠	🟡	🟡	🔴	🔴	🔴	🟠	🟢	🟢
Coupled SDM-population	🟢	🟢	🟢	🟡	🟠	🔴	🟢	🟠	🟡	🟠
Occupancy dynamics	🟢	🟢	🔴	🟢	🟢	🟠	🟢	🟠	🟡	🟡
Abundance dynamics (DRM)	🟢	🟢	🟢	🟢	🟢	🔴	🟢	🟠	🟠	🔴
Demographic distribution	🟠	🟠	🟠	🟠	🟢	🟠	🟠	🟠	🟠	🔴
Eco-physiological	🟠	🟠	🟠	🟢	🟢	🟢	🟠	🟠	🔴	🔴
Individual-based model	🟢	🟢	🟢	🟡	🟠	🟡	🟢	🟡	🟠	🔴

🟢 high/easy/always provided or dealt with

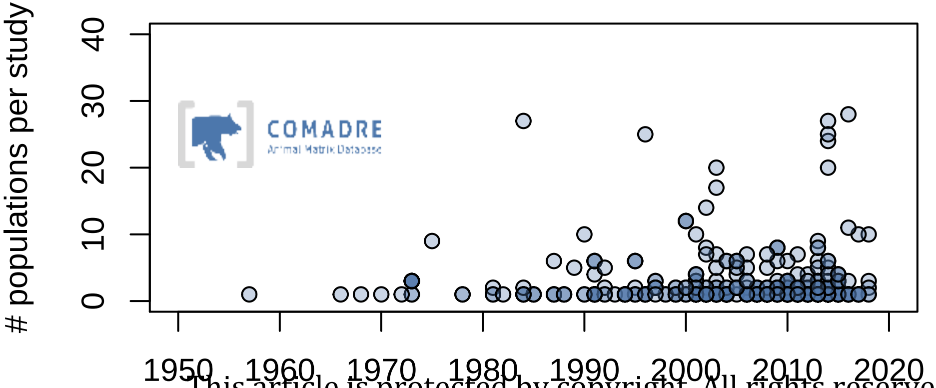
🟡 moderate/only in some implementations/ less susceptible or better relative to most other model classes

🟠 quite poor/rare or not demonstrated yet/more susceptible or worse relative to most other model classes

🔴 low/hard/not provided or dealt with



populations per study
0
10
20
30
40
1950
1960
1970
1980
1990
2000
2010
2020
COMPADRE
Plant Matrix Database



populations per study
0
10
20
30
40
1950
1960
1970
1980
1990
2000
2010
2020
COMADRE
Animal Matrix Database