



# Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact modelling

Brooke L. Bateman<sup>1†\*</sup>, Helen T. Murphy<sup>2</sup>, April E. Reside<sup>1</sup>, Karel Mokany<sup>3</sup> and Jeremy VanDerWal<sup>1</sup>

<sup>1</sup>Centre for Tropical Biodiversity and Climate Change Research, School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia, <sup>2</sup>CSIRO Ecosystem Sciences and Climate Adaptation Flagship, PO Box 780, Atherton, Qld 4883, Australia, <sup>3</sup>CSIRO Ecosystem Sciences, Climate Adaptation Flagship, PO Box 1700, Canberra, ACT 2601, Australia

## ABSTRACT

**Aim** Species distribution models (SDMs) generally use correlative relationships between the species location and the associated environment to project the species potential distribution under climate change. While projecting a future suitable climatic space is relatively simple using SDMs, predicting a species ability to occupy that space relies on understanding dispersal capacity; a lack of knowledge about species-specific dispersal ability, varying geographical contexts and technical constraints of simple SDMs has limited the consideration of dispersal in most studies. We review the current treatment of dispersal in SDM studies addressing the effects of climate change and explore how incorporating ‘partial-dispersal’ scenarios could lead to more realistic projections of species distributions into the future.

**Location** Global.

**Methods** We consider the implications for projected distributions of incorporating full- and no-dispersal scenarios in SDMs and identify a range of methods and their associated information needs for implementing partial-dispersal scenarios.

**Results** While simplistic and easy to implement, full- and no-dispersal scenarios are only realistic in a few situations. Although implementing partial-dispersal scenarios may require information that is lacking for many species, we argue that even relatively simple partial-dispersal models, with fairly basic knowledge needs, improve projections of altered distributions under climate change. More complex models, using more sophisticated modelling approaches, have been tested in a few cases and provide robust projections.

**Main Conclusions** While climate change SDM outputs have proved useful, we highlight that careful selection of dispersal scenarios, relevant to the particular questions being addressed, is necessary for appropriate interpretation of the model outputs when projecting into novel environments (e.g. future climates). A number of methods have been developed for incorporating partial-dispersal scenarios in SDMs; however, the data and computation requirements currently limit their application to large numbers of species, highlighting the need for other techniques and generic user-friendly modelling platforms.

## Keywords

climate change, correlative models, dispersal, future scenarios, movement ability, species distribution modelling.

\*Correspondence: Brooke L. Bateman, Centre for Tropical Biodiversity and Climate Change Research, School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia.  
E-mail: brooke.bateman@gmail.com

†Current Address: SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, 53706, USA

## INTRODUCTION

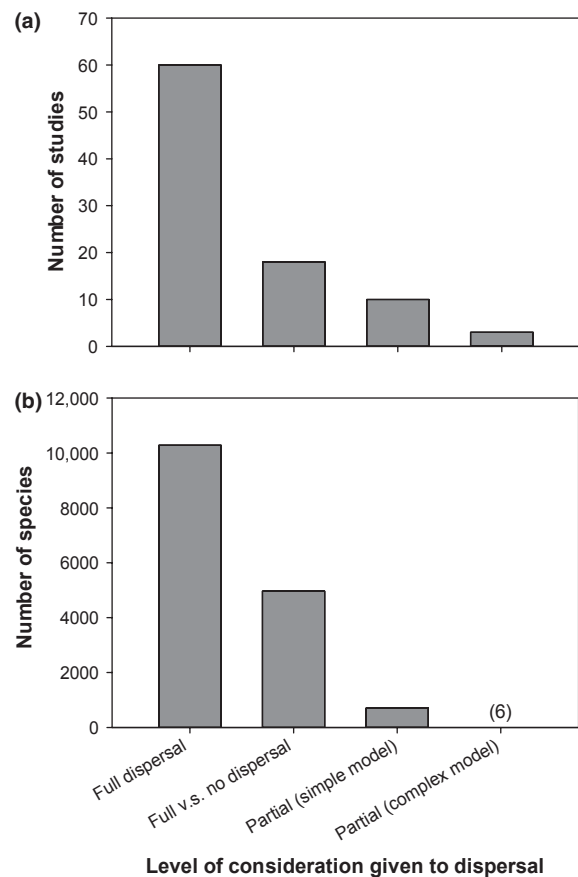
Species distribution models (SDMs) are widely used to understand the potential consequences of climate change for

the distribution of species (Pearson & Dawson, 2003; Araújo *et al.*, 2005; Martinez-Meyer, 2005; Hijmans & Graham, 2006; Jimenez-Valverde *et al.*, 2008; Thuiller *et al.*, 2008; Elith & Leathwick, 2009; Fitzpatrick & Hargrove, 2009), to

project future distributions of invasive species (Thuiller *et al.*, 2005b) and aid in conservation decision-making (Loiselle *et al.*, 2003; Sinclair *et al.*, 2010; Shoo *et al.*, 2011). While mechanistic modelling approaches based on physiological processes exist (see Kearney & Porter, 2009; Kearney *et al.*, 2010), most applications of SDMs are correlative (phenomenological) due to their accessibility, relative ease of use, minimal data needs and availability of modelling algorithms (Weller, 1999). Correlative SDMs require only occurrence data and information on the ‘environment’ at these locations to model the distribution of a species, which can be used to formulate hypotheses about a species niche (Jimenez-Valverde *et al.*, 2008). This model can then be used to project the potential distribution, which correspond to areas in geographical space that have suitable conditions for a species (Araújo & Guisan, 2006).

Climate warming is predicted to be occurring at a mean global velocity of 0.42 km per year (0.11–0.46 km per year) (Loarie *et al.*, 2009), and species are expected to respond to such changes by shifting their geographical distributions to follow suitable climatic conditions (Collingham & Huntley, 2000; Tingley *et al.*, 2009). Although adaptation *in situ* does occur (Huntley *et al.*, 2006), species have historically responded to rapid rates of climate change by shifting, expanding or contracting their geographical distribution (Huntley & Thompson Webb, 1989; Davis & Shaw, 2001; Huntley *et al.*, 2010). Present-day climate change is already having a noticeable impact on the distribution of species climatic niche space (VanDerWal *et al.*, 2013) and species distributions, with latitudinal and altitudinal range shifts increasingly documented (Parmesan & Yohe, 2003; Parmesan, 2006; Chen *et al.*, 2011). However, while projecting a future suitable climatic space is relatively simple using SDMs, predicting a species ability to occupy that space relies on understanding inherent dispersal capacity as well as barriers and conduits to dispersal. Due to their accessibility and their frequent use, it is imperative that the assumptions of SDMs are fully considered in interpreting results. Failure to adequately consider an appropriate dispersal scenario is often highlighted as a limitation to SDM climate change projections (Weller, 1999; Thuiller *et al.*, 2008).

Most SDM studies that make future predictions of species under climate change use full- or no-dispersal scenarios (Peterson *et al.*, 2002; Araújo *et al.*, 2004; Thomas *et al.*, 2004; Guisan & Thuiller, 2005; Thuiller *et al.*, 2005a,b; Pearson, 2006). A search of the ISI Web of Science using the key words ‘biodiversity’ and ‘climate change’ and ‘model\*’ (restricted to 33 international journals most commonly publishing projections of biodiversity under climate change) revealed that the majority of SDM studies solely used full-dispersal scenarios in climate change projections (Fig. 1). There are a small fraction of species without any limitations on dispersal and colonization and, equally, there are some species that completely lack the capacity to disperse (Weller, 1999). In reality, species have varying degrees of dispersal ability, and observed rates of distribution shift vary greatly



**Figure 1** (a) The number of papers published from 2007 to 2012 that have projected changes in the spatial distribution of species under climate change, as a function of the level of consideration given to dispersal in the predictive process. The same data are presented in (b) but expressed in terms of the number of species for which projections have been made. Studies were identified by searching ISI Web of Science using the key words ‘biodiversity’ and ‘climate change’ and ‘model\*’ restricted to 33 international journals most commonly publishing projections of biodiversity under climate change.

both among species and across taxonomic groups (Walther *et al.*, 2002; Berg *et al.*, 2010; Chen *et al.*, 2011). Despite this, the ability to simulate realistic dispersal scenarios under climate change has been limited by: (1) lack of knowledge about the dispersal abilities of species; (2) varying historical, geographical, anthropogenic, temporal and ecological mechanisms that are unique to the region a given species will need to disperse to or within; and (3) technical constraints of the modelling (McConkey *et al.*, 2012). As there is a no ‘one size fits all’ approach, and ecological knowledge is needed, most SDM studies fall back on all or nothing dispersal scenario approaches (Fig. 1). Recently, however, researchers have begun using a variety of approaches in an effort to incorporate more realistic dispersal into SDMs (Sorenson *et al.*, 1998; Midgley *et al.*, 2006; Gaston *et al.*, 2008; Dullinger *et al.*, 2012; Reside *et al.*, 2012)— often termed ‘partial dispersal’ scenarios.

Here, we review how correlative dispersal scenarios have been applied to date in SDM research and provide examples for a range of climate change-specific topics where dispersal ability should be considered. Our review provides the reader with the broad range of options for consideration when choosing the best dispersal scenario for their predictive models. In addition, we discuss the current trend in the use of 'hybrid' models that incorporate demographic or life history factors into SDM studies and highlight the simple or complex methodologies these models require (Table 1). The implications of different dispersal scenarios and their associated information requirements are considered.

### Full-dispersal

Full-dispersal scenarios in SDMs are the most commonly applied in climate change research (Fig. 1). This scenario assumes that a species (or taxa, community, etc.) could reach all geographical areas that are predicted to be suitable in future climate projections (Franklin, 2010). This scenario is generally the simplest to apply, often being the default output in SDM programmes. As a result, many studies provide no justification for applying the full-dispersal scenario, and it is common for no mention of dispersal processes to be made. Despite this, specific life history traits and biogeographical barriers can limit the ability of a species to migrate or disperse (Clark *et al.*, 2003), and full-dispersal is likely to be unrealistic except for the most vagile species

(Barbet-Massin *et al.*, 2012). For instance, the failure to keep pace with shifting climates has been highlighted across many taxa including trees (Conway, 2008), reptiles and amphibians (Araújo *et al.*, 2006), butterflies (Menéndez *et al.*, 2006; Devictor *et al.*, 2012) and birds in Europe (Roche *et al.*, 1997; Farmer & Parent, 1997). Mobile marine species (Robinson *et al.*, 2011), larger mammals and migratory birds (Sutherland *et al.*, 2000) are more likely to keep pace with climate change via dispersal compared with plants, reptiles and amphibians. Despite this expectation that large ranging and mobile species will have the greatest dispersal ability, actual shifts exhibited by species in response to climate change may rely on many factors, such as availability of suitable habitat, degree of habitat fragmentation and biotic interactions. There is some empirical evidence from recent distributional range shifts, suggesting that variation within a taxonomic group can be large and that the specific ecology of each species should be assessed where possible (Chen *et al.*, 2011).

Biogeographical barriers such as oceans, mountain ranges and deserts may limit dispersal (Pearson & Dawson, 2003; Guisan & Thuiller, 2005). The relative likelihood of dispersal across large natural barriers will depend on both the scale and magnitude of the barrier and its relation to the dispersal ability of the species. It might be unrealistic for a small reptile to cross an ocean, but reasonable for a migratory bird. Species specialized to a particular habitat type will be limited to the rate of change and establishment of that habitat in

**Table 1** Examples of studies incorporating partial-dispersal with SDMS for climate change modelling

Example	No of species	Dispersal Scenario	Method
Proteaceae plants in South Africa Midgley <i>et al.</i> (2006)	336	Full, none and partial (simple)	Migration rate per decadal time slice; dispersal distance determined broadly based on dispersal vector
Australian tropical savanna birds Reside <i>et al.</i> (2012)	243 (28 partial-dispersal scenarios)	Full, none or partial (simple)	Species assigned to a particular scenario depending on level of habitat specificity; dispersal distance assumed 3 km per year for all species in the partial-dispersal scenario
Selecting protected areas to accommodate species range shifts with climate change Hannah <i>et al.</i> (2007)	1695 (495 partial-dispersal scenarios)	Full or partial (simple)	Time step restricted dispersal further restricted by known dispersal distance radius, different assumptions for different taxa
Trees Iverson <i>et al.</i> (2004)	5	Partial (complex)	Distance decay dispersal function driven by abundance near the range boundary and habitat beyond the range boundary; using SHIFT
Dynamics of range margins for meta-populations of Lagomorphs Anderson <i>et al.</i> (2009)	2	Partial (complex)	Dispersal modelled via exponential function based on distance between suitable patches; three dispersal rates for each scenario (high, medium and low); incorporates a spatially explicit meta-population model
Mountain plants Engler & Guisan (2009)	287	Full, none and partial (complex)	Dispersal distance assigned to each species based on seven dispersal 'types'; implemented in MigClim
Persistence of an Oak tree under climate change Conlisk <i>et al.</i> (2012)	1	None and partial (complex)	Dispersal rate dependent on distance between patches rate of dispersal declines with increasing distance between patches; average and maximum dispersal distances applied; within-patch and between-patch dispersal; 30 dispersal scenarios used in model, three in sensitivity analysis (no-dispersal, low, high) and dispersal as a function of carrying capacity of receiving patch

new areas (Huntley, 1995). Therefore, the use of a full-dispersal scenario can be detrimental to conservation applications where gains in range are overestimated, and losses underestimated (Midgley *et al.*, 2006).

Although there are limitations to full-dispersal scenarios, they may be appropriate in applications where understanding the potential distribution is the desired output. This includes situations where pre-emptive conservation strategies are necessary, such as assisted migration (Hoegh-Guldberg *et al.*, 2008; Willis *et al.*, 2009) or the identification of future potential refugial areas, restoration sites and land acquisition (Shoo *et al.*, 2011; Anderson *et al.*, 2012). In addition, long-distance dispersal does occur and stochastic events such as hurricanes or altered circulation patterns could bring species long distances to areas they have not occurred in before (Hellmann *et al.*, 2008), assuming that enough individuals will disperse to form a viable population. In this case, full-dispersal scenarios would allow for these potential sites to be identified to aid in future ecological surveys that may allow for the discovery of new populations (Raxworthy *et al.*, 2003).

Understanding the potential range expansions of invasive species will likely require the use of full-dispersal scenarios. Some species introductions are facilitated by human movements (Hellmann *et al.*, 2008) and thus have a greater chance of filling their potential distributions. Invasive species examples globally highlight this; the Asian house gecko (*Hemidactylus frenatus*) is an avid stowaway that is well adapted to human habitats and has undergone a large global range expansion due to human facilitated movement (Hoskin, 2010), while the introduced cane toad (*Bufo marinus*) is adept at using roads to speed up its range expansion in Australia (Brown *et al.*, 2006). Purposeful movements of species outside of their native ranges by humans to 'rescue' them from climate change have also been documented (McLachlan *et al.*, 2007). Thus, full-dispersal scenarios may be useful in such cases to determine the potential impact of these invasive species (Thuiller *et al.*, 2005a,b).

## No-dispersal

To deal with the inherent limitation of the full-dispersal scenario, no-dispersal scenarios are often applied to future projections in conjunction with full-dispersal scenarios (Fig. 1). The justification being that the real outcome is likely to be somewhere between the no- and full-dispersal scenarios (Pitelka, 1997; Coetzee *et al.*, 2009; Marini *et al.*, 2009), and thus, the full range of possible distribution changes have been assessed (Pearson *et al.*, 2006). Like full-dispersal, no-dispersal scenarios are a commonly applied method due to their simplicity, although they are also unrealistic for most species. No-dispersal scenarios are generated by restricting future predictions of suitable habitat to the extent of the current distributions. Thus, by applying a no-dispersal scenario, it is assumed that future sites that might become suitable for a species remain unoccupied. The assumption that a species

will not move from its current range may generate overly pessimistic predictions of range losses in future climates for many species. For example, where no-dispersal scenarios have been applied to future predictions of birds (Jetz *et al.*, 2007; Coetzee *et al.*, 2009; Marini *et al.*, 2009), the chance of over-stating extinction risk is high due to the recorded distributional plasticity of many bird species (Brown *et al.*, 2001; Tingley *et al.*, 2009).

No-dispersal scenarios have been used as the 'worst case scenario' in SDMs; however, they are appropriate for some analyses, mainly where species lack the capacity to disperse due to intrinsic factors, and when a species is unable to colonize a new area due to extrinsic factors. Poor dispersers may include reptiles and amphibians, for whom dispersal distances are often small (tens of metres), and dispersal events result in a high risk of mortality (Bonnet *et al.*, 1999; Massot *et al.*, 2008). Climate change and increased temperatures are predicted to further inhibit dispersal ability in these taxa (Massot *et al.*, 2008). No-dispersal scenarios may also be appropriate for projecting future distributions of slow dispersers when using coarse grid scales. Many climate change prediction models use grid sizes up to 50 × 50 km; therefore, no-dispersal scenarios more realistically reflect the effect of climate change on the ranges of species that migrate slowly over smaller scales.

Extrinsic factors preventing dispersal include geographical barriers such as mountain peaks, where no higher altitude is available. Alpine species restricted to cooler, high altitude mountain tops are better represented by a no-dispersal scenario, as these species lose suitable habitat as climate space shifts upslope (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Parmesan, 2006; Dirnböck *et al.*, 2011). For example, the mountain pygmy possum (*Burramys parvus*) is restricted to a small high altitude distribution in Australia that is predicted to disappear with small increases in global temperature (Brereton *et al.*, 1995; Hughes, 2011). Mountain-top frog species already occupying the coolest refuges will be unable to disperse to cooler higher altitudes as climate space shifts upslope (Marra *et al.*, 1998; Knudsen *et al.*, 2011). In addition, species current distributions may be limited by factors beyond climate, and dispersal ability hampered by more than just landscape scale barriers (e.g. disturbances, habitat requirements interspecific interactions) (Huntley *et al.*, 2010; Bateman *et al.*, 2012). For example, habitat specificity limits dispersal where the habitat is clearly delineated. This is the case with soil or rock type for many mycophagous (fungus-eating) mammals in Australia (Laurance, 1997; Claridge, 2002), for reptiles such as the broad-headed snake (*Hoplocephalus bungaroides*) (Studds & Marra, 2007) and sand dune lizard (*Uma inornata*) (Barrows *et al.*, 2010), as well as for salamanders restricted to single cave systems (Niemiller *et al.*, 2010). In addition, human land-use and fragmentation may dramatically reduce habitat connectivity in some regions (Fischer & Lindenmayer, 2007), making no-dispersal scenarios appropriate for poor dispersers (Lu *et al.*, 2012).

## Partial-dispersal

Where partial-dispersal models are applied in projecting changes in the distributions of species, ‘simple’ models that incorporate dispersal attributes to restrict or buffer an otherwise full-dispersal scenario are most common (Fig. 1, Table 2). More ‘complex’ models use relatively sophisticated modelling approaches that combine the outcomes of SDMs with one or a combination of dispersal capacity, demographic knowledge, habitat information, the temporal nature of climate change and other factors influencing capacity to occupy a changed distribution (Table 2). These complex models, sometimes referred to as ‘hybrid’ or ‘coupled’ models, have only been applied and tested in a few cases (Fig. 1), but are becoming increasingly accessible (Engler & Guisan, 2009; Franklin, 2010; Midgley *et al.*, 2010; Engler *et al.*, 2012).

### Simple models of dispersal

There are several means by which basic attributes of dispersal can be incorporated into SDMs to improve projected outcomes compared with full- or no-dispersal models (Table 1). If maximum likely dispersal distance of a species is known, then this information can be used to determine whether a species will be able to reach a given projected potential distribution. This approach was taken by Lu *et al.* (2012), where known dispersal distances of threatened bird species were used to determine whether patches of suitable habitat in a fragmented landscape were able to be reached. If the species dispersal ability is unknown, other methods could be applied that account for estimated distances of dispersal, implemented in a time series to allow for a controlled dispersal projection. Future potential distributions of a species could be restricted by buffering a selected dispersal distance

**Table 2** The degree to which full-, no- and partial-dispersal approaches consider important factors influencing the future distribution of species, where black dots indicate ‘almost always’ and grey dots indicate ‘sometimes’

Factors influencing future distribution	Consideration given to dispersal			Complex model
	Full	None	Simple model	
Future climate	●	●	●	●
Current distribution		●	●	●
Dispersal attributes			●	●
Temporal nature of climate change			●	●
Habitat configuration			●	●
Biogeographical barriers			●	●
Demographic attributes				●
Interspecific interactions				●
Other change drivers (e.g. disturbance)				●

around the current distribution of that species for each future time period. Examples of this are presented in Midgley *et al.* (2006) and Williams *et al.* (2005) where different migration rates were selected for different plant seed dispersal agents, and these estimates were applied over several time slices throughout the projection. Potential migration rates for different species have been derived using paleo-data (Morin & Thuiller, 2009), or based on simple assumptions (Fitzpatrick *et al.*, 2008). Hannah *et al.* (2002) and Reside *et al.* (2012) each modelled species distributions over several time steps, allowing species to reach suitable habitat within a dispersal radius based on ecological knowledge of the species being modelled. Although applying fixed dispersal distances may risk ignoring potential long-distance dispersal events, they are relatively simple to apply to many species (Fig. 1b) and can capture key elements of dispersal limitation over time.

The application of simple dispersal scenarios in predicting climate change outcomes for many species could be greatly facilitated by the development of new user-friendly modelling platforms. This software could combine correlative habitat suitability models, with simple dispersal models allowing automated application across many species, regardless of the type of taxa. It is possible that this objective could be implemented through adaptation of existing packages such as *MigClim* (Engler & Guisan, 2009; Engler *et al.*, 2012) to be more taxonomically generic.

### Complex models of dispersal

Several software packages are available to combine dispersal processes and demographic information with SDMs in projecting distributional changes under climate change (Table 1). The *BioMove* (Midgley *et al.*, 2010) and *MigClim* (Engler & Guisan, 2009; Engler *et al.*, 2012) packages are specifically designed for modelling terrestrial plant species, although *MigClim* is potentially general enough to be adapted to other taxa. *BioMove* incorporates SDM outputs with various demographic information (Midgley *et al.*, 2010). Here, the dispersal ability of plant species is modelled by scaling demographic rates with the suitability of habitat, as well as incorporating disturbance and changes in vegetation structure. Iversen *et al.* (2004) incorporated SDMs with SHIFT, a programme that estimates dispersal abilities based on species abundances in the landscape and colonization probabilities. This model depends on the importance of species abundance at the boundary (termed source strength) and the density of the forest beyond the boundary (sink strength) to determine migration rates of trees. These modelling packages now allow the relatively simple incorporation of dispersal processes into climate change projections for individual species; however, the practical capacity of these approaches to evaluate more than a handful of species is unclear (Fig. 1b).

Some sophisticated modelling approaches have combined SDMs with spatially explicit meta-population models to



project altered distributions of species over time, under climate change (Keith *et al.*, 2008; Anderson *et al.*, 2009; Engler & Guisan, 2009; Lawson *et al.*, 2010; Conlisk *et al.*, 2012; Dullinger *et al.*, 2012; Fordham *et al.*, 2012; Regan *et al.*, 2012). These models project the abundance in one or more age classes for each grid cell at each time point, based on the abundance at the previous time point, dispersal from neighbouring grid cells and the predicted habitat suitability (from the SDM) (Clark *et al.*, 2003; Franklin, 2010). By incorporating dispersal processes over time, these meta-population models provide both spatially and temporally explicit projections, allowing for the timing of major changes in the distribution of a species under scenarios of climate change to be clearly identified. Importantly, these models assume that the SDM predicted probability of occurrence for a species is directly linked to a number of important attributes, such as the initial population size in each grid cell, demographic rates and the carrying capacity for that species in each location over time (Keith *et al.*, 2008; Dullinger *et al.*, 2012). These key assumptions of spatially explicit meta-population modelling approaches remain largely untested.

Other recent advances in SDMs incorporate dynamic processes such as range expansions with demographic information to predict changes in relation to life history characteristics (Anderson *et al.*, 2009; Brook *et al.*, 2009). A significant drawback of these more complex models is that they require reliable information on demographic rates (e.g. reproduction, mortality) and the dispersal kernel for the species being modelled. Uncertainty regarding demographic parameters requires much greater modelling effort per species in exploring the possible range of outcomes for a species under climate change (e.g. Dullinger *et al.*, 2012). In addition, important ecological factors may be oversimplified in demographic models, ignoring differential responses among individual life history stages, the effects of extreme and variable climate, regional differences in populations and demographics, the direct or indirect effects of climate on demography, and the influence of biotic interactions and how these factors affect dispersal success and population growth and establishment (Smolik *et al.*, 2010; Conlisk *et al.*, 2012; Dullinger *et al.*, 2012; Fordham *et al.*, 2012). The reliability of the models will therefore depend on the ecological relevance of the demographic information included (Fordham *et al.*, 2012).

Although these coupled models – or hybrid models – show promise, caution is warranted; each modelling component contains its own assumptions and uncertainties. When these different modelling techniques are used in conjunction, the compounding effects of these uncertainties can put reliability of model outputs into question (Langford *et al.*, 2011; Conlisk *et al.*, 2013). Outputs from the different combinations of the components of a coupled model can yield vastly different results and predictions making it difficult for their use in management decisions (Fordham *et al.*, 2012; Regan *et al.*, 2012; Conlisk *et al.*, 2013).

### *Modelling dispersal with knowledge shortfalls*

There is a range of simple ways in which we can extend existing knowledge on dispersal abilities for a small number of species to the vast majority of species for which we have little information. A relatively simplistic approach is to use a realistic intermediate dispersal scenario for species within an assemblage based on average dispersal values for the taxa. For example, the development of allometric relationships between basic physiological properties (e.g. body size) and dispersal attributes generated for well-studied species could be used to estimate dispersal properties for poorly studied species (Thomson *et al.*, 2011). In addition, well-studied species could be used to parameterize mechanistic models of dispersal for poorly studied species (Nathan *et al.*, 2002; Murphy *et al.*, 2008). Species could also be allocated to functional groups based on basic physiological dispersal attributes (e.g. seed size) or habitat specificity (Reside *et al.*, 2012), with well-studied species in each functional group used as surrogates to provide key dispersal information for poorly studied species (Dennis & Westcott, 2006, 2007; Huntley *et al.*, 2010). Alternatively, organisms can be grouped by factors such as common traits, life history or trophic position (Berg *et al.*, 2010). For example, generalist species are often better dispersers than specialists, not based on dispersal capacity per se, but rather on the ability to occupy a broader ecological niche as generalists are less limited by the availability of specific resources (Berg *et al.*, 2010; Sekar, 2012). Species in higher trophic positions are often better dispersers, as larger body sizes, and greater home ranges confer greater mobility than smaller, lower trophic position species (Berg *et al.*, 2010; Angert *et al.*, 2011). The next step would be to assess how these groupings could be paired with appropriate partial-dispersal scenarios. Meier *et al.* (2011) found that comparing projections from realistic dispersal kernels with those using full- or no-dispersal scenarios allowed for the identification of specific traits which could be used to suggest an appropriate dispersal scenario. Here, early-successional tree species were better at tracking climate change and did so at close to full-dispersal, while mid- and late-successional species responded slowly, and more in line with no-dispersal.

An appropriate surrogate for a dispersal scenario where actual dispersal capacity is uncertain could be generated by buffering the known distribution of a species by an appropriate distance from the range edge. The dispersal probability could be weighed by abundance or occupancy at the range edge, with higher abundances given a higher probability weighing. Iverson *et al.* (2004) demonstrated that abundance at range edge was more important than habitat availability beyond the edge in determining how far and fast North American trees migrate. If there is limited ecological knowledge about the species, then habitat suitability derived from SDMs could be used as a surrogate for abundance (Murphy *et al.*, 2006; VanDerWal *et al.*, 2009).

### Dispersal and habitat contiguity

Most dispersal scenarios assume a uniform dispersal rate for all qualities of the matrix regardless of landscape factors (but see Meier *et al.*, 2011). To account for this, distributions can also be clipped by biogeographical boundaries which are known to limit species (Williams *et al.*, 2010) or by selecting only contiguous areas (Peterson *et al.*, 2002; Peterson, 2003). Human-induced barriers, such as fragmentation, urbanization and anthropogenic habitat destruction, can also affect dispersal ability, as has been shown for butterflies and other insect species, reptiles and amphibians, and rainforest birds (Mattoni *et al.*, 1997, 2001; Ojima *et al.*, 1999; Collingham & Huntley, 2000; Araújo & Pearson, 2005; Russell *et al.*, 2005; Araújo *et al.*, 2006; Gaston *et al.*, 2008; Southwood & Avers, 2010). For example, the movement to future climatically suitable locations for the endangered Quino checkerspot butterfly (*Euphydryas editha quino*) is blocked by anthropogenic land-use changes, such as urbanization and fragmentation, in the landscape (Mattoni *et al.*, 1997, 2001). Dispersal ability can be particularly hampered when suitable patches are spaced widely apart or habitat availability is decreased (Collingham & Huntley, 2000). In such situations, land-use change data can be used to account for altered landscapes (Pearson, 2006), and connectivity via dispersal corridors (Graham *et al.*, 2010) or chains of 'stepping stone' suitable habitat over time (Williams *et al.*, 2005) can be accounted for (Collingham & Huntley, 2000; Meier *et al.*, 2011). Here, probability of dispersal is influenced by neighbouring cells and the connectivity between them.

### CONCLUSIONS

Here, we highlight that current climate change projections of species distributions often assume inappropriate dispersal scenarios, which can lead to unreliable projections of altered distributions. We examined how dispersal can be incorporated into SDMs in different ways, and our review outlines the appropriateness of different approaches to study species or systems with varying levels of knowledge. Partial-dispersal scenarios, uniquely tailored to each situation, are likely to provide the most robust projections of altered distributions under climate change. Although a number of methods have been developed for incorporating partial-dispersal in SDMs, the data and computation requirements can make their application to large numbers of species challenging. This highlights the need for continued development and refinement of techniques and generic user-friendly modelling platforms. Additionally, significant new research effort is required in collecting and collating dispersal data for a broad range of species, as well as the development of new methods of model parameter calibration to account for the lack of data availability that often prevents researchers from applying dispersal scenarios in SDMs. To provide the most useful models of climate change predictions for a species, selecting the most appropriate dispersal scenario is imperative.

### ACKNOWLEDGEMENTS

HM and KM receive support from the CSIRO Climate Adaptation Flagship, and KM was additionally supported by a grant from the Australia–India Strategic Research Fund.

### REFERENCES

- Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B*, **276**, 1415–1420.
- Anderson, A.S., Reside, A.E., VanDerWal, J.J., Shoo, L.P., Pearson, R.G. & Williams, S.E. (2012) Immigrants and refugees: the importance of dispersal in mediating biotic attrition under climate change. *Global Change Biology*, **18**, 2126–2134.
- Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.
- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.
- Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, **10**, 1618–1626.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712–1728.
- Barbet-Massin, M., Thuiller, W. & Jiguet, F. (2012) The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology*, **18**, 881–890.
- Barrows, C.W., Rotenberry, J.T. & Allen, M.F. (2010) Assessing sensitivity to climate change and drought variability of a sand dune endemic lizard. *Biological Conservation*, **143**, 731–736.
- Bateman, B.L., VanDerWal, J., Williams, S.E. & Johnson, C.N. (2012) Biotic interactions influence the projected distribution of a specialist mammal under climate change. *Diversity and Distributions*, **18**, 861–872.
- Berg, M.P., Kiers, E.T., Driessen, G., Van Der Heijden, M., Kooi, B.W., Kuenen, F., Liefting, M., Verhoef, H.A. & Ellers, J. (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, **16**, 587–598.
- Bonnet, X., Naulleau, G. & Shine, R. (1999) The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation*, **89**, 39–50.

- Brereton, R., Bennett, S. & Mansergh, I. (1995) Enhanced greenhouse climate change and its potential effect on selected fauna of south-eastern Australia: a trend analysis. *Biological Conservation*, **72**, 339–354.
- Brook, B.W., Akçakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G. & Araújo, M.B. (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters*, **5**, 723–725.
- Brown, S., Hickey, C., Harrington, B. & Gill, R. (2001). *The U.S. shorebird conservation plan*, 2nd edn. Manomet Center for Conservation Sciences. (ed. by M. C. f. C. Sciences), Manomet, MA.
- Brown, G.P., Phillips, B.L., Webb, J.K. & Shine, R. (2006) Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation*, **133**, 88–94.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Claridge, A.W. (2002) Ecological role of hypogeous ectomycorrhizal fungi in Australian forests and woodlands. *Plant and Soil*, **244**, 291–305.
- Clark, J.S., Lewis, M., McLachlan, J.S. & HilleRisLambers, J. (2003) Estimating population spread: what can we forecast and how well? *Ecology*, **84**, 1979–1988.
- Coetsee, B.W.T., Robertson, M.P., Erasmus, B.F.N., Van Rensburg, B.J. & Thuiller, W. (2009) Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography*, **18**, 701–710.
- Collingham, Y.C. & Huntley, B. (2000) Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications*, **10**, 131–144.
- Conlisk, E., Lawson, D., Syphard, A.D., Franklin, J., Flint, L., Flint, A. & Regan, H.M. (2012) The roles of dispersal, fecundity, and predation in the population persistence of an oak (*Quercus engelmannii*) under global change. *PLoS ONE*, **7**, e36391.
- Conlisk, E., Syphard, A.D., Franklin, J., Flint, L., Flint, A. & Regan, H. (2013) Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Global Change Biology*, **19**, 858–869.
- Conway, C.J. (2008). Standardized North American Marsh Bird Monitoring Protocols Wildlife Research Report #2008-01. U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ.
- Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.
- Dennis, A. & Westcott, D. (2006) Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia*, **149**, 620–634.
- Dennis, A. & Westcott, D.A. (2007). Estimating dispersal kernels produced by a diverse community of vertebrates. *Frugivory and seed dispersal: theory and its application in a changing world*. (ed. by A. Dennis, R. Green, E. Schupp and D. Westcott), pp. 201–228. CAB International Publishing, Wallingford.
- Devictor, V., van Swaay, C., Brereton, T. *et al.* (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.
- Dirnböck, T., Essl, F. & Rabitsch, W. (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, **17**, 990–996.
- Dullinger, S., Gattlinger, A., Thuiller, W. *et al.* (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, **2**, 619–622.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.
- Engler, R. & Guisan, A. (2009) MigClim: predicting plant distribution and dispersal in a changing climate. *Diversity and Distributions*, **15**, 590–601.
- Engler, R., Hordijk, W. & Guisan, A. (2012) The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. *Ecography*, **35**, 872–878.
- Farmer, A.H. & Parent, A.H. (1997) Effects of the landscape on shorebird movements at spring migration stopovers. *The Condor*, **99**, 698–707.
- Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.
- Fitzpatrick, M.C. & Hargrove, W.W. (2009) The projection of species distribution models and the problem of non-analog climate. *Biodiversity and Conservation*, **18**, 2255–2261.
- Fitzpatrick, M.C., Gove, A.D., Sanders, N.J. & Dunn, R.R. (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: the Banksia (Proteaceae) of Western Australia. *Global Change Biology*, **14**, 1337–1352.
- Fordham, D.A., Resit Akçakaya, H., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B.A., Yates, C. & Brook, B.W. (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357–1371.
- Franklin, J. (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321–330.
- Gaston, K.J., Jackson, S.F., Cantú-Salazar, L. & Cruz-Piñón, G. (2008) The ecological performance of protected areas. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 93–113.



- Graham, C.H., VanDerWal, J., Phillips, S.J., Moritz, C. & Williams, S.E. (2010) Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography*, **33**, 1062–1069.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, **11**, 485–495.
- Hannah, L., Midgley, G., Anelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R. & Williams, P. (2007) Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, **5**, 131–138.
- Hellmann, J.J., Byers, J.E., Bierwagen, B.G. & Dukes, J.S. (2008) Five potential consequences of climate change for invasive species. *Conservation Biology*, **22**, 534–543.
- Hijmans, R.J. & Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. (2008) Assisted colonization and rapid climate change. *Science*, **321**, 345–346.
- Hoskin, C.J. (2010) The invasion and potential impact of the Asian House Gecko (*Hemidactylus frenatus*) in Australia. *Austral Ecology*, **36**, 240–251.
- Hughes, L. (2011) Climate change and Australia: key vulnerable regions. *Regional Environmental Change*, **11**, 189–195.
- Huntley, B. (1995) Plant species' response to climate change: implications for the conservation of European birds. *Ibis*, **137**, S127–S138.
- Huntley, B. & Thompson Webb, I.I.I. (1989) Migration: species' response to climatic variations caused by changes in the earth's orbit. *Journal of Biogeography*, **16**, 5–19.
- Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G. (2006) Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, **148**, 8–28.
- Huntley, B., Barnard, P., Altwegg, R., Chambers, L., Coetzee, B.W.T., Gibson, L., Hockey, P.A.R., Hole, D.G., Midgley, G.F., Underhill, L.G. & Willis, S.G. (2010) Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. *Ecography*, **33**, 621–626.
- Iverson, L.R., Schwartz, M.W. & Prasad, A.M. (2004) How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography*, **13**, 209–219.
- Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, e157.
- Jimenez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions*, **14**, 885–890.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, **3**, 203–213.
- Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B. & Rebelo, T.G. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.
- Knudsen, E., Lindén, A., Both, C. *et al.* (2011) Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, **86**, 928–946.
- Langford, W.T., Gordon, A., Bastin, L., Bekessy, S.A., White, M.D. & Newell, G. (2011) Raising the bar for systematic conservation planning. *Trends in Ecology & Evolution*, **26**, 634–640.
- Laurance, W.F. (1997) A distributional survey and habitat model for the endangered northern Bettong *Bettongia tropica* in tropical Queensland. *Biological Conservation*, **82**, 47–60.
- Lawson, D.M., Regan, H.M., Zedler, P.H. & Franklin, J. (2010) Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Global Change Biology*, **16**, 2518–2529.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.
- Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G. & Williams, P.H. (2003) Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology*, **17**, 1591–1600.
- Lu, N., Jia, C.-X., Lloyd, H. & Sun, Y.-H. (2012) Species-specific habitat fragmentation assessment, considering the ecological niche requirements and dispersal capability. *Biological Conservation*, **152**, 102–109.
- Marini, M.Â., Barbet-Massin, M., Esteves Lopes, L. & Jiguet, F. (2009) Predicted climate-driven bird distribution changes and forecasted conservation conflicts in a neotropical savanna. *Conservation Biology*, **23**, 1558–1567.
- Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884–1886.
- Martinez-Meyer, E. (2005) Climate change and biodiversity: some considerations in forecasting shifts in species' potential distributions. *Biodiversity Informatics*, **2**, 42–55.
- Massot, M., Clobert, J. & Ferrière, R. (2008) Climate warming, dispersal inhibition and extinction risk. *Global Change Biology*, **14**, 461–469.
- Mattoni, R., Pratt, G., Longcore, T., Emmel, J. & George, J. (1997) The endangered quino checkerspot butterfly, distribution modelling. *Diversity and Distributions*, **14**, 885–890.

- Euphydryas editha quino* (Lepidoptera: Nymphalidae). *Journal of Research on the Lepidoptera*, **34**, 99–118.
- Mattoni, R., Longcore, T., Zonneveld, C. & Novotny, V. (2001) Analysis of Transect Counts to Monitor Population Size in Endangered Insects The Case of the El Segundo Blue Butterfly, *Euphilotes bernardino* Allyn. *Journal of Insect Conservation*, **5**, 197–206.
- McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H. & Santamaria, L. (2012) Seed dispersal in changing landscapes. *Biological Conservation*, **146**, 1–13.
- McLachlan, J.S., Hellmann, J.J. & Schwartz, M.W. (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, **21**, 297–302.
- Meier, E.S., Lischke, H., Schmatz, D.R. & Zimmermann, N.E. (2011) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, **21**, 164–178.
- Menéndez, R., Megías, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society B*, **273**, 1465–1470.
- Midgley, G.F., Hughes, G.O., Thuiller, W. & Rebelo, A.G. (2006) Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity and Distributions*, **12**, 555–562.
- Midgley, G.F., Davies, I.D., Albert, C.H., Altwegg, R., Hannah, L., Hughes, G.O., O'Halloran, L.R., Seo, C., Thorne, J.H. & Thuiller, W. (2010) BioMove – an integrated platform simulating the dynamic response of species to environmental change. *Ecography*, **33**, 612–616.
- Morin, X. & Thuiller, W. (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **90**, 1301–1313.
- Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2006) Distribution of abundance across the range in eastern North American trees. *Global Ecology & Biogeography*, **15**, 63–71.
- Murphy, H., Hardesty, B., Fletcher, C., Metcalfe, D., Westcott, D. & Brooks, S. (2008) Predicting dispersal and recruitment of *Miconia calvescens* (Melastomataceae) in Australian tropical rainforests. *Biological Invasions*, **10**, 925–936.
- Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W. & Levin, S.A. (2002) Mechanisms of long-distance dispersal of seeds by wind. *Nature*, **418**, 409–413.
- Niemiller, M.L., Osbourn, M.S., Fenolio, D.B., Pauley, T.K., Miller, B.T. & Holsinger, J.R. (2010) Conservation status and habitat use of the West Virginia Spring Salamander (*Gyrinophilus subterraneus*) and Spring Salamander (*G. porphyriticus*) in General Davis Cave, Greenbrier Co West Virginia. *Herpetological Conservation and Biology*, **5**, 32–43.
- Ojima, D., Garcia, L., Elgaali, E., Miller, K., Kittel, T.G.F. & Lockett, J. (1999) Potential climate change impacts on water resources in the great plains. *Journal of the American Water Resources Association*, **35**, 1443–1454.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearson, R.G. (2006) Climate change and the migration capacity of species. *Trends in Ecology & Evolution*, **21**, 111–113.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography*, **12**, 361–371.
- Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P. & Lees, D.C. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704–1711.
- Peterson, A.T. (2003) Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. *Global Change Biology*, **9**, 647–655.
- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R.H. & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.
- Pitelka, L.F. (1997) Plant migration and climate change. *American Scientist*, **85**, 464.
- Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. & Townsend Peterson, A. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, **426**, 837–841.
- Regan, H.M., Syphard, A.D., Franklin, J., Swab, R.M., Markovchick, L., Flint, A.L., Flint, L.E. & Zedler, P.H. (2012) Evaluation of assisted colonization strategies under global change for a rare, fire-dependent plant. *Global Change Biology*, **18**, 936–947.
- Reside, A.E., VanDerWal, J. & Kutt, A.S. (2012) Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios. *Ecology and Evolution*, **2**, 705–718.
- Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P. & Richardson, A.J. (2011) Pushing the limits in marine species distribution modeling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, **20**, 789–802.
- Roche, E.A., Cohen, J.B., Catlin, D.H., Amirault-Langlais, D.L., Cuthbert, F.J., Gratto-Trevor, C.L., Felio, J. & Fraser, J.D. (2012) Range-wide piping plover survival: correlated patterns and temporal declines. *Journal of Wildlife Management*, **74**, 1784–1791.
- Russell, A.P., Bauer, A.M. & Johnson, M.K. (2005). *Migration in amphibians and reptiles: an overview of patterns and orientation mechanisms in relation to life history strategies*. Migration of Organisms), pp. 151–203. Springer, Berlin Heidelberg.

- Sekar, S. (2012) A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? *Journal of Animal Ecology*, **81**, 174–184.
- Shoo, L.P., Storlie, C., VanDerWal, J., Little, J. & Williams, S.E. (2011) Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Global Change Biology*, **17**, 186–193.
- Sinclair, S.J., White, M.D. & Newell, G.R. (2010) How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society*, **15**, 8 [online].
- Smolik, M.G., Dullinger, S., Essl, F., Kleinbauer, I., Leitner, M., Peterseil, J., Stadler, L.M. & Vogl, G. (2010) Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant. *Journal of Biogeography*, **37**, 411–422.
- Sorenson, L.G., Goldberg, R., Root, T.L. & Anderson, M.G. (1998) Potential effects of global warming on waterfowl populations breeding in the northern Great Plains. *Climatic Change*, **40**, 343–369.
- Southwood, A. & Avers, L. (2010) Physiological, behavioral, and ecological aspects of migration in reptiles. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, **180**, 1–23.
- Studds, C.E. & Marra, P.P. (2007) Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Research*, **35**, 115–122.
- Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P. (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, **4**. Article 16.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, **99**, 1299–1307.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005a) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.
- Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005b) Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, **11**, 2234–2250.
- Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137–152.
- Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences USA*, **106**, 19637–19643.
- 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. *American Naturalist*, **174**, 282–291.
- VanDerWal, J., Murphy, H.T., Kutt, A.S., Perkins, G.C., Bateman, B.L., Perry, J.J. & Reside, A.E. (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, **3**, 239–243.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Weller, M.W. (1999) *Wetland birds: habitat resources and conservation implications*, Cambridge. Cambridge University Press, UK.
- Williams, P., Hannah, L.E.E., Andelman, S., Midgley, G.U.Y., Araújo, M., Hughes, G., Manne, L., Martinez-Meyer, E. & Pearson, R. (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, **19**, 1063–1074.
- Williams, S.E., VanDerWal, J., Isaac, J., Shoo, L.P., Storlie, C., Fox, S., Bolitho, E.E., Moritz, C., Hoskin, C. & Williams, Y.M. (2010) Distributions, life history characteristics, ecological specialisation and phylogeny of the rainforest vertebrates in the Australian Wet Tropics bioregion. *Ecology*, **91**, 2493.
- Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S. & Huntley, B. (2009) Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conservation Letters*, **2**, 46–52.

## BIOSKETCH

**Brooke Bateman** is a postdoctoral research associate in the SILVIS Lab (<http://silvis.forest.wisc.edu/>) at the University of Wisconsin-Madison and is a former member of and current collaborator with the Centre for Tropical Biodiversity and Climate Change Research (<http://www.jcu.edu.au/ctbcc/index.htm>) at James Cook University. Her current research interests are in spatial ecology and conservation, and the effect of extreme weather events on wildlife populations and communities.

Author contributions: J.VDW, B.L.B., A.E.R. and H.T.M. conceived the ideas; B.L.B., A.E.R. and K.M. led the literature search and analysis; B.L.B., H.T.M., A.E.R., K.M. and J.VDW were involved in writing and revising of the manuscript.

Editor: Wilfried Thuiller