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ESSAY REVIEW

Moving forward: insights and applications of moving-habitat models for climate change ecology

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Summary

1. Predicting and managing species' responses to climate change is one of the most significant challenges of our time. Tools are needed to address problems associated with novel climatic conditions, biotic interactions and greater climate velocities.

2. We present a spatially explicit moving-habitat model (MHM) and demonstrate its versatility in tackling critical questions in climate change research, including dispersal in multiple spatial dimensions, population stage structure, interspecific interactions, asymmetric range shifts, Allee effects and the presence of infectious diseases. The model utilizes integrodifference equations to track changes in population density over time in a habitat that is moving. The model is quite flexible and can accommodate variation in demography, dispersal patterns, biotic interaction and stochasticity in the velocity of climate change.

3. The methods provide a general mechanistic understanding of the underlying ecological processes that drive a system. Field data can be readily incorporated into the model to give insight into specific populations of interest and inform management decisions.

4. *Synthesis.* Moving-habitat models unite ecological theory, data-centred modelling and conservation decision support under a single framework. Their ability to generate testable hypotheses, incorporate data and inform best management practices proves that these models provide a valuable framework for climate change biologists.

Key-words: biotic interactions, climate change, integrodifference equation, range shift, simulation model, velocity of climate change

Moving-habitat models: a new opportunity

Climate change is one of the most significant challenges of our time. Scientists and resource managers need to document species' current responses, predict future responses and identify which species are most vulnerable to extinction (Cassar *et al.* 2006; IPCC 2014). The challenge is how best to predict and manage the impacts of climate change on species given the breadth of biotic and abiotic factors that determine vulnerability to climate change.

Predicting the effects of climate change on species and developing effective management plans require understanding complex biological responses that are likely to change with climate (Staudinger *et al.* 2013). For instance, species may respond to climate change by shifting their distribution or phenology, acclimating or adapting to changes, or going extinct (Aitken *et al.* 2008; Cleland *et al.* 2012; Valladares *et al.* 2014). In addition, the climatic factors affecting species, and how they affect species, will vary over a species distribution (Garcia *et al.* 2014; Lenoir & Svenning 2015; Harsch & HilleRisLambers 2016). It is, therefore, not possible to predict how a species will respond to climate change by documenting the species response to a single climate variable (temperature) at a single position (upper distribution limit) (Harsch & HilleRisLambers 2016). Finally, intra- and interspecific biotic interactions, which are likely to change with climate change, will influence population responses (Gilman *et al.* 2010; Post 2013; Urban, Zarnetske & Skelly 2013). Some invasive species and pathogens are expected to benefit from climatic changes, placing additional pressure on other species (Bebber, Ramotowski & Gurr 2013; Sorte *et al.* 2013).

Other factors, such as the rate of warming and human land use, must also be considered. Increased warming may prevent

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*Correspondence author. E-mail: harsch.melanie@gmail.com many species from tracking future spatial shifts in suitable habitat, even if they can keep pace now (Schloss, Nuñez & Lawler 2012; Buckley, Tewksbury & Deutsch 2013; Corlett & Westcott 2013). Human activity and land use have constrained species' responses through habitat fragmentation and habitat loss (Mantyka-Pringle, Martin & Rhodes 2012). Both increased rates of climate change and land use impinge upon a species' ability to track spatial shifts in suitable habitat, increasing its vulnerability to extinction.

What approaches to these issues will be most effective? Given the variety of challenges, the framework should be generalizable. Since threats to biodiversity are immediate (Butchart *et al.* 2010; Urban 2015), approaches that involve short experimental or observational periods are preferred over approaches that involve longer periods. Finally, frameworks should be able to make predictions for new conditions. We begin with a brief survey of quantitative models that are generalizable, that are easy to implement and that address future conditions. We then introduce a new model, a moving-habitat model (MHM), and explore its advantages.

Quantitative models of species' responses to climate change vary from statistical to analytical. Species distribution models (SDMs) statistically relate current population distributions to environmental variables. In the context of climate change, SDMs then use global circulation models and other tools to project future suitable habitat (Elith & Leathwick 2009). SDMs have faced criticism for failing to include biological processes, such as dispersal, as well as for making assumptions about niche conservatism and population–environment equilibrium (Araújo & Peterson 2012). Many of these criticisms are being addressed (Boulangeat, Gravel & Thuiller 2012; Giannini *et al.* 2013; Clark *et al.* 2014; Thuiller *et al.* 2015). As with all models, care must be taken when extrapolating beyond species' current conditions (Sinclair, White & Newell 2010; Harsch *et al.* 2012).

Reaction–diffusion equations (RDEs) have been used extensively to study invasion, persistence and pattern formation (see, e.g., Okubo 1980; Shigesada & Kawasaki 1997). RDEs assume continuous growth and dispersal, with dispersal based on the Gaussian distribution. Recent RDEs have modelled climate change using shifting boundary conditions or shifting growth functions that force populations to track suitable habitat (Potapov & Lewis 2004; Berestycki *et al.* 2009; Leroux *et al.* 2013; Berestycki, Desvillettes & Diekmann 2014; Li *et al.* 2014). These models can accommodate single species (Berestycki *et al.* 2009; Leroux *et al.* 2013; Li *et al.* 2014) as well as competing species (Potapov & Lewis 2004; Berestycki, Desvillettes & Diekmann 2014). RDEs can easily incorporate field data to provide risk estimates (Leroux *et al.* 2013), but care must be taken since RDEs cannot capture frequent long-distance dispersal events.

Individual-based models (IBMs) simulate individuals over space by defining rules for growth, specifying dispersal probabilities between locations and shifting an environmental gradient over time to represent climate change (Best *et al.* 2007; Brooker *et al.* 2007; Prasad *et al.* 2013; Bocedi *et al.* 2014). Investigators have examined single species (Travis 2003; Bocedi *et al.* 2014) and interacting species (Best *et al.* 2007; Brooker *et al.* 2007). IBMs can account for long-distance dispersal, which can shape the outcome of competition during climate change (Brooker *et al.* 2007). Since IBMs rely on simulation, they are suited for incorporating multiple complex factors, though often at a high computational cost.

In this article, we focus on a fourth modelling approach, integrodifference equations (IDEs), which model space as continuous and time as discrete. They are the discrete-time analogues of RDEs. Recent IDE models have considered a variety of spatial problems, including optimal pest control (Martinez, Lenhart & White 2015), measuring spread speeds for structured populations (Bateman *et al.* 2015), competition in patchy landscapes (Williams, Snyder & Levine 2016) and the influence of dispersal on Allee effects (Goodsman & Lewis 2016). IDEs are well suited for both applied and theoretical problems; they are easy to construct and implement; and, along with simple extensions, they can address nearly all of the challenges (at least partially) for prediction and management outlined above.

Integrodifference equations can be applied to a variety of climate change problems. For examples, IDEs can be used to evaluate how traits and life-history strategies influence a species' ability to track climate change. By incorporating mean dispersal distance and stage structure of four species (*Primula vulgaris*, *Dipsacus sylvestris, Pinus nigra*, *Pinus palustris*) into an IDE with a moving habitat, Harsch *et al.* (2014a) show that relative importance of different demographic transitions (survival, growth, reproduction) shifts with increasing velocity of climate change. All four species showed decreased importance of survival (stasis and shrinkage). In other words, being able to remain in the same stage contributed less and less to the growth rate of the population as speed increased. This is because a population's distribution can shift only as fast as newly established seedlings at the expanding range front can mature and disperse new seeds (Clark, Lewis & Horvath 2001).

In the following section, we provide a brief description of the IDE model that we developed to evaluate and predict the effects of climate change on species. We call this model a MHM, although the approaches described above could also fall under this name. We focus on the conceptual development of the model; a more detailed description is provided in Zhou & Kot (2011, 2013), Harsch *et al.* (2014a,b), and Kot & Phillips (2015). In 'Building upon foundations: adding complexity and new insights' section, we discuss insights gained from MHMs on the importance of dispersal, the interaction between dispersal and habitat shape, trade-offs between demographic parameters, and potential for evolution in a changing climate. In 'Extending MHMs: potential applications to global change biology' section, we discuss further applications of MHMs, primarily for climate change but also for other global changes. In this section, we outline four applications using simple models. These four examples are available as interactive web applications. Links are provided in Table 1.

Table 1. Online interactive web applications

Model	URL
Basic model	https://movinghabitatmodel.shinyapps.io/BasicModel/
Allee effects	https://movinghabitatmodel.shinyapps.io/AlleeEffects/
Change in range size	https://movinghabitatmodel.shinyapps.io/rangesize/
Biotic interactions: competition/facilitation	https://movinghabitatmodel.shinyapps.io/BioticInteractions/
Biotic interactions: infectious agent	https://movinghabitatmodel.shinyapps.io/InfectionModel/

Equations for each model may be found at the corresponding URLs. Code for the basic model can be found at: https://doi.pangaea.de/10.1594/PANGAEA.867779.

Laying foundations: a basic MHM

Moving-habitat models track the density of a population over a spatial domain at discrete-time steps using the IDE

$$n_{t+1}(x) = \int_{-\frac{L}{2}+ct}^{\frac{L}{2}+ct} k(x-y)f[n_t(y)]\mathrm{d}y. \qquad \text{eqn 1}$$

In this basic model, we integrate over the spatial domain or habitat to tally the population. The habitat is a simple line segment represented by the interval $[-L/2+ct, L/2+ct]$. The habitat may represent any spatial scale of interest, from a small patch to an entire range (thus our usage of 'moving habitat' rather than 'range shift' or other similar terms). Although conceptually similar to a real landscape, all points within the habitat are assumed to be equivalent, with identical growth and dispersal occurring. The habitat moves by a fixed increment of c in each time step (Fig. 1, column 4). The parameter c, like the velocity of climate change (Loarie *et al.* 2009), represents the speed of movement of suitable climatic conditions.

The function $n_t(x)$ describes the population density at time t at every location x along the one-dimensional habitat (L). The spatial gradient is continuous, whereas time is discrete, so that $n_t(x)$ represents the population density at the tth time step (Fig. 1). Between each time step, the habitat moves, due to climate change, and the population goes through two separate stages (Fig. 1). During the first stage (or sedentary growth stage), individuals along the habitat grow, reproduce and die. At each point x along the habitat (L), the local population n_t (x) produces offspring (or propagules) according to some growth function f [n_t (x)], such as Beverton–Holt growth (Fig. 1, column 3). In the second (or dispersal) stage, propagules disperse according to the dispersal kernel $k(x-y)$. A dispersal kernel is the probability distribution of the displacement of a propagule during the dispersal stage. Examples include the Gaussian, Laplace and Cauchy distributions (Fig. 1, column 4). For a fixed propagule source location y, $k(x-y)$ is the probability density of a propagule dispersing to destination x. At the end of the dispersal stage, the contribution from all sources y is tallied up by the integral in eqn (1). Propagules that land outside the habitat are tallied (Fig. 1).

Parameterizing model (1) involves estimating the dispersal kernel, growth function, habitat size and velocity of climate change. The first three components (dispersal, growth and habitat size) are not unique to MHMs and belong to a much larger literature of IDEs and other population-dynamic models.

Estimating dispersal kernels may involve measuring seed shadows (Clark 1998), identifying and quantifying multiple dispersal vectors (Nathan *et al.* 2008), measuring average lifetime displacement or converting from a measured distribution of dispersal distances to a dispersal kernel (Cousens & Rawlinson 2001). Recent advanced approaches to parameterizing IDE dispersal kernels include using climate projections to fit wind dispersal models (Bullock *et al.* 2012), collecting onsite

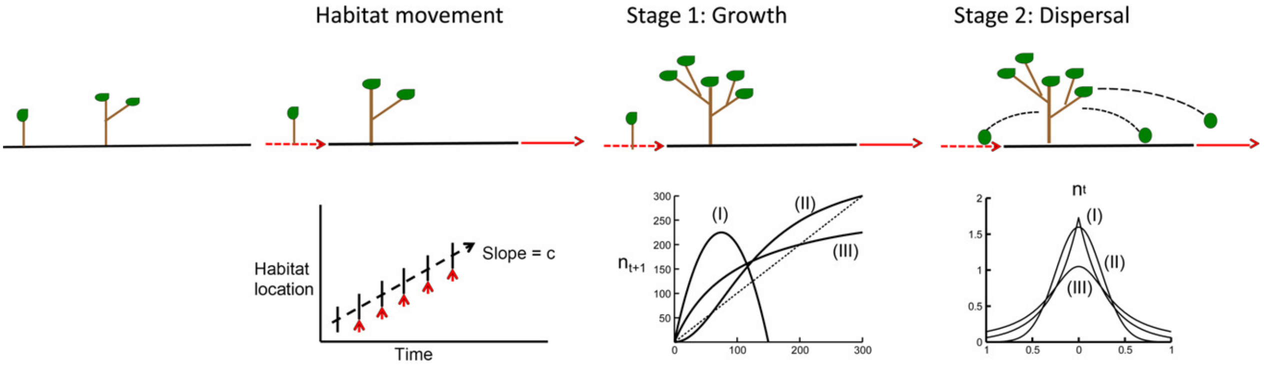

Fig. 1. Conceptual representation of the two population-level stages of the moving-habitat model. First, the suitable habitat moves by a specified amount (c; red arrows). Then, in stage 1, individuals grow, reproduce and die. Individuals (propagule or adult) outside the patch (dashed red line) do not grow or reproduce. Density-dependent growth can take the form of overcompensation (I), depensation (II) or compensation (III). In stage 2, propagules (green dots) disperse. Common dispersal kernels include the Laplace (I), Gaussian (II) and Cauchy (III) distributions. Habitat movement and the two stages are repeated for each time step. [Colour figure can be viewed at wileyonlinelibrary.com]

data on wind speed and tree canopy heights (Caplat, Nathan & Buckley 2012), incorporating complex movement of dispersal vectors such as birds (Neupane & Powell 2015), and using experimental warming to anticipate changes in seed release rates (Teller, Zhang & Shea 2016).

For MHMs, it is common to select a flexible family of dispersal kernels or to rely on the type of kernel commonly used for a particular taxon. To generate hypotheses, investigators have varied dispersal parameters and determined the effect on population dynamics (Zhou & Kot 2011; Harsch *et al.* 2014a; Phillips & Kot 2015).

Parameterizing growth functions depends on whether density-dependent growth is present. For some populations, with little or no density dependence, the growth function is simply the product of a constant net reproductive rate and the number of females. For populations with density-dependent growth, it is necessary to fit parameters that describe depensation (Berec & Mrkvička 2013), compensation (Brown, Downing & Leibold 2016) or overcompensation (Jarvis *et al.* 2016) (see Fig. 1, column 2 for examples). Although model (1) is not a structured population, estimating demographic parameters for structured models has an extensive literature (see, e.g., Caswell 2001). We consider a stage-structured MHM briefly.

Estimating habitat size depends on the scale at which the model is applied. If the habitat length *L* represents an entire range, the habitat may be set by environmental metrics, such as mean temperatures corresponding to upper and lower critical thermal limits. Model (1) effectively assumes that fecundity is optimal anywhere within the habitat but zero elsewhere and would be especially appropriate when individual performance is uniform within a certain range and declines sharply outside. If model (1) is used at a small scale, where *L* corresponds to the length of a patch, we rely on estimates of patch size (e.g., the size of meadows for networks of butterfly populations).

In uses of model (1) to date, the velocity of climate change *c* is a ‘free parameter’ that is varied to assess the impact of increasing velocities of change on populations. However, there are multiple estimates of climate velocity at global (Loarie *et al.* 2009), continental (Dobrowski *et al.* 2013) and regional (Mote & Salathe 2010) resolutions. When ecologically relevant, movement rates of other habitat delimiters such as rising tree lines and invading species may be used as proxies for *c*.

Exact solutions to model (1) are only obtainable for very simple cases, so numerical simulation is a standard method of exploration. However, many analytical approximations have been developed that reduce computation time and enable cross-validation of numerical results (Zhou & Kot 2013; Kot & Phillips 2015; Phillips & Kot 2015).

The speed (*c*) with which the habitat moves has a profound impact on population persistence. In both the basic (Zhou & Kot 2011, 2013) and extended models (Harsch *et al.* 2014a; Phillips & Kot 2015), the population collapses once the speed becomes too large. In particular, there is a critical speed c^*, beyond which the population cannot track its habitat (Fig. 2). Above the critical speed, the population growth rate λ drops below 1 and the population tends towards extinction (grey area in Fig. 2). (See Zhou & Kot 2011, for a mathematical definition of λ.) The critical speed is higher for populations with longer habitat length (Fig. 2a) and higher reproductive rates. The dependence of the critical speed on mean dispersal distance, however, is not monotonic. Higher mean dispersal distance may help the population keep up with rapid climate change, but the effect is reversed when the suitable habitat is too small or the population does not produce enough propagules. In the latter situations, a high mean dispersal distance may cause the population to overdisperse and lose too many propagules through the habitat boundaries (Fig. 2b).

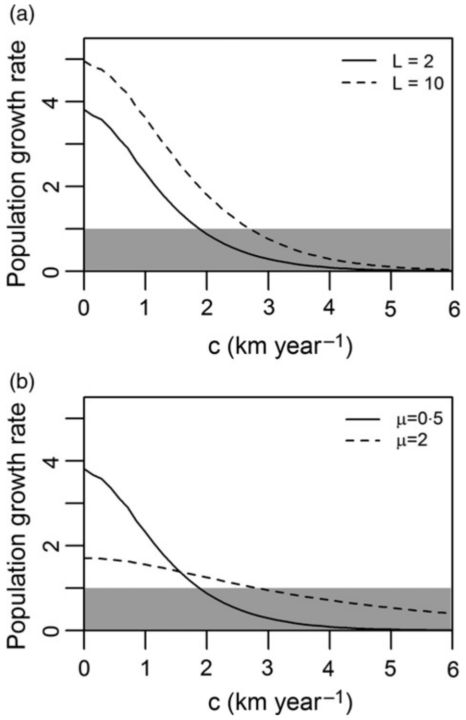

Fig. 2. Comparison of population growth rate λ with increasing values of *c* (km yr^{-1}) between shorter and longer (a) habitat lengths (*L*) and (b) mean dispersal distances (μ). White area of figure represents $\lambda > 1$ (growing population) and grey area represents $\lambda < 1$ (declining population). In all cases, the dispersal kernel is the Laplace distribution. For (a), the mean dispersal distance is 0·5 km and habitat length is either 2 km (solid line) or 10 km (dashed line). For (b), the habitat length is 2 km and mean dispersal distance is either 0·5 km (solid line) or 2 km (dashed line).

The shape of the dispersal kernel also affects the critical speed. Different dispersal kernels with the same mean dispersal distance may yield different critical speeds (Zhou & Kot 2011, 2013; Kot & Phillips 2015), but these speeds will always be finite, as long as the amount of suitable habitat is finite for the population (Zhou 2013). Since the critical speed cannot exceed a population’s speed of invasion, populations with finite invasion speeds will always tend towards extinction under extremely rapid climate change. In contrast, populations with long-distance dispersal kernels that lead to accelerating waves of invasion can tolerate much higher speeds of climate change. The basic model can be further explored using the interactive web application (Table 1).

Building upon foundations: adding complexity and new insights

Simple MHMs provide a foundation for incorporating greater complexity and realism. We provide two examples in this section. First, we relax assumptions regarding habitat structure (Phillips & Kot 2015) by modelling habitat with a two-dimensional rectangle rather than a line segment. A more realistic habitat structure can address complex dispersal patterns and inform management decisions on the shape of reserves and migration corridors. Second, we incorporate life-history structure, allowing us to explore the relative importance of life-history stages on persistence with climate change (Harsch *et al.* 2014a) and on potential evolutionary responses.

INTERACTIONS BETWEEN DISPERSAL AND HABITAT DIMENSIONS

As presented thus far, MHMs assume that habitat length (in the direction parallel to climate change) is limited but habitat width (in the perpendicular direction) is unlimited. For many populations, this assumption is simplistic. Dispersal barriers such as roads and mountains limit habitat width. Thus, one-dimensional MHMs overestimate persistence. To tighten persistence estimates, we model the habitat with a simple rectangle of length *L* and width *W*. At each time step, the rectangle shifts by *c* units, due to climate change, in the direction of *L* (Fig. 3a). We use a two-dimensional dispersal kernel to describe the redistribution of propagules during the dispersal stage.

The two-dimensional model has many ecological applications; we focus here on reserve design. Questions surrounding the best designs for nature reserves and migration corridors are abundant. Many reserve designs (or geometries) are possible (Gilbert-Norton *et al.* 2010). When the habitat is stationary ($c = 0$), the model identifies the minimum habitat length and width for a species to persist (the critical patch size). When the habitat is moving ($c > 0$), the model identifies the optimal corridor length and width that maximize persistence during climate change (Phillips & Kot 2015).

The optimal migration corridor configuration depends on the kurtosis of the dispersal kernel (Fig. 3b). Kurtosis is a standardized measure of the fourth moment of the distribution that quantifies the relative proportion of probability in the peak, shoulders and tails. If the dispersal kernel is platykurtic, it is

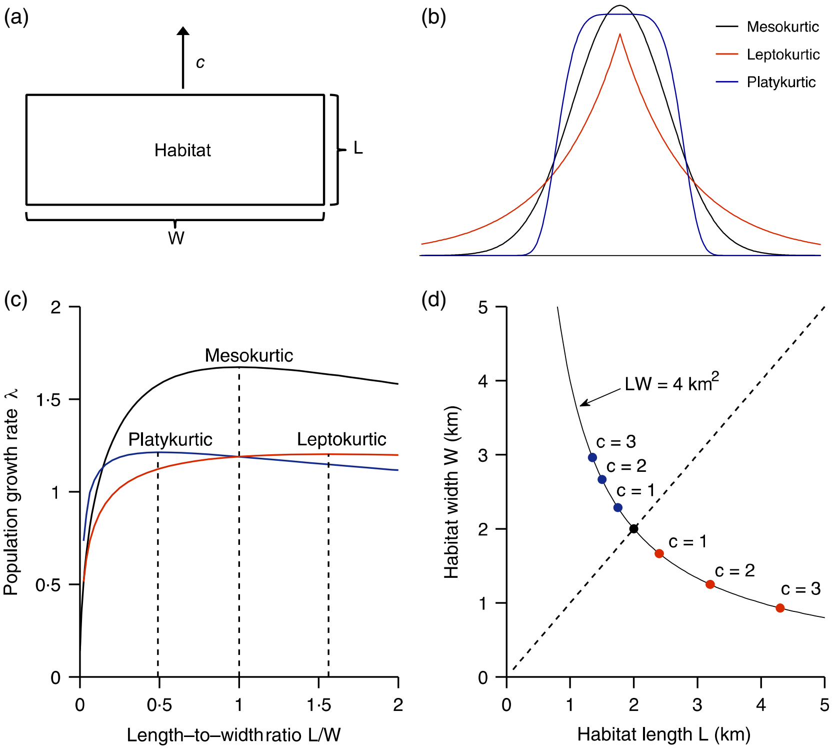

Fig. 3. (a) Conceptual diagram of a two-dimensional moving habitat. The habitat, with width *W* and length *L*, moves by *c* units per time step in the direction parallel to length. Area outside the habitat is inhospitable. (b) Kurtosis is a broad descriptor of probability distribution shape. High kurtosis occurs when probability mass is smaller near the shoulders and greater in the peak, the tails or both (Caswell 2001). Platykurtic distributions (blue) have probability mass concentrated in the shoulders. Leptokurtic distributions (green) have probability mass concentrated in the peak and/or tails. Mesokurtic distributions (red) such as the Gaussian have an intermediate shape. (c) Population growth rate λ as a function of the habitat length-to-width ratio under a constraint on habitat area. The optimal habitat shape depends on the kurtosis of the dispersal kernel: platykurtic kernels favour wider habitats (blue), leptokurtic kernels favour longer habitats (green) and mesokurtic kernels favour square habitats (red). (d) The effect of kurtosis on the best habitat shape increases with the velocity of climate change, *c*. We constrained habitat area by setting the product $LW = 4$ km^2 and plotted the optimal lengths and widths as *c* increases from 1 to 3 km yr^{-1}. For platykurtic kernels, width becomes more important with increasing *c* (blue dots); for leptokurtic kernels, length becomes more important (green dots); for mesokurtic kernels, length and width are always equally important (red dots). [Colour figure can be viewed at wileyonlinelibrary.com]

best to have a wide corridor ($W > L$), and the optimal length-to-width ratio is less than 1 (Fig. 3c, blue line). When the dispersal kernel is leptokurtic, it is best to have a long corridor ($W < L$) with a length–width ratio larger than 1 (Fig. 3c, green line). When the dispersal kernel is mesokurtic, habitat length and width are equally important (Fig. 3c, red line).

Results from two-dimensional MHMs indicate that the corridor should be designed according to the population's dispersal pattern. For example, many butterflies display negative exponential distributions of dispersal distances among patches or meadows (Stevens, Turlure & Baguette 2010), which leads to a leptokurtic dispersal kernel. Montane species such as the Rocky Mountain Apollo butterfly (*Parnassius smintheus*) are moving upslope due to direct warming effects and encroaching tree lines (Matter *et al.* 2011). As encroaching trees fragment networks of suitable meadow habitat, intervention may be necessary to ensure that the species tracks its habitat upslope. The species' leptokurtic dispersal kernel suggests that connections between habitats upslope is more important than connections between habitats along equal elevations (Phillips & Kot 2015). Please note that although many species of conservation interest may disperse differently depending on the geometry and composition of the corridor (see, e.g., Caswell & Neubert 2005), our model assumes passive dispersal that is identical from all source locations.

As the speed that the habitat moves (in the direction of L) increases, dispersal has an even greater effect on the best corridor design. Habitat length increases in importance for leptokurtic (Fig. 3d, red dots) and width increases in importance for platykurtic dispersers (Fig. 3d, blue dots). These patterns may be counterintuitive because the habitat moves in the direction of length, yet increasing length is not always the best choice. For species with leptokurtic dispersal, a greater length means more propagules fall within the habitat in the direction that the habitat is shifting. For species with platykurtic dispersal, there is little advantage to having a long, narrow habitat as few, if any, propagules will land at the furthest edges of the habitat and propagules falling to the side of the habitat will not persist. Increasing values of c will accentuate the problem. A wider habitat captures propagules falling along the width of the habitat along with individuals falling within the length of the shifted habitat. Increasing habitat width is a better way to assure persistence as the speed that the habitat moves increases for populations with platykurtic dispersal.

EFFECT OF LIFE HISTORY ON PERSISTENCE DURING HABITAT MOVEMENT

We can easily extend model (1) to accommodate species with distinct life-history stages. Stage-structured MHMs

$$n_{t+1}(x) = \int_{-\frac{L}{2}+ct}^{\frac{L}{2}+ct} [K(x-y) \circ A] n_t(y) \mathrm{d}y \qquad \text{eqn 2}$$

incorporate dispersal data [in matrix $\boldsymbol{K}(x-y)$] along with demographic data (e.g., stage- or age-structured life-history tables, in population projection matrix $\boldsymbol{A}$) on a moving habitat. The model explores the trade-offs in life-history parameters for persistence with increasing climate change velocity (Harsch *et al.* 2014a). We observe similar trajectories in shifts in the relative importance of growth, fecundity and stasis with increasing values of c across four plant species (*D. sylvestris*, *P. vulgaris*, *P. nigra* and *P. palustris*). Dispersal occurs in the reproduction stage for all four plants. Whether plants can use rapid adaptation to cope with climate change is uncertain (Shaw & Etterson 2012; Alberto *et al.* 2013), but the model results suggest the traits on which directional selection may occur.

Across all four species, the relative importance (elasticity) of different demographic vital rates (growth, fecundity and stasis) shifted towards lower relative importance of longevity and greater relative importance of growth and fecundity as the speed that the habitat moves increased (Fig. 4). Traits associated with longevity, such as seedbanks and delayed maturation, became less advantageous as the speed that the habitat moves increased, whereas reaching reproductive maturity quickly (growth) and reproducing (fecundity) became increasingly advantageous. This result is consistent with results from simulation models (Pearson *et al.* 2014) and empirical studies (Perry *et al.* 2005; Lenoir *et al.* 2008). Maturation age is likely a complex critical determinant in both species' sensitivity to climate change and ability to respond to changing climatic conditions. Higher speeds of habitat movement could, for example, select for earlier maturation, potentially affecting dispersal ability and reproductive rate (Perry *et al.* 2005; Gardner *et al.* 2011; Amundsen *et al.* 2012; Stevens *et al.* 2014). Whether the benefit of increased dispersal frequency outweighs the costs of earlier maturation has yet to be determined.

The consistent response across species with contrasting life-history strategies—increasing relative importance of fecundity and decreasing relative importance of longevity—also suggests the potential for strong selective pressure and rapid evolution for some species in a moving habitat (Jump & Peñuelas 2005; Bell & Collins 2008; Logan, Cox & Calsbeek 2014). Rapid evolution has been identified in fishery species in response to consistent, strong selective pressure (Mollet, Kraak & Rijnsdorp 2007; Poos, Brännström & Dieckmann 2011). In commercial fisheries, selective pressure acts on size class; during climate change, selective pressure acts on generation time (Mitchell & Maher 2006). In both cases, there is a trade-off between the cost associated with earlier reproduction (lower fecundity, less resources for offspring, greater probability of mortality) and the cost associated with waiting (decreased survival probability) (Gărdmark & Dieckmann 2006; Poos, Brännström & Dieckmann 2011). Smaller body size and shorter generation times are expected to decrease extinction risk due to climate change (Purvis *et al.* 2000; Cardillo *et al.* 2005). However, climate change is also expected to increase variability in resource availability, breeding season length and extreme weather events (IPCC 2014). Thus, although smaller body size and faster generation times may allow species to respond more rapidly to climate change, the trade-off between rapid growth and longevity (a

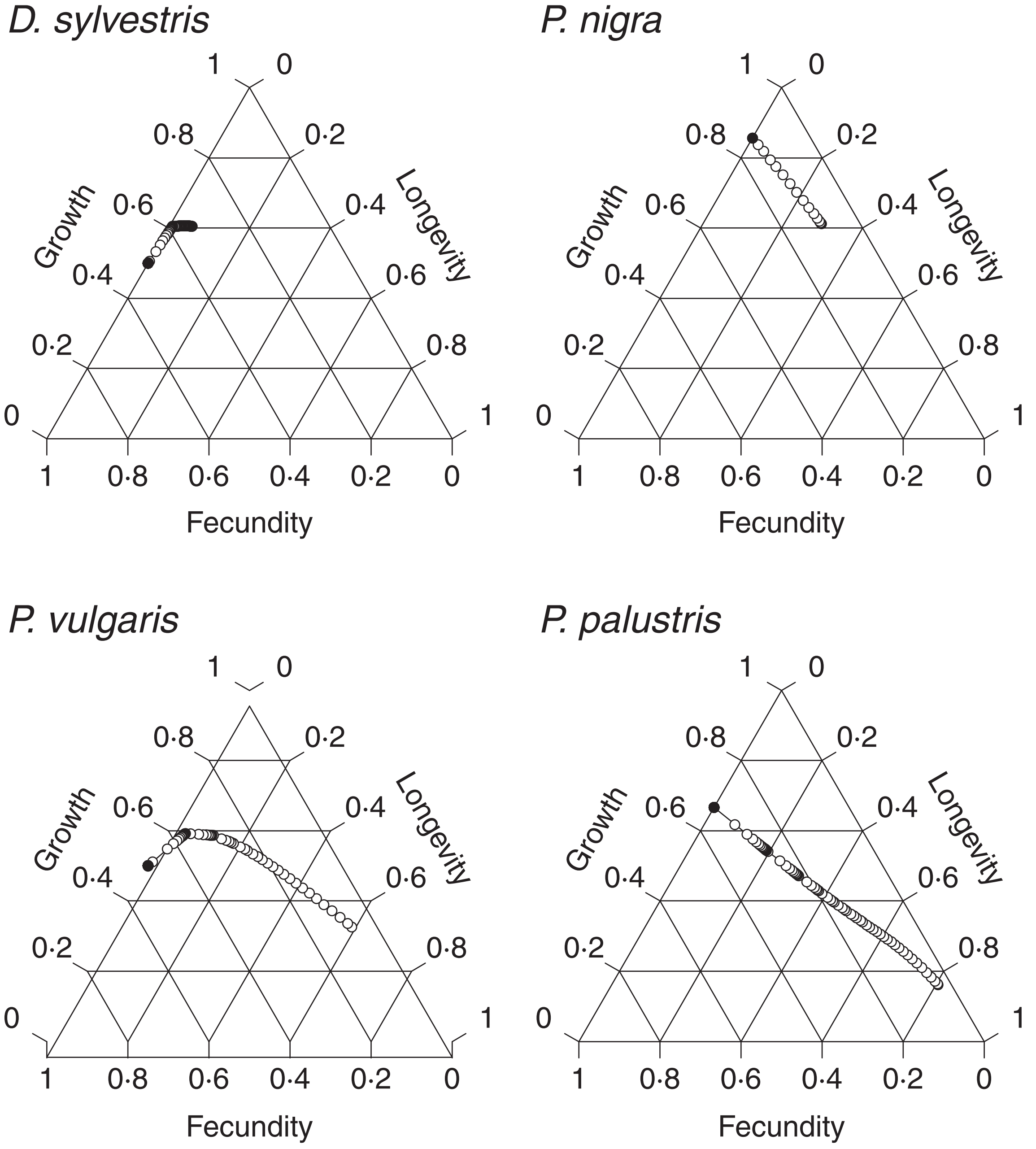

Fig. 4. Ternary plots of summed elasticities of population growth rate to changes in growth, stasis and fecundity for *Dipsacus sylvestris*, *Pinus nigra*, *Primula vulgaris* and *Pinus palustris*. The trajectory of change in the elasticity of growth, stasis and fecundity with increasing shift rate (*c/L*) follows the black line with the start point (habitat not shifting) defined by the first open circle and the end point (maximum shift rates) by the black dot. Further description of the stage-structured moving-habitat model along with parameter values, dispersal kernels and projection matrices is provided in Harsch *et al.* (2014a).

trait associated with persistence) may come at a cost under variable conditions.

Although model (2) does not address evolutionary dynamics directly, there are a number of ways for MHMs to address adaptation. One approach is to account explicitly for life-history trade-offs. Santini *et al.* (2016) used an IDE similar to model (2), along with data on trait covariances in mammals, to study spread rates in comparison to climate velocities. Applying similar analysis on a finite moving habitat would give a more accurate prediction of selective pressures under climate change. Another approach is to overlay a spatial component on a quantitative genetic model, such as that of Chevin, Lande & Mace (2010). They derived a critical rate of environmental change above which a population cannot adapt quickly enough. It would be informative to use a combined spatial–genetic model to compare their critical speed with the critical speed of habitat movement. Other possible templates for addressing adaptation with MHMs include IBMs (Schiffers *et al.* 2013), models of the evolution of dispersal kernels (Perkins *et al.* 2013) and adaptive dynamics analysis (Williams, Snyder & Levine 2016).

Extending MHMs: potential applications to global change biology

Research on the effects of climate change on organisms focuses on three broad areas: (i) individual phenological and physiological responses, (ii) population-level responses such as distribution shifts and (iii) community reorganization, including biotic interactions. MHMs have thus far focused on addressing distribution shifts in populations (Zhou & Kot 2011, 2013; Harsch *et al.* 2014a; Kot & Phillips 2015; Phillips & Kot 2015). However, the models can address other scales of biotic change. Below, we outline a non-exhaustive set of research questions related to individual, population and community responses that could be addressed using the MHM. Explorative case studies are provided for the population- and community-level responses. These case studies are accessible online as interactive web applications (Table 1). Case studies build upon the basic MHM by adding (i) Allee effects, (ii) asymmetric shift rates between upper and lower range margins, (iii) competitive and facilitative interactions between two species and (iv) infectious disease dynamics. We begin our discussion of potential applications by describing how phenological changes could be addressed using a MHM. We then highlight interesting outcomes for the Allee effect, asymmetric shift rate and biotic interaction case studies.

Phenological and physiological changes in response to climate change are measured for individuals. However, the effect of phenological and physiological changes has implications for population dynamics, community interactions and ecosystem functioning. For instance, changes in pollinator emergence time are expected to affect plant reproductive success (Thomson 2010; Thomson *et al.* 2010). Temporal mismatch in predator–prey cycles due to phenological shifts in one or more species may cascade through the trophic web, affecting ecosystem dynamics (Winder & Schindler 2004). Phenological shifts can be assessed using MHMs by considering models of the form

$$n_{t+1}(x) = \int_0^T h(y - ct)k(x, y)f[n_t(y)]\mathrm{d}y. \qquad \text{eqn 3}$$

Here, the interval [0, *T*] reflects the temporal timing of a phenological process of interest, rather than the spatial domain over which a species occurs. As with the basic model, time is discrete, but here, the phenological response has a distribution within each year. The integral is across all possible timings [0, *T*] of the phenological response. The kernel $k(x, y)$ describes the probability of a parent with phenotype y producing offspring with phenotype x. The function $h(y - ct)$ captures the shift in the optimal phenotype over time. It corrects the assumption that the growth function $f[n_t(y)]$ is constant across all phenological timings and was originally developed to take account for varying habitat suitability over space (Zhou 2013). Equation (3) resembles equations used in integral projection models (IPM). This is not a coincidence. IPMs, like IDEs, model a continuous variable (space for IDEs and demographic state such as size for IPMs) over discrete time to estimate demographic functions, such as population growth. IPMs have been considered to be analogous to IDEs (Briggs *et al.* 2010) or to be a type of IDE (Ghosh, Gelfand & Clark 2012). The key difference between the two approaches is in the form and interpretation of the kernel, as well as the interpretation of system dynamics. Of course, the two approaches can be integrated to include both continuous space and continuous demographic state (Jongejans *et al.* 2011).

For many populations, population growth rate is density dependent, which is another factor that is likely to change over time and with increasing velocities of climate change (Roques *et al.* 2008). Density dependence may be included in the growth function (e.g., Beverton–Holt and Ricker functions). For many range-expanding populations, low population density at range margins could lead to Allee effects (Garnier, Roques & Hamel 2012), whereby the population growth rate is negative due to lack of mates, insufficient group size to protect against predation, inbreeding depression or other causes. In the first interactive web application, we include Allee effects in the basic model. Exploration of the web application shows that for a population to persist, the Allee coefficient, which controls the severity of the effect, must decrease as the speed that habitat moves, due to climate change, increases (Fig. 5a). This is because fewer propagules fall within the shifted patch at each time step as the speed increases.

Additional advances in the model can be achieved by considering spatial structure. The climatic factors influencing range limits may differ between upper and lower limits (Ettinger, Ford & HilleRisLambers 2011). Thus, the velocity of climate change is unlikely to be equal between lower and upper habitat limits, resulting in either expansion or contraction of the total habitat size. The second web application explores the consequences of asymmetric (or unequal) shift rates between habitat limits. Populations tend to do better when the habitat is expanding (due to more rapid movement at the upper limit compared with lower limit) and worse when the habitat is contracting (due to more rapid movement at the lower limit compared with the upper limit) (Fig. 5b). However, when the velocity of climate change varies stochastically between time steps, population size may not change as expected based on whether the habitat size is, on average, expanding or contracting (Fig. 5b). Although such deviations are likely to be transient, a single bad year is sufficient to cause a population to go extinct.

Community-level responses to climate change, especially biotic interactions, are challenging to model. Evidence exists that biotic interactions are important in a changing climate (HilleRisLambers *et al.* 2013), yet the temporal effects of higher velocities of climate change on biotic interactions remain largely unexplored. MHMs can be extended to include multiple species to evaluate how species interactions will affect persistence in a changing climate. Possible interactions include competition, facilitation and predation, among others. The effects of competition, facilitation and predation are evident in the third web application. Depending on the type and

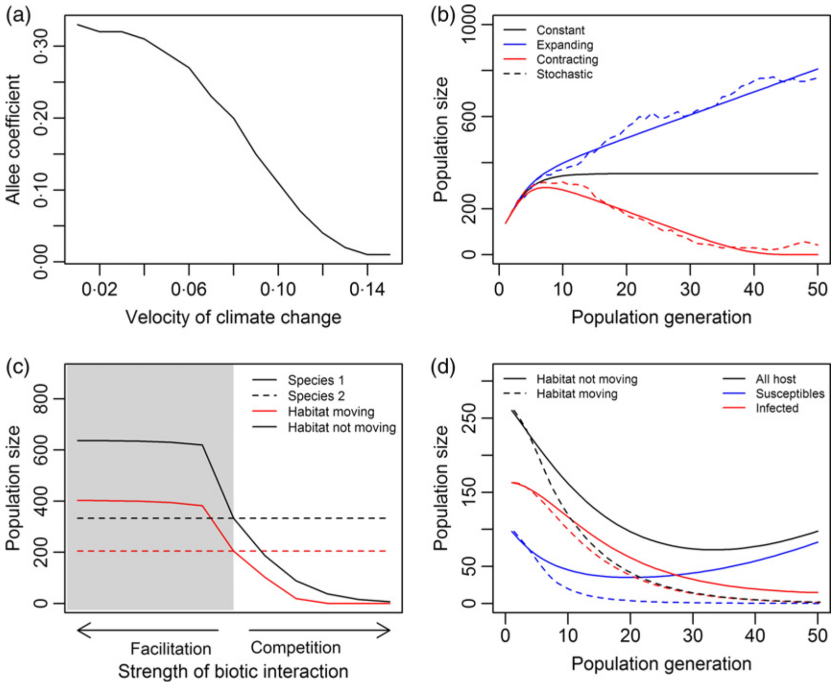

Fig. 5. (a) The maximum Allee coefficient for a given velocity of climate change resulting in a population size greater than 0 after 50 time steps. In this case study, the mean dispersal distance is slightly greater than the velocity of climate change (c + 0·8 km). (b) Effect of asymmetric shift rates on population size. Solid lines indicate results when c (0·5 in this case study) is deterministic and dashed lines when c is stochastic. Line colour indicates results when habitat size does not change (black line), is expanding (blue line) or contracting (red line). The mean dispersal distance is set to 1 km. (c) Change in total population size of a species after 50 times steps as the strength of the biotic interaction (facilitation or competition) by an interacting species increases on a stationary (black lines) and a moving habitat (red lines). In this example, species 2 (dashed lines) affects species 1 (solid lines) but species 1 has no effect on species 2. Shaded section of graph represent when species 2 facilitates species 1. We set c to 1 and the mean dispersal distance for both species to 1·5 km. (d) Change in total population size (black lines), the size of the subpopulation infected (red lines), and the size of the subpopulation susceptible but not yet infected (blue lines), both when the habitat is not moving (solid lines) and when the habitat is moving (dashed lines). We set c to 1, the mean dispersal distance to 0·75 km for the host species and 1 km for the infectious agent, a maximum reproduction rate of 20 and the population density at which half the maximum are produced at 100, a mortality of 10% for infected individuals, and a half-saturation constant of infection of 150. Initially, 60% of the host population are infected. In all case studies, the habitat length is set to 5 km, and we specify a Gaussian dispersal kernel, a carrying capacity of 100, and a net reproductive rate of 2. [Colour figure can be viewed at wileyonlinelibrary.com]

strength of biotic interactions, biotic interactions can alleviate or exacerbate the negative effects of climate change-induced moving habitats (Fig. 5c).

Moving-habitat models are sufficiently flexible to address questions about complex community structures or dynamics. For instance, how does increased competition or predation pressure following the introduction of non-native species affect persistence in a changing climate? Does the spatial ordering of species along an elevational or latitudinal gradient matter? We expect that the presence of a strong competitor or absence of a facilitator inhibits a species' ability to track its moving habitat (Gilman *et al.* 2010). Species differ in their sensitivity and ability to respond to climatic changes, potentially resulting in no-analogue communities. Under what conditions are no-analogue communities likely to form, and for how long? These questions could be explored using MHMs.

Another critical question is how climate change will affect the spread of infectious diseases (Ghini, Bettiol & Hamada 2011). The fourth web application explores how dispersal ability and infection rate affect the spread of an infectious agent and persistence of the host population within increasing velocities of climate change. This application is a simple susceptible–infectious (SI) model imposed on a moving habitat, demonstrating how climate change affects SI disease dynamics (Fig. 5d). The speed with which the habitat moves, due to climate change, cannot be ignored when considering future interactions between susceptible populations and infectious agents. In the SI MHM, susceptible densities fall more rapidly than infected densities until the entire population goes extinct (Fig. 5d). We did not consider generation times of the host and infectious agent or the possibility that the infectious agent could disperse to a new host population in this simple example. Both factors could be incorporated into a more complex MHM. In addition, the models can extend to include any number of species, interactions and trophic structures. The modelling framework presented can provide a more complete understanding of the interdependency of a community and the consequences of climate change at the community level.

In addition to the effects of competition, facilitation, predation and infection dynamics, our model can address direct anthropogenic effects such as overharvesting, habitat fragmentation and invasive-species introduction. Recently, researchers have used IDEs to develop optimal strategies for harvesting populations (Zhong & Lenhart 2012) and for controlling pest species (Lamoureaux *et al.* 2015; Martinez, Lenhart & White 2015). Applying these methods on a moving habitat would suggest how harvesting (or control) should change in light of climate change. Investigators have considered habitat fragmentation using IDEs with alternating suitable and unsuitable patches. Models of structured (Gilbert *et al.* 2014; Reimer, Bonsall & Maini 2016) and unstructured populations (Kawasaki & Shigesada 2007; Ramanantoanina & Hui 2016) have yielded conditions for successful spread. Adding habitat movement could involve overlaying a shifting suitability function (a Gaussian curve, for example) on a landscape of good and bad patches, combining the threats of habitat movement and fragmentation. IDEs have a long history of use for invasive species. Recent developments include modelling competing genotypes of pest species (Kanary *et al.* 2014) and calculating more accurate spread speeds for stage-structured invasives (Bateman *et al.* 2015). An interesting way to incorporate climate change would be to develop the IDE analogue of the RDE found in Li *et al.* (2014). Their model including only one shifting habitat edge, with the other end open to represent a population invading novel, suitable area. Such a model would be more appropriate for invasive species that are only constrained at the trailing range margin.

Conclusions

Moving-habitat models are powerful tools that can address many of the challenges associated with climate change ecology. We have discussed ways to examine (i) whether populations can keep pace with their moving habitats (eqn 1), (ii) population responses such as adaptation (eqn 2) and phenology shift (eqn 3), (iii) the effects of limited habitat size due to fragmentation or dispersal barriers (Interactions between dispersal and habitat dimensions section), (iv) differential effects of climate change on upper and lower range margins (Interactive application 3) and (v) both intra- and interspecific biotic interactions during climate change (interactive applications 2, 4 and 5). The ability to touch on multiple aspects of climate change ecology with simple modifications to model (1) makes MHMs advantageous.

The framework presented is flexible on the spectrum from theoretical to applied questions. Although model (1) is not, in general, exactly solvable, numerous methods allow for close analytical approximations (Zhou & Kot 2011, 2013; Kot & Phillips 2015). MHMs are tractable enough that general results can be obtained without always relying on intensive numerical simulation. For use in applied problems, MHMs draw on a history of quantifying dispersal kernels, growth functions and, more recently, rates of climate change. Although dispersal kernels can be difficult to estimate, the payoff is the ability to incorporate detailed information such as weather patterns, multiple dispersal vectors and dispersal initiation processes. For investigators new to IDEs, the basic model presented is easy to implement in computing environments such as R (R code available through PANGAEA at https://doi.pangaea.de/10.1594/PANGAEA.867779).

Most work to date on MHMs has been hypothesis development. Testable claims include (i) that species with rapid development will have the advantage during climate change (Harsch *et al.* 2014a), (ii) that intermediate levels of dispersal are best for species tracking their habitats (Zhou & Kot 2011), (iii) that the shape of this dispersal mediates the importance of habitat shape (Phillips & Kot 2015) and (iv) that Allee effects can negate the benefits of long-distance dispersal (interactive application 2). Linking these hypotheses with simulation and experimental approaches is an exciting prospect.

Should MHMs be used instead of other approaches, such as SDMs, RDEs or IBMs? No – the real benefit to climate change ecology comes from communication and comparison between model types. By itself, a MHM is best suited when complex or long-distance dispersal mechanisms play a key role, when discovering underlying mechanisms is desirable, and when a computationally simple approach is needed. In the context of other methods, MHMs are an excellent way to cross-validate analytical results from RDEs, test whether species can track projected habitats from SDMs and understand the mechanisms behind patterns observed in IBMs. Given the rapid and widespread effect of climate change on ecosystems, we strongly advocate using predictive quantitative models to aid management decisions. MHMs provide a way to explore potential species responses to climate change and identify testable hypotheses that will aid management in a changing world.

Authors' contribution

M.H. conceived the article. M.H., A.P., Y.Z., D.S.R. and M.-R.L. wrote the underlying code for the online simulation models. M.H. developed and deployed the online simulation models. M.H., A.P. and Y.Z. wrote the manuscript. M.K. provided significant guidance and editing of the manuscript and mathematical models. All authors contributed to manuscript development and revisions.

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Data accessibility

Data and code for Effect of life history on persistence during habitat movement section can be found at the Dryad Digital Repository https://doi.org/10.5061/dryad.mg1tb (Harsch *et al.* 2014b).

Code for the online web applications can be found at https://doi.pangaea.de/10.1594/PANGAEA.867779 (Harsch & Phillips 2016).

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