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Incorporating movement in species distribution models

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Abstract

Movement in the context of species distribution models (SDMs) generally refers to a species' ability to access suitable habitat. Movement ability can be determined by some combination of dispersal constraints or migration rates, landscape factors such as patch configuration, disturbance, and barriers, and demographic factors related to age at maturity, mortality, and fecundity. Including movement ability can result in more precise projections that help to distinguish suitable habitat that is or can be potentially occupied, from suitable habitat that is inaccessible. While most SDM studies have ignored movement or conceptualized it in overly simplistic ways (e.g. no dispersal versus unlimited dispersal), it is increasingly important to incorporate realistic information on movement ability, particularly for studies that aim to project future distributions such as climate change forecasting and invasive species applications. This progress report addresses the increasingly complex ways in which movement has been incorporated in SDM and outlines directions for further study.

Keywords
species distribution model, dispersal, migration, climate change, invasive species

I Introduction

Species distribution models (SDMs) are widely considered to be the framework de rigeur for studying the geographic distribution of plants and animals, as well as related biological phenomena such as invasion risk and vector-borne diseases, at spatial scales ranging from landscape to global. In addition to providing a robust methodology for applications aimed at quantitatively assessing the correlation between species and their environment, SDMs have also been used to examine conceptual issues related to their effective implementation, such as the effects of scale (Guisan et al., 2007; Pradervand et al., 2014), uncertainty (Beale and Lennon, 2012), and semantics (Soberón and Nakamura, 2009), among many others.

One issue of longstanding importance involves the selection of appropriate environmental factors to use in the model and, in addition to species' ecological requirements, this decision is informed by the objectives (e.g. explanation versus prediction, estimating potential versus actual distribution) and the spatial scale of the study. Soberón and Peterson (2005) introduced the "BAM" framework to illustrate the individual and joint effects of three types of factors that are

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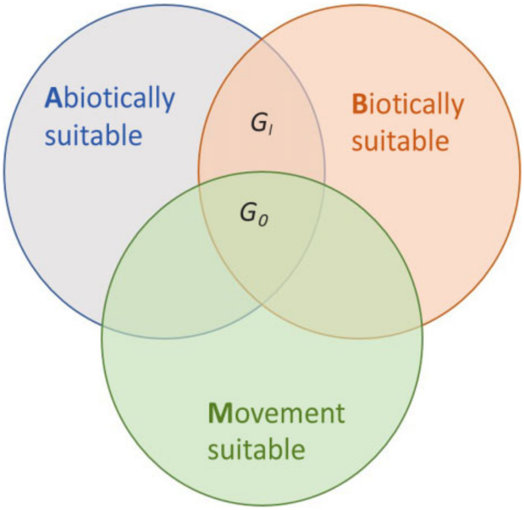

Figure 1. "BAM" diagram illustrating the three factors that determine species distributions: biotic, abiotic, and movement (modified from Soberón, 2007).

most important in determining species distributions: biotic (**B**), abiotic (**A**), and movement (**M**) (Figure 1). Biotic factors represent interactions with other species; therefore "biotic suitability" describes an area that contains either positive interactions (e.g. mutualism, facilitation) or the absence of negative interactions (e.g. competition, predation). Abiotic factors associated with physiological tolerance such as temperature and precipitation represent the area within which the intrinsic growth rate of the species is positive, and "movement suitable" refers to the area that has been or will be accessible to the species within a certain timeframe. This diagram can be used to explore conceptual issues related to species distributions: for example, the intersection of the three components (G_O) represents a species' actual distribution; G_I represents area that is suitable but currently inaccessible, and could therefore be invaded or occupied through relocation or assisted migration (see also Peterson et al., 2011; Soberón, 2007).

In spite of the relative importance of each of these factors, the majority of SDM studies have traditionally been based solely on abiotic factors. Of the three, biotic factors are the most dynamic and far more difficult to measure: species interactions can vary across time, as a function of abiotic factors, and even among different populations of the same species. Additionally, the effects of biotic interactions are often superseded by abiotic factors at spatial scales that are typical of SDM studies, although biotic factors have been incorporated successfully at macro-scales (see De Araújo et al., 2014; Heikkinen et al., 2007).

Factors related to movement and accessibility have been addressed even less frequently in SDM applications until very recently (see Franklin, 2010). Most SDM studies that include movement have used terms such as "dispersal limitations," "dispersal capacity/ability/potential," or "migration rates" somewhat interchangeably to describe a rate of spread (e.g. 50 km/century) that is either species-specific or general enough to apply across all species. Although dispersal is defined broadly as the movement of organisms away from their parent or source, its impacts can occur at the individual (survival, reproduction), population/community (composition), and species (geographic distribution/range) level (Nathan, 2001). It should be noted that the concept of "movement" used here reflects its usage in recent SDM applications and refers to the cumulative, collective movement of species or populations across a broad time scale, not to the daily movement of a single individual. While there are studies that have estimated dispersal limits based on individual-level movement (e.g. using random walk models; see Cunze et al., 2013; Hawkes, 2009), the estimated parameters are still implemented at the species level. In addition to the ability to *access* suitable environments that is represented by dispersal and migration rates, "movement suitability" can also be used to describe contingent demographic factors that can facilitate dispersal or migration, such as the distribution and configuration of suitable patches (Anderson, 2013; Fordham et al., 2013).

The BAM framework can also be used to guide data collection and model calibration. Barve et al. (2011) suggest that accessibility (**M** in Figure 1) be used to determine the appropriate spatial extent for calibrating SDMs. If data are collected throughout the geographic space that is accessible to a species, observations of absence will more likely be associated with abiotically unsuitable conditions (instead of suitable but inaccessible) – this is particularly important for applications that use presence-only data, in which pseudo-absence or background data are sampled from the remaining study area and whose environmental profiles are highly dependent on the spatial extent.

This progress report is the third in a series that focuses on recent methodological advancements in SDMs (see also Miller, 2012, 2014). Here we review the ways in which movement factors have been included in SDMs and highlight two application areas in which movement is a particularly important component: the effects of climate change on species distributions and the spread of invasive species.

II SDM applications: climate change and invasive species

Incorporating movement factors is particularly important for use in SDMs for which the main research objective is to identify changes in distributions over time, particularly in the context of climate change. Current climate conditions are changing, with some climate combinations disappearing locally and even globally and new ones emerging (“novel” or no-analogue climates). Loarie et al. (2009) derived an “index of velocity of temperature change” based on the ratio of the spatial gradient of temperature increase and the annual rate of increase in temperature, which can be interpreted as the rate of movement (e.g. for a species) in order for temperature to remain constant. They calculated a global mean of 0.42 km/yr, with velocities in tropical and subtropical coniferous forest biomes having the lowest index (0.08 km/yr) while flooded grasslands and savannas had the highest (1.26 km/yr). A recent meta-analysis using data for 23 taxonomic groups in different regions across Europe and North America found that species distributions have shifted to higher latitudes at a median rate of 16.9 km/decade and based on data for 31 taxonomic groups found that distributions shifted to higher elevations at a median rate of 11 m/decade (Chen et al., 2011).

SDMs are an important tool for exploring how changing climate conditions will affect species distributions. If the new conditions are still within the range it can tolerate, a species can persist; otherwise it will need to colonize new suitable areas that are accessible. Engler and Guisan (2009) used the terms “potentially suitable” and “potentially colonizable” to address this important distinction between all suitable areas ($G_O \cup G_I$ in Figure 1), and the subset of suitable areas that are currently accessible to the species (G_O in Figure 1), respectively.

Both climate change and invasive species studies violate one of the standard assumptions of SDM, i.e. that species are in equilibrium with the environment. However, in contrast to many climate change studies, where insufficient movement may result in projections of extinction, invasive species studies are characterized by assumptions of excessive movement and usually on much shorter time scales. Studies of invasive species distributions are further complicated by the fact that observations of “absence” are unreliable, as it is unknown whether they are associated with unsuitable areas or simply suitable areas that have not been reached yet, but see Elith et al., 2010 for a data treatment strategy that attempts to approximate an equilibrium in order to model cane toad invasion in Australia. Information on species–environment relationships is often based on characteristics of the species in its native range, while it has been observed that actual distributions can be very different in the native range compared to the introduced range (Dullinger et al., 2009). Movement can be a particularly confounding parameter to estimate, as invasive species movement can be human-assisted or facilitated by random long distance events and subsequently movement of invasive species in an SDM context focuses on post-establishment distributions.

III Dispersal limitations and migration rates

Both climate change and invasive species studies require information on future distributions and spread in order to be used effectively to inform management decisions. In its most basic implementation, incorporating movement in these applications involves refining a projected species distribution map to distinguish (abiotically and sometimes biotically) suitable and accessible locations from suitable and inaccessible where accessibility is a function of dispersal limitations or migration rates (represented as movement suitability, **M**, in Figure 1). Although they refer to slightly different processes, dispersal and migration both involve movement that has potential to lead to new gene flow and therefore are considered to be similar enough to be used interchangeably here to describe a species' ability to access or colonize new areas. While the issue of "accessibility" for a species has been addressed sporadically in SDM studies, it has been defined and implemented in different ways.

1 No dispersal and unlimited dispersal

One of the first ways in which movement was incorporated in SDM involved refining projections of suitable areas in the context of climate change based on one of two extreme scenarios: either no dispersal occurred and the projected distribution was constrained to be within the current distribution (also referred to as null migration) or dispersal was unlimited and the species could move anywhere new suitable habitat occurred (also referred to as full migration) (Araújo et al., 2006; Lawler et al., 2006; Midgley et al., 2006). The results could be interpreted as representing the range of outcomes, with no dispersal being the worst case scenario and unlimited dispersal representing the best case scenario. While the ability to represent the uncertainty associated with projections from these two extreme scenarios was an improvement over previous studies that ignored dispersal and therefore implicitly assumed it was unlimited, neither of these scenarios was realistic for most of the species to which they were applied. An assumption of no dispersal might be appropriate for species with low dispersal capacity (e.g. reptiles) or mountainous species that are unable to shift to higher elevations. No dispersal might also be applicable for a coarse-scale study where the model grid cell size far exceeds actual dispersal ability. Otherwise, projections based on no dispersal could overestimate extinction rates.

Assuming unlimited dispersal may be more appropriate for invasive species studies than climate change studies, as overestimating potentially invaded areas is less problematic than overestimating future distributions (although the management implications can be expensive and time-intensive). Unlimited dispersal may be a more realistic assumption for highly mobile species such as migratory birds as well, but they are also subject to barriers and contingent factors related to patch size and configuration. Assumptions of no dispersal or unlimited dispersal are overly simplistic and the results can be so variable that knowing the real outcome falls somewhere between the two extremes may be of limited use.

2 Parametrized constraints

Due to the wide range of results associated with no dispersal and unlimited dispersal approaches, more recent studies have begun to use empirically derived or theoretically based dispersal rates to modify projected suitability distributions. These dispersal limitations can be parametrized based on observed rates or rates estimated using paleo data, or derived from known rates for species with similar traits associated with dispersal ability (e.g. body size, habitat generalist versus specialist). Based on an extensive literature review, Vittoz and Engler (2007) developed a typology of seven different "dispersal types" that can be used to describe typical dispersal distances for plants in temperate regions. The dispersal types were classified based on similarity of dispersal agent (e.g. wind, animal), including precise information on the mechanism used in agent dispersal (e.g. for animals, whether the seeds are consumed or carried externally) and species traits that affect dispersal efficiency (e.g. height).

a Fixed rates. The simplest way to include a parametrized dispersal constraint in an SDM involves using a fixed rate of dispersal/migration, and applying the appropriate time-based distance as a buffer around the current distribution to constrain the projected distribution. To assess the invasion risk of the killer shrimp (*Dikerogammarus villosus*) in the River Great Ouse in the UK, Gallardo et al. (2012) used the mean of reported dispersal velocities (100 km/yr) of downstream spread of the killer shrimp in the Rhine River on mainland Europe, alongside a low speed (20 km /yr) and intermediate speed (60 km/yr) of dispersal which may better match the velocity of the Great Ouse. They found that while the fastest velocity predicted the greatest area of invasion risk within 5 years, the northern part of the catchment is under serious invasion risk with all 3 dispersal models. In a study investigating the effects of climate change on 336 Proteaceae species in the Cape Floristic Region of South Africa, Midgley et al. (2006) compared projections based on no migration and unlimited migration rates to two parametrized rates based on dispersal agents: wind (~4 km/yr) or ants and rodents (~1.5 km/yr). While they found that unlimited migration resulted in the most variable projections with respect to species range changes, between the two parametrized constraints, the more mobile wind-dispersed species had greater range reductions over a 50 year period, likely due to their reliance on marginally suitable habitat. They also found that modeling range change in decadal 'time slices' produced different results for year 2050 projections compared to the results from a single 50 year time step.

Hsu et al. (2012) used the maximum dispersal distance suggested in previous studies for tropical plants in East Asia, including that associated with annual typhoon events (1 km/yr), to determine the fixed migration rate of forests in Taiwan, irrespective of the dispersal agents. They also investigated the interaction between highly mobile epiphytes that depend on these forest species and found that all forest types, with the exception of broadleaf lowland forests, were projected to experience significant range contractions by 2100. Consequently, specialist epiphytes, particularly those that depended on old growth forest, were particularly at risk in the presence of climate change, in spite of their high mobility.

As empirical data on dispersal velocity are rarely directly available, other studies have used post-glacial rates of migration for similar species to derive limitations. Cole et al. (2011) used Holocene midden data to estimate a potential natural migration rate for the Joshua tree as 2 km over 60–90 years. For faster moving tree species, Iverson et al. (2011) implemented a dispersal rate of 50 km/century in their SHIFT model based on fossil pollen interpretation. However, rates that are based on post-glacial migrations may not be equivalent to current or future migration rates due to the fragmentation of the landscape by anthropogenic land use and the absence of other more frequent long-distance dispersal events, referred to as "Reid's paradox of rapid plant migrations" (Clark et al., 1998).

b Dispersal kernels. Dispersal kernels extend these fixed rates of movement by calculating the probability density function describing the number (or density) of dispersal units as a function of distance (and in some cases direction) from the source. While only recently introduced in SDM, dispersal kernels have been widely studied in population biology, starting with Skellam's (1951) diffusion model which included reproduction, dispersal distance, abundance and life history characteristics. Dispersal kernels can be differentiated by two types of models for seed dispersal: phenomenological and mechanistic (Nathan and Muller-Landau, 2000). Phenomenological models fit a mathematical function to observed (or hypothesized) data in order to describe the distribution of distances of offspring from the seed source, ignoring the roles of dispersal vectors in the process, while mechanistic models use data on factors influencing the dispersal process to parameterize the kernels, such as wind speed, diaspora terminal velocities, and movement of animal vectors (Nathan et al., 2003).

One advantage of using dispersal kernels instead of a fixed migration rate is their ability to accommodate long-distance dispersal (LDD) events. LDD events are rare and unpredictable, but they can play an important part in determining the broad-scale processes of population spread (Nathan et al., 2008). Specification of fat-tailed kernels (a kernel with a tail that drops off more slowly than that of any negative exponential kernel) has facilitated the inclusion of LDD in phenomenological kernels (Clark et al., 1998) and mechanistic models continue to gain recognition for their power to identify the vectors most likely to transport seeds over these scales of interest, such as migratory animals or those with large home ranges (Nathan et al., 2008).

Most of the SDM studies that used dispersal kernels have focused on invasive species (Ellis et al., 2010; Williams et al., 2008), although there are some examples that addressed the impact of climate change on species distributions (Conlisk et al., 2012; Nathan et al., 2011; Summers et al., 2012). Williams et al. (2008) combined an expert-based suitability index with a phenomenological dispersal kernel to predict potential locations of an invasive weed species in Victoria, Australia. They relied on previously published empirical studies of dispersal distances of their species and related species in other locations to derive a dispersal curve that showed highest likelihood of seed dispersal within 250 m of the source population but still allowed for the low probability of a rare long-distance dispersal of 5 km. They used this distance-based kernel to generate a likelihood of seed arrival, with which they combined information on wind direction in order to produce a dispersal plume of seeds. Summers et al. (2012) estimated the vulnerability to climate change for 584 plant species in Australia as a function of abiotic factors (climate, soil), four different climate change scenarios, and what they called "adaptive capacity," which was a generic Euclidean distance-based dispersal kernel for each species. A species was considered vulnerable if its projected distribution contracted or shifted and they identified higher elevation and southern latitude areas as areas containing the most vulnerable species.

In a study investigating the impact of spatial habitat configuration on the occurrence and abundance of alpine plant species in the Calcareous Alps in Austria, Dullinger et al. (2011) accounted for connectivity between patches based on parameterized multi-vector mechanistic dispersal kernels for both wind and animal vectors. Wind dispersal kernels were based on the analytical WALD model (Katul et al., 2005) which uses an inverse Gaussian probability density function of dispersal distances based on wind speed, terminal seed velocity, release height, and height of surrounding vegetation. Animal dispersal kernels were modeled by combining simulations of animal movements with estimates of seed detachment or gut survival rates. These mechanistic models were more closely related to abundance patterns than simple presence/absence, and the long-distance dispersal probabilities of the animal kernels indicated the ability of alpine plants to adapt to a rapidly warming climate may depend on these large mammals.

Likewise, single-vector models should also include mixed dispersal rates. For example, dispersal capacity based on spatial location within the entire population has been observed in plants and invertebrates, with populations in the expanding front producing more dispersive offspring (e.g. larger winged seeds) than the more established population within the range (Cwynar and MacDonald, 1987; Simmons and Thomas, 2004). Dispersal may also change with climate change. Decisions regarding when to disperse, as well as the distances covered by dispersal, are affected by abiotic factors, and any climate-change driven changes in these could affect dispersal rates (Travis et al., 2013). In a study on the meadow brown butterfly in Europe, Delattre et al. (2013) found that at lower temperatures dispersal distance was greater across a fragmented landscape, but at warmer temperatures across a continuous landscape. In a series of studies investigating the use of SDM to predict the spread of the invasive forest pathogen that causes sudden oak death (SOD) in the Western US, several different conceptualizations of dispersal constraints were combined with other abiotic, biotic, and spatial factors to increase the precision of projected spread (Václavík and Meentemeyer, 2009; Václavík et al., 2010, 2012). They calculated the "potential force of invasion" using a negative exponential dispersal kernel where the distance represents the Euclidean distance between a target cell and each potential source of invasion and does not involve species-specific dispersal characteristics (Václavík and Meentemeyer, 2009). They found that for almost all models, including dispersal constraints increased the accuracy of projected spread. In a subsequent study on early detection of SOD in Oregon, they used a similar measure of dispersal constraint, "dispersal pressure," also a function of the inverse distance between potential invasion source and a target, but modified because no true absence data were available (Václavík et al., 2010). They found that dispersal pressure was the most important variable used in the models, compared to abiotic factors (climate, topography) and host abundance and susceptibility.

In a subsequent study of SOD spread, Václavík et al. (2012) tested the importance of explicitly incorporating spatial autocorrelation in SDM and found that both spatial models used outperformed non-spatial models. Along with spatially structured environmental variables, dispersal constraints contribute to strong spatial clustering in species distributions. For invasive species whose distributions are not necessarily driven by environmental controls, or whose environmental tolerances or dispersal processes are not well known in their introduced range, incorporating fine-scale spatial autocorrelation may represent an alternative way to constrain projections, especially in the early stages of colonization.

Dispersal kernels have been successfully used to model movement in studies where the species of focus is a passive disperser (i.e. wind-blown seeds) (Boulangeat et al., 2012; Dullinger et al., 2011; Summers et al., 2012), as well as for active dispersers, such as bird species (Brotons et al., 2012; Conlisk et al., 2012). Dispersal kernels that are based on Euclidean distance ignore the important influence landscape configuration has on movement, therefore recent studies have employed landscape-based "effective" distances to model movement ability more realistically (Adriaensen et al., 2003; Ellis et al., 2010).

c Landscape-derived metrics. Landscape structure and composition can also affect dispersal ability. If two environmentally suitable areas are equidistant from a source area, but one is connected by a corridor, while the other is isolated by a barrier, a Euclidean distance-based kernel would consider them equally accessible. Effective distances are therefore used when Euclidean distance between two locations may not be the best representation of likely movement. In a study on climate change effects on the Caspian whip snake, a species with particularly low dispersal ability, Sahlean et al. (2014) calculated a "maximum dispersal range" using a cost surface based on geomorphological features, ecological conditions, and human impacts to refine projected distributions. Ellis et al. (2010) explored the importance of "potential connectivity" (the degree to which habitats are linked based on dispersal ability and landscape structures) to study the spread of sudden oak death in Northern California. They found that models that included connectivity in addition to environmental variables outperformed models based on either environmental variables or connectivity solely, and that the results were better when connectivity was modeled using a dispersal kernel based on effective distance (land-cover-based friction values) compared to Euclidean distance.

In an area containing 127 breeding ponds in Geneva, Switzerland, Ray et al. (2002) modeled the potential migration zones for two amphibian species as a function of a friction surface and maximum migration distances derived from the literature, both according to land use values. For each species, they assigned "migration costs" to land use cells surrounding the ponds based on energy expense and mortality risk and used least-cost path analysis to determine connectivity.

Much like dispersal rates, measured energy costs of landscape variables can be difficult to obtain for many species, meaning least-cost paths are either only developed for well-studied species, or parametrized by subjective expert opinions. In a recent study on modeling migration in response to climate change for 26 *Anolis* lizard species in Hispaniola, Algar et al. (2013) modeled dispersal cost surfaces for each species based on the inverse of climatic suitability for each 1 km grid cell, and a second modified surface that included cost to reach another known occurrence of the species. They incorporated the cost surface variables in an SDM, along with climate and a "morphological similarity surface" (a proxy for biotic interactions) and found that the importance of the dispersal cost variables suggested that environmental barriers had prevented species from reaching abiotically suitable areas.

d Incorporating demographic information. An even more advanced way of addressing movement in SDM involves incorporating demographic information with dispersal limitations, generally applied using cellular automaton (CA) simulation models to add a more dynamic component to the output from an SDM. CA models are matrix simulations of local (grid cell level) behavior that act according to a set of rules based on the neighborhood, cell states and time constraints (Silva et al., 2008). In addition to facilitating the incorporation of demographic information such as functional traits, reproductive potential, and species abundance, the spatially explicit and stochastic nature of CA allow for variation in values assigned to grid cells that is not possible using global parameters or landscape-based parameters.

Several software packages have been introduced that share the general goal of combining demographic and dispersal information with SDM to explore the spatial consequences of climate change. SHIFT was developed to study tree species and simulates the colonization probability of individual species propagules as a function of the surrounding cells' current abundance, habitat quality, and an inverse-power function of distance (including rare occurrence of long-distance dispersal events) at 1 km resolution (Iverson et al., 1999, 2004, 2011). Species abundance at range boundaries is weighted more heavily than abundance inside the range. Results from a study using five tree species from the Eastern U.S. showed that migration was limited for all five species and the potential effects of long-distance dispersal events were negligible (Iverson et al., 2004).

MigClim was developed by Engler and Guisan (2009) to simulate species-specific dispersal constraints that can be used in conjunction with habitat suitability information. Dispersal constraints are a function of dispersal distance and kernel (including potential long-distance dispersal events), dispersal barriers, propagule production potential since the time the cell became colonized, and habitat "invasibility" (based on suitability from SDM output and can also include biotic factors). Using inputs of the dispersal parameters and maps of initial distribution, subsequent distributions based on changing climate conditions, and permanent barriers, a CA model was used to identify future suitable habitats that are accessible. Testing a 100 year climate projection on two virtual species), they found that the potentially suitable distribution ($G_O \cup G_I$) and the potentially colonizable distribution (G_O) could differ by as much as 95% depending on the climate scenario and dispersal distances used.

Midgley et al. (2010) developed BioMove as a hybrid approach that combines population viability analysis (age-specific mortality and fecundity, age at maturity), and landscape-level processes such as dispersal, disturbance, and habitat structure, with the output from a SDM to study dynamic range simulations. The dispersal parameters used are species-specific values for mean dispersal distance and the fraction of seeds subject to long-distance dispersal events, although because the seed movement is undirected, BioMove is currently only appropriate for plant species, as animals experience directed movement. While all three of these software packages were developed for use with plant species, MigClim is general enough to be used with other taxa.

Benito et al. (2014) developed a model that incorporates a stochastic distribution of potential dispersal outcomes to study the range shifts of 176 plant species in Andalusia. They estimated an appropriate dispersal kernel for each species based on previous studies (Vittoz and Engler, 2007) or expert knowledge, but due to unreliable information they excluded the potential for long-distance dispersal events. They combined habitat suitability with simulated dispersal distance drawn from each species' dispersal kernel to generate a probability of presence, on which they used binomial trials to simulate colonization and local extinction for two different climate warming scenarios. They found that while simulations using dispersal showed a slight decrease in the percentage of species that were projected to become extinct compared to simulations with no dispersal, simulations that included dispersal were much more effective at preventing critical range contraction for most species.

Integrodifferential-equation models (IDEs) are increasingly being used to study the spread of invasive species. IDEs consider a change in population density as a result of two processes: population growth and dispersal. Growth occurs during a sedentary stage, modeled in the simplest form using a nonlinear map such as the compensatory model and in the second stage, progeny disperse based on the probability density function obtain from a dispersal kernel (Neubert et al., 2000). Population growth then occurs in the next time step on the re-dispersed individuals, and the process continues. The combination of these two equations allows population spread to be calculated by modeling the dispersal of individuals, and then relating the results to the population.

IV Conclusion

Movement is an important factor that determines the distribution of a species by distinguishing between suitable environmental conditions that are accessible and those that are not. Although there are some SDM research objectives that obviate the incorporation of movement, such as projecting new suitable habitat for assisted migration or generating a "worst case scenario" of the spread of an invasive species or vector-borne disease, the goal of most SDM studies is to produce a precise and accurate estimate of species distribution. While progress has been made in SDM studies that incorporate movement, in the span of a decade studies have gone from ignoring movement to acknowledging two extreme movement scenarios (no dispersal compared to unlimited dispersal) to developing sophisticated dynamic hybrid models that include demographic information with dispersal. Despite this progress, there are still many questions left to address.

We conclude this progress report with some recommendations and "best practices" that have emerged from the papers discussed above:

- More realistically defined dispersal constraints are obviously preferable, but when the appropriate data are unavailable (or the computational time is excessive), estimates based on similar species, similar dispersal agents, or similar morphometry should be used instead. Failing that, spatial autocorrelation can be used as a proxy for some of these factors, especially for invasive species whose dispersal behavior may be less predictable.
- Selection of dispersal type should be informed by, among other things, the study objective (climate change, invasive species), the time frame, the types of habitat in the study area, and the type of taxa studied.
- The application of the rate of movement over time should be better studied. As movement is a function of both dispersal/rate and suitable environmental conditions that change over time, there will be differences in projections based on a single time step compared to several individual time steps. Midgley et al. (2006) reported differences in projected distributions for a single 50 year time step compared to that produced using five decadal time slices. Time steps for invasive species studies are generally much shorter and the effect of varying time steps should also be investigated in more detail.
- Contingent demographic factors related to suitable habitat patch size and configuration are also an important component of movement, but their role in dispersal/migration over broad time frames has been less studied.
- More studies that compare different dispersal rates applied to the same data should be conducted in order to better understand the uncertainty associated with different dispersal/migration assumptions. In particular, more studies that incorporate a mechanism to assess the performance of different dispersal rates and/or functions (e.g., using past data to project to present) are needed.

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