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1 Introduction

2 Movement is a ubiquitous ecological process that operates across many spatial and temporal scales and
3 influences most facets of organism life. ; however, 'movement' has only recently been incorporated in
4 species distribution models (SDMs). SDMs provide a powerful spatial ecological framework for studying
5 the geographic distribution of a wide range of organisms and are frequently used to address questions
6 pertaining to ecological processes involving climate change, invasion risk and biogeographic hypotheses
7 (Franklin 2009; Peterson *et al.* 2011). For SDMs that include movement, it has predominantly been
8 conceptualized as (temporally and spatially) broad-scale processes like dispersal or migration (Franklin
9 2010; Bateman *et al.* 2013; Miller and Holloway 2015), based on population-level models of movement
10 (e.g. distance or kernel-based rates of movement), or as a measure of accessibility with which to select
11 the appropriate spatial extent for model calibration, validation, and comparison (Barve *et al.* 2011; Saupe
12 *et al.* 2012; Qiao *et al.* 2015).

13 Movement patterns and processes vary substantially across taxa, landscapes and individuals,
14 consequently, developing a generalized framework for incorporation has been difficult. Moreover, as
15 movement occurs across such a broad range of spatiotemporal scales, its conceptualization should not be
16 restricted to the aforementioned narrow and specific movement processes. In spite of the ecological
17 significance, the incorporation of movement has lagged behind other methodological advancements. By
18 not implementing measures of movement within SDM, projections of species distributions ignore one of
19 the most important ecological processes that cause patterns of current and future geographic ranges of
20 species. The incorporation of movement in SDMs should provide not only more accurate representations
21 of the distribution of a species, but also an increased understanding for ecological processes that relate
22 to habitat characteristics (e.g. climatic preferences), functional traits (e.g. behavior, physiology), and
23 fitness components (e.g. survival, growth). The aim of this review is to provide a quantitative synthesis in
24 order to recognize how movement has been incorporated in SDM to date, identify the under-studied
25 components of incorporating movement, and outline emerging trends in this burgeoning research
26 frontier.

27 Meta-Analysis of Movement in SDM

28 The ISI Web of Knowledge (<http://apps.webofknowledge.com/>) was used to conduct a comprehensive
29 search for journal articles that satisfied a query of both SDM and 'movement' as words in the article topic.
30 While the current terminology used to refer to correlative species-environment models is converging on
31 'species distribution models', they have previously been referred to as 'predictive vegetation models'
32 (Franklin, 1995), 'niche models' (Peterson *et al.* 2007) and 'predictive habitat distribution models' (Guisan
33 and Zimmermann, 2000). While conceptual differences between terms do exist (e.g. modelling the actual
34 versus potential distribution - Peterson *et al.* 2011), in order to correctly identify any article which could
35 be considered under the SDM framework, all four terms were used within the search and for the purposes
36 of this review can be considered synonymous. A variety of terms associated with organism movement
37 were identified by Holyoak *et al.* (2008) in their quantitative study in a special issue of the *Proceedings of*
38 *the National Academy of Science* introducing movement ecology. They identified 15 general movement
39 terms from the literature, with four key terms used in 98% of the studies surveyed; movement, migration,

dispersal and gene flow. The four SDM terms and 15 movement terms identified by Holyoak *et al.* (2008) were used as search parameters, and while these parameters are relatively broad, we felt this was necessary in order to complete a comprehensive review. An article was deemed relevant if it referred to the movement of whole genes, progeny, organisms, populations, or species (Supplementary Information 1). The search was conducted so that every journal article published up to and including December 31st 2015 is included, with the search considered complete as of March 9th 2016.

The last decade has seen a surge in the incorporation of movement within SDM, with between 20-25% of all SDM studies (n.b. total number of SDM studies was calculated using the total articles returned from the four SDM terms, controlled for by the overlap observed in articles from the SDM and movement searches) published since 2010 implementing a method of movement within the analysis, or discussing but not implementing movement (Figure 1). In total, 595 relevant articles were identified across 180 journals, illustrating just how inter-disciplinary SDM has become. We distinguished between articles that explicitly implemented movement, compared to those that only discussed movement, and it can be seen that the proportion of studies explicitly accounting for movement has increased in recent years (Figure 1). When movement was only discussed in the article, discussion ranged from explicitly stating that dispersal was not incorporated in the study but an acknowledgement was made asserting that this likely increased uncertainty in projections (e.g. Garner *et al.* 2015), to studies that highlighted the importance of SDMs for plant migration, but made no further mention of movement factors or processes (e.g. Meineri *et al.* 2012).

Movement Terminology

SDMs are used across a number of disciplines, so it is therefore vital that if movement is to be successfully incorporated into SDMs, then one must be clear in the definitions and terms used. When concepts are not well defined, it distorts communication with scientists across (and beyond) the discipline, alienates the public through ambiguous, imprecise and unstandardized answers, and it distracts from the primary aims of the research (Hall *et al.* 1997). SDM researchers addressing questions related to range shifts in response to the changing climate or to track the spread of invasive species have used terms such as 'dispersal limitations', 'dispersal capacities', 'migration rates', and 'spread rates' interchangeably to refer to the cumulative movement of a species or a population across a broad time scale and often across multiple generations (Miller and Holloway 2015). Definitions of movement behaviors are still strongly debated throughout the ecological disciplines (Dingle and Drake 2007), with terms such as 'migration' or 'dispersal' causing highly emotive responses across both the scientific and public realms (Milner-Gulland *et al.* 2011). As such, it is not the purpose of this article to re-visit the debate surrounding movement definitions, but rather to provide a discussion on how movement concepts have been used in SDM, and illustrate the need for clear and concise definitions without the assumption of consensus.

Dispersal (48.15%) was the predominant term used to describe movement when studies across all taxa and spatiotemporal scales were considered, followed by migration (12.58%), and then movement (8.40%), with a total of 32 general terms used to describe organism movement (Supplementary Information 1). Only a handful of studies actually defined the terms they used. For example, Pittiglio *et al.* (2012) used the term transit corridor to refer to the seasonal movement of elephants in Tanzania, while Ai *et al.* (2012) defined dispersal limitation as spatially limited dispersal in local communities. Only 46 studies (7.73%)

used a single movement term throughout the entirety of their paper. Some repetition in movement terms may have occurred due to researchers citing work which used a different term or referred to a different movement pattern; however, most of the repetition occurred due to researchers using multiple terms to refer to the same movement behavior. Moreover, in 37 (6.22%) studies we could not distinguish the predominant movement term used.

Dispersal and migration were often used interchangeably to refer to the same movement behavior, in particular movement in response to changing climates. Table 1 highlights the number of times migration or dispersal was recorded as the general term used to refer to movement in response to climate change or finer-scale daily or seasonal movements. Unsurprisingly, dispersal was the predominant term used for both movement patterns (as it was also the predominant term across all movement patterns), but it was used twice as much to describe tracking of the changing environment. The use of migration to describe the tracking of the changing environment is perhaps the most contradictory to the general consensus of what constitutes migration (e.g. the movement between two habitats on a predictable basis - Hansson and Åkesson 2014). Movement in response to climate change does not represent regular trips, and with the overwhelming use of dispersal to describe this movement pattern, migration should perhaps not be used in this context. However, the use of dispersal in the context of climate change is also slightly ambiguous with colonization. When movement over multiple generations is simulated (e.g. in response to climate change), an assumption of success at each stage of dispersal is inherently assumed in the dispersal models. Researchers need to emphasize any ambiguous definitions when modelling movement in an SDM context. Clarification of the movement patterns being simulated will only become more pertinent as methods continue to advance and the inclusion of multiple movement processes in models becomes a regular occurrence.

What is Moving?

Species Groups

SDM studies addressing movement did so for a number of different organisms, ranging from amoebas (Aguilar and Lado 2012; Aguilar *et al.* 2014) to elephants (Richmond *et al.* 2010; Pittiglio *et al.* 2012). However, the majority of studies which addressed movement did so for plant taxa (Figure 2). These outnumbered all other taxon groups across all SDM applications with the exception of projecting the current distribution (for which the majority of the movement patterns studied resulted from processes such as foraging). While initially surprising that plants were recorded undertaking 'regular movements', communities of plants undergo regular turnover, and this is an important determinant in the maintenance of a species distribution. Many bird species epitomize animal movement, and it is therefore perhaps less surprising that these species constitute the second most studied group, recording equal coverage between applications of movement (with the exception of invasive spread). Plants and birds are the most studied species groups on the planet (Lomolino *et al.* 2006), with bird atlases collected with regularity since the 1960s (Sharrock 1976), and a disproportionately high number of available telemetry datasets for birds on data repositories such as Movebank (<https://www.movebank.org/>). These datasets will provide researchers with the most comprehensive data to evaluate the different movement models implemented by SDM researchers and will allow more rigorous testing and evaluation of movement models.

Of greater ecological concern are the under-studied species. Arthropods (insects, arachnids, crustaceans) constitute over half of the species recorded on the planet, but are relatively understudied compared to plants. This trend is not unique to SDM studies, with the paucity of entomologists in relation to other taxon specialists well documented (Lomolino *et al.* 2006). Arthropod species can undertake vast migration excursions (e.g. monarch butterflies), and therefore should be more readily studied. Moreover, in recent years, amphibians have suffered global and substantial losses (Pounds 2001; Alford *et al.* 2007; Blaustein *et al.* 2011). Subsequently, there is a pressing need to study these species in response to global change; however, only six studies investigated the impact of global change on amphibians and incorporated a measure of dispersal alongside this. While amphibians are considered relatively poor dispersers, they have been recorded undertaking relatively long migrations between breeding and hunting locations (e.g. 3 km Ray *et al.* 2002), meaning that future projections of these species should incorporate a measure of dispersal.

Individuals, Populations, or Species

As noted by Levin (1992), patterns at one level of organization can often be understood as the collective behavior of aggregates of smaller units. This is pertinent when studying species distributions, and while the focus of SDMs are often aimed towards population or species-level patterns, various levels of organization were recorded in the meta-analysis (Figure 3). Questions related to dispersal and colonization are population-level processes; however, many of the factors responsible for animal movement operate on an individual scale (Jönsson *et al.* 2016). The differences between Eulerian (population) and Lagrangian (individual) approaches to movement are important to consider here, particularly as methods to model movement in SDM are increasing in complexity. Both approaches deal with population-level movement, but one can be considered a top-down method while the other is bottom-up. The Lagrangian approach involves discrete steps and segments and is useful for tracking detailed movements of individuals, while the Eulerian approach describes the expected pattern of space use by an individual or population (Smouse *et al.* 2010). Movements of individuals contain the most detail concerning movement and environmental interactions, but emergent population- or species-level patterns are the focus of SDM. Subsequently, Lagrangian approaches to modelling movement have lagged, despite support for such approaches by ecologists and modelers alike (Tang and Bennett 2010).

Recent developments in the fields of movement ecology and computational movement analysis are beginning to address this long-standing issue. The potential of individual-based models to simulate the inherent relationship between movement and the environment while aggregating individual movement to the population level has seen an increase in the use of spatial simulation models to understand animal movement, and are subsequently beginning to be observed within the SDM framework (Martinez *et al.* 2012; Adams *et al.* 2015). For example, Martinez *et al.* (2012) used a parameterized individual-based model which incorporated competition, facilitation and dispersal limitations to estimate a realistic rate of tree line 'migration' (or dispersal as defined in this review) under climate change in the Pyrenees. Similarly, Adams *et al.* (2015) used an individual-based cellular automata model based on dispersal constraints to model invasive spread of a non-native weed in Australia over a period of five to ten years. While the potential to estimate population level redistributions of species using individual-based models within SDM is promising, currently only one study has addressed this beyond plants (Zurrell *et al.* 2012). Furthermore,

all of these studies used a gridded representation of an individual, meaning explicit idiosyncratic movement patterns are amalgamated to a grid and subsequently lost. These methods begin to bridge the gap between population and individual movements; however, these models could be argued to be grid-based population models. Furthermore, discretizing movement into a gridded structure can result in an over-estimation of movement distances (Chipperfield *et al.* 2011), meaning research needs to be directed towards addressing these methodological artefacts. The uptake of Lagrangian movement paths within SDM therefore remains a challenging but potentially rewarding research frontier.

The 'BAM' Framework

To illustrate the individual and joint effects of three factors deemed most important in determining species distributions, Soberón and Peterson (2005) developed the heuristic 'BAM' framework (Figure 4a). In this framework, biotic factors (**B**) represent interactions with other species (i.e. competition, predation), abiotic factors (**A**) represent the physiological tolerances of a species (i.e. temperature, precipitation) and movement factors (**M**) refer to the area that has been or will be accessible to a species within a certain timeframe (i.e. dispersal, connectivity). The intersection of suitable biotic and abiotic factors beyond movement factors represent the invadable distribution (G_i), or where a species could survive if such areas were accessible. This area can be considered analogous with the species potential distribution. The occupied distribution (G_o) represents the intersection of suitable biotic, abiotic, and movement factors, or where species are actually found. This area is often considered synonymous to the species actual distribution. Central to this framework is **M**, as the inclusion of movement allows the species range to be considered a dynamic entity, as it is the inaccessibility to G_i that is preventing an area from being occupied. The importance of abiotic and biotic factors is well established in SDM applications, while the incorporation of movement has lagged. The incorporation of **M** has generally been considered useful for predicting G_o , the actual distribution of species, but less so when G_i or the potential distribution is sought. Despite this, there is substantial overlap in the theories and methodologies implemented by researchers predicting both G_i and G_o , and furthermore many of the assumptions within modelling the potential distribution could be improved alongside a measure of movement.

Recently, Barve *et al.* (2011) identified three implications of **M** within SDM: model calibration, validation, and comparison. The choice of geographic extent has been found to significantly alter the projected environmental drivers during SDM calibration (VanDerWal *et al.* 2009). If the geographic extent used in an SDM is beyond the dispersal capacity of the species, then the model will project the species to be absent due to the abiotic or biotic conditions, when in fact it is absent due to factors related to **M** (Barve *et al.* 2011). Such models would under-predict the species potential distribution under changing climates and possibly lead to incorrect extinction predictions. Similarly, the use of absence or pseudo-absence test data beyond the dispersal capacity of a species will improve the accuracy of the projection in model evaluation and validation. Areas beyond the dispersal capacity are projected as having a low habitat suitability due to the lack of presence observations rather than unsuitable abiotic and biotic conditions (Barve *et al.* 2011). These assumptions can inflate accuracy metrics, identify incorrect or spuriously correlated environmental drivers, and undermine the robustness of SDM results. Finally, comparisons of niche similarity are an important application for many studies investigating biogeographic hypotheses (Warren *et al.* 2008). These comparisons require an estimate of background area, which should be

considered the equivalent of **M**, meaning the aforementioned issues associated with model calibration and validation could cause insufficient representation of movement and significant repercussions on model inference.

Various 'BAM' scenarios exist, with different assumptions of **B**, **A**, and **M** strongly influencing all phases of model configuration (Figure 4). For example, Saupe *et al.* (2012) used virtual species to explore the implications of different BAM scenarios, explicitly pertaining to **A** and **M**. They found that models that assumed total accessibility and abiotic suitability (Figure 4c) failed to perform better than random expectations. They cited this example as being similar to island species, whose distribution is most likely the result of dispersal limitations (**M**) rather than abiotic conditions (**A**). Similarly, **M** can be thought of in terms of invasive species (Figure 4d), which cannot disperse to suitable abiotic and biotic habitats under their own ability. Figure 4d would also represent a scenario where favorable abiotic and biotic conditions have shifted under climate change, but the species lacks the dispersal capacity required to keep track, which would result in a species going extinct. These conceptualizations of **M** within the BAM framework have led to an increased understanding of model interpretation (Barve *et al.* 2011; Saupe *et al.* 2012; Qiao *et al.* 2015), with a number of studies explicitly acknowledging **M** when defining modelling extent, pseudo-absence selection or model validation (Belaire *et al.* 2014; Escobar *et al.* 2014; Strubbe *et al.* 2015; McQuillan and Rice 2015; Mateo *et al.* 2015; Bradley *et al.* 2015).

A criticism of BAM is that it fails to regularly account for the dynamic nature of the three factors, and in particular it could benefit from a representation of time. This is eluded to in Figure 4d, where time is an important construct of shifting both **A** and **B** beyond locations deemed accessible to the species, but it cannot be depicted in this static representation. Another example is the fact that **B** and **M** are inherently linked. When organisms traverse through a landscape, biotic resources can be depleted while the individual is in the area (e.g. herbivory) and replenish while the individual is absent. For example, the reintroduction of wolves to Yellowstone National Park in the mid-1990s changed elk movement patterns and dramatically transformed the distribution of biotic resources in a short space of time (Turner *et al.* 2001). While **M** has been used to describe contingent demographic factors that can facilitate dispersal or migration, such as the distribution and configuration of suitable patches required to maintain populations (Anderson, 2013; Fordham *et al.*, 2013), these landscape constructs such as fragmentation, connectivity, and species-area relationships are still represented as static entities. Subsequently, the BAM framework currently lacks the detail required to incorporate these dynamic relationships and this singular or static representation of **M** will therefore have to be revisited as increasingly complex representations of movement processes are incorporated more readily within SDM.

Applications of Movement in SDM

As stated, applications of movement in SDM have consisted of either coupling the statistical model of abiotic and biotic suitability with a measure of dispersal in response to climate change or invasive spread, or as a measure of accessibility with which to select the appropriate spatial extent for model calibration, validation, and comparison. However, movement occurs across a broad range of spatiotemporal scales and as such should not be restricted to these narrow and specific movement behaviors. Following this meta-analysis, Figure 5 was developed as a conceptual diagram illustrating the patterns of movement that

were identified as having been studied within SDM, and the following sub-sections will discuss how these patterns of movement have been implemented, and identify the conceptual and methodological issues associated with them.

Tracking Changing Environmental Conditions

Incorporating movement factors is particularly pertinent for SDMs for which the main focus is to identify changes in distributions over broad time-scales. Climate conditions and land cover are changing, and SDMs are an important tool for exploring how these changes will affect species distributions. If the new abiotic and biotic conditions are still within the range the species can tolerate, it can persist; otherwise it will need to colonize new suitable areas. Most applications involve refining a projected species distribution map to distinguish (abiotically and biotically) suitable and accessible habitat from suitable and inaccessible habitat, with accessibility measured as a function of dispersal (Miller and Holloway 2015). However, when dispersal has been implemented in SDM research, it has often taken one of two extreme approaches: either unlimited or no dispersal (e.g. Araújo *et al.* 2006; Lawler *et al.* 2006; Araújo and Luoto 2007). Unlimited dispersal assumes that there are no barriers to movement and that distance is not a limiting factor, implying that any suitable habitat which is present in the study area can become occupied. Conversely, no dispersal assumes the opposite, with dispersal not possible, and the future suitable habitat is restricted to locations that overlap with the original distribution.

The use of both unlimited dispersal and no dispersal ('all or nothing') was recorded in a quarter of the studies investigating distribution shifts under climate change. While these two approaches overly simplify movement, using both together is an improvement on studies that overlooked dispersal (and thus implicitly assumed unlimited dispersal). Furthermore, due to their extreme variation, these implementations of dispersal can be used to represent the uncertainty associated with the effects of climate change, as the actual dispersal capacity will most likely be found somewhere in the middle of those two predictions. A number of methods have begun to emerge in the literature, ranging from a fixed rate of dispersal applied as a time based distance buffer (Hsu *et al.* 2012; Gallardo *et al.* 2012; Jaeschke *et al.* 2013), to complex probabilistic dispersal kernels (Summers *et al.* 2012; Alagador *et al.* 2014; Bush *et al.* 2014). A summary of these dispersal models is provided by Miller and Holloway (2015) in a recent review on the subject; however, these methods used to simulate dispersal vary greatly in terms of implementation. Recently, Holloway *et al.* (2016) compared the accuracy and uncertainty of 20 dispersal models for future projections (1990 to 2010) of breeding British birds. They found that the choice of dispersal model and how it is implemented could significantly influence the results both in terms of accuracy and the area predicted as present. The choice of dispersal model undoubtedly introduces uncertainty into projections, and while a handful of studies have compared the results (Engler and Guisan, 2009; Cunze *et al.* 2013; Holloway *et al.* 2016) more extensive testing across different taxa and spatial scales is needed.

Moreover, when extrapolating species-environment relationships across time, there is also the assumption that the biotic and abiotic factors will remain constant for every intermediate time period. While a postulate of equilibrium is necessary for projecting the model in space and time (Guisan and Thuiller 2005), for long time periods (e.g. 100 years) it is highly unlikely that the biotic and abiotic factors

will remain the same. Dispersal is commonly simulated as a one-step process (e.g., from the current period $[t_1]$ to the future period $[t_2]$); however, it could be simulated as a multiple-step process (e.g., from the current period $[t_1]$ to a number of chronological intermediate periods $[t_{1a}, t_{1b}, t_{1c}]$ to the future period $[t_2]$) (Midgely *et al.* 2006), accounting for some of the inherent uncertainty related to the assumption of homogeneity of abiotic and biotic factors. For models simulating dispersal as a multiple step process, at each intermediate time-step the dispersal model is coupled with a corresponding statistical model of abiotic and biotic suitability. The next dispersal event then originates from the area predicted present based on suitability and accessibility for this time period. If the abiotic and biotic conditions alter significantly, then the number of steps used to model dispersal could greatly influence the projected distributions. For example, in a study investigating the effects of climate change on 336 Proteaceae species in South Africa, Midgely *et al.* (2006) found that the resulting ranges of species in 2050 were larger by approximately 10% when dispersal was simulated as a single 50-year time-step compared to when dispersal was simulated in decadal time-steps. Due to these vast differences in areal extent of future projections of geographic ranges, the uncertainty arising from modelling future distributions in multiple time-steps needs to be explored further.

Invasive Spread

Invasive species are often characterized by excessive movements within relatively short time periods, and this movement can be a particularly confounding parameter to estimate, as species movement can be human-assisted or facilitated by long distance dispersal events. This has meant that movement of invasive spread in an SDM context has focused on post-establishment distributions (Miller and Holloway 2015). This is illustrated in Figure 5 as this movement pattern is depicted as expanding from a single point in space and time (e.g. the location of release or escape). Methods for incorporating post-establishment spread of invasive species in SDM studies are broadly similar to those used to investigate the impacts of climate change on distributions, meaning the research challenges and frontiers are mostly similar.

However, if dispersal processes are not well known, incorporating fine-scale spatial autocorrelation (see Miller 2012 for a discussion in SDM) may represent an alternative way to constrain predictions, especially in the early stages of colonization. For example, Václavík *et al.* (2012) used autocovariate logistic regression and spatial eigenvector modelling to incorporate spatial information into the model outputs in order to constrain projections of Sudden Oak Death in California, and found that these proxies for dispersal better predicted the presence of the pathogen compared to models calibrated only on abiotic factors. Invasive organism distributions are often driven by factors beyond environmental controls, and so a direct set of abiotic and biotic predictors may not be plausible. Indirect gradients and surrogate factors therefore remain important, and studies that have used dispersal kernels (Meentemeyer *et al.*, 2008; Ellis *et al.* 2010) or simple distance metrics (Václavík *et al.* 2010) have found that dispersal pressure was a better indicator of invasive distributions than abiotic and biotic factors alone.

Disease Spread

Infectious diseases can present a serious threat to both wildlife and humans, and subsequently an increasingly utilized application area of SDMs in recent years has been in understanding and predicting the geography of vector-borne diseases (González *et al.* 2010; Signorini *et al.* 2014; Campbell *et al.* 2015). Again, the challenges of modelling the spread of diseases within an SDM context have a number of analogs

with modeling invasive spread. However, modelling infectious diseases that subsequently impact humans is a unique challenge due to the movement capacity of people as disease vectors. Gardner *et al.* (2012) addressed this by coupling risk analysis and infection data alongside suitable climatic factors for dengue fever. By incorporating infection data, estimations for 'at risk' airports and travel routes could be made, identifying specific 'high risk' airports, and in turn allowing more effective surveillance of these diseases (Gardner and Sarkar 2013; 2015). The use of network models alongside SDM could allow for research to address not only disease spread through human vectors but also inform on pre-establishment human-facilitated movements for invasive species.

Seasonal Movement

For species that move, some parts of their geographic range may temporally experience abiotic and biotic conditions beyond the tolerance of the organism. As a result, species may migrate seasonally to track the changing resources (e.g. wildebeest migrations in Africa to track seasonal rainfall patterns). However, the movement activities associated with seasonal migration may exist 'outside' what would constitute a species distribution. For example, the large swath of the Atlantic Ocean between Greenland and mainland Europe over which barnacle geese migrate is not suitable habitat. While abiotic (e.g. wind speed, direction) and biotic (e.g. increased predation) factors play important roles in determining the success of these specific migration events, there is little overlap with the movement factors as established in the 'BAM' framework. Subsequently, the need to incorporate a dynamic temporal dimension within such models, as well as the 'BAM' framework, persists.

A simple delineation of summer and winter habitats is a common method used to account for these migrations (e.g. Martin *et al.* 2011), and begins to address the dynamic nature of a species distribution. A key issue associated with seasonal migrations in SDM is the observation of a species during the migration, which is subsequently in climatic conditions beyond the species tolerance. The example provided for the barnacle geese was extreme, but for many migrating species the differences in abiotic and biotic conditions across the migration corridor will be less obvious. The use of these 'migration sightings' in any statistical model assumes that this species can survive in these conditions on a permanent basis, and the resultant projection will most likely over-predict the distribution (Sinclair *et al.* 2010).

Projecting habitat suitability along a migration corridor could address some of the issues associated with the temporal variability in predicting the distribution of migrating species distributions. For example, Hefley *et al.* (2015) projected the abiotic and biotic conditions for stopover habitat along the migration path of the whooping crane in Nebraska, USA, and identified areas that could support high densities of individuals during migration. This study does well to address variables along a migration pathway; however, the need to explicitly address the suitability of migration zones persists, and should be a key focus of researchers working with migratory species.

The use of temporally explicit variables removes some of the uncertainty in the seasonal distributions of species (Gscwheng *et al.* 2012; O'Connor *et al.* 2012). For example, O'Connor *et al.* (2012) incorporated Julian day in their generation of an SDM projecting the fall distribution of American shad and striped bass in the Hudson River Estuary, and found that it was the most important determinant of fish presence. Similarly, Gscwheng *et al.* (2012) matched telemetry data with abiotic conditions obtained at a monthly

temporal period, and projected monthly distribution models of the Eleonora's falcon in Madagascar. These methods begin to identify that resource use for mobile animals is not uniform in space or time, although projections are still representative of a static species-environment relationship, albeit at a finer temporal resolution.

Regular Movements

Regular movements maintain the distribution of a population or species, and include behaviors such as foraging (searching for food), homing (returning to home), bounding (marking home range limits), and biotic interactions (e.g., movement in response to predation) (Figure 5). These movements were distinguished as different from seasonal migration, as all of these movement behaviors also occur within the seasonal distribution of a species (e.g. foraging occurs in both breeding and wintering habitats). Explicit information of movement activity in locality data is rare, and while some studies have generated projections of suitable habitat for different activities such as nesting and foraging (Smart *et al.* 2012; Brambilla and Saporetto 2014; D'Elia *et al.* 2015), most presence data is absent of 'animal activity'. This means most projections of a species distribution inherently assume that the habitat is suitable for a multitude of activities (e.g. foraging, nesting, etc.) which are representative of the regular movements of species. The application of activity to animal observations is routinely undertaken in animal behavior studies, identifying areas where inter-disciplinary research could bridge the gap needed within the SDM discipline.

Mobile species utilize several patches of suitable habitat within their home range, meaning species observations may be recorded in an environment which is unsuitable for them on a permanent basis. Due to the fragmentation of suitable habitat, animals often have to traverse through an inhospitable matrix (e.g. forests separated by an open meadow or urban area). Subsequently the aforementioned issue relating to using sightings of presence in unsuitable habitat in model calibration persists. However, as regular movements occur at a finer spatiotemporal scale, this issue could be controlled for by observing the environmental variables at a neighborhood scale (Ashcroft and Major 2013). Subsequently, for many mobile animals, the use of a focal statistic summarizing the abiotic and biotic conditions within a specified neighborhood may better represent what is available to it within its home range. For example, black grouse utilize a mixture of moorland (for mating) and woodland (for shelter) habitats, and Geary *et al.* (2013) identified the habitat richness of different land cover types within various neighborhood scales and incorporated this into the statistical model. The use of a focal statistic to describe the proportion of land cover types as an indicator of habitat suitability and connectivity in SDM has been found to have equal or higher predictive power than a local model, and can also help to clarify the influence of the other environmental factors that are contributing to the distribution of a mobile species (Czucz *et al.* 2011; Ashcroft and Major 2013; Betts *et al.* 2014).

A number of methods have been proposed to incorporate a focal model, ranging from the simplistic definition of a neighborhood around a point (Arthur *et al.* 1996), to using distance from points (Cooper and Millsaugh 1999), weighted distances (Hjermann 2000), and topographic barriers (Matthiopoulos 2003), as covariates in the model. The methods used to identify accessible neighboring features have been found to significantly alter the importance of the environmental variables in such statistical models (Forrester *et al.* 2009; Holloway and Miller 2014), meaning how researchers define 'accessible' in these

models can have large implications on model projections. Currently, the methods used in SDM to describe the surrounding and available habitat do not explicitly incorporate geographic context and results are subject to uncertainty pertaining to the accessibility, connectivity, and availability of habitat within a neighborhood. Research needs to be directed to find models which better illustrate these issues of accessibility for mobile species. This concept is perhaps closest to Anderson's (2013) definition of 'movement suitability' which describes the contingent demographic factors that can facilitate dispersal, such as the distribution and configuration of suitable patches, and if realistic models of movement can be generated that reliably simulate these regular movements, then these could be used to identify accessibility to all features of an individual's home range, including nesting locations, boundaries, biotic interactions as well as suitable habitat.

Gene Flow

Recently, phylogeographic analysis has been integrated with SDM as a multi-faceted approach to address the processes of how current distribution patterns of genes, populations and species were shaped (Carstens and Richards 2007). The ability to use SDMs to 'hindcast' species distributions has provided researchers with a means to characterize the spatial distribution of previous suitable climatic conditions for species, and these past projections have been used to determine the potential distribution and refugia areas during the late Quaternary (e.g. Veloz *et al.* 2012). The coupling of SDMs and phylogeographic analyses can be considered complementary, as information is provided about potential dispersal corridors from habitat suitability and genetic similarity, with both approaches used to explore and assess each other (Peterson *et al.* 2004). The testing of biogeographic hypotheses has recently 'exploded' in terms of its application in SDM, with 120 studies (20.27%) explicitly addressing a biogeographic hypothesis identified in the meta-analysis. Studies have explored several biogeographic questions such as speciation mechanisms (e.g. Raxworthy *et al.* 2008), niche shifts (e.g. Hill *et al.* 2013), and dispersal versus vicariance hypotheses (e.g. Bendiksy *et al.* 2014). Several methods have been utilized to explore gene migrations with the majority of methods identifying the most likely divergence scenario for each species using mtDNA or microsatellite data from phylogenetic analyses (e.g. MIGRATE - Inoue *et al.* 2015). The most likely gene migration pattern is then obtained from population-isolation analyses (Mellick *et al.* 2014), with the results used to identify barriers to colonization or the differences between isolated populations. For example, Chang *et al.* (2012) coupled SDM with an analysis of population genetic structure and demography to investigate the effect of historical climate changes on the endemic Hainan Island partridge, and concluded that its current distribution is representative of its *in situ* refuge and not dispersal from the mainland.

These models are more exploratory compared to the more predictive 'climate change' and 'invasive spread' movement patterns which have been incorporated more readily in SDM. However, if these methods do well to explain historical movements in response to changing climates, then they have the potential to be used to predict future changes. Recently, Razgour (2015) used a landscape genetics approach to investigate the future range shifts of the gray long-eared bat in Iberia. Implementation of the landscape genetics framework (which identified landscape variables that impede or facilitate gene flow movement) with SDM was similar to many other methods used to simulate dispersal in response to climate change, with the outputs from the landscape genetic analysis used to restrain the potentially

suitable abiotic and biotic future habitat. Subsequently, there exists the possibility to combine research from both movement patterns, and use the more empirical data and analysis used in gene migration studies to predict future changes in the distribution of species, as well as identifying possible divergent events.

Movement Data as Response Data

With the recent technological advances in satellite tracking, movement data is becoming increasingly ubiquitous in habitat studies. Such technology permits continuous monitoring of individual animals, which can provide more objective information on the habitat preferences of individual species than can be achieved from other observation strategies or opportunistic sightings (Dambach and Rödder 2012). Subsequently, a number of studies have begun using the locations obtained from telemetry data as the response data in SDM (e.g. Edrén *et al.* 2010; Gscwheng *et al.* 2012; D'Elia *et al.* 2015). Despite the vast potential to use telemetry data within an SDM framework, a number of new conceptual issues related to this data type have arisen.

Spatial imprecision is an inherent problem associated with the collection of telemetry data as observations are subject to variability in precision, measured as the distribution of differences between the central location and GPS-estimated locations (Frair *et al.* 2010). Another issue associated with using telemetry data is the fact that the sequential observations of an individual are not independent, and subsequently spatially and temporally autocorrelated, meaning any statistical inference associated with this data requires special considerations (Boyce *et al.* 2010). Finally, idiosyncratic preferences of individuals may influence the habitat suitability. If a single individual contributes more locations to the analysis, then the subsequent SDM may be biased towards the individual's habitat preferences. Table 2 identifies the methods currently implemented to address these new issues, and research should be directed towards developing a deeper understanding of how the different methodologies influence SDM outputs.

How should movement be represented?

Finally, this research has highlighted a difference in how movement has been incorporated within SDM. For studies investigating the impact of global change on future distributions, the predominant methodology has been to couple the statistical model of abiotic and biotic suitability with a dispersal model (also known as hybrid models in the literature). Whereas for movement patterns indicative of finer temporal scales (e.g. regular movements), a spatial variable representative of movement, connectivity or dispersal has been generated and incorporated in the statistical model. These two approaches both incorporate movement into SDM, but do so in very different conceptual and methodological manners.

Moreover, Schymanski *et al.* (2013) have suggested that the coupling of a dispersal model with a correlative habitat suitability map into a hybrid model may create a new problem. When calibrating the correlative species-environment relationship, the effects of dispersal limitation could already be included in the habitat suitability projection (as it was essentially fit to reproduce the observed distribution). Therefore, dispersal may already be a latent factor included in the model, with another environmental variable already accounting for some of the effects of dispersal. By coupling this with a dispersal model,

the same process may be incorporated in the overall model twice, propagating uncertainty and incorrectly accounting for effects of movement.

The differentiation between explanation and prediction of the correlative model being fit should be considered in this argument, but so too is the fact that perfect statistical independence between environmental variables is perhaps unrealistic of real-world variables. Propagation of environmental variables most likely exists in most SDMs. Omitting movement from a model based on the possibility that dispersal may already be incorporated is the same as omitting abiotic or biotic factors for the same reasons. Simple assumptions of dispersal limitation have been simulated to explore the effect of each of the BAM factors (Saupe *et al.* 2012; Qiao *et al.* 2015), so a virtual ecologist approach (Miller 2014) could be a method to explore exactly how much error would be propagated through such ‘noisy’ dispersal assumptions. This argument is perhaps more pertinent for the Barve *et al.* (2011) definition of **M** representing accessibility based on historical dispersal rather than dispersal or invasive spread into new habitats over space and time. However, it is important to consider that the decision to generate hybrid models or to generate a variable of dispersal potentially has wide ranging consequences beyond the simple differences in user decisions and assumptions made. Therefore, future research should aim to quantify the uncertainty between projections, as well as any assumptions of a latent dispersal variable.

Conclusion

Incorporating movement should now be a compulsory aspect of any study projecting the current or future distributions of species. This review has investigated and reported results across a broad range of taxa, for multiple movement processes at a range of spatial and temporal scales. The results from the meta-analysis have identified a number of key findings pertaining to dispersal in response to climate change and regular movements, as well as opening a dialogue regarding the incorporation of multiple scales of movement in SDM research. Here we conclude with the identification of a number of future research trajectories for the continued incorporation of movement within species distribution modelling:

1. Further exploration of the differences in dispersal models used in climate change studies is needed. Only one study (Holloway *et al.* 2016) has extensively compared the dispersal models for birds, meaning continued investigation across different spatiotemporal scales and taxa is still needed.
2. The assumption of abiotic and biotic homogeneity over time should be revisited. Significant differences between implementations of models which simulated dispersal as a one-step process and as a multiple-step process were found. Future research should be directed towards further exploring this fundamental issue, focusing on how often the temporal period should be deconstructed and if data coverage allows, the accuracy of intermediate time-periods could be evaluated in order to identify whether errors in these models propagate.
3. The exploration of how movement can be incorporated for different species groups should continue to be investigated. In particular, the less frequently studied species (Figure 2) should be of key concern.
4. How can spatial simulation continue to address individual-based simulations of animal movement? To date, individual-based models in SDM have focused on the movement of

- individuals as grids, so research should investigate how using movement paths can be incorporated in SDM.
5. A number of studies have begun using the locations obtained from telemetry data as the response data in SDM (e.g. Gschweng *et al.* 2012). Despite the vast potential to use telemetry data within an SDM framework, a number of new conceptual issues related to this data structure, such as precision, autocorrelation, and idiosyncratic preferences have arisen. Various methods have been implemented for data filtering, but to date they all remain untested as to their impact on SDM results.
 6. What are the differences between coupling the statistical model with a model of dispersal compared to incorporating a movement variable in the statistical model? When calibrating the correlative species-environment relationship, the effects of dispersal limitation may be a latent factor included in the model (Schymanski *et al.* 2013). Subsequently, to what extent does coupling the statistical model with a dispersal model propagate potential bias in prediction? Virtual species with known properties could be used to answer this question and quantify any error or uncertainty.
 7. Finally, research should continue to focus on integrating multiple scales of movement within SDM. Movement undoubtedly occurs across fine and broad spatial and temporal scales, meaning the most informative models will be those that continue to bridge the gap between scales.

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809

810 Tables

811 *Table 1: The number of times dispersal or migration was used to refer to the tracking of changing*
812 *environmental conditions or regular movement. The value in the brackets refers to the number of times*
813 *the main terms were indistinguishable.*

814

	Track Environment	Changing Daily Movements	or Seasonal
Dispersal	91 (10)	35 (1)	
Migration	37 (10)	27 (1)	

815

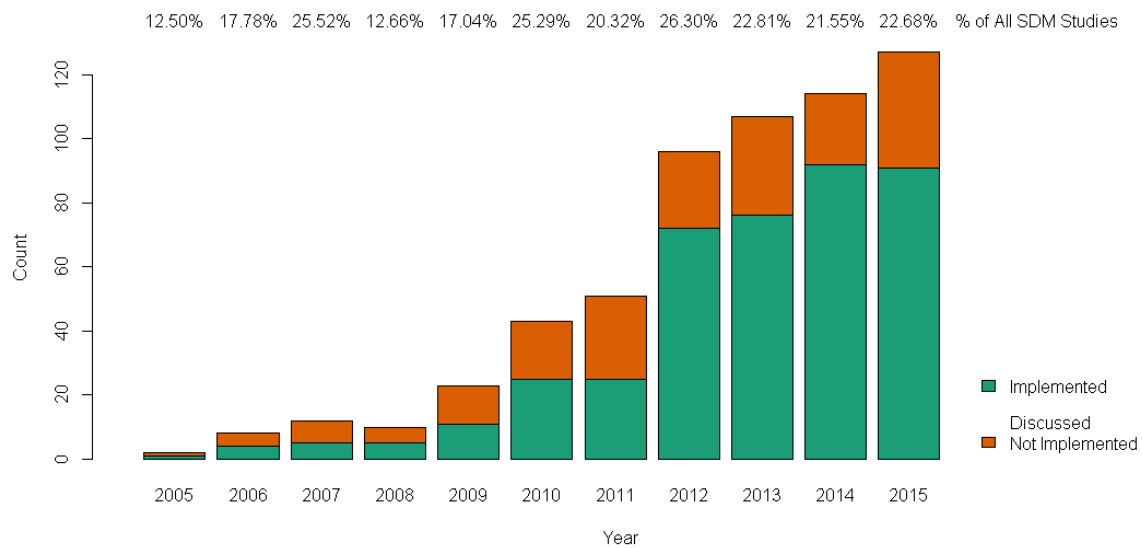
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818 Table 2: Description of the different filtering methods used to control for unique issues associated with using telemetry data as response data. SE:
819 Spatial Error, SAC: Spatial Autocorrelation, TAC: Temporal Autocorrelation, IP: Individual Preferences.

Method	Description	SE	SAC	TAC	IP	Source
Spatial Accuracy Filtering	Selection of locations which have a spatial accuracy estimated within a predefined distance (often coupled with the spatial resolution of the environmental variables).	X				D'Elia <i>et al.</i> 2015
Density Contouring	When large spatial error exists, density contours including a predefined proportion of observations (e.g. 50%) are generated, with presence points created within. Use of a higher proportion (e.g. 90%) can then be used as the extent with which to generate pseudo-absences.	X				Torres <i>et al.</i> 2015
Grid Filtering	Removal of observations which all fall into the same environmental grid.		X			Monnet <i>et al.</i> 2015
Removal of serial correlation.	Specification of a time-period after which observations are no longer autocorrelated. Use of exploratory analysis of autocorrelations and partial-autocorrelations of the deviance residuals.		X	X		Fortin <i>et al.</i> 2005
Best Daily Location	Selection of one observation within a 24-hour period which has the highest spatial accuracy.	X	X	X		Abecasis <i>et al.</i> 2014
Bootstrapping Individuals	Use of a bootstrapping procedure to randomly select a fixed number of records for each animal, pooling the records and then creating an SDM.				X	Edrén <i>et al.</i> 2010
Removal of Individuals	Systematically removing one individual from the analysis to identify significant changes in accuracy.				X	Gscwheng <i>et al.</i> 2012
No filtering	No data-filtering (beyond extreme outliers) undertaken and all data considered in analysis.					Meisingset <i>et al.</i> 2013

820 Figures

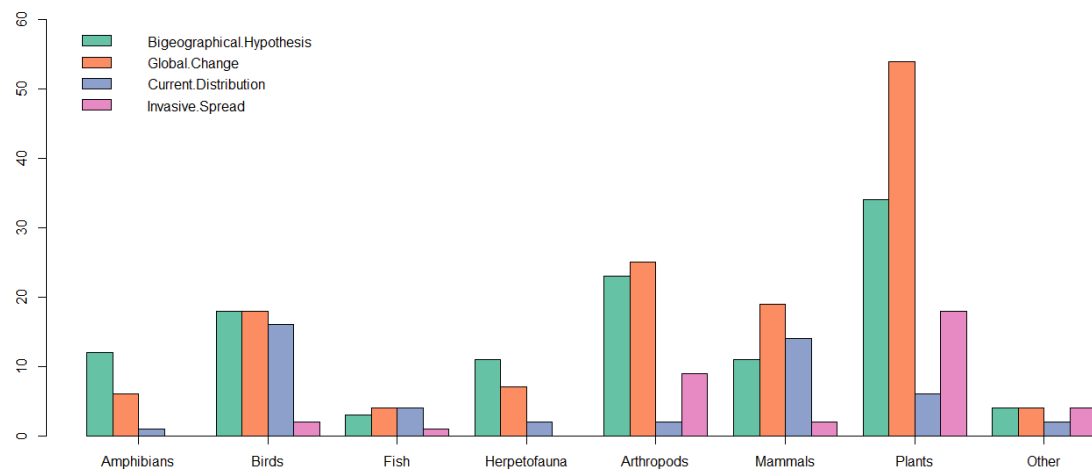


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822 *Figure 1: The number of SDM articles per year in which movement was implemented, or discussed but not*
 823 *implemented since 2005 (n.b. two SDM articles pre-2005 discussed movement but were not included in*
 824 *the above figure).*

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828 *Figure 2: The number of SDM studies applying movement for a species group.*

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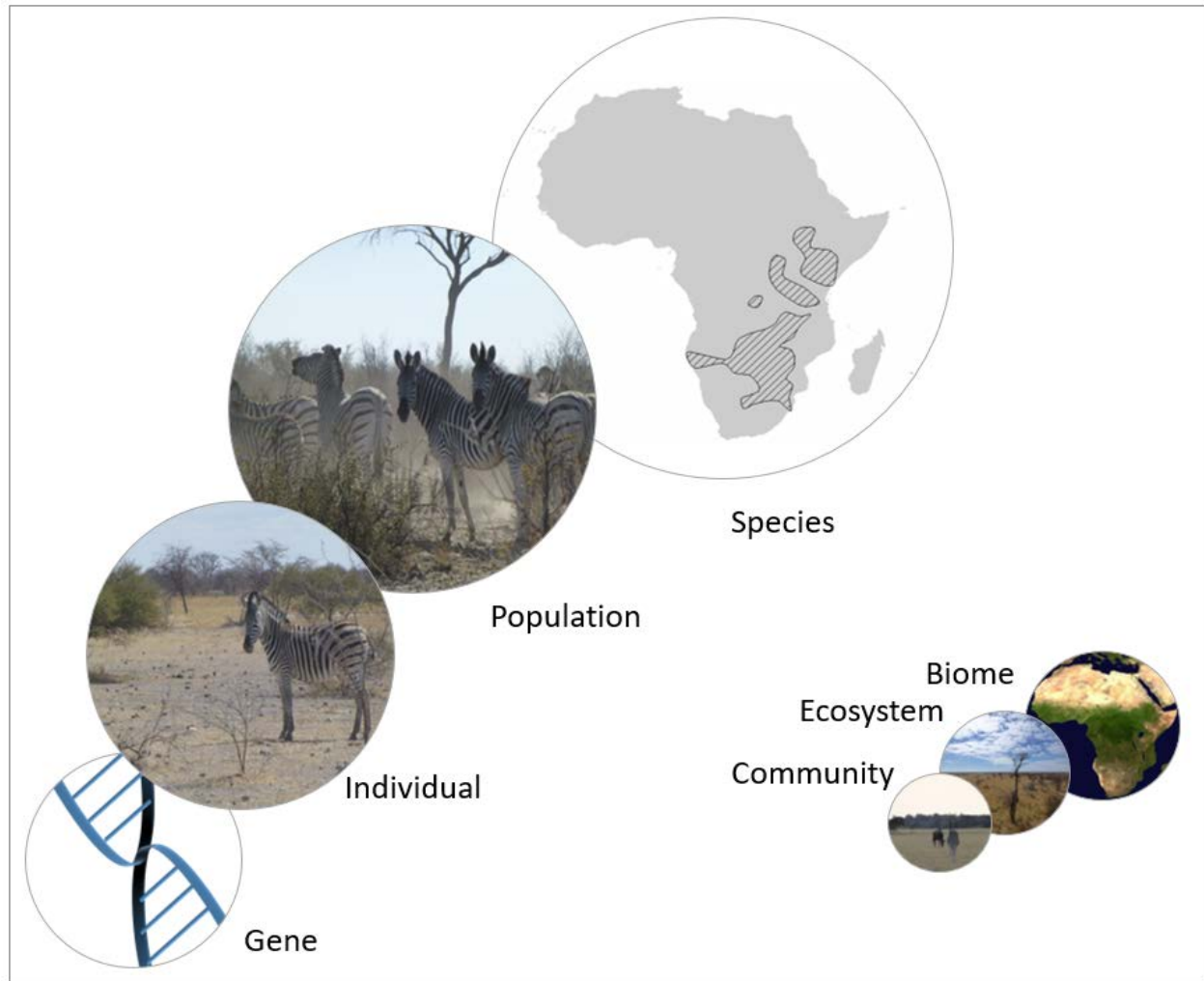
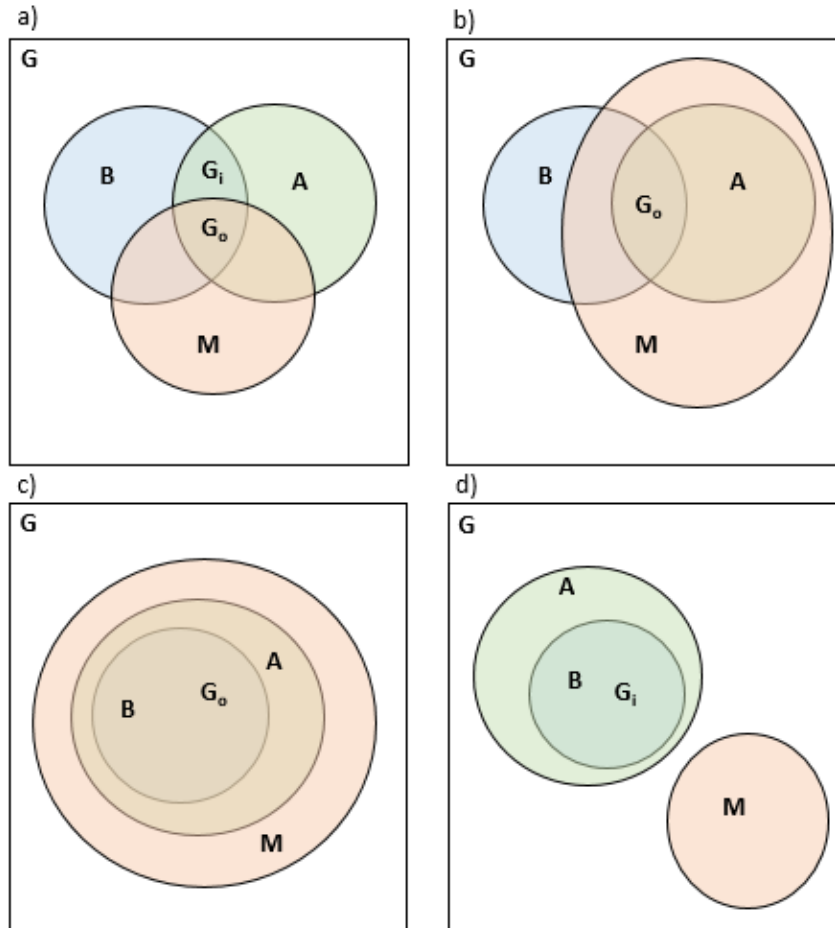
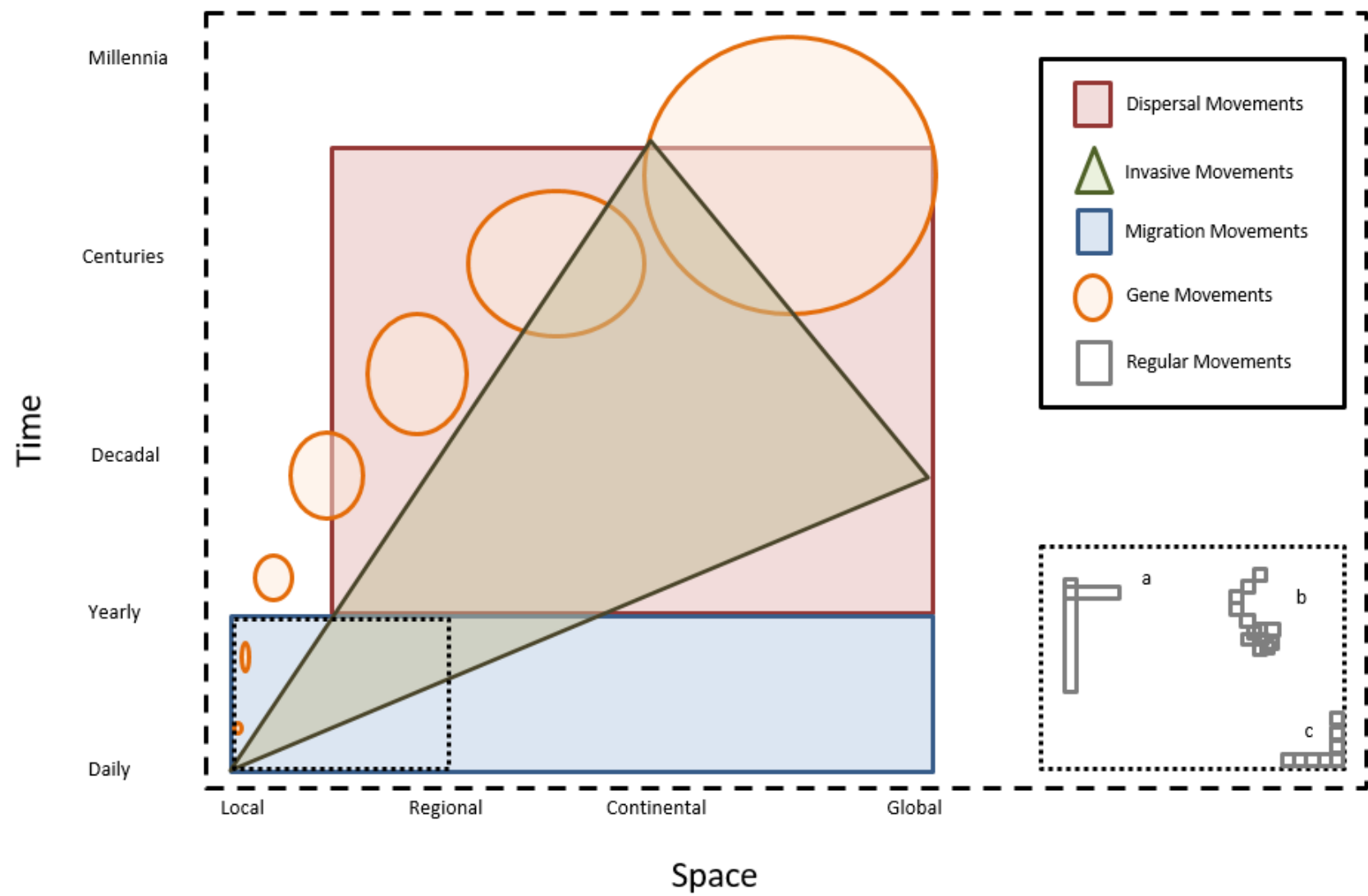


Figure 3: Levels of organization for which movement has been investigated within an SDM context.



837 *Figure 4: Different 'BAM' scenarios, a) represents the classic 'BAM' framework that depicts the interaction*
 838 *between biotic (B), abiotic (A), and movement (M) factors. G is the geographic space within which the*
 839 *analysis occurs, G_i is the invadable (abiotic and biotic) suitable area. Finally G_o represents the occupied*
 840 *(abiotic and biotic) suitable area and is therefore the actual distribution, b) represents a situation where*
 841 *all the combined suitable abiotic and biotic area is accessible, so the invadable area is null, c) represents*
 842 *a situation where all of A and B are accessible, and so movement does not restrict the distribution.*
 843 *Finally d) represents a situation where neither A or B is accessible. This could represent the potential*
 844 *area of an invasive species, or where potentially abiotic and biotic conditions have shifted under climate*
 845 *change, but the species lacks the dispersal capacity required to keep track, which could result in a species*
 846 *going extinct. Modified from Peterson et al. (2011).*



849 *Figure 5: The spatiotemporal scales of movement applications within species distribution modelling. Dispersal movements represent the*
850 *processes through which species move in response to changing environmental conditions. Typically, these movements are modeled at a temporal*
851 *scale greater than a year, despite yearly dispersal events of individuals. While local dispersal events have been known to occur, often this*
852 *movement takes a species into a new geographic area, and as such is depicted as being between local and regional scales. Invasive movements*
853 *within an SDM context are often simulated as spreading from a single point of invasion through both space and time. Migration movements*
854 *represent the seasonal migration processes that many species undertake, either tracking seasonal changes in resources, or movement between*
855 *different habitat types. Due to the variety of seasonal movements, these can range from very local migrations (e.g. amphibians) to global*
856 *migrations (e.g. albatrosses). Gene movements represent the flow of genes through populations. This process can occur on very short time*
857 *periods within local populations, or over many millennia at a much coarser spatial scale. Finally, regular movements maintain the distribution*
858 *of a population and species, and include behaviors such as a) interactions (e.g. movement in response to predation or competition), b) foraging*
859 *(e.g. searching for resources) and bounding (e.g. marking home range limits). These movements are markedly different from seasonal*
860 *movements, as these activities operate within seasonal habitats.*

Supplementary Information 1: The number of articles returned from different ISI Web of Knowledge search parameters. Terms representing the correlative species-environment models are species distribution models (SDM), niche models (NM), predictive habitat distribution models (PHDM), and predictive vegetation models (PVM).

Movement Term	SDM	NM	PHDM	PVM
Diffusion	3	1	0	0
Dispersal	266	106	0	2
Distance Travelled	0	0	0	0
Gene Dispersal	0	0	0	0
Gene Flow	45	55	0	0
Habitat Use	41	12	1	0
Interconnectivity	1	0	0	0
Locomotor Activity	0	0	0	0
Migration	103	35	0	0
Movement	55	18	0	0
Passage	2	0	0	0
Population Connectivity	7	1	0	0
Site Fidelity	2	0	0	0
Transport	11	9	0	0
Traverse	1	1	0	0

In total there were 32 general terms used to describe organism movement. In alphabetical order, these were: assisted migration, colonize, connectivity, corridor, diel turnover, diffusion, dispersal, dispersal limitation, dispersal pressure, distance to, emigration / immigration, forage, gene flow, geographic background, geographic distance, habitat selection, habitat use, interconnectivity, jump dispersal, migration, movement, partial dispersal, passage, population connectivity, propagule limited, shift, site fidelity, spread, track, transit corridors, transport, traverse.