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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,

40 dispersal and gene flow. The four SDM terms and 15 movement terms identified by Holyoak *et al.* (2008)  
41 were used as search parameters, and while these parameters are relatively broad, we felt this was  
42 necessary in order to complete a comprehensive review. An article was deemed relevant if it referred to  
43 the movement of whole genes, progeny, organisms, populations, or species (Supplementary Information  
44 1). The search was conducted so that every journal article published up to and including December 31<sup>st</sup>  
45 2015 is included, with the search considered complete as of March 9<sup>th</sup> 2016.

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

## 58 **Movement Terminology**

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

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

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

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

## 101 **What is Moving?**

### 102 ***Species Groups***

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

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

### 130 ***Individuals, Populations, or Species***

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

146 Recent developments in the fields of movement ecology and computational movement analysis are  
147 beginning to address this long-standing issue. The potential of individual-based models to simulate the  
148 inherent relationship between movement and the environment while aggregating individual movement  
149 to the population level has seen an increase in the use of spatial simulation models to understand animal  
150 movement, and are subsequently beginning to be observed within the SDM framework (Martinez *et al.*  
151 2012; Adams *et al.* 2015). For example, Martinez *et al.* (2012) used a parameterized individual-based  
152 model which incorporated competition, facilitation and dispersal limitations to estimate a realistic rate of  
153 tree line 'migration' (or dispersal as defined in this review) under climate change in the Pyrenees. Similarly,  
154 Adams *et al.* (2015) used an individual-based cellular automata model based on dispersal constraints to  
155 model invasive spread of a non-native weed in Australia over a period of five to ten years. While the  
156 potential to estimate population level redistributions of species using individual-based models within SDM  
157 is promising, currently only one study has addressed this beyond plants (Zurrell *et al.* 2012). Furthermore,

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

### 165 **The 'BAM' Framework**

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

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

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

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

215 A criticism of BAM is that it fails to regularly account for the dynamic nature of the three factors, and in  
216 particular it could benefit from a representation of time. This is eluded to in Figure 4d, where time is an  
217 important construct of shifting both **A** and **B** beyond locations deemed accessible to the species, but it  
218 cannot be depicted in this static representation. Another example is the fact that **B** and **M** are inherently  
219 linked. When organisms traverse through a landscape, biotic resources can be depleted while the  
220 individual is in the area (e.g. herbivory) and replenish while the individual is absent. For example, the  
221 reintroduction of wolves to Yellowstone National Park in the mid-1990s changed elk movement patterns  
222 and dramatically transformed the distribution of biotic resources in a short space of time (Turner *et al.*  
223 2001). While **M** has been used to describe contingent demographic factors that can facilitate dispersal or  
224 migration, such as the distribution and configuration of suitable patches required to maintain populations  
225 (Anderson, 2013; Fordham *et al.*, 2013), these landscape constructs such as fragmentation, connectivity,  
226 and species-area relationships are still represented as static entities. Subsequently, the BAM framework  
227 currently lacks the detail required to incorporate these dynamic relationships and this singular or static  
228 representation of **M** will therefore have to be revisited as increasingly complex representations of  
229 movement processes are incorporated more readily within SDM.

### 230 **Applications of Movement in SDM**

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

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

#### 240 ***Tracking Changing Environmental Conditions***

241 Incorporating movement factors is particularly pertinent for SDMs for which the main focus is to identify  
242 changes in distributions over broad time-scales. Climate conditions and land cover are changing, and  
243 SDMs are an important tool for exploring how these changes will affect species distributions. If the new  
244 abiotic and biotic conditions are still within the range the species can tolerate, it can persist; otherwise it  
245 will need to colonize new suitable areas. Most applications involve refining a projected species  
246 distribution map to distinguish (abiotically and biotically) suitable and accessible habitat from suitable and  
247 inaccessible habitat, with accessibility measured as a function of dispersal (Miller and Holloway 2015).  
248 However, when dispersal has been implemented in SDM research, it has often taken one of two extreme  
249 approaches: either unlimited or no dispersal (e.g. Araújo *et al.* 2006; Lawler *et al.* 2006; Araújo and Luoto  
250 2007). Unlimited dispersal assumes that there are no barriers to movement and that distance is not a  
251 limiting factor, implying that any suitable habitat which is present in the study area can become occupied.  
252 Conversely, no dispersal assumes the opposite, with dispersal not possible, and the future suitable habitat  
253 is restricted to locations that overlap with the original distribution.

254 The use of both unlimited dispersal and no dispersal ('all or nothing') was recorded in a quarter of the  
255 studies investigating distribution shifts under climate change. While these two approaches overly simplify  
256 movement, using both together is an improvement on studies that overlooked dispersal (and thus  
257 implicitly assumed unlimited dispersal). Furthermore, due to their extreme variation, these  
258 implementations of dispersal can be used to represent the uncertainty associated with the effects of  
259 climate change, as the actual dispersal capacity will most likely be found somewhere in the middle of  
260 those two predictions. A number of methods have begun to emerge in the literature, ranging from a fixed  
261 rate of dispersal applied as a time based distance buffer (Hsu *et al.* 2012; Gallardo *et al.* 2012; Jaeschke *et al.*  
262 2013), to complex probabilistic dispersal kernels (Summers *et al.* 2012; Alagador *et al.* 2014; Bush *et al.*  
263 2014). A summary of these dispersal models is provided by Miller and Holloway (2015) in a recent  
264 review on the subject; however, these methods used to simulate dispersal vary greatly in terms of  
265 implementation. Recently, Holloway *et al.* (2016) compared the accuracy and uncertainty of 20 dispersal  
266 models for future projections (1990 to 2010) of breeding British birds. They found that the choice of  
267 dispersal model and how it is implemented could significantly influence the results both in terms of  
268 accuracy and the area predicted as present. The choice of dispersal model undoubtedly introduces  
269 uncertainty into projections, and while a handful of studies have compared the results (Engler and Guisan,  
270 2009; Cunze *et al.* 2013; Holloway *et al.* 2016) more extensive testing across different taxa and spatial  
271 scales is needed.

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



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

### 291 ***Invasive Spread***

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

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

### 311 ***Disease Spread***

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

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

#### 324 **Seasonal Movement**

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

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

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

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

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

### 359 **Regular Movements**

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

373 Mobile species utilize several patches of suitable habitat within their home range, meaning species  
374 observations may be recorded in an environment which is unsuitable for them on a permanent basis. Due  
375 to the fragmentation of suitable habitat, animals often have to traverse through an inhospitable matrix  
376 (e.g. forests separated by an open meadow or urban area). Subsequently the aforementioned issue  
377 relating to using sightings of presence in unsuitable habitat in model calibration persists. However, as  
378 regular movements occur at a finer spatiotemporal scale, this issue could be controlled for by observing  
379 the environmental variables at a neighborhood scale (Ashcroft and Major 2013). Subsequently, for many  
380 mobile animals, the use of a focal statistic summarizing the abiotic and biotic conditions within a specified  
381 neighborhood may better represent what is available to it within its home range. For example, black  
382 grouse utilize a mixture of moorland (for mating) and woodland (for shelter) habitats, and Geary *et al.*  
383 (2013) identified the habitat richness of different land cover types within various neighborhood scales and  
384 incorporated this into the statistical model. The use of a focal statistic to describe the proportion of land  
385 cover types as an indicator of habitat suitability and connectivity in SDM has been found to have equal or  
386 higher predictive power than a local model, and can also help to clarify the influence of the other  
387 environmental factors that are contributing to the distribution of a mobile species (Czúcz *et al.* 2011;  
388 Ashcroft and Major 2013; Betts *et al.* 2014).

389 A number of methods have been proposed to incorporate a focal model, ranging from the simplistic  
390 definition of a neighborhood around a point (Arthur *et al.* 1996), to using distance from points (Cooper  
391 and Millsaugh 1999), weighted distances (Hjermann 2000), and topographic barriers (Matthiopoulos  
392 2003), as covariates in the model. The methods used to identify accessible neighboring features have been  
393 found to significantly alter the importance of the environmental variables in such statistical models  
394 (Forrester *et al.* 2009; Holloway and Miller 2014), meaning how researchers define 'accessible' in these

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

#### 405 **Gene Flow**

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

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

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

#### 439 **Movement Data as Response Data**

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

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

#### 458 **How should movement be represented?**

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

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

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

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

## 488 **Conclusion**

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

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

- 511 individuals as grids, so research should investigate how using movement paths can be  
512 incorporated in SDM.
- 513 5. A number of studies have begun using the locations obtained from telemetry data as the  
514 response data in SDM (e.g. Gschweng *et al.* 2012). Despite the vast potential to use telemetry  
515 data within an SDM framework, a number of new conceptual issues related to this data  
516 structure, such as precision, autocorrelation, and idiosyncratic preferences have arisen.  
517 Various methods have been implemented for data filtering, but to date they all remain  
518 untested as to their impact on SDM results.
- 519 6. What are the differences between coupling the statistical model with a model of dispersal  
520 compared to incorporating a movement variable in the statistical model? When calibrating  
521 the correlative species-environment relationship, the effects of dispersal limitation may be a  
522 latent factor included in the model (Schymanski *et al.* 2013). Subsequently, to what extent  
523 does coupling the statistical model with a dispersal model propagate potential bias in  
524 prediction? Virtual species with known properties could be used to answer this question and  
525 quantify any error or uncertainty.
- 526 7. Finally, research should continue to focus on integrating multiple scales of movement within  
527 SDM. Movement undoubtedly occurs across fine and broad spatial and temporal scales,  
528 meaning the most informative models will be those that continue to bridge the gap between  
529 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

	<b>Track Environment</b>	<b>Changing</b>	<b>Daily</b>	<b>or</b>	<b>Seasonal</b>
<b>Dispersal</b>	91 (10)		35 (1)		
<b>Migration</b>	37 (10)		27 (1)		

815

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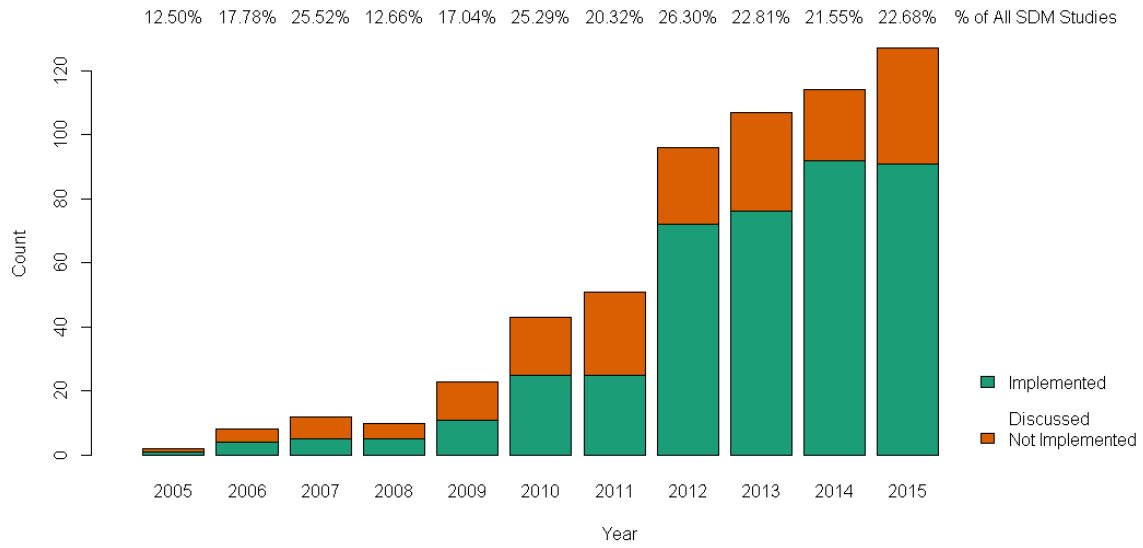
817

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.*

<b>Method</b>	<b>Description</b>	<b>SE</b>	<b>SAC</b>	<b>TAC</b>	<b>IP</b>	<b>Source</b>
<b>Spatial Accuracy Filtering</b>	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
<b>Density Contouring</b>	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
<b>Grid Filtering</b>	Removal of observations which all fall into the same environmental grid.		X			Monnet <i>et al.</i> 2015
<b>Removal of serial correlation.</b>	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
<b>Best Daily Location</b>	Selection of one observation within a 24-hour period which has the highest spatial accuracy.	X	X	X		Abecasis <i>et al.</i> 2014
<b>Bootstrapping Individuals</b>	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
<b>Removal of Individuals</b>	Systematically removing one individual from the analysis to identify significant changes in accuracy.				X	Gscwheng <i>et al.</i> 2012
<b>No filtering</b>	No data-filtering (beyond extreme outliers) undertaken and all data considered in analysis.					Meisingset <i>et al.</i> 2013



820 Figures

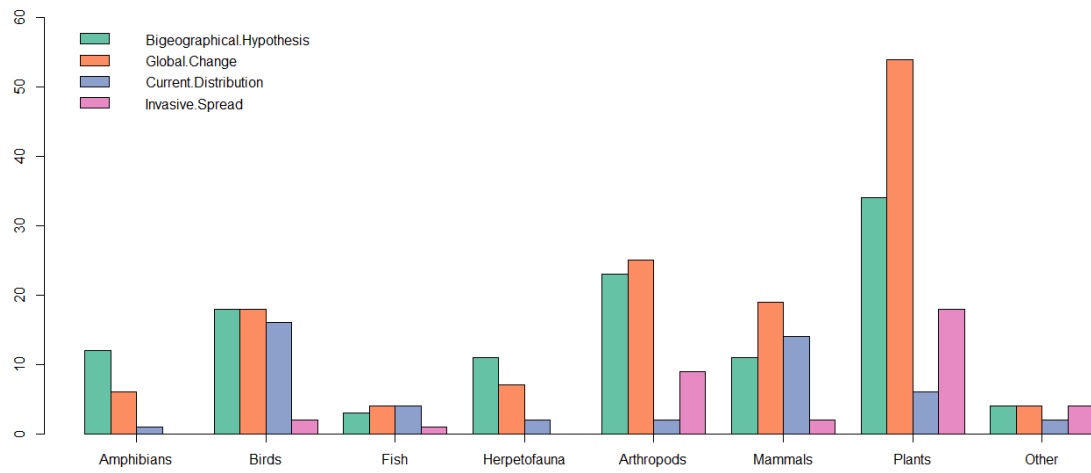


821

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).*

825

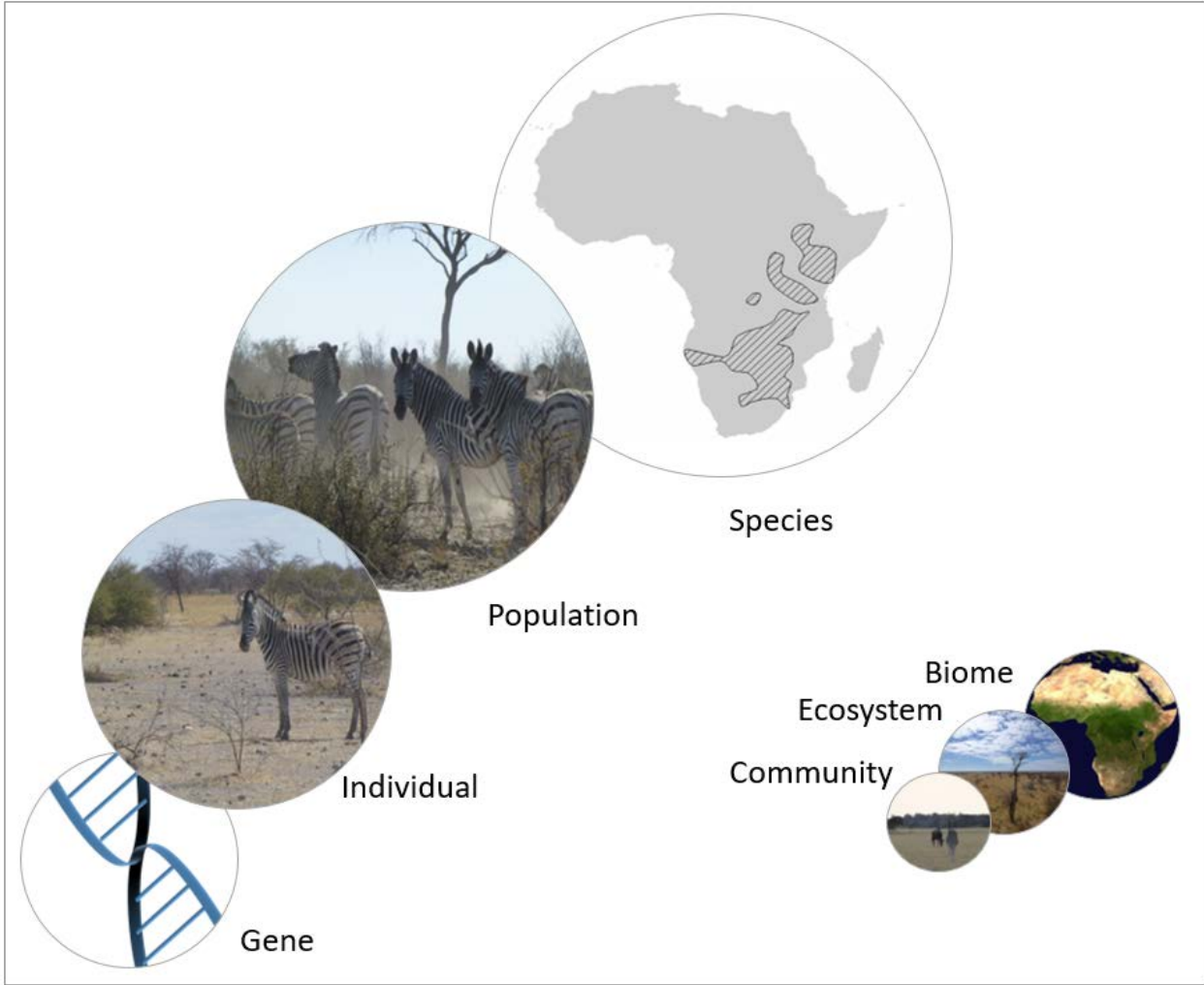
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828 *Figure 2: The number of SDM studies applying movement for a species group.*

829



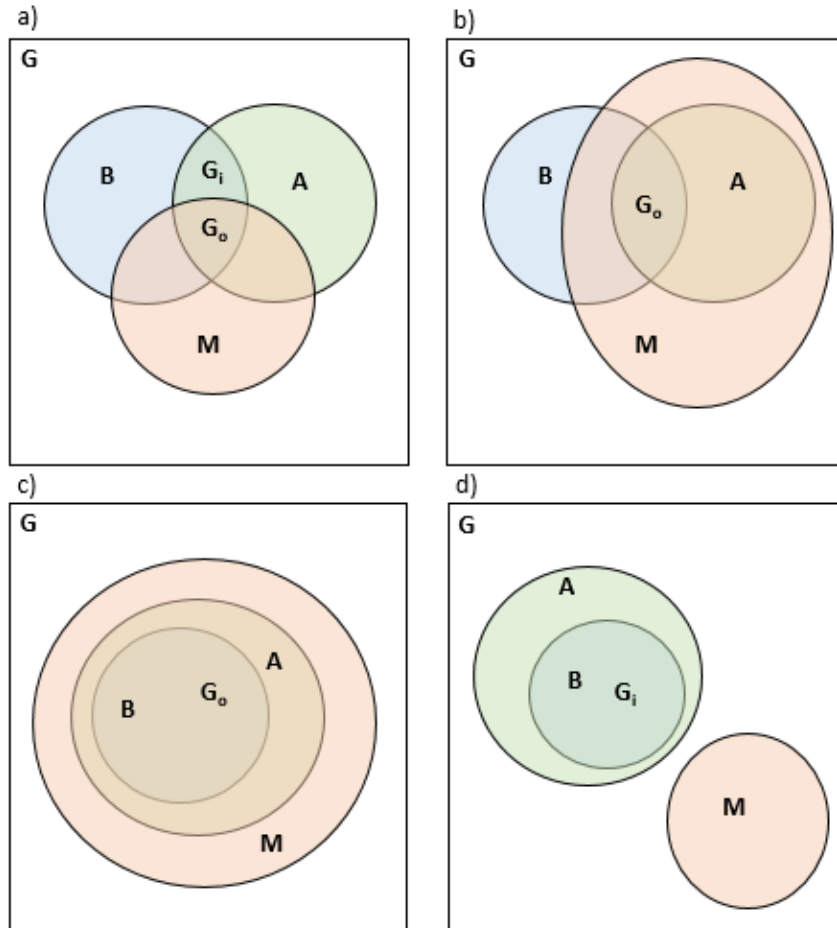
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831 *Figure 3: Levels of organization for which movement has been investigated within an SDM context.*

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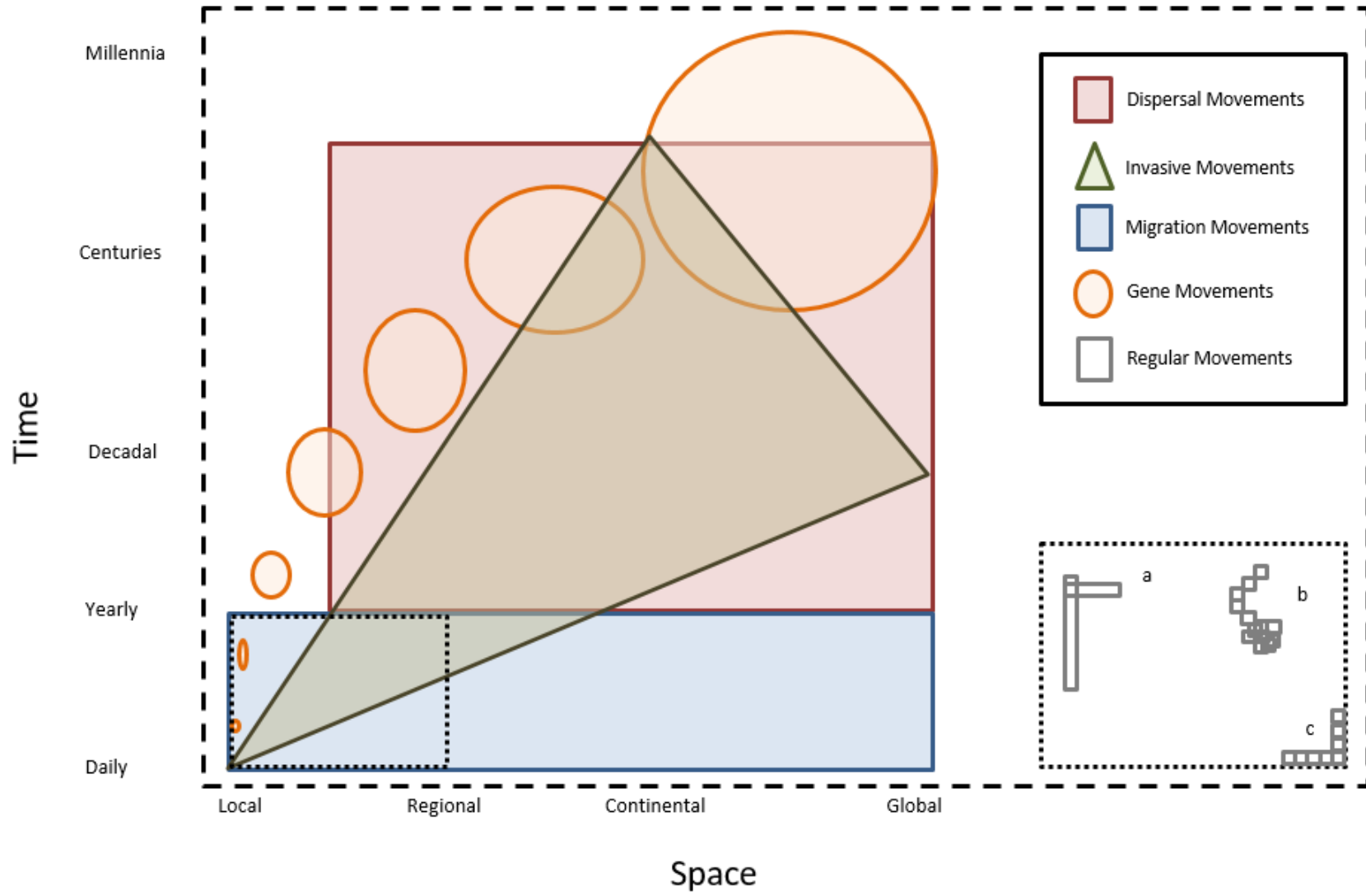
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837 *Figure 4: Different 'BAM' scenarios, a) represents the classic 'BAM' framework that depicts the interaction*  
 838 *between biotic (B), abiotic (A), and movement (M) factors. G is the geographic space within which the*  
 839 *analysis occurs, G<sub>i</sub> is the inadmissible (abiotic and biotic) suitable area. Finally G<sub>o</sub> 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 inadmissible 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.*

861 *Supplementary Information 1: The number of articles returned from different ISI Web of Knowledge search*  
 862 *parameters. Terms representing the correlative species-environment models are species distribution*  
 863 *models (SDM), niche models (NM), predictive habitat distribution models (PHDM), and predictive*  
 864 *vegetation models (PVM).*  
 865

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

866  
 867

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