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Review

# A quantitative synthesis of the movement concepts used within species distribution modelling

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ABSTRACT

Movement is a ubiquitous ecological process that influences the distribution of all species. In spite of this ecological significance, the incorporation of movement in species distribution models (SDMs) has lagged in comparison with other methodological and conceptual advancements. Many studies still ignore movement processes in applications inherently linked to movement (e.g. tracking changes in climate), and moreover, finer scale movements (e.g. foraging) have been neglected even more severely. We reviewed almost 600 research articles published in the last decade to identify important trends in the way that movement has been explicitly incorporated in SDM. We note that the conceptual differences associated with the 'object' whose movement is of interest, as well as subtler differences among taxon groups (e.g. plants v animals) and levels of organization (e.g. individuals, populations, species) that have significant implications for how movement processes occur, have hindered more substantial integration of these concepts. Finally, we highlight novel and unique methodological issues such as the use of successive telemetry data as response data in these correlative models. The gaps and trends identified in this review should foster future research in this burgeoning research area.



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## 1. Introduction

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

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

## 2. Meta-Analysis of movement in SDM

The ISI Web of Knowledge (http://apps.webofknowledge.com/) was used to conduct a comprehensive search for journal articles that satisfied a query of both SDM and 'movement' as words in the article topic. While the current terminology used to refer to correlative species-environment models is converging on 'species distribution models', they have previously been referred to as 'predictive vegetation models' (Franklin, 1995), 'niche models' (Peterson et al., 2007) and 'predictive habitat distribution models' (Guisan and Zimmermann, 2000). While conceptual differences between terms do exist (e.g. modelling the actual versus potential distribution – Peterson et al., 2011), in order to correctly identify any article which could be considered under the SDM framework, all four terms were used within the search and for the purposes of this review can be considered synonymous. A variety of terms associated with organism movement were identified by Holyoak et al. (2008) in their quantitative study in a special issue of the *Proceedings of the National Academy of Science* introducing movement ecology. They identified 15 general movement 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 and 26% 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 (Fig. 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 (Fig. 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).

## 3. 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