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EDITORIAL

Multi-scale habitat selection modeling: introduction to the special issue

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Scale is the lens through which we view spatial and temporal heterogeneity and interpret ecological relationships (Wiens 1989; Levin 1992; Wu and Hobbs 2002; Wu et al. 2006). Indeed, how environmental structure at various scales affects the distribution, abundance and fitness of organisms has been a major focus of ecology since its inception. Moreover, there is growing consensus that it is critical not only to identify the operative scale(s) for the expression of these ecological relationships, but that multi-scale approaches to habitat modeling will yield stronger and more reliable inferences (e.g., Grand et al. 2004; Holland et al. 2004; Wasserman et al. 2012; Weaver et al. 2012; Shirk et al. 2014; Zeller et al. 2014). Given longstanding awareness of the importance of scale in species–environment relationships (Wiens 1976) and growing recognition of the advantages of multi-scale approaches for elucidating these relationships (Mayor et al. 2009), why do so few studies use multi-scale approaches to identify the relevant operative scale(s)? This basic question was the motivation for this special issue on multi-scale habitat modeling.

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Objective and organization

To provide focus for this special issue, we must define what we mean by "multi-scale habitat modeling". First, "habitat modeling" refers generally to quantitative approaches to determine how the physical, chemical and biological resources and conditions in an area affect occupancy patterns, survival and reproduction. In this context, "multi-scale" habitat modeling refers to any approach that seeks to identify the scale, or scales (in space or time), at which the organism interacts with, or is limited by, the environment.

Given this focus, our objective for this special issue is to review the origin and evolution of multi-scale habitat modeling and provide a diversity of multi-scale applications that highlight the versatility and utility of multi-scale approaches in habitat modeling. By reviewing the conceptual foundation for multi-scale modeling and demonstrating a broad range of multi-scale applications, we hope to promote greater adoption of multi-scale approaches in future habitat modeling studies. To this end, we begin this issue with three review papers, as follows:

- McGarigal and coauthors examine the conceptual origins of multi-scale habitat selection modeling, survey the leading edge of multi-scale habitat selection modeling through a review of recent literature, and provide a synthesis and recommendations aimed at advancing the science of multi-scale habitat selection modeling.

- Miguet and coauthors dig deeper into the underlying hypotheses concerning what determines the operative scale(s) of habitat selection, or what they refer to as the "scale of effect", and review the literature to determine the degree of empirical support for various predictions derived from these hypotheses.
- Yackulic and Ginsberg examine scale in the context of species distribution modeling, with particular attention to how multiple scale-dependent processes operating at different levels of biological organization under changing environmental conditions can affect range dynamics.

The most common response variable for habitat selection studies is occurrence. We next present three case study applications that illustrate the use of occurrence data in multi-scale approaches. All three approaches varied the extent of the ecological neighborhood around use locations and random locations in conjunction with model selection to identify the best operative scales of predictor variables.

- Timm and coauthors developed a multi-scale, single-level point selection function corresponding to Johnson's (1980) second-order selection to examine Mexican spotted owl (*Strix occidentalis lucida*) nest/roost locations within a study area in northern Arizona, USA.
- Comfort and coauthors developed a multi-scale, single-level point selection function corresponding to Johnson's (1980) third-order selection to examine northern spotted owl (*S. occidentalis caurina*) use of fire-induced hard versus soft edges within home ranges in southern Oregon, USA.
- Vergara and coauthors developed a multi-scale, single-level point selection function corresponding to Johnson's (1980) second-order selection to examine the distributions and niche divergence of two sympatric martin species (*Martes martes* and *M. foina*) within a study area in northern Spain.

The following three studies illustrate multi-scale approaches to habitat selection based on alternative response variables (e.g., capture rate) and/or simple model extensions to account for context dependency. All three studies also varied the extent of the ecological neighborhood around use locations and random locations in conjunction with model selection to identify the best operative scales of predictor variables.

- Mateo-Sánchez and coauthors developed multi-scale, single-level point selection functions corresponding to Johnson's (1980) second-order selection to examine context-dependent habitat selection of brown bears (*Ursus arctos*) within a study area in northern Spain. They used model selection to identify and compare the optimal multi-scale, multi-variable models among seasonal and temporal (multiple years) periods, with an emphasis on elucidating shifts in habitat selection over time.
- Rostro-Garcia and coauthors adopted a multi-scale, single-level approach to identify the landscape features that predict livestock predation by tiger (*Panthera tigris*) and leopard (*P. pardus*) in Bhutan. They identified the optimal multi-scale, multi-variable model for each species and elucidated differences in the operative scales of predictors between species.
- Chambers and coauthors developed multi-scale, single-level point selection functions corresponding to Johnson's (1980) second-order selection to examine habitat selection of several species and guilds of bats (Chiroptera) within a study area in southwestern Nicaragua. They similarly identified the optimal multi-scale, multi-variable model for each species and elucidated differences in the operative scales of predictors among species and guilds.

Next we present three studies that illustrate multi-scale approaches to habitat selection during animal movement within a seasonal home range or during dispersal based on telemetry data, with a focus on estimating resistant surfaces for connectivity modeling.

- Zeller and coauthors developed multi-scale, single-level step and path selection functions corresponding to Johnson's (1980) third-order selection to examine the sensitivity of estimated resistance surfaces to the choice of selection function (step or path), scale (single or multi-scale), prediction framework (paired or unpaired logistic regression) and GPS collar sampling interval for pumas (*Puma* *concolor*) within seasonal home ranges in southern California. They varied the spatial extent of the available neighborhood around used steps and path segments and used a variety of performance criteria to evaluate and compare resistance surfaces.

- Cushman and coauthors developed a multi-scale, single-level path selection function to create a resistance surface from which to examine landscape connectivity under a variety of landscape change scenarios for dispersing lions (*P. leo*) in southern Africa. They used a combination of unique approaches to evaluate multiple scales, including randomly shifting used paths by varying displacement distances to define "available" in the path selection function, and varying the potential dispersal distance of lions in the connectivity modeling.
- Krishnamurthy and coauthors developed a multi-scale, single-level path selection function to create a resistance surface for dispersing tigers in central India. Similar to Cushman et al. above, they varied the displacement distance of the randomly shifted paths to define "available" in the path selection function and used model selection to identify the best operative scales of predictors.

Lastly we present two studies that illustrate new or enhanced methods for multi-scale habitat modeling of occurrence and abundance, and that highlight the opportunities that exist for expanding the current multi-scale modeling toolbox.

- Fletcher and coauthors developed a likelihood-based method for uniting presence–absence and presence-only data into a single integrated distribution model. They used this approach to create a multi-scale, single-level point selection function corresponding to Johnson's (1980) second-order selection to examine the distribution of Sherman's fox squirrels (*Sciurus niger shermani*) within a study area in north-central Florida. They similarly varied the spatial extent of the neighborhood around detection (for the presence-only data) and trapping (for the presence–absence) locations and used model selection to identify the best operative scales of predictors and compare modeling approaches, with an emphasis on evaluating the relative performance of the integrated distribution model.
- Chandler and Hepinstall-Cymerman developed a likelihood-based method for estimating the operative scale of predictors when predicting abundance that can easily be extended to other classes of statistical models. They used this approach to create a multi-scale, single-level point selection function to examine site-level abundance of Canada warblers (*Cardellina canadensis*) within a study area in North Carolina, USA. Importantly, they used maximum likelihood procedures to estimate the operative spatial scale for each predictor.

Synthesis and major findings

The empirical studies presented in this special issue illustrate the utility of using multi-scale approaches in a wide variety of habitat modeling applications, including the development of point, step and path selection functions for predicting occurrence, abundance, movement and other responses. Importantly, the applications in this issue add to the growing consensus that multi-scale models produce stronger and more reliable inferences than their single-scale alternatives. However, despite the superior performance of multi-scale models in most cases, Miguet and coauthors show in their review that our theoretical understanding of the mechanisms that govern these multi-scale relationships is still in its infancy, as the empirical evidence is either lacking or equivocal for many of the predictions that derive from hypotheses explaining what determines the operative scale(s).

The empirical studies presented in this issue also clearly indicate a strong emphasis in current research on spatial scaling of neighborhood extent, with the most common approach being the smoothing of predictors within ecological neighborhoods defined at various bandwidths. Despite the focus on neighborhood spatial extent in this issue, it is important to remember that scale exists in other dimensions, including spatial grain and temporal grain and extent, among others, and that multi-scale modeling must expand its scope to include these other dimensions if we are to fully embrace the multi-scale paradigm.

Although there is widespread recognition of the importance of multi-scale analyses for modeling habitat relationships, the review papers in this issue reveal that a large majority of published habitat ecology papers still do not explicitly consider scale, let alone address multiple spatial or temporal scales. Moreover, even among multi-scale studies, scale optimization, which is critical to assess scale dependence, is rarely done. Instead, in most studies the operative scale(s) of predictors are selected a priori based on available data or expert knowledge rather than using empirical approaches. When empirical scale optimization is used it is almost always based on a discrete set of a priori scales and a two-stage optimization approach where the optimal scale for each covariate is determined univariately and the optimized covariates are combined into a single multi-scale, multi-variable model. This two-stage approach is practical but not ideal, as it optimizes the scale of each covariate univariately based on its marginal explanatory power rather than conditionally on the other covariates. Methods for empirically identifying the optimal operative scale(s) of multiple predictors in a single stage without requiring the pre-specification of discrete scales have only recently been explored. In this regard, Chandler and Hepinstall-Cymerman in this issue present a very promising method for estimating the operative scale of predictors in models of abundance that does not require prior specification of discrete scales. Their approach should be extendable to models of occurrence and other more complex model structures.

The review papers in this issue also reveal that little attention has been given to integrating multi-scale approaches across multiple levels of organization (e.g., individual, population, metapopulation). In their review, Yackulic and Ginsberg focus on how the interaction between processes operating at various levels of biological organization interact with the spatial configuration of environmental conditions (landscape context) at different spatial scales to determine how species are distributed relative to environmental conditions. It is clear that we must give greater attention to the processes generating scale-dependent patterns at each level of biological organization, and address dynamic or nonequilibrium landscapes and populations, if we are to advance our theoretical understanding of multi-scale species-habitat relationships.

In conclusion, it is our hope that this special issue will rekindle interest in multi-scale habitat modeling and will provide useful examples of the analytical approaches to do so. While the empirical studies presented here are by no means comprehensive in terms of the multi-scale approaches used, they do exemplify the most common approaches being used today and serve as a springboard for researchers interested in extending these approaches to other applications. Most importantly, these studies illustrate the stronger inferences about species–environment relationships that derive from adopting a multi-scale approach.

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