Landscape Ecol
DOI 10.1007/s10980-016-0374-x

RESEARCH ARTICLE

Multi-scale habitat selection modeling: a review and outlook

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Received: 27 June 2015 / Accepted: 24 March 2016

Abstract
Context Scale is the lens that focuses ecological relationships. Organisms select habitat at multiple hierarchical levels and at different spatial and/or temporal scales within each level. Failure to properly address scale dependence can result in incorrect inferences in multi-scale habitat selection modeling studies.
Objectives Our goals in this review are to describe the conceptual origins of multi-scale habitat selection modeling, evaluate the current state-of-the-science, and suggest ways forward to improve analysis of scale-dependent habitat selection.
Methods We reviewed more than 800 papers on habitat selection from 23 major ecological journals published between 2009 and 2014 and recorded a number of characteristics, such as whether they addressed habitat selection at multiple scales, what attributes of scale were evaluated, and what analytical methods were utilized.
Results Our results show that despite widespread recognition of the importance of multi-scale analyses of habitat relationships, a large majority of published habitat ecology papers do not address multiple spatial or temporal scales. We also found that scale optimization, which is critical to assess scale dependence, is done in less than 5 % of all habitat selection modeling papers and less than 25 % of papers that address "multi-scale" habitat analysis broadly defined.
Conclusions Our review confirms the existence of a powerful conceptual foundation for multi-scale habitat selection modeling, but that the majority of studies on wildlife habitat are still not adopting multi-scale frameworks. Most importantly, our review points to the need for wider adoption of a formal scale optimization of organism response to environmental variables.

Keywords Scale · Habitat · Habitat selection · Resource selection · Resource selection function · Wildlife habitat relationships · Species–environment relationships

Electronic supplementary material The online version of this article (doi:10.1007/s10980-016-0374-x) contains supplementary material, which is available to authorized users.

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Introduction

The environment is structured across scales in space and time, and organisms perceive and respond to this structure at different scales. Indeed, how

Published online: 07 April 2016

environmental structure affects the distribution, abundance and fitness of organisms has been the focus of ecology since its inception. Given longstanding awareness of the importance of scale in species–environment relationships (see references below), why do so few studies give explicit attention to identifying the relevant scale(s)? This basic question was the motivation for this review and this special section on multi-scale habitat selection modeling.

To provide focus for this review, we must define what we mean by "multi-scale habitat selection modeling". First, "habitat selection 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 selection modeling refers to any approach that seeks to identify the scale, or scales (in space or time), at which the organism interacts with the environment to determine it being found in, or doing better in, one place (or time) over another.

Given this focus, we seek to compliment the excellent review of multi-scale habitat selection by Mayor et al. (2009) by: (1) exploring the conceptual origins of multi-scale habitat selection modeling, with particular attention to several seminal publications that provided the conceptual motivation for the modern multi-scale perspective; (2) reviewing the current state-of-the-art in habitat selection modeling through a review of the literature between 2009 and 2014, focusing on the prevalence and characteristics of multi-scale approaches; and (3) providing a brief synthesis and offering recommendations aimed at advancing the science of multi-scale habitat selection modeling.

Conceptual origins of the multi-scale perspective

The multi-scale perspective cannot be fully understood or appreciated without giving due credit to several seminal publications that either introduced a critical concept or summarized it in a form that transformed mainstream ecological thinking. While it is impossible to identify and review all important contributions, we distinguish four as foundations of the modern multi-scale perspective on habitat selection.

Space–time scaling of ecological systems

One of the seminal concepts is that ecological patterns and processes interact across scales in space and time, such that as the spatial scale of the phenomenon increases so does the temporal scale over which it operates. Stommel (1963) provided one of the first formal expressions of this concept in physical oceanography, in which he described and graphically portrayed the correlated scales of spatial and temporal variability in sea level. Since the introduction of the Stommel diagram, there have been myriad incarnations of this basic theme for describing the scaling of ecological phenomena (e.g., Haury et al. 1978; Delcourt et al. 1983), including the eventual depiction of space–time scaling of habitat selection across a gradient from fine to coarse scales (Mayor et al. 2009). One of the major implications of this concept is that reliable predictions about a particular phenomenon (e.g., selection of food resource patches within an individual's home range) require that one observes the system at the right scale(s) in both space and time (Wiens 1989). Determining the best scale(s) at which to describe habitat selection is a major focus of current multi-scale habitat selection modeling.

Organism-centered perspective

Another monumental contribution to the modern perspective on habitat selection was the shift from an anthropocentric to organism-centered perspective on species–environment relationships. While others also contributed to this paradigm shift, Wiens (1976) brought this concept to the forefront of ecological thinking in his seminal publication on population responses to patchy environments, where he stated: "…it is essential that the fabric of spatial scales on which patchiness is expressed be unraveled, and the structure of spatial heterogeneity be related to the variations in environmental states on diverse time scales. The key to achieving this is in shedding our own conceptions of environmental scale and instead concentrating on the perceptions of the organisms, attempting to view environmental structure through their senses." While an organism-centered perspective is central to the multi-scale approach (as discussed below), adopting non-arbitrary, biologically relevant scales for the analysis of species-environment relationships still remains a major challenge today

(Wheatley and Johnson 2009). Analyzing a priori selected biologically meaningful scales (e.g., Schaefer and Messier 1995) or using empirical methods post hoc to chose the best scale(s) (e.g., Thompson and McGarigal 2002) for the organism under consideration is indeed the predominant focus of current multi-scale habitat selection modeling.

Multi-level habitat selection

Building on the previous two conceptual advances, Johnson (1980) solidified these concepts into a multi-scale, hierarchical framework for studying habitat selection. He proposed a four-level framework: 1st order = selection of the physical or geographical range of a species; 2nd order = selection of a home range of an individual or social group; 3rd order = selection of various habitat patches within the home range; and 4th order = selection of specific resources within a habitat patch. This framework is now so widely adopted (or in a slightly modified form, e.g., Meyer and Thuiller 2006) that few recent papers in habitat selection modeling do not explicitly discuss it. Importantly, the Johnson (1980) framework proposes hierarchically organized "levels" of habitat selection wherein changes in spatial/temporal "scale" among levels is implicit rather than explicit (as discussed further below).

Ecological neighborhoods

The concept of "ecological neighborhoods", proposed by Addicott and others (1987), which we consider to be the final foundational idea in modern multi-scale habitat selection modeling, states that "the ecological neighborhood of an organism for a given ecological process is the region within which that organism is active or has some influence during the appropriate period of time." Central to this concept is the idea that each ecological process (e.g., foraging, predator–prey interaction, competition, territorial aggression) has an appropriate neighborhood size (i.e., spatial scale) determined by the time scale appropriate to that process for that organism. The "neighborhood" can be thought of in many ways, but in the context of habitat selection it is useful to think of it as the area within which environmental variation influences habitat selection. Consequently, the neighborhood can take on any size or shape depending on the process under consideration (e.g., selecting a food resource patch or nesting/denning site, selecting a home range, dispersing, etc.), giving rise to the multi-scale perspective. Determining the right neighborhood size(s) is in fact a major focus of current multi-scale habitat selection modeling.

The awakening

We believe that the seminal works described above were all critical to the development of multi-scale habitat selection modeling, but by themselves were not sufficient catalysts. We suggest that a mass "awakening" with respect to the importance of scale in ecology was spearheaded by two pivotal publications. The first was the classic paper by Wiens (1989) on spatial scaling in ecology, in which he captured the essence of this new scale paradigm in his opening statement: "Acts in what Hutchinson (1965) has called the 'ecological theatre' are played out on various scales of space and time. To understand the drama, we must view it on the appropriate scale." In this paper, he described several effects of scale, emphasizing that our ability to discern causal mechanisms and make reliable predictions depends fundamentally on the scale (in space and time) of observation and analysis, and that choosing the appropriate scale(s) is critical for robust inference. More importantly, he presented a multi-scale framework for investigating ecological phenomena (such as habitat selection), emphasizing that the scale of analysis must be matched to the objective and the organism under study, and introduced the concept of "scale domains", which are portions of the scale spectrum within which particular ecological phenomena are consistent. Furthermore, he advocated study designs and analytical methods that would allow researchers to identify these domains of scale, which was essentially a call for multi-scale designs and analytical methods that are the basis for modern multi-scale habitat selection modeling.

The second pivotal publication was the immensely impactful paper by Levin (1992) in which he defined the problem of pattern and scale as the central problem in ecology. He argued that "each individual and each species experiences the environment on a unique range of scales, and thus responds to variability individualistically. Thus, no description of the variability and predictability of the environment makes sense without reference to the particular range of scales that are relevant to the organism or process being examined.” Like Wiens (1989), not only did he call broadly for a “science of scale”, but he provided the ecological rationale and justification for what would become the multi-scale habitat selection modeling paradigm.

Given that several decades have passed since this scale awakening, our goal in this review was to determine how extensively habitat selection modeling research has adopted the multi-scale paradigm, and to describe the perspectives and approaches that dominate its application today. Mayor et al. (2009) subjectively synthesized the literature on habitat selection at multiple scales, while also reviewing and suggesting several analytical approaches for multi-scale habitat selection modeling. We sought to evaluate their assertion that multi-scaled research on habitat selection has proliferated by objectively quantifying the prevalence of multi-scale approaches in habitat selection studies, and also describe the approaches used for multi-scale habitat selection modeling in the 5 years since their review.

Methods

We selected 23 ecological journals most likely to publish papers on habitat selection, including most of the higher impact journals, as well as single taxa-specific journals for mammals, birds, reptiles and amphibians, and insects (Table 1). Next, we conducted a literature search of these journals using Web of Science and the following criteria: years = 2009–2014, and key words = “habitat selection” OR “habitat modelling” OR “habitat modeling” OR “resource selection”. This resulted in 859 papers distributed unevenly among the journals (Table 1), but with a relatively even distribution across years (range 115–165). Based on the abstracts, we determined whether each paper: (1) included some form of quantitative analysis, method development or review of methods in habitat selection modeling, and (2) also used a multi-scale approach (as defined below). This left us with 223 papers for full review, after which we determined that 50 additional papers did not qualify as quantitative and multi-scale. We evaluated the remaining 173 papers according to 36 different attributes organized into five major groups, as described and numbered in the following sections.

Taxonomic focus

We classified each paper to one of the following taxonomic groups based on the primary focus of the study: (1) bird, (2) herp, (3) insect, (4) mammal, (5) plant. There were few other taxa that had only a single paper which we ultimately dropped from the multivariate analysis described below.

Multi-level versus multi-scale

Perhaps the most challenging aspect of our review was determining what to include under the “multi-scale” umbrella and how to categorize the various approaches for addressing scale. Here, we made a critical distinction between multiple “levels” and multiple “scales”, as has been advocated by others (e.g., Mayor et al. 2009; Wheatley and Johnson 2009), as this is a major source of confusion in determining what constitutes multi-scale habitat selection modeling (Fig. 1).

For our purposes (and consistent with Mayor et al. 2009), “level” refers to a constructed organizational hierarchy, wherein either: (a) the environment is treated as being hierarchically structured in space (e.g., forest, stand, tree, and leaf) or time (e.g., annual, seasonal, lunar, and daily light cycles) AND it is assumed that this structure induces a response by the focal organism leading to differential habitat selection across levels; or (b) the focal organism’s behavior is treated as being hierarchically structured in space (e.g., population range, individual annual/seasonal home range, resource patch, and individual resource item, as in Johnson 1980) or time (e.g., generation time, breeding cycle, foraging period, and individual feeding bout) AND it is assumed that different behavioral mechanisms lead to differential habitat selection across levels. Importantly, in a multi-level study, as defined here, each level requires a separate analysis of habitat selection because it is assumed that the mechanisms or processes of habitat selection are different at each level. In addition, all multi-level studies are implicitly multi-scale as well, because as the organizational level changes the absolute scale (in space and/or time) changes as well. We further classified multi-level studies based on whether the levels were defined in the spatial, temporal or spatiotemporal domains, as follows:

Table 1 List of journals searched for papers on habitat selection, habitat modeling or resource selection between 2009 and 2014 and the number of papers deemed either multi-level (and thus at least implicitly multi-scale) or multi-scale as defined in the text

Journal	Number of papers
Journal of Wildlife Management	162
Biological Conservation	76
Journal of Mammalogy	76
Journal of Animal Ecology	71
Ecology	69
Ecography	50
Landscape Ecology	45
Condor	45
Ecological Modelling	43
Journal of Applied Ecology	39
Ecological Applications	37
Biodiversity and Conservation	28
Journal of Herpetology	20
Diversity and Distributions	19
American Naturalist	18
Ecology Letters	15
Journal of Biogeography	14
Conservation Biology	14
Ecological Entomology	9
Ecological Monographs	6
Annual Review of Ecology Evolution and Systematics	2
Frontiers in Ecology and the Environment	1
Journal of Ecology	0

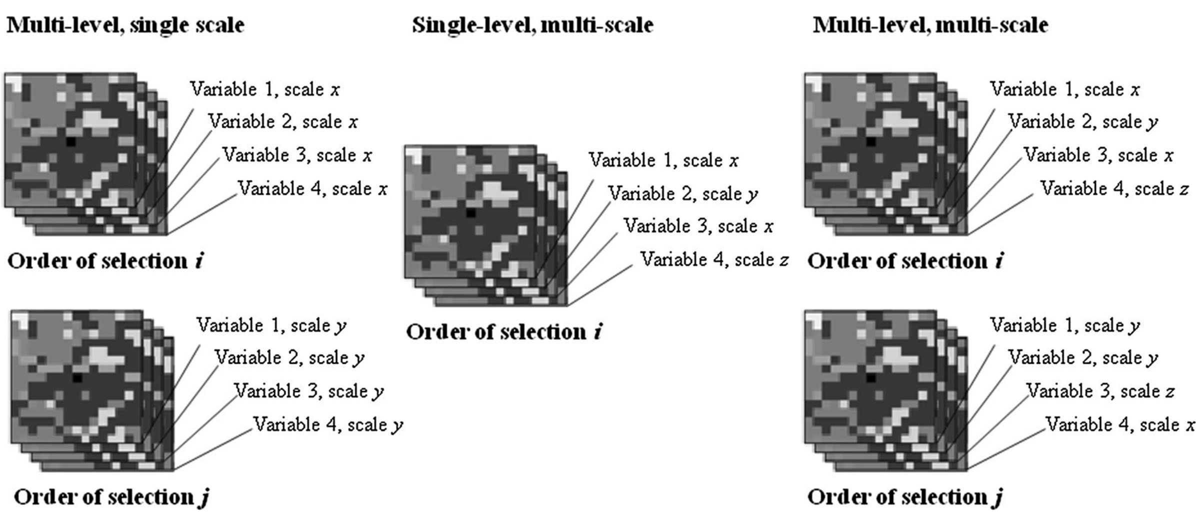

Fig. 1 Conceptual diagram illustrating the distinction among three broad classes of multi-scale habitat selection models: *1* multi-level, single-scale, *2* single-level, multi-scale, and *3* multi-level, multi-scale

(6) *Multi-level in space (mlSpace)* In this design, levels exhibited a clear spatial hierarchy but without a corresponding temporal hierarchy; e.g., when habitat selection was assessed using spatially nested subsets of observations over the same sampling period (e.g., home range

placement within the study area using all the observations, versus selection within the 95 % utilization distribution (UD), versus selection within the 50 % UD).

(7) *Multi-level in time (mlTime)* In this design, levels exhibited a clear temporal hierarchy but without a corresponding spatial hierarchy; e.g., when habitat selection was assessed using temporally nested time periods over the same spatial extent (e.g., seasonal within-home range selection versus annual within-home range selection).

(8) *Multi-level in both space and time (mlBoth)* In this design, levels varied concurrently in both space and time; e.g., when habitat selection was assessed at the species' home range level versus within-home range level, corresponding to Johnson's (1980) level 2 and 3 selection. Importantly, in this approach, as the level increased, not only did the spatial extent of the analysis increase (e.g., from home range to study area) but the observational units for the analysis represented an integration of the raw observational data over some longer time period (e.g., from individual point locations to a collection of point locations accumulated over a longer sampling interval corresponding to, say, a seasonal or annual home range).

Scale, on the other hand, refers explicitly to the grain of observation (i.e., the smallest/shortest unit of observation) and extent of analysis (i.e., the spatial extent or duration over which observations are made), and is typically measured in units of distance, area, volume, or time. Therefore, within a single level (as defined above), a multi-scale study involves the explicit consideration of explanatory variables measured at more than one spatial and/or temporal scale, with many variations on how to choose and analyze relationships across scales, as discussed below. As with multi-level studies, we further classified multi-scale studies based on whether the scales were defined in the spatial, temporal or spatiotemporal domains, as follows:

(9) *Multi-scale in space (msSpace)* In this design, scales exhibited a clear spatial hierarchy; e.g., when habitat variables were measured within concentric ambit radii around used and random locations.

(10) *Multi-scale in time (msTime)* In this design, scales exhibited a clear temporal hierarchy; e.g., when habitat variables were measured over varying time periods (e.g., mean daily maximum temperature versus mean monthly maximum temperature).

(11) *Multi-scale in both space and time (msBoth)* In this design, scales varied concurrently in both space and time; e.g., when habitat variables measured at coarser spatial scales also represented longer periods of time (e.g., habitat along movement paths defined at different detection intervals, such that longer periods between detections resulted in integrating habitat conditions over greater spatial extents).

We also classified studies based on the analytical approach (or strategy) for assessing habitat selection at multiple scales, which we loosely grouped into five classes, roughly in order of increasing complexity, as follows:

(12) A priori *single scale (ms1)* In this study, the investigator pre-selected one scale for all covariates within each level, and thus the study would have to have been multi-level to qualify as "multi-scale".

(13) A priori *separate scales (ms2)* In this approach, the investigator a priori selected a single, but potentially different scale for each covariate, and ultimately included at least two different scales across the suite of covariates, making the analysis technically multi-scale. Importantly, in this approach the investigator made no attempt to empirically determine the best scale for each covariate (as in ms4–5 below), but instead relied on independent information (usually "expert" knowledge of the biology of the focal species) to select an ecologically meaningful scale for each covariate. In addition, each covariate was modeled separately; no attempt was made to combine variables measured at different scales into a single multi-variable model (as in ms3 below).

(14) A priori *multiple scales (ms3)* This approach was identical to ms2 above, except that the explanatory variables, measured at multiple scales represented across variables, were

combined into a single multi-variable, multi-scale model.

(15) *Pseudo-optimized single scale (ms4)* In this approach, the investigator evaluated all covariates simultaneously across a range of scales and used statistical measures to select the single best scale for the model. Importantly, in this approach the investigator used empirical means to determine the best scale (as opposed to ms2–3 above), but forced all covariates to be included at the same scale. Note, we refer to this approach as "pseudo-optimized" because the variables were evaluated at a predetermined and limited number scales (i.e., the solution was constrained by the a priori selected scales). Also, one could argue that since all the covariates entered the final model at the same scale that this was not a truly multi-scale approach; however, we considered any approach that evaluated explanatory variables at multiple scales, regardless of whether multiple scales were retained in the final model, as multi-scale.

(16) *(Pseudo-)optimized multiple scales (ms5)* In the most common version of this approach, the investigator evaluated each covariate separately across a range of pre-specified scales and used statistical measures to select the single best scale for each covariate, and then combined the covariates (at their best univariate scale) into a single multi-variable, multi-scale model. Importantly, in this approach the investigator used empirical means to determine the best scale for each variable (as in ms4 above), but the investigator also allowed the variables to enter the multi-variable model at different scales. Hence, the final model in this approach was truly multi-scale. Note, we refer to this approach as "pseudo-optimized" for the reason discussed above, but also because the best scale was determined univariately based on the variables marginal explanatory power across scales and not multivariately (or conditionally) in the context of the full multi-variable model. In an alternative version of this approach, which we encountered in only two studies, the investigator evaluated all of the covariates simultaneously across a continuous range of scales such that the best scale for each variable was identified conditioned on the other covariates. Importantly, in this approach the investigator did not pre-define a limited set of scales; instead, a numerical optimization algorithm was used to search the multi-dimensional parameter space to find the optimal multi-scale solution.

Data type

We classified each paper based on the type of response variable for the habitat selection assessment: (17) occurrence derived from surveys, (18) occurrence derived from telemetry (or simulated), (19) abundance estimated from either surveys or telemetry, (20) movement path characteristics from telemetry.

Statistical method

We classified each paper based on the primary statistical analysis method used: (21) generalized linear modeling, (22) occupancy modeling, (23) maximum entropy, (24) homerange analysis, (25) Bayesian modeling, (26) compositional analysis, (27) unconstrained ordination analysis, (28) regression tree analysis.

Conditional habitat selection

We classified each paper based on whether habitat selection was analyzed conditional on: (29) species, for studies involving multi-species comparisons; (30) demographic group (e.g., sex, age class, or reproductive status); (31) behavioral state (e.g., resting versus foraging); (32) temporal context, such as activity periods (e.g., diurnal versus nocturnal, or seasonal); and (33) spatial context, such that habitat selection varied with geographic location. With regards to conditional habitat selection, the typical approach was to build a separate model for each class (e.g., species, demographic group, behavioral state, time period or geographic area). However, in some cases the investigator used special analytical methods to deal with conditional habitat selection, including: (34) geographically weighted regression, (35) conditional (or paired, or case-controlled) logistic regression, and (36) individual-based, state-space modeling.

Statistical analysis

Our primary analysis of the 36 attributes listed above consisted of a simple summary of the frequency of papers in each class within each of the five major attribute groups. However, to evaluate patterns of similarity among papers across these characteristics we also conducted a polythetic hierarchical agglomerative clustering (PAHC) analysis. PAHC agglomerates entities based on their multivariate similarity, fusing entities into clusters hierarchically across fusion distances (McGarigal et al. 2000). Given that the characteristics that we recorded for each paper were nominal, we transformed them into 36 binary variables recording whether each paper had that particular characteristic or not. PAHC operates on a distance matrix recording the distances in multivariate space among all entities to be clustered. Given the binary nature of the attributes recorded for each paper, we used the Jaccard distance measure, which is appropriate for binary data given it weights positive matches but not negative matches (Legendre and Legendre 1998), and we used Wards minimum variance fusion strategy to build clusters. We implemented PAHC with the HCLUST function in R. To describe the strength of the clustering structure we computed the agglomerative coefficient using the CLUSTER package in R (Kaufman and Rousseeuw 1990). PAHC depicts the major patterns of clustering but does not describe the characteristics of these clusters (e.g., what is different in terms of the characteristics of papers that make them up). To describe the characteristics of the clusters we used discriminant analysis, which is a multivariate method that defines orthogonal axes that maximally discriminate a priori defined groups based on their multivariate characteristics (McGarigal et al. 2000). To describe the strength of discrimination we computed the Kappa statistic, which is a measure of classification improvement over chance (Cohen 1960), and to distinguish the multivariate attributes that best discriminated among groups we used the discriminant loadings or structure coefficients (McGarigal et al. 2000).

Results and discussion

A complete listing of the 859 papers identified by our search and the results of the complete evaluation of the final 173 papers is included in Appendix A. In addition, we provide a detailed statistical summary of these papers with respect to the full suite of evaluation criteria along with example references from the papers we reviewed in Appendix B. Here, we summarize only what we deem to be the most important finding.

Despite the strong call for multi-scale approaches to the study of habitat selection (Wiens 1989; Levin 1992; Mayor et al. 2009) and the rising interest in scale in ecology since the “awakening” (Schneider 2001), only 20 % (173/859) of the papers published between 2009 and 2014 that met our search criteria qualified as quantitative, multi-scale approaches based on our most liberal definition of “multi-scale” (i.e., including multi-level, single scale studies). Of those papers pursuing a multi-scale approach, there was a clear distinction between two major groups based on the multivariate analysis. Specifically, there was a strong hierarchical clustering of the papers (agglomerative coefficient = 0.94; Fig. 2), with two highly dominant clusters. The discriminant analysis indicated almost perfect separation between these two groups of papers (Kappa = 0.97, $p < 0.001$), largely based on the multi-level versus multi-scale attributes (Table 2). Specifically, the variable loadings and the group means indicated that all papers in cluster 1 were conducted at multiple levels, but with a single scale of analysis at each level (ms1). Conversely, all papers in cluster 2 were conducted at multiple scales of analysis (either ms2, 3, 4 or 5). Thus the main separation between the two dominant clusters were between studies conducted at single versus those conducted at multiple scales. In addition, there was nearly complete separation between clusters for the variables mlspace and mlboth, which are studies that were conducted at multiple levels (with levels defined in space or both space and time, respectively). Thus the two main clusters were conceptually divided into cluster 1 being multi-level, single scale papers (e.g., Indermaur et al. 2009; Tanferna et al. 2013; Beatty et al. 2014) and cluster 2 being multi-scale papers, most of which were single-level (e.g., Pennington and Blair 2011; Poulin and Villard 2011; Jamoneau et al. 2012).

The strength and nature of this two-cluster solution sheds light on the major differences in the context, methods and scope in which multi-scale analysis has been employed in the past several years in habitat selection modeling. Most basically, the clustering shows dramatic separation of “multi-scale” papers

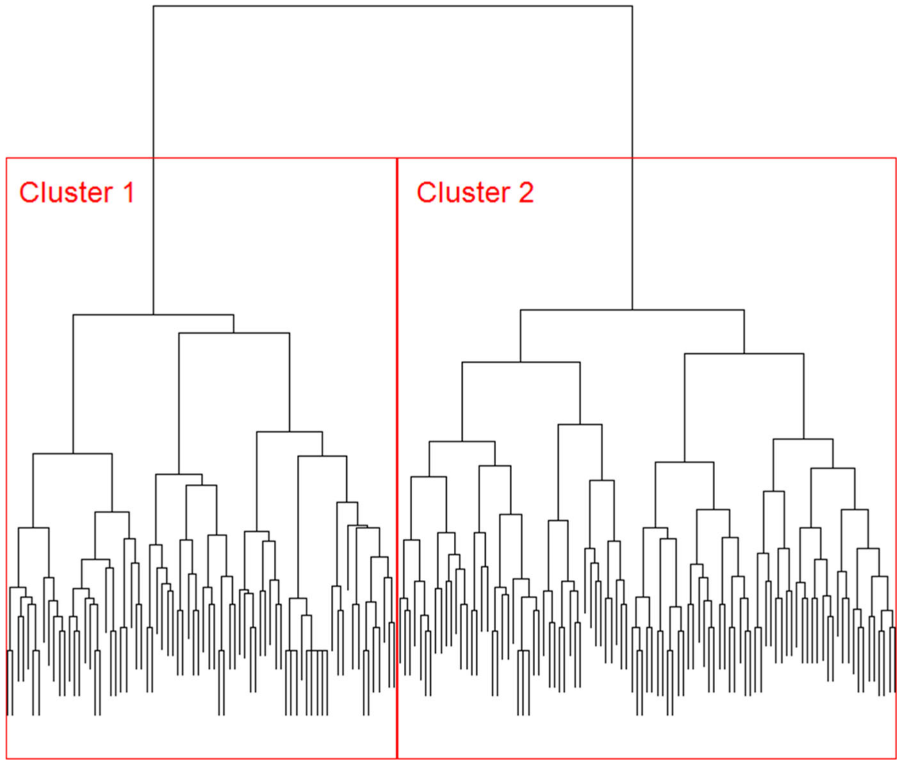

Fig. 2 Polythetic agglomerative hierarchical clustering of 173 habitat selection papers based on 36 evaluation criteria (variables) using Jaccard's dissimilarity coefficient and Ward's minimum variance fusion criterion, with the two dominant clusters enclosed in *red boxes*. Note, the branches of the tree along the *x-axis* represent the individual papers and the height of the tree along the *y-axis* represents the fusion distance (based on Ward's minimum variance) at which papers and clusters of papers aggregated into larger clusters. (Color figure online)

Table 2 Results of discriminant analysis of multivariate differences between the two dominant clusters of habitat selection papers. Polythetic agglomerative hierarchical clustering of 173 papers based on 36 evaluation criteria (variables) produced two dominant clusters. Linear discriminant analysis was used to describe the multivariate differences between clusters. Variable loadings or structure coefficients (i.e., correlation between each variable and the linear discriminant axis) for the variables that best discriminated between clusters (loadings >0.25) are shown

Variable	Description	Loading
mlSpace	Multiple levels in space	0.40
mlBoth	Multiple levels in both space and time	0.43
ms1	A priori single scale for all covariates within each level, and thus the study would have to have been multi-level to qualify as "multi-scale"	0.98
ms2	A priori separate scale for each variable analyzed univariately	−0.43
ms3	A priori separate scale for each covariate (i.e., at least two different scales across all variables) combined into a single multi-variable model	−0.37
ms4	Pseudo-optimized single scale, multi-variable model; multiple covariates at the same scale evaluated across multiple scales to select the best single scale, mult-variable model	−0.28
ms5	(pseudo-)optimized multi-scale, multi-variable model; multiple covariates evaluated separately or jointly across multiple scales and the best scale for each covariate combined into a single multi-scale, multi-variable model	−0.35
msSpace	Multiple scales in space	−0.91
Composition	Compositional analysis (Aebischer et al. 1993)	0.30

into two very distinct groups in the application of multi-scale habitat selection modeling. The first faction, corresponding to cluster 1, we call "hierarchical modelers" after Johnson (1980). The central point that motivates this group's analyses is that habitat is selected at hierarchical levels. In this category we include all papers that are explicitly multi-level (and thus implicitly multi-scale) as described above. The second faction, corresponding to cluster 2, we call "scale modelers" after Wiens (1989). The central point that motivates this group's analyses is that organisms scale the environment differently and that each may respond to each environmental variable at a different scale. Thus, the critical attribute of analyses for scale modelers would be scale optimization, in which each environmental variable included in the model would be evaluated at several scales to find the scale at which the organism most strongly responds. Papers grouped into cluster 2 were universally multi-scale in analysis, and often used optimization methods to identify the best scales of selection. Based on our classification above, only analytical approaches ms4 (pseudo-optimized single scale) and ms5 ((pseudo-)optimized multiple scales) qualify as scale-optimized based on these criteria, because scale type ms4 optimizes the scale of response for all variables simultaneously and chooses the single scale at which the collective of variables has the strongest response, while scale type ms5 optimizes each variable independently or jointly and combines them into a multi-variable, scale-optimized model.

There are several important insights that arise from this categorization. First, a simple difference of proportions test indicates that hierarchical modelers far outnumber scale modelers. For example, 57 % (99/173) of papers that met our most liberal "multi-scale" criteria, as described above, qualify as hierarchical modelers, while only 23 % (40/173) are in the scale modelers group. This difference is highly significant ($X^2 = 40.5$, df = 1, $p < 0.001$). Second, these categories are not necessarily mutually exclusive. That is, it is possible to be both a hierarchical and a scale modeler, for example by implementing a multi-level study with multi-scale optimization at each level (e.g., DeCesare et al. 2012; LeBlond et al. 2011; McNew et al. 2013). Evaluating this intersection we find that scale modelers are much more likely to also be hierarchical modelers than vice versa. Only 12 % (12/99) of multi-level papers also use multi-scale optimization, while 30 % (12/40) of scale-optimized papers also analyze multiple levels ($X^2 = 5.2$, df = 1, $p = 0.023$).

Further insights can be obtained from evaluating a Venn diagram that shows the proportion of all "multi-scale" papers that are: (a) single-level, not scale optimized, (b) multi-level, not scale optimized, (c) single-level, scale optimized, and d) multi-level, scale optimized (Fig. 3). A remarkable 24 % (42/173) of "multi-scale" papers in our review are neither multi-level nor scale optimized. In these papers, a priori single scales were chosen for each variable, and for which only a single level was analyzed. Thus they neither qualify as hierarchical or scale modelers, as we defined them above. The majority (53 %, 91/173) of "multi-scale" papers are multi-level, but not scale optimized. A total of 18 % (32/173) of "multi-scale" papers are single-level and scale optimized. Finally, only 5 % (8/173) of all "multi-scale" papers are both multi-level and scale optimized.

There are several important implications of these observations. First, a multi-level study design is not always warranted, given that many relevant ecological questions do not require analysis at multiple levels (e.g., analysis of habitat selection within home ranges). Thus, it is not necessary for strong inferences in multi-scale modeling to adopt the multi-level framework of Johnson (1980). Conversely, strong inferences in multi-scale modeling do require scale

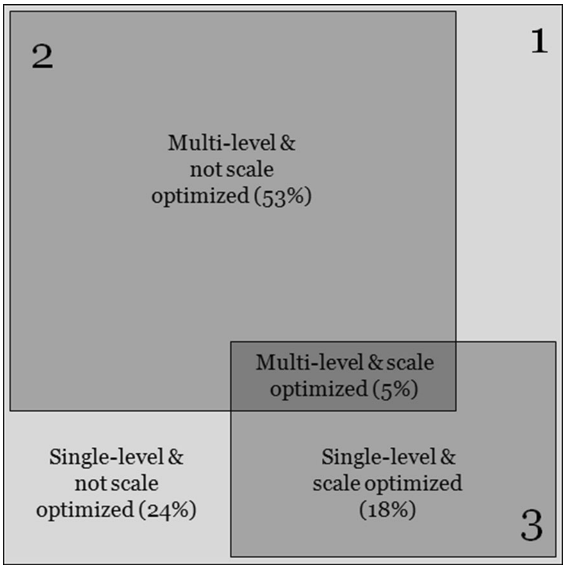

Fig. 3 Venn diagram depicting the proportions of multi-scale habitat selection papers (broadly defined) that are the various combinations of multi-level and scale-optimized. The area of the *square labeled 1* represents the total number of multi-scale papers reviewed (n = 173). The area of the *square labeled 2* represents the number of multi-level papers (n = 99). The area of the *square labeled 3* represents the number of scale-optimized papers (n = 40)

optimization, since each species will scale the environment uniquely and it is difficult to robustly postulate the operative scale for each variable a priori. Indeed, the central lesson to emerge from Wiens (1989) and Levin (1992) and the body of work they inspired is that habitat models that do not optimize scale relationships may produce incorrect inferences regarding the nature and importance of relationships between species responses and environmental variables (e.g., Thompson and McGarigal 2002; Grand and Cushman 2003; Grand et al. 2004; Shirk et al. 2014). Thus, the pattern that emerges from this review is somewhat troubling. It appears that a large portion of the field has adopted a multi-level paradigm without implementing multi-scale optimization of variables within levels. Without multi-scale optimization inferences even from multi-level models are equivocal regarding the influence of scale on species responses.

Collectively these observations convince us of the critical importance of wider adoption of scale optimization methods, particularly by the branches of the field that have typically applied multi-level habitat selection models. Our broad definition of "multi-scale" included any analysis that included multiple levels or measured any variables at different scales. However, scale-optimized models account for less than 25 % of all "multi-scale" habitat papers and less than 5 % (40/859) of all habitat selection papers that we reviewed. Scale optimization we believe is a key step toward robustly assessing the sensitivity of habitat relationships to the scale of analysis and we believe is critical to reliable and clear inferences about how the environment interacts with species perceptions, behavior and population responses. We urge workers in the field to reconsider the importance of multi-scale analysis in general and in particular the critical role that scale optimization plays in obtaining clear and accurate inferences in habitat ecology.

Synthesis and recommendations

Based on our tracings of the conceptual origins of multi-scale habitat selection modeling, our review of habitat selection modeling papers published between 2009 and 2014 (including the statistical summary provided in Appendix B), and building on the previous review by Mayor et al. (2009), we reached several major conclusions regarding the state-of-the-science in multi-scale habitat selection modeling.

First, the seminal works by Stommel (1963), Wiens (1976), Johnson (1980), and Addicott and others (1987), and the critical syntheses on ecological scale provided by Wiens (1989) and Levin (1992) provide a solid conceptual foundation for multi-scale habitat selection modeling. Given this foundation, the frontiers in multi-scale habitat selection modeling lie more on the technical side—for example, finding accessible technical solutions for incorporating the ecological dynamics (i.e., context dependency) of habitat selection into models and the numerical optimization of spatial scales.

Second, although there has been substantial research on multi-scale habitat selection modeling over the past 25 years, it is apparent that the majority of habitat studies still are not using a multi-scale framework. Moreover, the literature is fraught with inconsistent use of terminology pertaining to scale in habitat selection studies. In particular, the conflation of "level" and "scale" in the literature may be distracting investigators from attending to issues of scale. Specifically, investigating habitat selection at multiple levels may be interpreted as fulfilling the objective of a multi-scale assessment, and may lead investigators to neglect multi-scale optimization.

Third, we identified a strong division in the habitat selection literature between so-called hierarchical modelers who apply analyses to multiple-levels of habitat selection and so-called scale modelers who apply some form of scale optimization to identify the characteristic scale of habitat selection for each environmental variable. Generally, hierarchical modelers have eschewed multi-scale optimization within levels, even though such optimization is critical to provide strong inferences about scale dependence in habitat relationships. A very small proportion of all habitat selection papers have applied scale optimization even though most studies that have done so have demonstrated large improvements in predictive power and ecological interpretability of results when scale is optimized.

Fourth, there is a strong and perhaps appropriate emphasis on spatial extent (i.e., varying the ecological neighborhood size) in multi-scale habitat selection modeling studies, but this may have resulted in too little attention being given to the role of spatial grain as well as temporal scale. Very few studies have evaluated environmental variables across different grains, despite the demonstrated sensitivity of habitat selection to spatial grain (e.g., Thompson and McGarigal 2002). In addition, very few studies have incorporated environmental variables measured at different temporal scales. Arguably, temporal scale is more difficult to address for practical reasons owing to data limitations. For example, whereas it is relatively easy to quantify environmental conditions across different spatial neighborhood sizes, it is much more difficult to assess environmental conditions at a location across different temporal extents, since the temporal resolution of most extant environmental data is limited. Nevertheless, it is important to recognize that just as organisms have the ability to perceive environmental conditions over varying spatial scales, they also have the ability to perceive environmental conditions over varying temporal scales. For example, memory allows individuals to act on the basis of previously experienced conditions (e.g., Avgar et al. 2013). Overall, multi-scale habitat selection modeling studies have not examined habitat selection comprehensively across spatiotemporal gradients in both grain and extent.

Fifth, there is a strong and perhaps appropriate emphasis on predicting species occurrence in multi-scale habitat modeling studies, but this may have resulted in too little attention being given to other measures of individual performance, such as survival and reproduction. Indeed, very few studies have attempted to couple multi-scale habitat selection with population dynamics. This may be due to the practical difficulties of obtaining data on population demography, but it may also reflect a lack of attention to scale in population modeling compared to species distribution modeling.

Sixth, there are myriad analytical approaches and statistical modeling methods now available for multi-scale habitat modeling. Among the varied approaches, a resources selection function (RSF) analyzed in a generalized linear modeling (GLM) framework is the most popular, given it is both intuitive and flexible (see Appendix C for a detailed description of alternative multi-scale approaches for RSFs). RSFs can accommodate data in a wide variety of forms, including observations representing point locations, movement steps, movement paths, and home ranges. Moreover, GLMs can accommodate a wide variety of response variables (e.g., occurrence, counts, density, and other discrete and continuous measures of individual performance). A particularly appealing aspect of GLMs is the relative ease of incorporating a hierarchical or multi-level structure to the model, which has been used prominently to account for non-independent observations, detectability, spatial structuring processes, and context-dependency. Moreover, the likelihood-based framework of GLMs has facilitated the use of model selection methods based on Information Criteria (e.g., AIC) to contest models representing different scales of habitat selection. Other continuum-based approaches such as those reviewed by Mayor et al. (2009) and individual-based, multi-state models (Patterson et al. 2008) also hold great promise but have yet to achieve widespread use in multi-scale habitat selection modeling studies.

Lastly, the studies we reviewed confirmed the conclusions reached by Mayor et al. (2009) regarding the importance of scale in habitat selection. First, and most importantly, habitat selection is scale-dependent. Indeed, questions of habitat selection cannot be answered without either implicit or explicit consideration of scale, since determining the disproportionate use of resources or environmental conditions requires measurements of those resources or environmental conditions, and measurement implies scale. However, these studies also affirm that it is not sufficient to simply select a scale for measurement, since habitat selection measured at one scale is often insufficient to predict habitat selection at another scale (Wheatley 2010; Norththrup et al. 2013). Thus, conducting a habitat selection study in a scale-explicit manner is necessary, but not sufficient. Second, different species select habitat at different scales and, moreover, individuals may select different habitat components at different scales. Therefore, there is no single correct or "characteristic" scale at which to undertake research on habitat selection (Wiens 1989; Holland et al. 2004). Given the complex, multi-scaled nature of habitat selection, it is often impossible to pre-select the best scales for measurement and analysis. Thus, it is preferable to use multi-scaled approaches coupled with empirical means to determine the characteristic scale(s), within limits (Meyer and Thuiller 2006). Indeed, such approaches generally produce superior results than single-scale approaches (e.g., Boscolo and Metzger 2009; Kuhn et al. 2011; Sáncheza et al. 2013; Zeller et al. 2014, although see Martin and Fahrig 2012). Third, not only is habitat selection species-specific and scale-dependent, but it can also be context-dependent. Specifically, selection of habitat can depend on demographic class, behavioral state, and/or location in space and/or time. An important finding in this regard is that selection for or against particular resources or environments can depend on whether they are limiting in a particular area or at a particular time. Consequently, a study conducted at a place where and/or time when a particular environment is not limiting may suggest that selection is neutral for that condition, when in fact the spatiotemporal context of the study could be masking a strong selection for that condition where or when it is limiting (e.g., Cushman et al. 2011, 2013).

Based on the conclusions above, we offer the following recommendations to guide future studies involving multi-scale habitat selection modeling:

(1) Adopt a consistent conceptual framework and terminology for referencing multi-scale habitat selection modeling studies, with particular attention to distinguishing between multi-"level" and multi-"scale" studies. Although distinguishing between levels and scales can be difficult, we believe that doing so will promote attention to multi-scaled approaches within levels.

(2) Clearly define the level(s) of habitat selection under investigation, with explicit attention to distinguishing among multiple levels in both space and time, and justify the definition given the research question. Although any hierarchically organized scheme for defining levels is acceptable, the use of Johnson's (1980) hierarchy (or widely adopted modifications of it, e.g., Meyer and Thuiller 2006) will facilitate cross-study comparisons.

(3) For each level of habitat selection under investigation, make the scale(s) of measurement and analysis explicit with regards to grain and extent in space and time (and easy for the reader to identify), and provide a biological and/or empirical justification for the choices of scale(s).

(4) For multi-level studies modeling occurrence in a GLM framework, consider sampling used and available locations in a hierarchically nested manner that ensures the conditionality of the predicted values across levels so that the single-level results can be combined into single multi-level RSF, as in DeCesare et al. (2012). Such approaches that integrate selection across levels into a single spatial depiction of habitat may best facilitate conservation (Storch 2003).

(5) Whenever possible, evaluate multiple scales of selection within a level. Specifically, measure the resources and/or environmental conditions at an appropriate range of scales (in space and time, as appropriate), and use empirical methods to compete the scales against each other to identify the best scale for each covariate. Ideally, allow each variable to enter the final model at a different scale, producing a truly optimized multi-scale, multi-variable model. In addition, provide a biological and/or empirical justification for the range of scales or specific scales evaluated. Even when a priori biological knowledge suggests a particular scale for one or all of the explanatory variables, there is likely enough uncertainty to warrant an optimized multi-scale evaluation.

(6) Whenever possible, use a true optimization approach (i.e., one that doesn't require a priori selection of discrete scales) to identify the best scale(s) for each covariate in the final single-level model. While truly optimized multi-scale methods exist for certain limited applications (e.g., Guenard et al. 2010; Latombe et al. 2014), for many applications suitable methods do not yet exist or are not yet readily accessible to a wide range of ecologists. In the interim, it may be sufficient to use a pseudo-optimized multi-scale analytical approach in which the covariates are evaluated across a sufficient range and number of discrete scales univariately and then combined into a single, multi-scale model. Nevertheless, developing better and more efficient technical solutions to scale optimization is an important frontier.

(7) When conducting a multi-scale analysis within a level compare the results of the multi-scale approach to the best single-scale approach. Few studies have conducted such formal comparisons, and although the majority of studies that have done so have shown the multi-scale approach to be superior, there is much still to be learned about the conditions under which a single-scale approach may be sufficient or even superior (e.g., Martin and Fahrig 2012).

(8) Consider the context-dependency of habitat selection when designing a study and analyzing the data. Specifically, consider the potential for habitat selection to vary among demographic groups, behavioral states, and/or location in space and time. Accordingly, consider designs and analytical approaches that allow habitat selection to be quantified in a context-dependent manner. A simple approach is to fit separate models for each unique context (e.g., each behavioral state, study site, or time period). A more complex approach is to use analytical methods that allow for continuously varying context, including methods such as conditional logistic regression and individual-based, multi-state modeling. In particular, consider approaches that allow the choice of predictors, their effect sizes and, importantly, their characteristic scales to vary with the context, as in Shirk et al. (2014).

(9) Lastly, if you think like the focal species, a multi-level, multi-scale (and scale-optimized) approach will almost certainly emerge as best way to evaluate habitat selection.

Acknowledgments This work was supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-0907995 (Zeller) and the Joint Fire Sciences Project # 12-1-06-56 (Wan, Timm, McGarigal, and Cushman). This manuscript was also improved by the suggestions of several anonymous reviewers.

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