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Original Research Article

Scale relativity of species-habitat models

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ABSTRACT

Scale has been identified as a central unifying concept in ecology, yet few empirical studies examine its importance *per se* when quantifying species-habitat relationships. Means and associated variances of ecological variables are known to aggregate unpredictably among observational scale sizes; however, the empirical implications of these scaling effects remain to be fully examined when building and interpreting species-environment models. Here we explore scale-based modeling implications using radio-telemetry data of adult and dispersing-juvenile northern flying squirrels linked to LiDAR-derived fine-grain forest structure data. We construct and rank the same set of candidate species-habitat models across a continuum of 14 biologically relevant observational scales to examine whether scale alone can affect species-habitat model selection. Our results demonstrate differential relative model support (via AIC weights) whereby upwards of seven different “best models” can be generated with varying levels of support entirely contingent upon the scale within which they were quantified. Further, we show this effect to be different for male, female, and dispersing-juvenile animals. We conclude that a continuum-based approach and an understanding of model relativity among scales is a fundamental but absent step in the building and interpretation of most multi-scale ecological models.

1. Introduction

Scale has been espoused as the central, unifying issue in ecology (Levin, 1992), and fundamental to all ecological investigations (Wiens, 1989). It is defined ecologically as “the spatial or temporal dimension of an object or process, characterized by both grain and extent” (Turner et al., 1989; Gustafson 1998; Dungan et al., 2002; Schneider 2001). Several authors have urged for more focus on scale *per se* (Sandel and Smith, 2009 and references therein) including the addition of scale as an explicit factor in investigations (Meentemeyer and Box, 1987; Weins, 1989; Wheatley, 2010; Laforge et al., 2015), and recent reviews consistently identify scale as fundamental to research design and interpretation (Wheatley and Johnson, 2009; Jackson and Fahrig, 2015; McGarigal et al., 2016). Nonetheless, our general understanding of scale in ecology remains limited, a fact evidenced by its continued uninformed use in study design (Wheatley and Johnson, 2009; McGarigal et al., 2016), even though the empirical implications of scale to any ecological investigation are potentially profound (e.g., de Knegt et al., 2010; Wheatley, 2010; Lechner et al., 2012; Martin and Fahrig, 2012).

There are two central scale issues that require much examination: (1) how ecological variables and their associated variance quantify along a scale continuum, and the implications any scaling effects (or lack thereof) have on ecological investigation (e.g., Wu, 2004; de Knegt et al., 2010; Wheatley, 2010), and (2) how observational scale affects the selection and interpretation of ecological models. As the former has been addressed in some detail elsewhere (e.g., Wheatley and Johnson, 2009, de Knegt et al., 2010; Wheatley, 2010) herein we focus on the latter using an applied example in species-habitat modeling, a field of study where issues of scale or data aggregation are ubiquitous yet under-examined or entirely overlooked.

In species-habitat modeling, ecologists first must choose an observational scale; namely a grain, extent, or time-step within which to group their observations. This scale choice has implications for both means and variances of sampled metrics, an effect commonly referred to in the geographical sciences as the modifiable area unit problem, or MAUP (Wrigley, 1979; Jelinski and Wu, 1996). Generally the MAUP indicates that, depending on how a researcher chooses to aggregate their observations, different variance structures can be produced from the same data contingent upon observational scale (e.g., Fig. S1). Because different variance structures are associated with scale, we must then expect different mathematical relationships between dependent and independent variables as a function of scale; and it then becomes an insightful exercise, both methodologically and ecologically, to explore model fit and selection for the same set of models among observational scales. Such explorations have only started to emerge as methodology

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in model development as attempts to eliminate the scale issue (e.g., DeCesare et al., 2012; McGarigal et al., 2016), but these remain uncommon and their implications arguably underappreciated.

For example, such methods have been advocated within a univariate context whereby uni-variable models are competed against each other amongst scales, and the scales with the best uni-variate model support are then combined into a global multi-scale multi-variable model (e.g., McGarigal et al., 2016). This approach is appealing and intuitive, particularly where dependent variables are categorical or non-continuous and thus non-scalar, thereby enabling an examination of how independent variables scale while effectively holding the response variable constant (e.g., logistic and multinomial regressions). Examples of this approach have emerged though remain relatively uncommon (e.g., DeCesare et al., 2012; McGarigal et al., 2016) as researchers claim to have transcended scale dependency or to have effectively removed scale as a lurking variable in their multi-variate analyses. However, by doing so issues of scale still abound, if not become amplified.

The uni-variate approach described above requires two important and, we argue, tenuous assumptions. First, researchers must be willing to overlook the basic parametric assumption of equal sampling probability from a defined population for both dependent and independent variables. In a uni-variate multi-scale approach, because each variable can be sampled from a different scale (i.e. variable-specific smaller or larger observational scales), one effectively creates different sampling probabilities from different sized sampling populations (amongst scales) and then forces these into the same model. The individuals sampled amongst each variable do not have equal probabilities of being sampled, and the populations for each variable are each defined differently as a function of scale (i.e., observational extent or size); some populations will be smaller, while others much larger thereby achieving more data explorations than *a priori* hypothesis testing. Second and more importantly, this approach requires that the dependent variable is scale-independent, enabling an exploration of independent-variable scale effects while holding variation associated with the dependent variable constant. However, aside from logistic or multinomial contexts, variation associated with most dependent variables is also a function of scale. Whenever dependent variables are continuous and spatially explicit (e.g., energy budgets, behavioral metrics, wildlife-telemetry data, etc.) then the choice of scale becomes important to both dependent and independent variables, and scale issues quickly become complex (e.g., Fig. 1). In these contexts and because the MAUP *de facto* applies to both dependent and independent variables, uni-variate scale optimization (e.g., McGarigal et al., 2016) or scale transcendence (e.g., DeCesare et al., 2010) becomes difficult to interpret both mathematically and ecologically and, particularly in multi-variate multi-model contexts, is better replaced with a continuum-based approach.

By contrast, a continuum-based approach is where multiple scales are examined relative to each other along a relevant section of the scale continuum, and where both dependent and independent variables are re-calculated for each scale examined. That is, within each scale the same set of candidate models for all proposed hypotheses are included, whereby any changes in relative model support can be compared among scales. This model-relativity continuum-based approach requires that the data feeding all models at a single scale are quantified at that same scale, both adhering to sampling-based parametric assumptions and enabling both independent and dependent variables to scale accordingly. This approach assumes *a priori* that, because variables are known to quantify unpredictably contingent upon scale, then relative multi-variate candidate-model support (e.g., ROC scores, AIC weights, etc.) will also change across scales, whereby the best-ranked model at scale A may not be the best-ranked at scale B. Because of the emergence of the uni-variate approach described above (e.g., also see Holland et al., 2004), the scale-continuum approach has not been applied to species-environment modeling, but would add considerable insight into whether scale is a lurking variable, and would also enhance a researcher's ability to provide an ecological interpretation of their results.

Within the context of scale, this ecological interpretation is important because an individual animal's perception of scale (*sensu* Weins, 1989; Levin, 1992) should be different depending on their species, sex, and their life-history stage. In other words, not all aspects of an animal's biology can be observed using one observational scale. Different observational scales are often required to examine or compare (say) local foraging movements versus natal dispersal movements. For example, scale-based perception of habitat structure should differ for a dispersing juvenile exploring adjacent-habitat areas and looking to leave the natal home range versus a lactating female who is staying close to a single nest site nursing altricial young, versus an independent male foraging or searching for mates. Each life-history stage has different spatial requirements, and these will be scale-dependent. That is, if we quantified habitat associations for dispersing juveniles using the same observational scale as for maternal females, not only might we be overlooking the lurking variable of scale, but our interpretation of our subsequent results may be confounded and misled; for expecting meaningful habitat-relationships to surface for a dispersing juvenile when examining this through a scale more relevant to a post-partum female is naive.

These are practical sampling reasons for using multiple observational scales, but there is also a fundamental theoretical reason that receives almost no attention: namely, the ability to predict patterns and processes across scales (Wheatley and Johnson, 2009). Cross-scalar predictability should be the paramount question in scalar ecology, but is missing from almost all multi-scale studies, and is a concept in jeopardy with the recent advent of optimized-scale models. Cross-scale predictability is not a new concept. Wiens (1989), for example, clearly outlined why the identification of “domains of scale” is key to our understanding of ecological systems contending that if the scale spectrum is not variable (i.e. every change in scale does not bring with it changes in patterns and processes), there may be domains of scale over which patterns and processes are predictable. If we can predict how observations will change among domains (the space between known break-points in pattern or process), we may be able to extrapolate observations among scales. However, if we optimize our predictive models by combining variables from disparate scales into one global model, then cross-scale predictability is lost as we attempt to control or remove scale as an analytical issue, rather than understand it as a key aspect of ecological investigation and model interpretation.

Here, we demonstrate the importance of directly examining scaling effects (rather than attempting to remove or control them) using a continuous-dependent variable of telemetry-based activity budgets collected from northern flying squirrels (*Glaucomys sabrinus*), with independent habitat-structure variables derived from Light Detection and Ranging (LiDAR) data along a biologically relevant range of the scale continuum. This squirrel-LiDAR system is particularly well-suited to examine a continuum-based approach to species-habitat modeling. LiDAR-derived habitat data enable habitat features to be quantified from the same data source across many scales, facilitating a true multi-scale approach and avoiding a non-scalar multi-design approach (i.e., see Wheatley and Johnson 2009). Additionally, in this system both the independent and dependent variables scale, whereby changes in observational scale result in different amounts of squirrel-telemetry points aggregating amongst spatial scales. Northern flying squirrels are relatively easy to capture and radio-collar, too, enabling an examination of whether scaling effects are similar among sexes and between adults versus dispersing juveniles when scale-based habitat perceptions would be most prominent and ecologically relevant.

Our analysis has two main objectives. The first is to empirically demonstrate a continuum-based approach to species-habitat model selection, combining the scaling effects of both dependent and independent variables into one scale-relative analysis. Based on the unpredictable nature of the scale continuum observed elsewhere (Wheatley, 2010) we predict that observational scale will greatly