SPECIAL FEATURE

Scale for resource selection functions

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ABSTRACT

Resource selection functions (RSFs) are statistical models defined to be proportional to the probability of use of a resource unit. My objective with this review is to identify how RSFs can be used to unravel the influence of scale in habitat selection. In wildlife habitat studies, including radiotelemetry, RSFs can be estimated using a variety of statistical methods, all of which can be used to explore the role of scale. All RSFs are bounded by the resolution of data and the spatial extent of the study area, but also allow predictor covariates to be measured at a variety of scales. Conditional logistic regression permits designs (e.g. matched case) that relate the process of habitat selection to a limited domain of resource units that might better characterize what is truly 'available' to the animal. Scale influences the process of habitat selection, e.g. food resources are often selected at fine spatial scales, whereas landscape patterns at much larger scales typically influence the location of home ranges. Scale also influences appropriate sampling in many ways: (1) heterogeneity might be obliterated (transmutation) if resolution or grain size is too large, (2) variance of habitat characteristics might be undersampled if extent or domain is too small, (3) timing and duration of observations can influence RSF models, and (d) both spatial and temporal autocorrelations can vary directly with the intensity of sampling. Using RSFs, researchers can examine habitat selection at multiple scales, and predictive models that bridge scales can be estimated. Using Geographical Information Systems, predictor covariates in RSF models can be measured at different scales easily so that the predictive ability of models at alternative spatial and temporal domains can be explored by the investigator. Identification of the scale that best explains the data can be evaluated by comparing alternative models using information-theoretic metrics such as Akaike Information Criteria, and predictive capability of the models can be assessed using *k*-fold cross validation.

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INTRODUCTION

Resource selection functions (RSFs) can be used to characterize the distribution and abundance of organisms (Boyce & McDonald, 1999; Manly *et al*., 2002; Nielsen *et al*., 2005). More broadly, overlays of RSFs for multiple species can be used to predict species diversity at a site (Nielsen *et al*., 2003). Likewise, species interactions in space can be modelled using RSF (Johnson *et al*., 2000; Hirzel & Le Lay, 2006). For example, RSFs have been used to map a predator and prey on the same landscape to identify habitats where encounters are likely to occur between predator and prey (Hebblewhite *et al*., 2005). Scale is a fundamental consideration in RSF studies because (1) the scale of the sampling scheme influences the strength of habitat associations, and

(2) ecological processes including habitat selection can occur on different spatio-temporal scales. RSFs are especially convenient structures for studying the influence of scale on habitat selection because they offer a framework that can be used to bridge spatio-temporal scales.

A RSF is defined as any function that is proportional to the probability of use (Manly *et al*., 2002). In context of scale, RSFs allow a mixture of sampling scales for covariates to be included in the same model. In the extremes, scale must be defined relative to: (1) resolution or grain, and (2) domain or extent (Turner *et al*., 2001). Resolution reflects how finely a resource unit or covariate is measured and often is limited by available data, e.g. a 30-m pixel. Resolution clearly limits the precision of spatial predictions, which appears to be especially important for

landscape-structure variables. The availability of data and feasibility of data collection can limit the resolution at which an investigation might take place.

Domain or extent is the size of the area under investigation. In some cases consistent patterns of habitat selection occur across spatial domains (Schaefer & Messier, 1995; Resetarits, 2005), but in other instances RSFs might vary substantially among scales, and the particular choice of domain depends on the objectives of the study (Boyce *et al.*, 2003). Fish predators have been shown to influence habitat selection by tree frogs at both regional and local scales leading Resetarits (2005) to conclude that habitat selection is 'a critical link between local communities and the regional dynamics of metacommunities in complex landscapes'. However, I caution that the scale at which habitat selection is measured can influence apparent species interactions. For example, mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) interactions were studied at different scales in Colorado (Whittaker & Lindzey, 2004). Although one might have concluded potential competitive interaction based on fine-scale selection of diet, seasonal spatial segregation at a larger scale showed that there was little potential for competitive interaction between the two species.

Beyond the scale components of resolution and extent, sample units can include covariates measured within buffers of arbitrary size. For example, we might characterize vegetation type as a discrete variable within a 30-m pixel, but road density within a 1-km radius buffer as a continuous variable. Such buffers can be useful for characterizing the context of a resource unit, for example, the configuration of vegetation patches can be quantified using FRAGSTATS (McGarigal & Marks, 1995) or other spatial pattern metrics (Perry *et al.*, 2002), and these context metrics can be used as covariates in the RSF model. For organisms with large area requirements, buffers might need to be large depending on the scale of the ecological processes influencing the use of a resource unit and the spatial pattern in vegetation (Johnson *et al.*, 2004b). For example, landscape heterogeneity measured at large spatial scales, even larger than the home range, appears to be necessary to characterize habitat selection by mule deer (Kie *et al.*, 2002).

My objective in this paper is to highlight the importance of scale in RSF investigations and to suggest some analysis protocols that allow efficient examination of the role of both temporal and spatial scales in habitat studies. Although in my outline I discuss temporal and spatial scales separately, these two dimensions are not independent. For example, body size is related to home-range area and longevity (Calder, 1984), i.e. space and time, so we might expect investigations for large animals to require large spatial and long temporal scales. Integrating time and space considerations, methods have been proposed to use movement rates to identify appropriate spatial scales of analysis for RSFs (Nams, 2005), e.g. identifying habitats used for foraging vs. interpatch movement (Johnson *et al.*, 2002).

SAMPLING DESIGNS

The scale of an RSF and the appropriate statistics for analysis are fundamentally tied to the sampling design. Manly *et al.* (2002)

provide a comprehensive review of alternative sampling designs for estimating RSFs. I will focus discussion on two designs that are most common in wildlife habitat studies: (1) used/unused or presence/absence designs, and (2) use/availability or presence/pseudo-absence designs (Pearce & Boyce, 2006). Scale can be studied using either of the two designs — primary differences relate to the feasibility of field sampling and the particular data available.

In the first design, a random sample of resource units is drawn, and each is inspected for the presence (= 1) or absence (= 0) of a species. Typically a generalized linear model (GLM) or a generalized additive model (GAM) would be used to estimate a resource selection function (Manly *et al.*, 2002; Hirzel & Le Lay, 2006). A special case of presence/absence is the case-control design where intensity of sampling of used and unused resource units is not random (Keating & Cherry, 2004).

One of the common difficulties with a presence/absence design is called an 'asymmetry of errors' where presence is observed and thereby known with certainty, but absence can be difficult to evaluate (MacKenzie, 2005). Temporal scale of sampling can be crucial to the correct detection of absences, because repeated sampling over a longer time might result in the detection of a presence in a resource unit where the species was initially absent (Johnson *et al.*, 2006). This may not a problem if the spatial and temporal domains of the study are carefully specified. For example, birds might be sampled using time–area counts for 12 min at sampling locations visited once during the month of June. But having to restrict the domain of application for the RSF might limit applications, for example if the objective is to characterize the habitats used by a species for purposes of distribution mapping.

Problems associated with accurately characterizing unused resource units or absences often are thought to be a particular problem for animals because they move around. However, I believe that the same problems exist for modelling plant distributions, typically at a much slower temporal scale. Many plants can exist for years in the seed bank, germinating after heavy rains or when conditions are otherwise favourable. Likewise many species of plants may exist undetected until a major disturbance resets the successional process. Clearly detection error can influence estimates of RSF models based upon presence/absence data (Gu & Swihart, 2004), and in some circumstances adjustments for detection bias are possible (Frair *et al.*, 2004).

The second design involves contrasting a sample of resource units where the species is known to occur (= 1) with a random sample of 'available' resource units (= 0) drawn without replacement within the domain of the area of study. We often assume an exponential or log-linear structure for an RSF:

$$\text{RSF} = w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + ... + \beta_k x_k) \tag{1}$$

for a vector x of k predictor covariates. The model coefficient, β_i, for the i-th habitat covariate, x_i, can be estimated using the corresponding coefficient from logistic regression so long as used resource units are relatively rare on the landscape (Manly *et al.*, 2002).

However, the RSF for a used/available design is best interpreted as a logistic discriminant function assuming a ratio of density functions for used (f_u) and available (f_a) resource units of the form (Seber, 1984: pp. 308–317):

$$\frac{f_u(x)}{f_a(x)} = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k), \qquad (2)$$

where again we estimate k model coefficients as in equation 1 using logistic regression (Keating & Cherry, 2004). The primary distinction here is that used and available resource units are drawn with replacement, and a resource unit is allowed to appear in both the used and available samples (Johnson *et al.*, 2006).

The form of the RSF model is flexible allowing polynomial terms and/or interaction terms. For example, for two covariates with both linear and squared terms for the first variable and an interaction between variables we would write:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2 + \beta_4 x_1 x_2) \qquad (3)$$

This approach is functionally identical to the distribution modelling used by plant ecologists where available points are labelled pseudo-absences (Pearce & Boyce, 2006), and is a common approach for analysing radiotelemetry data in wildlife studies (Mao *et al.*, 2005). As a caveat, the probabilities obtained from a logistic regression equation are not the appropriate values for such a used/available design (Manly *et al.*, 2002: p. 100) and one should use the exponential form of the $w(x)$ instead (eq. 1 or 2) to estimate values that are *proportional* to the probability of use. The RSF does not yield a discrete classification but rather a relative probability of use which is continuous. Also, the usual statistical methods for evaluating logistic regression are not appropriate for such a use-availability design, and the predictive ability of these models is best evaluated using k-fold cross validation (Boyce *et al.*, 2002; Johnson *et al.*, 2006). Using this method, models built using alternative scales can be compared by how well they predict patterns of use (distribution frequency) on the landscape.

A variation on the use/availability design is where the patterns of use on the landscape are characterized by a utilization distribution (UD), e.g. an adaptive kernel home-range estimator (Marzluff *et al.*, 2004). With this method the response variable becomes the intensity of use of a resource unit (pixel) from the UD, and a GLM is used to model the influence of predictor covariates as in the RSF. Such a resource utilization function (RUF) eliminates fine-scale resolution in occurrence data to a varying degree depending upon the magnitude of the smoothing parameter in the utilization distribution.

Yet another approach that has been used to study scale effects on habitat selection with use/availability data is ecological niche factor analysis (ENFA; Hirzel *et al.*, 2002). Again, predictor variables are measured at used sites and at random landscape locations. But no model-selection protocol is followed with ENFA and all predictor variables are retained in the model. A multivariate characterization of the sets of variables is obtained, and interpretation is based on how the predictor variables are loaded into factors or summary axes. By including variables measured at three spatial scales and examining how these variables loaded into an ENFA for bearded vultures (*Gypaetus barbatus*), Hirzel *et al.* (2004) were able to evaluate the importance of habitat selection at the three scales.

CHARACTERIZATION OF ABUNDANCE USING RSFS

Habitat models can be linked to population models, using the RSF to distribute individuals in a population across the landscape (Boyce & McDonald, 1999). However, scale is of crucial importance and can have large influence on population estimation. If grain size of the spatial sampling unit is fairly small so that few individuals are likely to occur within a single resource unit (pixel), the Boyce and McDonald (1999) method should yield reasonable results. However, if resource units are large so that a number of individuals might occur within a single resource unit, RSFs estimated using logistic regression might not be suitable. Instead, one could use a zero-inflated binomial model, with no guarantee that the ecological variables that determine occurrence in a resource unit will be the same variables that influence abundance within resource units (Nielsen *et al.*, 2005). As in any such study using GLMs, one should examine the data to assess which model is most appropriate. GLM links known to work well depending on the observed shape of the distribution of the data include the Poisson, zero-inflated Poisson (Ripley *et al.*, 2005), zero-inflated negative binomial (Nielsen *et al.*, 2005), or sometimes even ordinary least-squares linear regression (Radeloff *et al.*, 2000).

Abundance–occupancy relationships vary with colonization rate and the spatial distribution of habitats. When colonization rates are high, patterns of abundance and occupancy tend to be similar although usually not linear (Gaston *et al.*, 2000; Freckleton *et al.*, 2005). But with low to moderate rates of colonization, as in metapopulations, large-scale patterns can be complicated by local population processes such as local extinctions (Freckleton *et al.*, 2005). Such mechanisms can result in RSF models predicting a relative probability of occurrence that might be poorly correlated with the spatial pattern of abundance (Nielsen *et al.*, 2005), although not necessarily (Ripley *et al.*, 2005).

TEMPORAL SCALE

The temporal scale of sampling designs, involving both grain and extent, can be of crucial significance for the interpretation of RSFs. Often, for example, habitat-use patterns vary seasonally requiring that separate models be estimated for each season (Nielsen *et al.*, 2003, 2004). Bridging temporal scales might be necessary, e.g. winter habitats are important determinants of summer territory selection by yellowhammers (*Emberiza citronella*; Whittingham *et al.*, 2005). In addition, habitat-use patterns can vary depending on the time of day, thereby requiring careful specification of the temporal scale of sampling (Beyer & Haufler, 1994; Nielsen *et al.*, 2004). Radiotelemetry based on traditional VHF transmitters often involves sampling only during daylight hours, whereas new GPS-radiotelemetry permits

locations to be recorded at any hour. Likewise, because GPS-telemetry yields much more location data (fine grain) than VHF radiotelemetry, home-range size might be considerably larger than would be estimated with VHF-telemetry. This technologically induced change effectively alters the sampling domain in within-home-range analyses of habitat selection (Arthur & Schwartz, 1999).

A less obvious aspect of temporal scale is that different habitats might be selected in different years. Habitat selection can be influenced by events such as fires or hurricanes that altered vegetation many years previously. Thus, different RSFs might apply depending on environmental conditions. For example, in roe deer (*Capreolus capreolus*) habitat selection was weak during good years when preferred forage was widely available and survival did not vary with food availability among sites. However, animals that selected sites with preferred plants enjoyed significantly higher survival during drought years (Pettorelli *et al.*, 2005). To capture such patterns spanning multiple years, sampling must be on a temporal scale of sufficient duration to understand the significance of habitat selection that varies through time.

SPATIAL SCALE

Identifying the appropriate resolution or sample-unit size requires a detailed understanding of a species' ecology, and several studies have demonstrated that different ecological processes may function at different scales (Bissonette *et al.*, 1997; Mysterud *et al.*, 1999b; Anderson *et al.*, 2005). The size of sample units can have a large influence on attributes of habitat as well as population parameters, with large grain size effectively averaging out spatial heterogeneity occurring at finer resolution (Bowyer *et al.*, 1996). To select the size of sample units that best explains distribution, model-selection methods can be used to select among RSFs with alternative buffer sizes within which habitat covariates are measured. For example, in a study of the northern spotted owl (*Strix occidentalis caurina*) sample unit size was identified by measuring habitat covariates within buffer rings (like doughnuts) surrounding sample points, adding covariates measured in larger buffer rings as justified by data (Meyer *et al.*, 1998).

Identifying extent often is less objective. If the objective of a study is to map the distribution of a species across a large area, then used and available locations obviously should be drawn from a large area. If the objective is to use an RSF to identify habitats for management such as modifying vegetation by burning or mechanical methods, landscape or within-home-range scales of selection probably are most relevant (Johnson, 1980). To capture the details of forage selection requires that the analysis be done at yet a finer scale, as along movement paths (Fortin *et al.*, 2005b). There is no one best scale for habitat studies. Instead, the appropriate scale depends on the question at hand (Boyce *et al.*, 2003). For example, aligning habitat models with the scale at which resource management decisions are made might increase the utility of the models in habitat management (Hobbs, 2003).

Case-control or discrete-choice designs afford unique opportunities to specify spatial scale of sampling. By choosing available resource units within buffers surrounding used resource units, one has the potential to constrain available locations to match the scale at which the animal is actually selecting habitats (Arthur *et al.*, 1996; Johnson *et al.*, 2002). For example, if used locations were obtained using radiotelemetry with locations recorded every 5 h, it would make sense to plot the distribution of step lengths for 5-h intervals and use the maximum distance or some threshold distance to establish the radius for each buffer. Analysis is done using conditional logistic regression and matching of used locations with some arbitrary number of random landscape locations drawn from within each buffered resource unit; sometimes this is called matched-case or paired logistic regression (Compton *et al.*, 2002). This approach typically reflects habitat selection at a finer spatial and temporal scale tied to the actual location of the animal rather than contrasting use with overall average habitats within the spatial domain of the investigation. When trying to apply matched-case results at larger scales, one approach might be to map only those areas within the buffered landscape as representing limited available habitats for a species. Anything beyond such buffers could be masked as unused or non-habitat.

AUTOCORRELATION

Scales of both temporal and spatial autocorrelations also are relevant to RSFs (Olivier & Wotherspoon, 2005). Autocorrelation usually occurs because observations close together in time or space are likely to be more similar than those that are more widely separated. As such, autocorrelated observations are not independent and can interfere with statistical inference. Positive autocorrelation increases the chance of a type I error, meaning that we might conclude that there is a pattern when in fact, one does not exist. Sampling scale and autocorrelation are closely linked. If sampling the landscape sparsely over a very large scale, say for modelling distribution of a species, resource units might be essentially independent and not autocorrelated in space. At the opposite extreme, GPS-radiotelemetry affords vast quantities of data taken at short intervals such that the data are often highly autocorrelated in both space and time.

At fine to moderate spatial scales, landscapes almost always are autocorrelated, and this autocorrelation is fundamental to spatial patterns. Instead of being a 'problem', we should view autocorrelation as one of the structural attributes of the landscape that we need to understand (Legendre, 1993). One might explore the autocorrelation structure of landscape variables to identify the extent necessary to capture the variance of predictor variables. For example, Bailey *et al.* (1996) claimed that abiotic factors were primary drivers for large-scale distribution patterns of grazing herbivores, whereas biotic variables such as vegetation were more important at finer extents. Indeed, abiotic variables such as topography required a much larger spatial extent to capture the full range of variability than for vegetation variables in Yellowstone National Park documented by plotting the semivariance for landscape variables (Boyce *et al.*, 2003). An obvious corollary is that if the spatial domain is too small, we will not be sampling the full range of habitat heterogeneity, and as a consequence the

strength of habitat selection will not be appear to be as strong (Turner *et al.*, 1997; WallisDeVries & Laca, 1999; Boyce *et al.*, 2003).

A metric that can be used to characterize patterns of spatial autocorrelation of the landscape and to identify the dominant scales of heterogeneity is the three-term local quadrat variance (3TLQV; Dale, 1999). We used the distance at which the 3TLQV peaked to define a moving window for calculating the density of vegetation patches, i.e. a regional scale (Johnson *et al.*, 2004a). The best RSF models for caribou (*Rangifer tarandus*) that migrate vast distances across the Canadian Arctic included only these regional-scale covariates, whereas RSFs for grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) were improved by including both regional and local patch-scale covariates.

Often we can assume that landscape covariates are responsible for much of the spatial autocorrelation in animal-use locations. However, after building a RSF containing various landscape covariates, autocorrelation among the residuals would suggest that the variance in regression coefficients needs to be adjusted before applying significance tests (Cressie, 1993). In fact, for coarse-scale patterns that span the domain of the study area, one might even use UTM coordinates (including polynomials) as covariates to remove spatial trend in the data (Heikkinen *et al.*, 2004).

If autocorrelation remains in the residuals, either temporal or spatial, one approach is to reduce the degrees of freedom or inflate the variances for regression coefficients (β_is). Estimates of model coefficients are unbiased, but the variances are under-estimated when the autocorrelation is positive. One such post-hoc adjustment is the Newey–West estimator (Newey & West, 1987; Nielsen *et al.*, 2002). Alternatively one can adjust for autocorrelation using a mixed model, or using a data-clustering approach (Fortin *et al.*, 2005a). The reason to make these adjustments is to ensure valid inferences, i.e. to evaluate if a covariate is having a significant influence in the model. However, as Diniz-Filho *et al.* (2003) point out, accounting for spatial autocorrelation by incorporating spatial structure in the error term can de-emphasize predictors with strong autocorrelation and long-distance clinal structures, giving more importance to variables acting at smaller geographical scales. So, if possible, it is best to incorporate all the variables that account for the autocorrelation into the RSF (until there is zero autocorrelation in the residuals) to compare predictors at different scales.

Yet another approach is to develop autoregressive models where occurrence or abundance in nearby resource units is entered explicitly as a covariate in the RSF model. Specifically, autologistic regression involves recording a 0 or 1 for absence or presence of the species in adjacent or nearby resource units (Augustin *et al.*, 1996). When the autoregressive term is included in the model, this accounts for the autocorrelation such that the variances associated with the RSF model coefficients are unbiased and can be used to make valid inferences about the contribution of each covariate to the model. This is fine for hypothesis testing, but renders the model rather worthless for prediction because one must know the distribution of the organism to be able to predict its occurrence! To get around this problem, one can exploit the spatial autocorrelation explicitly by using kriging to interpolate between sampling locations, or at a larger scale one might use the Gibbs sampler to predict occurrence on the landscape (Augustin *et al.*, 1998; Osborne *et al.*, 2001; Teterukovskiy & Edenius, 2003). A simpler approach would be to employ a two-step process using the autologistic model for statistical inference and then drop the autoregressive term and refit the model again to obtain a predictive model.

Concern about autocorrelation sometimes may be a Red Herring (Diniz-Filho *et al.*, 2003). Although Dark (2004) claimed that autocorrelation is fundamentally important in building models of distribution, inspection of her results leads me to question this conclusion because model coefficients were virtually identical whether or not a spatially autoregressive model was used. If model prediction is the objective (Boyce *et al.*, 2002), using information-theoretic methods such as Akaike Information Criterion to select the best model (Burnham & Anderson, 2002) might be sufficient, and statistical significance might not be a concern (Johnson, 1999).

CONCLUSIONS

Generalizations about the effect that scale will have on habitat selection are few, because of enormous variation in landscapes and patterns of processes influencing resource selection. For example, muskoxen (*Ovibos moschatus*) appeared to select the same resources across scales, but this appears to be true because the arctic landscape had relatively little topographic relief and the same plant (*Carex aquatilis*) was distributed widely and available at all scales (Schaefer & Messier, 1995). RSFs can vary among scales when there exists substantial topographic relief such as in mountainous habitats (Bailey *et al.*, 1996; Boyce *et al.*, 2003) and when there are trade-offs between selection of different resources (Mysterud *et al.*, 1999a,b). Another generalization might be that foraging considerations are more likely to influence RSFs at finer scales, whereas predation, dispersal, and other population processes that operate across larger scales will exhibit an effect on resource selection when measured at the correspondingly larger scales (Anderson *et al.*, 2005; Fortin *et al.*, 2005b).

Matching the resolution of resource units with the resolution of the predictor covariates is usually a good idea (Guisan & Thuiller, 2005), but this depends more on the scale at which habitat selection is occurring. Some predictor covariates might best be measured at scales much larger than others, e.g. one might measure road density within a 1-km buffer, whereas forage should be measured with very fine resolution (Fortin *et al.*, 2005b).

Autocorrelation is inherent to most, if not, all landscapes, and should be viewed as an attribute rather than a problem. Measuring patterns of spatial autocorrelation for landscape variables can help one to select a domain for a study area that will capture the underlying variability. Incorporating into RSFs the relevant environmental covariates can capture this landscape autocorrelation. Ideally little spatial autocorrelation will remain amongst the residuals once the effect of the landscape is taken into account. Residual autocorrelation in distribution due to aggregation (positive) or competitive interactions (negative) can be modelled using autologistic regression (Augustin *et al.*, 1996).

Resource utilization functions (RUFs) entail estimating the intensity of use of the landscape with some home-range algorithm, e.g. the adaptive kernel method (Marzluff *et al.*, 2004). As such, considerable smoothing of the distribution is guaranteed, and we lose the ability to detect fine-scale habitat selection despite the fact that statistical inference adjustments for autocorrelation have been developed (Hepinstall *et al.*, 2003). In other words, by using the utilization distribution, RUFs guarantee substantial spatial autocorrelation in the patterns of use. If the UD smoothing compares favourably with the spatial autocorrelation of the landscape, or if the animals are using the landscape at a coarse scale, RUFs might perform similarly to RSFs. My concern is that considerable information about fine-scale habitat selection might be lost by using RUFs, so for reasons of scale I fail to see advantages to RUFs over RSFs.

Despite the paucity of generalizations that have emerged, it is clear that both spatial and temporal scales can be major considerations in efforts to model habitat selection by animals. RSF model coefficients, model predictive ability, and statistical inference can be influenced by the scale identified by the investigator, so it is crucial that the researcher understand the consequences of scale. More importantly, the process of habitat selection is fundamentally affected by ecological processes operating at different scales. Ecologists are still at a fairly naïve pattern-documentation phase in understanding the importance of scale. RSFs can be a powerful tool for identifying and modelling such scale-dependent processes.

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