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Defining the scale of habitat availability for models of habitat selection

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Abstract. Statistical models of habitat preference and species distribution (e.g. Resource Selection Functions and Maximum Entropy approaches) perform a quantitative comparison of the use of space with the availability of all habitats in an animal’s environment. However, not all of space is accessible all of the time to all individuals, so availability is, in fact, determined by limitations in animal perception and mobility. Therefore, measuring habitat availability at biologically relevant scales is essential for understanding preference, but herein lies a trade-off: Models fitted at large spatial scales, will tend to average across the responses of different individuals that happen to be in regions with contrasting habitat compositions. We suggest that such models may fail to capture local extremes (hot-spots and cold-spots) in animal usage and call this potential problem, homogenization. In contrast, models fitted at smaller scales, will vary stochastically depending on the particular habitat composition of their narrow spatial neighborhood, and hence fail to describe responses when predicting for different sampling instances. This is the now well-documented issue of non-transferability of habitat models. We illustrate this trade-off, using a range of simulated experiments, incorporating variations in environmental gradients, richness and fragmentation. We propose diagnostics for detecting the two issues of homogenization and non-transferability and show that these scale-related symptoms are likely to be more pronounced in highly fragmented or steeply graded landscapes. Further, we address these problems, by treating the neighborhood of each cell in the landscape grid as an individual sampling instance (with its own neighborhood), hence allowing coefficients to respond to the local expectations of environmental variables according to a Generalized Functional Response (GFR). Under simulation this approach is consistently better at estimating robust (i.e. transferrable) habitat models at smaller scales, and less susceptible to homogenization at larger scales. At the same time, it represents the first application of a GFR to continuous space
(rather than multiple, spatially distinct datasets), allowing the predictive advantages of this extension of species distribution models to become available to data from large-scale but single-site field studies.

Key words: climate change; habitat fragmentation; functional responses for species distributions; generalized linear model; animal habitat preference; predictive modeling; resource selection functions; simulation study; spatial scale; species distribution models; species ranges; statistical model.

Introduction

Species Distribution Models (SDM) have seen increased use, due to advances in data collection methods (GIS, GPS, radio telemetry) and flexible regression-based frameworks in software such as R (R Core Team, 2014). A large class of SDMs are used for identifying habitat preferences based on a comparison between habitat use and the availability of habitats in the study area (Johnson 1980). We will here refer to these approaches as habitat models (employing a species-independent definition of the term “habitat”, as a particular point in environmental, or niche-space - Hall et al. 1997, Aarts et al. 2008, Matthisopoulos et al. 2011, Matthisopoulos et al. 2015). The general class of habitat models includes notable examples of frameworks such as Resource Selection Functions (RSF - Boyce and McDonald 1999, Manly et al. 2002, also termed Habitat Selection Functions, HSFs - Aarts et al. 2012) and Maximum Entropy models (MaxEnt - Phillips et al. 2006, Elith and Leathwick 2009). Habitat models are predicated on the assumption that if organisms had no preference and could access all of the study area, then space use would be uniformly random. Therefore, when habitat use is disproportionate to habitat availability, this is taken to indicate preferential selection, possibly hinting at combinations of environmental
conditions that help species fulfil vital life history functions (Johnson 1980, Boyce & McDonald 1999, Aarts et al. 2012). However, a fundamental principle of habitat models has been largely neglected in their application to real data. Johnson (1980) conditioned his definition of preference on the availability of all habitats within an organism’s reach (Aarts et al. 2008) and several publications since have pointed out that estimates of preference (and subsequent predictions of space use) are conditional on the complete profile of availabilities in the environment (Boyce and McDonald 1999, Mysterud & Ims 1998, Mauritzen et al. 2003, Osko et al. 2004, Aarts et al. 2008, Godvik et al. 2009, Beyer et al. 2010, Matthiopoulos et al. 2011, Aarts et al. 2012, Aarts et al. 2013). In particular, three main problems have been identified: The sensitivity of habitat models on the defined size of the study region, changes in the environment’s composition and changes in population density.

Dependence on the size of the study region: Habitat models are frequently implemented at study scales decided during project planning, often on the basis of logistical constraints. For the particular example of use-availability data, Beyer et al. (2010) drew attention to the fact that the overall spatial scale of a study alters the representation of habitat availability, and hence changes subsequent estimates of preference. When based on arbitrarily extreme scales, the resulting regression coefficients in a habitat model can (alarmingly) lead an investigator to conclude that an animal shows any one of the three possible responses of preference, avoidance or indifference (positive, negative or zero regression slope) towards any environmental gradient.

Dependence on changing environments: Increasingly, habitat models fitted to data from one region are being used to predict space use in other regions, or to forecast species distributions in the future, particularly in view of habitat loss and climate change. Matthiopoulos et al. (2011) examined the consequences of such extrapolations. Using both simulated and real data, they
showed that habitat models fitted in one region are tied explicitly to the habitat availability prevailing in that region. Since it is unlikely that the availability of all habitats will remain the same in new regions or through time (ironically, environmental change is the instigator of most current conservation studies on habitat preference), the fitted habitat model coefficients may be ineffective for spatial prediction and forecasting.

**Dependence on changing population sizes:** Individuals in small populations can aggregate at high quality habitats, whereas individuals in crowded environments may be forced into sub-optimal habitats (McLaughlin et al. 2010). Habitat models fitted to these two situations would attest to different apparent strengths of preference for high-quality habitats. In recent work Matthiopoulos et al. (2015), have proposed a solution to this problem by modeling the dependence of habitat model coefficients on population density.

All three of the above types of dependence are manifestations of the same fact: apparent preference is conditional on habitat availability (as it is perceived by the observer, set by the environment, or experienced by the animal), and therefore any analytical protocol or ecological process that alters availability will also alter our insights into preference. This paper resolves the challenges of quantifying availability at a biologically relevant scale and accounting for an organism’s non-linear responses to the availability of all habitats within that scale.

Thinking about biologically relevant scales in habitat models requires us to trade off two types of bias against each other. At one extreme, models fitted over small study regions may miss the full diversity of environmental compositions occurring in the broader landscape and hence exclude the full range of animal responses to different environmental compositions. This will yield prediction bias when these models are applied in unobserved environments. Here, we will call this problem, *non-transferability*, because it causes models to be unusable outside the
confines of the data to which they were fitted. Conversely, larger study scales may encompass data from multiple individuals, hence averaging over divergent responses to a wide variety of habitat availabilities and compositions. In such cases, particularly in the presence of non-linear responses by higher animals, a habitat model with spatially stationary regression coefficients is asked to describe strong and varying responses to the same covariates, at different points in space. We hypothesize that this will lead to estimation bias because the model will underestimate usage hot-spots and over-estimate usage cold-spots. We will call this potential problem homogenization because it leads to a spatial flattening of a model’s estimates and subsequent predictions. Such scale-dependencies are inherent in all implementations of habitat models, however they may be fitted (e.g. via maximum likelihood, maximum entropy, or Bayesian methods) and they are likely to be more important when the study organisms respond non-linearly to their environment and environmental composition is variable across the study region.

Non-linear responses are caused by the complex relationship between habitat availability, and demography, behaviour and physiology (Mauritzen et al. 2003, Hebblewhite and Merrill 2008, Beyer et al. 2010). Mysterud and Ims (1998) pointed out that habitat preference may vary as a non-linear function of habitat availability and called this a ‘functional response in habitat selection’: the dependence of preference for any given habitat on the availability of all habitats in the landscape (Arthur et al. 1996, Mysterud and Ims 1998; Beyer et al. 2010). The existence of functional responses has been empirically demonstrated in a variety of animal taxa (Orians and Wittenberger 1991, Mysterud and Ims 1998, Mauritzen et al. 2003, Hebblewhite and Merrill 2008), making them a ubiquitous biological feature that habitat models need to account for.

While the problems caused by functional responses have been discussed (Boyce and MacDonald 1999, Mysterud and Ims 1999), they remained unresolved, due to a lack of practical treatment
and statistical implementation (Beyer et al. 2010). In 2011, Matthiopoulos et al. presented a method for incorporating functional responses into habitat models. Their derivation of a Generalized Functional Response (GFR) approach considers populations in different spatial regions, each with its own distinctive habitat composition. The GFR acknowledges that model coefficients must be allowed to vary when predicting spatial usage in different regions to reflect different animal responses to changes in the availability of all habitats in each region (Boyce, McDonald & Manly 1999). In biological terms, this quantifies how an individual uses the local habitat by taking into account the availability of all habitats within the surrounding region.

Matthiopoulos at el. (2011) show that conditioning local usage on regional availability of habitats can be achieved by introducing into the model’s linear predictor the regional expectations \( E(X), E(X^2), E(X^3), \ldots \) of each environmental covariate. In the simplest case, a GFR using first-order expectations involves just the means of the environmental covariates across each region \( E(X) = \bar{X} \). For example, in the case of a habitat \( \mathbf{x} \) characterized by two particular values \((x_1, x_2)\) of two environmental covariates \( X_1 \) and \( X_2 \), the linear predictor of a habitat model incorporating a first-expectation GFR would take the form:

\[
L(\mathbf{x}) = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 + \beta_1 \bar{X}_1 + \beta_2 \bar{X}_2 + \beta_{11} x_1 \bar{X}_1 + \beta_{12} x_1 \bar{X}_2 + \beta_{21} x_2 \bar{X}_1 + \beta_{22} x_2 \bar{X}_2 \quad (1)
\]

Where the \( \alpha_i \)'s denote the coefficients of the \( i^{th} \) environmental covariate, the \( \beta_i \)'s are the coefficients of the regional means and the \( \beta_{ij} \)'s denote the coefficients of the interaction between the \( i^{th} \) predictor and the regional mean for the \( j^{th} \) covariate. With more available data, higher-order expectations can also be included, but with diminishing gains in model performance. The coefficients of the linear predictor are estimated by fitting a model with an appropriate link function that depends on the usage data at-hand (see Aarts et al. 2012).
The GFR attempts to unify the responses of a species to different regions under the same habitat model, so central to this approach is the combination of data from different regions or sampling instances. By drawing information from different sampling instances a GFR can learn how the organism might respond in, as-yet unobserved, scenarios of availability. For both simulated (Matthiopoulos et al. 2011; Aarts et al. 2013) and real data (Matthiopoulos et al. 2011), the method has displayed superior predictive performance compared to standard habitat models.

The original version of the GFR, as presented by Matthiopoulos et al. (2011) used distinct sampling instances, and thus assumed that the spatial scale of the sampling instance was easy to define a-priori. This poses no problem when biologically informed study scales are available, such as the collective spatial extent of the wolf territories used by Matthiopoulos et al. (2011). In such cases, the scale of the study is identical to the scale of a sampling instance. If, however, such a scale does not readily recommend itself, then the GFR remains vulnerable to the dependence on study scale as outlined above. For example, in the case of nomadic animals, where decisions of space use are not made within the confines of an easily identifiable home range, it is not always clear how to define the spatial scale of a sampling instance. However, an alternative, pragmatic definition of the scale of the sampling instance would focus on the fundamental trade-off between homogenization and non-transferability (i.e. estimation v prediction bias). Assuming that data are available for study areas much larger than the range of a single individual, the appropriate scale for a sampling instance would be the one that finds an optimal conciliation between the two extremes. This poses a new problem: if the chosen scale to be used for sampling instances (and hence for calculating availability) is not the same as the size of each study area, then the sampling instance is not by default the same as the individual study. Instead, we suggest extracting multiple sampling instances at the appropriate scale from within...
any-one study. GFRs compare multiple sampling instances to gain insight into how the same species uses space in different regions. In a single, sufficiently large and heterogeneous region we could equivalently ask whether a GFR can gain the same insights by looking at different segments of the landscape. Indeed, by considering each point on the landscape as a unique vantage point we can try to quantify local usage in terms of proximate habitat availability (defined over a circular buffer zone). This would give rise to a point-by-point version of the GFR in a spatial grid, whereby the neighborhood of each cell in space is treated as a sampling instance.

We will use simulation to illustrate the implications of large and small study scales on the coefficients and predictions of habitat models. We will outline a set of diagnostic tools that are used to measure aspects of study scale dependence in model performance. Using these measures, we will investigate how landscapes with varying levels of fragmentation, resource gradients and resource abundances impact upon model performance. In each scenario, we assess the performance of a point-by-point GFR using as our baseline a habitat model fitted as a GLM.

Methods

Terminology on spatial scales

We consider three distinct spatial scales (Fig. 1a). We will use the term landscape to imply a spatial extent greater than the range which a single study animal can access and use. The study scale (a subset of the landscape) is the area over which data collection is carried out. Within the study scale, the objective is to model usage of each cell in the grid as a function of environmental covariates (e.g. the two layers in Figs 1b and 1c). Finally, the spatial scale of a sampling instance is referred to as the sampling scale, defined by a circle of radius $r$ around a point in the study.
For a standard GFR, the sampling scale is the same as the study scale, whereas for a point by-point GFR, the sampling instance is decoupled from the study scale. For example, consider a landscape described by environmental variables (Figs 1b and 1c) recorded on a grid of arbitrarily fine resolution. In contrast to the standard GFR which uses a landscape-wide expectation of availability for each covariate, the point-by-point GFR would evaluate local expectations from a sampling scale $r$ around each grid cell in the study area for which usage data (e.g. via telemetry, transects or quadrats) was available. Practically, this process yields additional data layers containing the expected values of each covariate within the radius of the sampling instance around each cell in the study area (e.g. Figs 1d and 1e).

**Simulation**

We used a set of features based on the simulated free-ranging foragers of Matthiopoulos et al. (2011) implemented in ‘R’ v3.0.3 (R Core Team 2014). We used a landscape of dimensions 100x100 with torroidal movement boundaries (animals exiting at one edge of the landscape re-entered at the opposite edge). Two resource layers were generated over the landscape as follows: For each resource, a pre-defined number of resource foci were placed randomly on the landscape (according to a planar intensity gradient of a given steepness). A pre-determined total amount of the resource was divided equally between the foci and the amount of resource at each focus was redistributed according to a Gaussian kernel, to create a given degree of spatial autocorrelation. The animal was assumed to acquire resources according to a Holling Type II functional response and the two resources were assumed to be non-substitutable. The animal accumulated one resource until satiation, before switching to the other. The reserves of the organism for each resource were depleted at a constant rate per unit of reserve. The simulation ran for a total of $1 \times 10^6$ units of time. If the individual’s reserves of either resource reached zero, then the animal
was assumed dead, and a new individual was generated at the centre-point of the landscape. If
$5 \times 10^3$ iterations passed with no animal mortality, then a new animal was generated at a random
point in the landscape, replacing the original. The data used for model fitting comprised the
counts of total visits to different cells in the grid and the two environmental layers. Landscape
parameter values were set at the start of each experiment, specifying the number of foci and their
associated smoothing intensity (collectively determining resource fragmentation), the steepness
of the planar gradient (determining the placement of foci), as well as the total abundance of both
resources in the landscape.

First, resource fragmentation was increased by reducing the number of resource foci from 1000
to 50 (Manipulation 1, Fig. 2 - the degree of Gaussian smoothing at each focus was kept fixed
throughout). Secondly, a southwest-to-northeast gradient of increasing steepness (starting from a
zero slope) was applied to the distribution of foci in the landscape (Manipulation 2, Fig. 2).
Finally, we altered the overall quantity of resource distributed across the system from 20 to 1
arbitrary units (Manipulation 3, Fig. 2). The overall amounts of food were calibrated to the
energetic requirements of our simulated organism, to make sure that 20 units corresponded to
superabundance and 1 corresponded to a value where survival became difficult. Each of these
manipulations was applied, in isolation, to a baseline environmental scenario (Fig. 2) specified
by 1000 foci (high homogeneity), 0% Gradient (no gradient) and 20 resource units (high
resource abundance). Each simulation experiment was replicated 30 times for each set of
parameters, to control for the effect of spurious (Monte Carlo) variation.
Model fitting

To study the effect of changing the scale of habitat availability on the coefficients of the habitat model, we sub-sampled the landscape at 36 study scales ranging from grids of 5x5 up to 40x40, centred at the mid-point of the landscape (see Fig. 1a). We also used a buffer zone comprising the outer 10 cells in the grid to mitigate against edge effects (dark edges in Fig. 1) in the resource distributions due to the smoothing operation used to generate the covariate layers. For each study scale, a GLM and a point-by-point GFR were fit to the data. Given that our usage data were recorded as counts on a grid, a log-link was fitted directly to the usage data. The linear predictor for this GLM took the form (compare with eq. (1)):

$$L(x) = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2$$

This GLM is used as our baseline habitat model for this paper. The data frame for the baseline habitat model comprised a row for each cell in the given grid (the cells contained in the dashed square in Fig. 1a). Each data frame row contained data on the usage of that cell and the local densities of the two resources within the cell. We assumed a complete survey of the cells in the study area, but a smaller sample would have been analysed identically.

The point-by-point GFR took the form of eq. (1), also fitted as a GLM, an extension of the baseline habitat model. However, instead of the terms $X_1$ and $X_2$ corresponding to landscape-wide expectations, they now denote data for local averages within the sampling instance (Figs 1d, 1e). The data frame for this model was identical to the one used for the baseline habitat model, but it was augmented with two columns containing these expectations. In order to decide on an appropriate sampling scale for the point-by-point GFR, for each study scale, radii of length 1-10 were tested. The models generated from different sampling scale sizes were compared using the Akaike Information Criterion (AIC), with the optimal model for each scale used for
comparison with the baseline habitat model. To compare the performance of the point-by-point GFR with the baseline habitat model we devised two novel diagnostics. Firstly, we sought to establish how the habitat model’s regression coefficients varied across different study scales. Coefficients derived from small regions of the landscape were expected to be highly specific to the circumstances in those regions (non-transferability). In contrast, we expect coefficients estimated from large study scales to be more general, and stable. As we move from small scales, to larger ones, we would therefore expect the coefficients to converge to their stable values. On this basis, we benchmarked model coefficients against the corresponding coefficient values ($\alpha_{i,40}$) estimated at the largest study scale (40x40) of each experiment. Hence, the deviation of the $i^{th}$ coefficient at scale $j$ was measured as $|\alpha_{i,40} - \alpha_{i,j}|$. A measure of non-transferability $C_j$ at the study scale $j$, was constructed by comparing the deviation at that study scale with the maximum deviation observed over all scales. The measure estimated for a given coefficient at the scale $j$ was averaged over all 30 trials of a given experiment and added across all coefficients ($i$) in the model,

$$C_j = \sum_i \left( \frac{1}{30} \sum \left( \frac{|\alpha_{i,40} - \alpha_{i,j}|}{\max(|\alpha_{i,40} - \alpha_{i,j}|)} \right) \right)$$  

(3)

When calculating $C_j$ of point-by-point GFR models, only the coefficients shared with the baseline habitat model were included. The transferability of habitat model coefficients that tends to minimize $C_j$ at larger scales is the result of the model using fixed coefficients to describe both weak and strong responses to the same habitat, at different points in the landscape. We therefore suggest that (particularly with the use of global smoothness models such as the GLMs used here), this will result in spatially dampened model output that under-estimates the peaks and
over-estimates the troughs of usage distributions. This effect can be identified from a scatter-plot of the fitted values against the actual usage data (Fig. 3). The slope ($s$) of the regression line in that scatter plot can identify if there is a dampening of model estimates by comparing it to a line of slope 1, corresponding to perfectly unbiased estimates (the black line in Fig. 3). Slopes below one indicate under-estimation of usage hotspots and over-estimation of cold spots (red line, Fig. 3). One minus this slope $s$ will therefore give a measure of how much under-estimation is occurring, with values closest to zero indicating minimal under prediction, and vice versa. This is a quantitative representation of the effect of homogenization described earlier in the paper. It is conceivable for the converse of this to occur at smaller study scales ($m > 1$), whereby the amplitude of predictions is increased due to the exclusion of the broader context of availability. However, this effect was only stochastically observed in individual trials of our experiments, and did not survive the averaging across the 30 replicates of simulation experiments.

**Results**

Results from the three simulated experiments manipulating resource fragmentation, gradient and abundance are shown in Fig. 4. Values plotted are averages across the 30 simulation repeats (more detailed plots showing simulation error can be found in the supplementary material). The size of each point is a proxy for the size of the study scale. The ideal value for both metrics is zero, because we desire transferable models that do not homogenize spatial predictions. Non-transferability can be seen in all scenarios, particularly at small study scales. Homogenization is found only in heterogeneous environments, such as landscapes with fragmented or steeply graded resources (Figs 4c-e and 4h-j). In these heterogeneous landscapes, a trade-off between transferability and homogenization is observed, with larger study-scales yielding high
transferability, but also high homogenization, and vice versa. This can be thought of as a manifestation of the bias-variance trade-off (Hastie, Tibshirani & Friedman 2011).

Under these heterogeneous conditions (Figs 4c-e and 4h-j), the point-by-point GFR performs better with regards to both metrics. Biologically, the GFR is better able to fit local hotspots of usage across all study scales, and generates models that (for the same study scale) are more transferrable. In the final resource abundance-altering set of experiments (Figs 4k-o), the performances of the baseline habitat model and point-by-point GFR are comparable, probably because overall resource abundance has no impact on landscape heterogeneity.

Discussion

With accelerating climate change and habitat loss, spatial predictions from habitat models have become important in the conservation and management of threatened or invasive species (Austin 2007, Elith & Leathwick 2009). Despite their widespread use, problems remain with the implementation of habitat models depending on the scale at which the spatial data were collected. Practical advice exists for selecting the study scale of a habitat model (Boyce 2006, Beyer et al. 2010, Northup et al. 2013), but in species (such as nomadic animals) where there is limited understanding of spatial limits, there is a risk of arriving at incorrect predictions by selecting a biologically irrelevant sampling scale.

In this paper, we identify an important scale-related trade-off between the processes of model transferability (prediction bias) and homogenization (estimation bias). Models fitted across large scales tend to estimate generic coefficients that are unable to describe extreme responses to habitat at particular regions in space. Such models tend to homogenize the true responses by
under-estimating areas of high usage and over-estimating low-usage areas. Our simulated experiments suggested that the issue of homogenization is likely to be lowest at small study scales, but in those cases coefficients are non-transferable and model predictions are the least robust to environmental change. Resolving this trade-off between sampling scales is more challenging in heterogeneous landscapes. Our simulations further identified that these scale-related effects become more pronounced in systems where habitats are fragmented or where resources are distributed over steep gradients.

In the literature, these issues have been identified with reference to particular types of data (e.g. Beyer et al. 2010 focus on use-availability designs) or particular model-fitting methodologies (e.g. Matthiopoulos et al. 2011 look at selection functions implemented as GLMs). However, problems of availability will potentially affect any study of mobile species in heterogeneous environments. Non-transferability and homogenization will occur in any study that i) collects data or generates predictions at a spatial resolution finer than the range of a single individual (so that single individuals may be observed using multiple grid cells) and, ii) is conducted over a region large and variable enough to encompass the ranges of many individuals (so that different individuals can be found in different habitat availabilities within their ranges).

Therefore, our methods will be particularly useful for habitat models fitted to fine-resolution and expansive datasets from animal species.

Predictive maps across space and time are likely to be the most pertinent for conservationists and managers (Guisan et al. 2013). An ever-expanding body of literature demonstrates that habitat models derived from one landscape are unlikely to make valid predictions elsewhere (Randin et al. 2006, Zurell et al 2009, McLaughlin et al. 2010, Sinclair et al. 2010, Matthiopoulos et al. 2011, Wenger & Olden 2012). This can be attributed to how habitat models
deal with habitat availability; they assume that as the availability of a habitat decreases or increases, then so too will its use by the animal. Animal responses are, however, not this straightforward, and the use of any type of habitat can vary non-linearly with availability (this is described as a “functional response in habitat selection” – Arthur et al. 1998, Mysterud & Ims 1998). As a result, predictions made in one landscape are unlikely to be adequate descriptions of animal responses in a system of differing habitat availability. Methodologies for dealing with functional responses (Mauritzen et al. 2003, Gilles et al. 2006, Hebblewhite and Merrill 2008, Matthiopoulos et al. 2011) compare multiple sampling instances to construct a picture of how the individual responds to changes in habitat availabilities.

Our present extension of the GFR framework that was introduced by Matthiopoulos et al. (2011) includes a continuous, point-by-point availability definition, which treats each point in the landscape as a sampling instance for which an appropriate $r$ can be retrieved via standard model-selection criteria. Here, we have found that the proposed point-by-point GFR performs favourably in comparison to a standard habitat model. By including interaction terms between environmental covariates and the mean values within the sampling instance, the point-by-point GFR is better equipped to capture patterns of space use even when the broader palette of environmental information is not available, as demonstrated by the method’s ability to improve transferability of models based on small study scales.

Collinearity between the local value of a variable and its expected value within a radius $r$ will arise if the radius is small, or if the resolution of the explanatory data is coarse. In such cases, the additional explanatory power of the expectation terms of the model will be low. If the study organisms perceive and respond to their environment over larger sampling scales, then collinearity should not be an issue because higher values of $r$ will automatically be selected by
AIC. If, however, the animals are relatively sessile (responding to local conditions only), then issues of habitat availability do not arise and the GFR approach is not strictly necessary. The point-by-point implementation extends the reach of the GFR framework because, by treating each point (rather than each study) as a sampling instance, it exploits the information and contrast, available within even single studies, on how animals respond to changes in regional availability (assuming, of course, that single studies are expansive enough to have recorded contrasting responses to a heterogeneous landscape).

The point-by-point GFR was also less susceptible to homogenisation, with coefficients which did not under-predict usage hotspots to the same degree as a standard habitat model. It may be argued that this comparison is not stringent enough because, by using a simple GLM, our baseline habitat model implementation was not sufficiently flexible to capture extremes in usage. For instance, a Generalized Additive Model (Hastie and Tibshirani 1990, Wood 2006) would have automatically directed sufficient local flexibility to the areas where the data presented extreme low/high responses. However, a GAM approach to extreme responses offers a purely heuristic description of the data, treating extremes in usage, almost as “exceptions to the rules”.

Putting aside, for the moment, individual variation in behaviour (which was absent from our simulation experiments), the apparent extremes in space use remain the manifestations of the same underlying behavioural rules. All animals in a population interact with their environment using a similar length of memory, range of perception and individual mobility. By managing to capture patterns of space use, while still inferring a single global sampling scale $r$, our approach remains faithful to this basic biological fact. A further reason for not using more elaborate models such as GAMs here is the fact that they remain vulnerable to non-transferability under environmental change. The ability of a GAM, or any other habitat model, to extrapolate under
changing habitat availability remains limited, unless it is augmented with terms capturing functional responses in habitat use. Implementation of GAMs with GFRs is possible (see supplementary material in Aarts et al. 2013) but computationally quite costly. Our approach uses resource averages calculated at variable radii around each grid cell in the data. Superficially, this could be confused with two other data analysis tricks encountered in landscape ecology. The first consists of fitting the spatial model at ever-coarser scales to try and reduce residual spatial autocorrelation in the results (Gibson et al. 2004, Whittaker and Lindzey 2004, Boyce 2006). This approach however leads to loss of information which our modeling retains by contrasting the finest resolution of the data together with expectations at the biologically relevant scale \( r \). The second trick sometimes employed by spatial analysts is the use of regional availability around points as additional covariates to capture neighborhood effects in the response data (Compton, Rhymer, & McCollough 2002, Swanson et al. 2013). This yields data frames identical to the ones we have used here for model fitting. However, our use of these neighborhood covariates in the model formula is different because it arises from the extension of habitat models by the GFR (complete with all pairwise interactions between neighborhood averages and local covariate values – see eq. 1).

As we have identified from our simulated data, study scales that minimize homogenization are typically the worst cases for transferability, and vice versa. The severity of this trade-off in real data sets remains to be investigated, however our simulation results suggest that it is likely to be the worst under conditions of high fragmentation and steep environmental gradients. When these symptoms of habitat availability are likely to be severe, the point-by-point GFR offers an easy to implement compromise between predictive accuracy and robustness under environmental change. Importantly, if in any given wildlife application the GFR does not outperform more
standard models (in the sense of model selection), then this will be readily measurable via methods such as information criteria or cross validation.

Our use of the AIC to identify the appropriate scale for measuring habitat availability is appealing from a statistical perspective. Model selection methods (such as the AIC) aim for a compromise between goodness of fit (estimation ability) and model parsimony (predictive ability), an objective that chimes well with our balancing a type of estimation error (homogenization) with prediction error (non-transferability). However, statistical model selection is not the only way to think about the problem. From a biological viewpoint it may be possible to derive, or explain, scales of availability in terms of an organism’s cognitive and movement abilities (sensu Compton et al. 2002). Such comparisons between statistically and ecologically proposed scales of availability will form an interesting component of the application of the point-by-point GFR to real data.

Elith and Leathwick conclude their 2009 review of SDMs by suggesting that augmenting methodologies with ecological theory would be beneficial for the advancement of the field. We strongly support this suggestion. The point-by-point GFR, proposed here, is a good example of an approach that is motivated by reasoning about the scales at which ecological phenomena (habitat selection) take place, but can in turn motivate ecological hypotheses by estimating characteristic scales from spatial data.

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**Supplementary material**

**APPENDIX A:** Expanded figures showing details of stochastic variability in results

**SUPPLEMENT 1:** Simulation R-code

**SUPPLEMENT 2:** Point-by-point GFR code in R
**Figure legends**

**Figure 1 (a):** Example spatial plot depicting two simulated resource layers (blue and orange) within the landscape (solid black border). The study scale (dashed black border) is the region for which data on usage were collected (variable study scales are examined in this paper). Under our proposed point-by-point GFR, the solid yellow point at the top left of the study area is the centre of a sampling instance and the yellow shaded circle indicates the disc of radius $r$ that makes up the sampling scale for the calculation of habitat availability. Within the study area, each point in the grey shaded area is in turn considered as a sampling instance with the circumscribed sampling scale $r$. **(b-c):** Spatial plots depicting the individual resource layers ($X_1$ and $X_2$) within the study region. **(d-e):** Plots of the average values ($\bar{X}_1$ and $\bar{X}_2$) of each resource around every point in the study region. The local averaging operation is carried out at the sampling scale (i.e. over a disc of radius $r$).

**Figure 2:** Environmental manipulations used for our simulated experiments. Of all scenarios, our baseline scenario was the most homogeneous and resource-rich. To this, we applied three manipulations. Manipulation 1: Fragmentation was generated by decreasing the number of foci seeded into the landscape. This led to areas of high and low richness by dividing the same amount of total resource among fewer patches. Manipulation 2: A resource gradient was generated by inclining the intensity with which foci were seeded along a southwest to northeast axis. Manipulation 3: Resource abundance was changed by reducing the amount of resource allocated to each focus.
Figure 3: An example from a habitat model fitted to simulated data of animal movement showing the log-transformed fitted and observed values of space-use in each grid cell of the spatial arena. The solid black line has slope 1 and represents exact matching of fitted and observed values. The difference between this and the slope of the regression line (dashed line) through the points indicates the problem of homogenization, whereby the habitat model under-estimates regions of high usage and over-estimates areas of low usage.

Figure 4: Scatterplots of homogenization against non-transferability measures, across the three manipulations (see Fig. 2) of habitat fragmentation (plates a-e), resource gradient (f-j) and abundance (k-o). Values for the simple habitat model (GLM) are shown in blue, and those for the point-by-point GFR in green. The size of the symbol used for each point in the scatterplot represents the study scale of the data set. A value of zero is desirable for both metrics, and is marked on both axes in red. Homogenization is low in landscapes with no gradient or little fragmentation (a, b, f, g and k-o). However, in fragmented (c-e) and steeply graded landscapes (h-i) homogenization occurs at all study scales, but is most severe at large ones. Non-transferability exists in all landscapes, with the coefficients of small study scales highly mobile, and those of larger scales more stable. In spatially variable environments a scale-related trade-off is observable; larger scales incur a penalty in homogenization, while smaller scales are non-transferable. The point-by-point GFR is shown to be superior with regards to both of these metrics, reducing homogenization at all study scales, and giving more transferable model coefficients at smaller scales.
Figure 1.

![Diagram of landscape with labels: Sampling scale, Study scale, X₁, X₂, X̅₁, X̅₂.](image)
Figure 2. Changes in biodiversity with increasing fragmentation, gradient, and decreasing abundance.
Figure 3.
Figure 4