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1 Defining the scale of habitat availability for models
2 of habitat selection

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

37 (rather than multiple, spatially distinct datasets), allowing the predictive advantages of this
38 extension of species distribution models to become available to data from large-scale but single-
39 site field studies.

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

44

45 **Introduction**

46 Species Distribution Models (SDM) have seen increased use, due to advances in data collection
47 methods (GIS, GPS, radio telemetry) and flexible regression-based frameworks in software such
48 as R (R Core Team, 2014). A large class of SDMs are used for identifying habitat preferences
49 based on a comparison between habitat use and the availability of habitats in the study area
50 (Johnson 1980). We will here refer to these approaches as habitat models (employing a species-
51 independent definition of the term “habitat”, as a particular point in environmental, or niche-
52 space - Hall et al. 1997, Aarts et al. 2008, Matthiopoulos et al. 2011, Matthiopoulos et al. 2015).
53 The general class of habitat models includes notable examples of frameworks such as Resource
54 Selection Functions (RSF - Boyce and McDonald 1999, Manly et al. 2002, also termed Habitat
55 Selection Functions, HSFs - Aarts et al. 2012) and Maximum Entropy models (MaxEnt - Phillips
56 et al. 2006, Elith and Leathwick 2009). Habitat models are predicated on the assumption that if
57 organisms had no preference and could access all of the study area, then space use would be
58 uniformly random. Therefore, when habitat use is disproportionate to habitat availability, this is
59 taken to indicate preferential selection, possibly hinting at combinations of environmental

60 conditions that help species fulfil vital life history functions (Johnson 1980, Boyce & McDonald
61 1999, Aarts et al. 2012). However, a fundamental principle of habitat models has been largely
62 neglected in their application to real data. Johnson (1980) conditioned his definition of
63 preference on the availability of *all* habitats within an organism's reach (Aarts et al. 2008) and
64 several publications since have pointed out that estimates of preference (and subsequent
65 predictions of space use) are conditional on the complete profile of availabilities in the
66 environment (Boyce and McDonald 1999, Mysterud & Ims 1998, Mauritzen et al. 2003, Osko et
67 al. 2004, Aarts et al. 2008, Godvik et al. 2009, Beyer et al. 2010, Matthiopoulos et al. 2011,
68 Aarts et al. 2012, Aarts et al. 2013). In particular, three main problems have been identified: The
69 sensitivity of habitat models on the defined size of the study region, changes in the
70 environment's composition and changes in population density.

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

79 *Dependence on changing environments:* Increasingly, habitat models fitted to data from one
80 region are being used to predict space use in other regions, or to forecast species distributions in
81 the future, particularly in view of habitat loss and climate change. Matthiopoulos et al. (2011)
82 examined the consequences of such extrapolations. Using both simulated and real data, they

83 showed that habitat models fitted in one region are tied explicitly to the habitat availability
84 prevailing in that region. Since it is unlikely that the availability of all habitats will remain the
85 same in new regions or through time (ironically, environmental change is the instigator of most
86 current conservation studies on habitat preference), the fitted habitat model coefficients may be
87 ineffective for spatial prediction and forecasting.

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

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

100 Thinking about biologically relevant scales in habitat models requires us to trade off two types
101 of bias against each other. At one extreme, models fitted over small study regions may miss the
102 full diversity of environmental compositions occurring in the broader landscape and hence
103 exclude the full range of animal responses to different environmental compositions. This will
104 yield prediction bias when these models are applied in unobserved environments. Here, we will
105 call this problem, *non-transferability*, because it causes models to be unusable outside the

106 confines of the data to which they were fitted. Conversely, larger study scales may encompass
107 data from multiple individuals, hence averaging over divergent responses to a wide variety of
108 habitat availabilities and compositions. In such cases, particularly in the presence of non-linear
109 responses by higher animals, a habitat model with spatially stationary regression coefficients is
110 asked to describe strong and varying responses to the same covariates, at different points in
111 space. We hypothesize that this will lead to estimation bias because the model will under-
112 estimate usage hot-spots and over-estimate usage cold-spots. We will call this potential problem
113 *homogenization* because it leads to a spatial flattening of a model's estimates and subsequent
114 predictions. Such scale-dependencies are inherent in all implementations of habitat models,
115 however they may be fitted (e.g. via maximum likelihood, maximum entropy, or Bayesian
116 methods) and they are likely to be more important when the study organisms respond non-
117 linearly to their environment and environmental composition is variable across the study region.

118 Non-linear responses are caused by the complex relationship between habitat availability, and
119 demography, behaviour and physiology (Mauritzen et al. 2003, Hebblewhite and Merrill 2008,
120 Beyer et al. 2010). Mysterud and Ims (1998) pointed out that habitat preference may vary as a
121 non-linear function of habitat availability and called this a 'functional response in habitat
122 selection': the dependence of preference for *any* given habitat on the availability of *all* habitats in
123 the landscape (Arthur et al. 1996, Mysterud and Ims 1998; Beyer et al. 2010). The existence of
124 functional responses has been empirically demonstrated in a variety of animal taxa (Orians and
125 Wittenberger 1991, Mysterud and Ims 1998, Mauritzen et al. 2003, Hebblewhite and Merrill
126 2008), making them a ubiquitous biological feature that habitat models need to account for.
127 While the problems caused by functional responses have been discussed (Boyce and MacDonald
128 1999, Mysterud and Ims 1999), they remained unresolved, due to a lack of practical treatment

129 and statistical implementation (Beyer et al. 2010). In 2011, Matthiopoulos et al. presented a
 130 method for incorporating functional responses into habitat models. Their derivation of a
 131 Generalized Functional Response (GFR) approach considers populations in different spatial
 132 regions, each with its own distinctive habitat composition. The GFR acknowledges that model
 133 coefficients must be allowed to vary when predicting spatial usage in different regions to reflect
 134 different animal responses to changes in the availability of all habitats in each region (Boyce,
 135 McDonald & Manly 1999). In biological terms, this quantifies how an individual uses the local
 136 habitat by taking into account the availability of all habitats within the surrounding region.
 137 Matthiopoulos et al. (2011) show that conditioning local usage on regional availability of
 138 habitats can be achieved by introducing into the model's linear predictor the regional
 139 expectations ($E(X)$, $E(X^2)$, $E(X^3)$...) of each environmental covariate. In the simplest case, a
 140 GFR using first-order expectations involves just the means of the environmental covariates
 141 across each region ($E(X) = \bar{X}$). For example, in the case of a habitat \mathbf{x} characterized by two
 142 particular values (x_1 and x_2) of two environmental covariates X_1 and X_2 , the linear predictor of
 143 a habitat model incorporating a first-expectation GFR would take the form:

$$144 \quad L(\mathbf{x}) = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 + \beta_1 \bar{X}_1 + \beta_2 \bar{X}_2 + \beta_{11} x_1 \bar{X}_1 + \beta_{12} x_1 \bar{X}_2 + \beta_{21} x_2 \bar{X}_1 + \beta_{22} x_2 \bar{X}_2 \quad (1)$$

145 Where the α_i 's denote the coefficients of the i^{th} environmental covariate, the β_i 's are the
 146 coefficients of the regional means and the β_{ij} 's denote the coefficients of the interaction between
 147 the i^{th} predictor and the regional mean for the j^{th} covariate. With more available data, higher-
 148 order expectations can also be included, but with diminishing gains in model performance. The
 149 coefficients of the linear predictor are estimated by fitting a model with an appropriate link
 150 function that depends on the usage data at-hand (see Aarts et al. 2012).

151 The GFR attempts to unify the responses of a species to different regions under the same habitat
152 model, so central to this approach is the combination of data from different regions or *sampling*
153 *instances*. By drawing information from different sampling instances a GFR can learn how the
154 organism might respond in, as-yet unobserved, scenarios of availability. For both simulated
155 (Matthiopoulos et al. 2011; Aarts et al. 2013) and real data (Matthiopoulos et al. 2011), the
156 method has displayed superior predictive performance compared to standard habitat models.

157 The original version of the GFR, as presented by Matthiopoulos et al. (2011) used distinct
158 sampling instances, and thus assumed that the spatial scale of the sampling instance was easy to
159 define *a-priori*. This poses no problem when biologically informed study scales are available,
160 such as the collective spatial extent of the wolf territories used by Matthiopoulos et al. (2011). In
161 such cases, the scale of the study is identical to the scale of a sampling instance. If, however,
162 such a scale does not readily recommend itself, then the GFR remains vulnerable to the
163 dependence on study scale as outlined above. For example, in the case of nomadic animals,
164 where decisions of space use are not made within the confines of an easily identifiable home
165 range, it is not always clear how to define the spatial scale of a sampling instance. However, an
166 alternative, pragmatic definition of the scale of the sampling instance would focus on the
167 fundamental trade-off between homogenization and non-transferability (i.e. estimation v
168 prediction bias). Assuming that data are available for study areas much larger than the range of a
169 single individual, the appropriate scale for a sampling instance would be the one that finds an
170 optimal conciliation between the two extremes. This poses a new problem: if the chosen scale to
171 be used for sampling instances (and hence for calculating availability) is not the same as the size
172 of each study area, then the sampling instance is not by default the same as the individual study.
173 Instead, we suggest extracting multiple sampling instances at the appropriate scale from *within*

174 any-one study. GFRs compare multiple sampling instances to gain insight into how the same
175 species uses space in different regions. In a single, sufficiently large and heterogeneous region
176 we could equivalently ask whether a GFR can gain the same insights by looking at different
177 segments of the landscape. Indeed, by considering each point on the landscape as a unique
178 vantage point we can try to quantify local usage in terms of proximate habitat availability
179 (defined over a circular buffer zone). This would give rise to a point-by-point version of the
180 GFR in a spatial grid, whereby the neighborhood of each cell in space is treated as a sampling
181 instance.

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

188

189 **Methods**

190 *Terminology on spatial scales*

191 We consider three distinct spatial scales (Fig. 1a). We will use the term *landscape* to imply a
192 spatial extent greater than the range which a single study animal can access and use. The *study*
193 *scale* (a subset of the landscape) is the area over which data collection is carried out. Within the
194 study scale, the objective is to model usage of each cell in the grid as a function of environmental
195 covariates (e.g. the two layers in Figs 1b and 1c). Finally, the spatial scale of a sampling instance
196 is referred to as the *sampling scale*, defined by a circle of radius r around a point in the study

197 region. For a standard GFR, the sampling scale is the same as the study scale, whereas for a point
198 by-point GFR, the sampling instance is decoupled from the study scale.

199 For example, consider a landscape described by environmental variables (Figs 1b and 1c)
200 recorded on a grid of arbitrarily fine resolution. In contrast to the standard GFR which uses a
201 landscape-wide expectation of availability for each covariate, the point-by-point GFR would
202 evaluate local expectations from a sampling scale r around each grid cell in the study area for
203 which usage data (e.g. via telemetry, transects or quadrats) was available. Practically, this
204 process yields additional data layers containing the expected values of each covariate within the
205 radius of the sampling instance around each cell in the study area (e.g. Figs 1d and 1e).

206 *Simulation*

207 We used a set of features based on the simulated free-ranging foragers of Matthiopoulos et al.
208 (2011) implemented in ‘R’ v3.0.3 (R Core Team 2014). We used a landscape of dimensions
209 100x100 with torroidal movement boundaries (animals exiting at one edge of the landscape re-
210 entered at the opposite edge). Two resource layers were generated over the landscape as follows:
211 For each resource, a pre-defined number of resource foci were placed randomly on the landscape
212 (according to a planar intensity gradient of a given steepness). A pre-determined total amount of
213 the resource was divided equally between the foci and the amount of resource at each focus was
214 redistributed according to a Gaussian kernel, to create a given degree of spatial autocorrelation.
215 The animal was assumed to acquire resources according to a Holling Type II functional response
216 and the two resources were assumed to be non-substitutable. The animal accumulated one
217 resource until satiation, before switching to the other. The reserves of the organism for each
218 resource were depleted at a constant rate per unit of reserve. The simulation ran for a total of
219 1×10^6 units of time. If the individual’s reserves of either resource reached zero, then the animal

220 was assumed dead, and a new individual was generated at the centre-point of the landscape. If
221 5×10^3 iterations passed with no animal mortality, then a new animal was generated at a random
222 point in the landscape, replacing the original. The data used for model fitting comprised the
223 counts of total visits to different cells in the grid and the two environmental layers. Landscape
224 parameter values were set at the start of each experiment, specifying the number of foci and their
225 associated smoothing intensity (collectively determining resource fragmentation), the steepness
226 of the planar gradient (determining the placement of foci), as well as the total abundance of both
227 resources in the landscape.

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

240

241 *Model fitting*

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

250
$$L(\mathbf{x}) = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 \tag{2}$$

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

256 The point-by-point GFR took the form of eq. (1), also fitted as a GLM, an extension of the
257 baseline habitat model. However, instead of the terms \bar{X}_1 and \bar{X}_2 corresponding to landscape-
258 wide expectations, they now denote data for local averages within the sampling instance (Figs
259 1d, 1e). The data frame for this model was identical to the one used for the baseline habitat
260 model, but it was augmented with two columns containing these expectations. In order to decide
261 on an appropriate sampling scale for the point-by-point GFR, for each study scale, radii of length
262 1-10 were tested. The models generated from different sampling scale sizes were compared using
263 the Akaike Information Criterion (AIC), with the optimal model for each scale used for

264 comparison with the baseline habitat model. To compare the performance of the point-by-point
 265 GFR with the baseline habitat model we devised two novel diagnostics.
 266 Firstly, we sought to establish how the habitat model's regression coefficients varied across
 267 different study scales. Coefficients derived from small regions of the landscape were expected to
 268 be highly specific to the circumstances in those regions (non-transferability). In contrast, we
 269 expect coefficients estimated from large study scales to be more general, and stable. As we move
 270 from small scales, to larger ones, we would therefore expect the coefficients to converge to their
 271 stable values. On this basis, we benchmarked model coefficients against the corresponding
 272 coefficient values ($\alpha_{i,40}$) estimated at the largest study scale (40x40) of each experiment. Hence,
 273 the deviation of the i^{th} coefficient at scale j was measured as $|\alpha_{i,40} - \alpha_{i,j}|$. A measure of non-
 274 transferability C_j at the study scale j , was constructed by comparing the deviation at that study
 275 scale with the maximum deviation observed over all scales. The measure estimated for a given
 276 coefficient at the scale j was averaged over all 30 trials of a given experiment and added across
 277 all coefficients (i) in the model,

$$278 \quad C_j = \sum_i \left(\frac{1}{30} \sum \left(\frac{|\alpha_{i,40} - \alpha_{i,j}|}{\max(|\alpha_{i,40} - \alpha_{i,j}|)} \right) \right) \quad (3)$$

279 When calculating C_j of point-by-point GFR models, only the coefficients shared with the baseline
 280 habitat model were included. The transferability of habitat model coefficients that tends to
 281 minimize C_j at larger scales is the result of the model using fixed coefficients to describe both
 282 weak and strong responses to the same habitat, at different points in the landscape. We therefore
 283 suggest that (particularly with the use of global smoothness models such as the GLMs used
 284 here), this will result in spatially dampened model output that under-estimates the peaks and

285 over-estimates the troughs of usage distributions. This effect can be identified from a scatter-plot
286 of the fitted values against the actual usage data (Fig. 3). The slope (s) of the regression line in
287 that scatter plot can identify if there is a dampening of model estimates by comparing it to a line
288 of slope 1, corresponding to perfectly unbiased estimates (the black line in Fig. 3). Slopes below
289 one indicate under-estimation of usage hotspots and over-estimation of cold spots (red line, Fig.
290 3). One minus this slope s will therefore give a measure of how much under-estimation is
291 occurring, with values closest to zero indicating minimal under prediction, and vice versa. This is
292 a quantitative representation of the effect of homogenization described earlier in the paper. It is
293 conceivable for the converse of this to occur at smaller study scales ($m > 1$), whereby the
294 amplitude of predictions is increased due to the exclusion of the broader context of availability.
295 However, this effect was only stochastically observed in individual trials of our experiments, and
296 did not survive the averaging across the 30 replicates of simulation experiments.

297

298 **Results**

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

308 transferability, but also high homogenization, and vice versa. This can be thought of as a
309 manifestation of the bias-variance trade-off (Hastie, Tibshirani & Friedman 2011).

310

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

317

318 **Discussion**

319 With accelerating climate change and habitat loss, spatial predictions from habitat models have
320 become important in the conservation and management of threatened or invasive species (Austin
321 2007, Elith & Leathwick 2009). Despite their widespread use, problems remain with the
322 implementation of habitat models depending on the scale at which the spatial data were
323 collected. Practical advice exists for selecting the study scale of a habitat model (Boyce 2006,
324 Beyer et al. 2010, Northup et al. 2013), but in species (such as nomadic animals) where there is
325 limited understanding of spatial limits, there is a risk of arriving at incorrect predictions by
326 selecting a biologically irrelevant sampling scale.

327 In this paper, we identify an important scale-related trade-off between the processes of model
328 transferability (prediction bias) and homogenization (estimation bias). Models fitted across large
329 scales tend to estimate generic coefficients that are unable to describe extreme responses to
330 habitat at particular regions in space. Such models tend to homogenize the true responses by

331 under-estimating areas of high usage and over-estimating low-usage areas. Our simulated
332 experiments suggested that the issue of homogenization is likely to be lowest at small study
333 scales, but in those cases coefficients are non-transferable and model predictions are the least
334 robust to environmental change. Resolving this trade-off between sampling scales is more
335 challenging in heterogeneous landscapes. Our simulations further identified that these scale-
336 related effects become more pronounced in systems where habitats are fragmented or where
337 resources are distributed over steep gradients.

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

349 Predictive maps across space and time are likely to be the most pertinent for conservationists
350 and managers (Guisan et al. 2013). An ever-expanding body of literature demonstrates that
351 habitat models derived from one landscape are unlikely to make valid predictions elsewhere
352 (Randin et al. 2006, Zurell et al 2009, McLaughlin et al. 2010, Sinclair et al. 2010,
353 Matthiopoulos et al. 2011, Wenger & Olden 2012). This can be attributed to how habitat models

354 deal with habitat availability; they assume that as the availability of a habitat decreases or
355 increases, then so too will its use by the animal. Animal responses are, however, not this
356 straightforward, and the use of any type of habitat can vary non-linearly with availability (this is
357 described as a “functional response in habitat selection” – Arthur et al. 1998, Mysterud & Ims
358 1998). As a result, predictions made in one landscape are unlikely to be adequate descriptions of
359 animal responses in a system of differing habitat availability. Methodologies for dealing with
360 functional responses (Mauritzen et al. 2003, Gilles et al. 2006, Hebblewhite and Merrill 2008,
361 Matthiopoulos et al. 2011) compare multiple sampling instances to construct a picture of how the
362 individual responds to changes in habitat availabilities.

363 Our present extension of the GFR framework that was introduced by Matthiopoulos et al.
364 (2011) includes a continuous, point-by-point availability definition, which treats each point in the
365 landscape as a sampling instance for which an appropriate r can be retrieved via standard model-
366 selection criteria. Here, we have found that the proposed point-by-point GFR performs
367 favourably in comparison to a standard habitat model. By including interaction terms between
368 environmental covariates and the mean values within the sampling instance, the point-by-point
369 GFR is better equipped to capture patterns of space use even when the broader palette of
370 environmental information is not available, as demonstrated by the method’s ability to improve
371 transferability of models based on small study scales.

372 Collinearity between the local value of a variable and its expected value within a radius r will
373 arise if the radius is small, or if the resolution of the explanatory data is coarse. In such cases, the
374 additional explanatory power of the expectation terms of the model will be low. If the study
375 organisms perceive and respond to their environment over larger sampling scales, then
376 collinearity should not be an issue because higher values of r will automatically be selected by

377 AIC. If, however, the animals are relatively sessile (responding to local conditions only), then
378 issues of habitat availability do not arise and the GFR approach is not strictly necessary.
379 The point-by-point implementation extends the reach of the GFR framework because, by treating
380 each point (rather than each study) as a sampling instance, it exploits the information and
381 contrast, available within even single studies, on how animals respond to changes in regional
382 availability (assuming, of course, that single studies are expansive enough to have recorded
383 contrasting responses to a heterogeneous landscape).

384 The point-by-point GFR was also less susceptible to homogenisation, with coefficients which
385 did not under-predict usage hotspots to the same degree as a standard habitat model. It may be
386 argued that this comparison is not stringent enough because, by using a simple GLM, our
387 baseline habitat model implementation was not sufficiently flexible to capture extremes in usage.
388 For instance, a Generalized Additive Model (Hastie and Tibshirani 1990, Wood 2006) would
389 have automatically directed sufficient local flexibility to the areas where the data presented
390 extreme low/high responses. However, a GAM approach to extreme responses offers a purely
391 heuristic description of the data, treating extremes in usage, almost as “exceptions to the rules”.
392 Putting aside, for the moment, individual variation in behaviour (which was absent from our
393 simulation experiments), the apparent extremes in space use remain the manifestations of the
394 same underlying behavioural rules. All animals in a population interact with their environment
395 using a similar length of memory, range of perception and individual mobility. By managing to
396 capture patterns of space use, while still inferring a single global sampling scale r , our approach
397 remains faithful to this basic biological fact. A further reason for not using more elaborate
398 models such as GAMs here is the fact that they remain vulnerable to non-transferability under
399 environmental change. The ability of a GAM, or any other habitat model, to extrapolate under

400 changing habitat availability remains limited, unless it is augmented with terms capturing
401 functional responses in habitat use. Implementation of GAMs with GFRs is possible (see
402 supplementary material in Aarts et al. 2013) but computationally quite costly.
403 Our approach uses resource averages calculated at variable radii around each grid cell in the data.
404 Superficially, this could be confused with two other data analysis tricks encountered in landscape
405 ecology. The first consists of fitting the spatial model at ever-coarser scales to try and reduce
406 residual spatial autocorrelation in the results (Gibson et al. 2004, Whittaker and Lindzey 2004,
407 Boyce 2006). This approach however leads to loss of information which our modeling retains by
408 contrasting the finest resolution of the data together with expectations at the biologically relevant
409 scale r . The second trick sometimes employed by spatial analysts is the use of regional
410 availability around points as additional covariates to capture neighborhood effects in the
411 response data (Compton, Rhymer, & McCollough 2002, Swanson et al. 2013). This yields data
412 frames identical to the ones we have used here for model fitting. However, our use of these
413 neighborhood covariates in the model formula is different because it arises from the extension of
414 habitat models by the GFR (complete with all pairwise interactions between neighborhood
415 averages and local covariate values – see eq. 1).

416 As we have identified from our simulated data, study scales that minimize homogenization
417 are typically the worst cases for transferability, and vice versa. The severity of this trade-off in
418 real data sets remains to be investigated, however our simulation results suggest that it is likely
419 to be the worst under conditions of high fragmentation and steep environmental gradients. When
420 these symptoms of habitat availability are likely to be severe, the point-by-point GFR offers an
421 easy to implement compromise between predictive accuracy and robustness under environmental
422 change. Importantly, if in any given wildlife application the GFR does not outperform more

423 standard models (in the sense of model selection), then this will be readily measurable via
424 methods such as information criteria or cross validation.

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

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

441

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445 work.

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532

533 **Supplementary material**

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

535 **SUPPLEMENT 1:** Simulation R-code

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

537 **Figure legends**

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

549

550 **Figure 2:** Environmental manipulations used for our simulated experiments. Of all scenarios, our
551 baseline scenario was the most homogeneous and resource-rich. To this, we applied three
552 manipulations. Manipulation 1: Fragmentation was generated by decreasing the number of foci
553 seeded into the landscape. This led to areas of high and low richness by dividing the same
554 amount of total resource among fewer patches. Manipulation 2: A resource gradient was
555 generated by inclining the intensity with which foci were seeded along a southwest to northeast
556 axis. Manipulation 3: Resource abundance was changed by reducing the amount of resource
557 allocated to each focus.

558

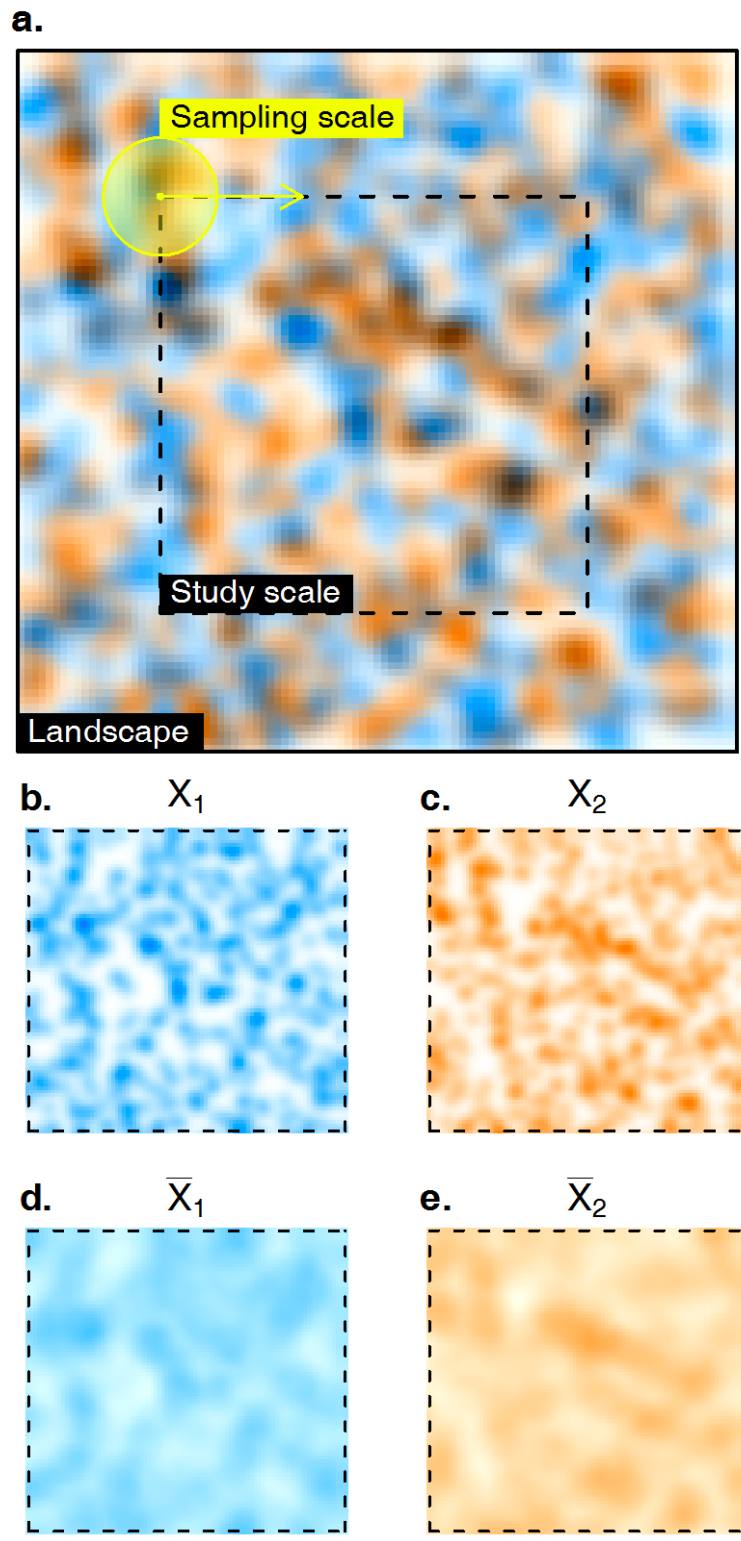
559 **Figure 3:** An example from a habitat model fitted to simulated data of animal movement
560 showing the log-transformed fitted and observed values of space-use in each grid cell of the
561 spatial arena. The solid black line has slope 1 and represents exact matching of fitted and
562 observed values. The difference between this and the slope of the regression line (dashed line)
563 through the points indicates the problem of homogenization, whereby the habitat model under-
564 estimates regions of high usage and over-estimates areas of low usage.

565

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

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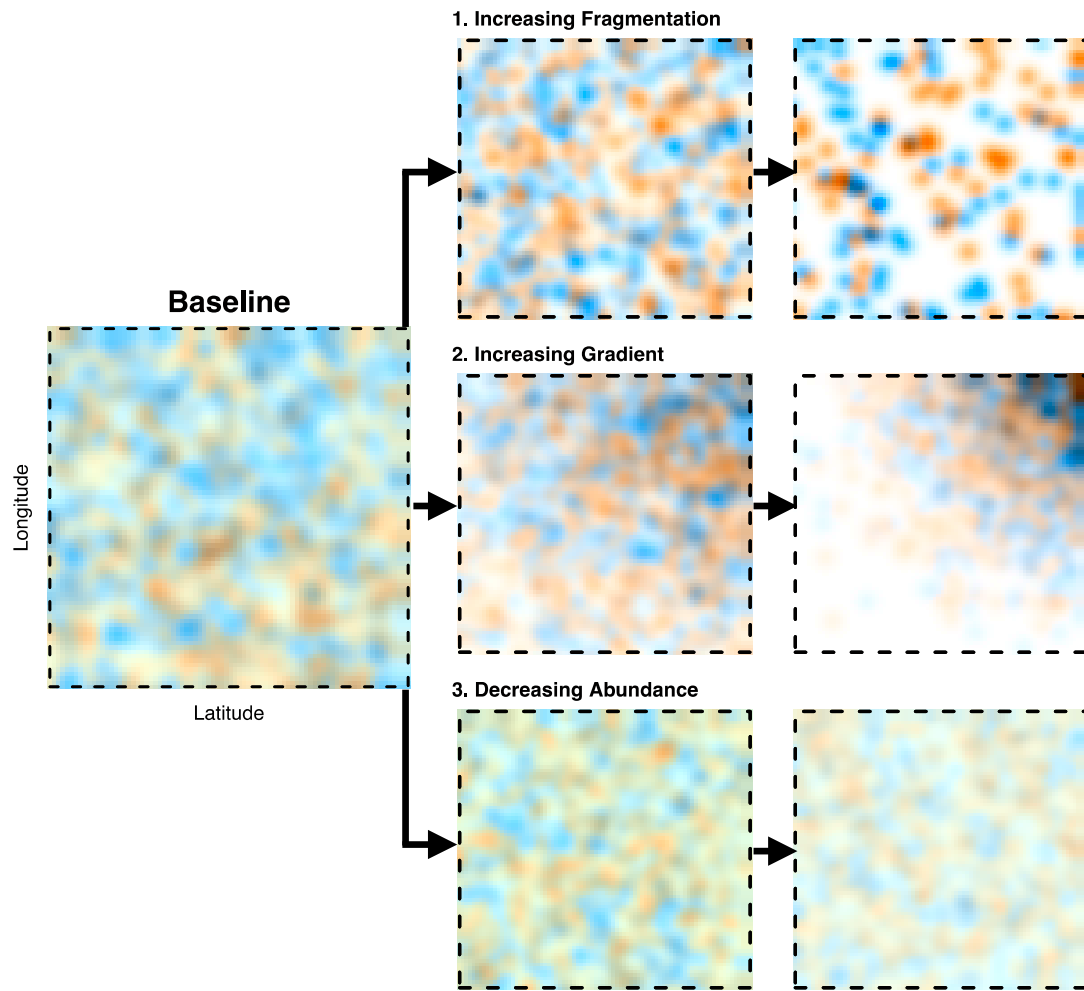
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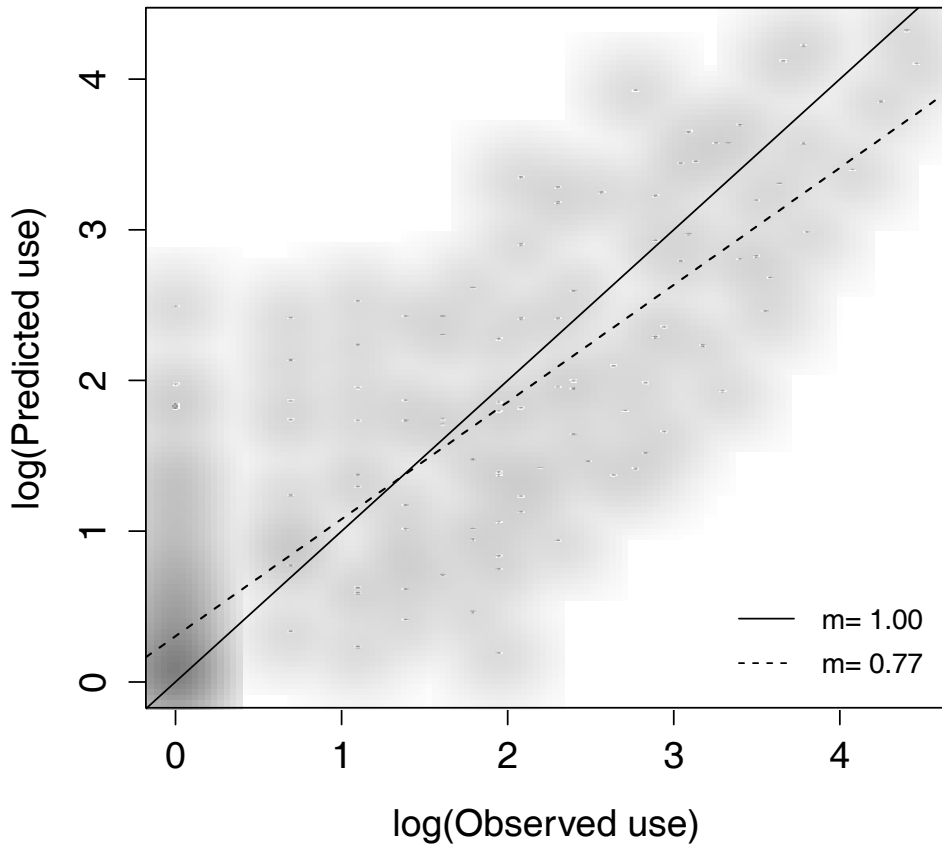
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Figure 1.



2.



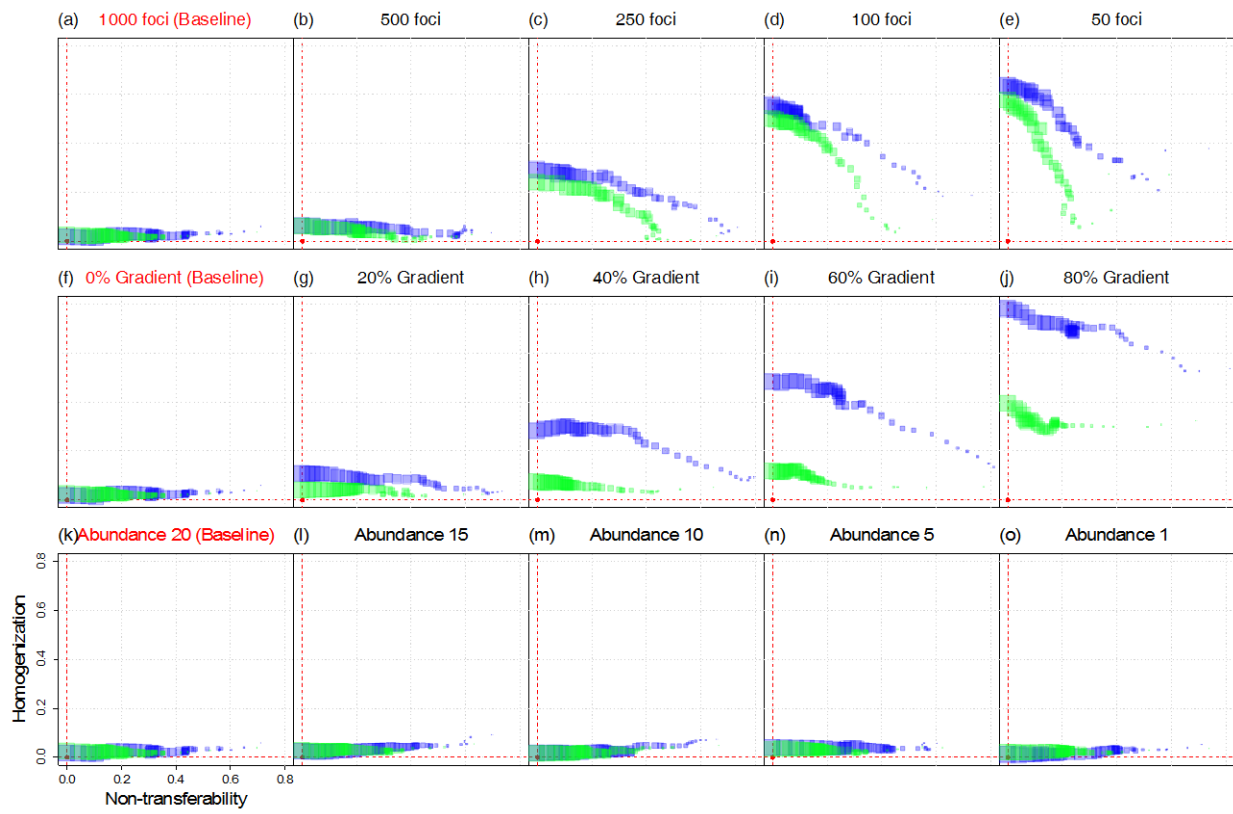
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Figure 3.



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Figure 4