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Within Reach? Habitat Availability as a Function of Individual Mobility and Spatial Structuring.

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1   # Within reach? Habitat availability as a function of

2   # individual mobility and spatial structuring

3   **Abstract**

4   Organisms need access to particular habitats for their survival and reproduction. However, even

5   if all necessary habitats are available within the broader environment, they may not all be easily

6   reachable from the position of a single individual. Many Species Distribution Models (SDMs)

7   consider populations in environmental (or niche) space, hence overlooking this fundamental

8   aspect of geographical accessibility. Here, we develop a formal way of thinking about habitat

9   availability in environmental spaces by describing how limitations in accessibility can cause

10   animals to experience a more limited or, simply, different mixture of habitats than those more

11   broadly available. We develop an analytical framework for characterizing constrained habitat

12   availability based on the statistical properties of movement and environmental autocorrelation.

13   Using simulation experiments, we show that our general statistical representation of constrained

14   availability is a good approximation of habitat availability for particular realizations of

15   landscape-organism interactions. We present two applications of our approach, one to the

16   statistical analysis of habitat preference (using step-selection functions to analyze harbor seal

17   telemetry data) and a second that derives theoretical insights about population viability from

18   knowledge of the underlying environment. Analytical expressions for habitat availability, such

19   as those we develop here, can yield gains in analytical speed, biological realism and conceptual

20   generality by allowing us to formulate models that are habitat-sensitive, without needing to be

21   spatially explicit.

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1. Introduction

Habitats within an environment can be thought of as a combination of different values of environmental variables (e.g. abiotic conditions or biotic resources). Individual organisms may require multiple habitats to meet their biological needs, but these habitats may not all be equally accessible. Across species and life stages, individuals vary in their mobility, from complete sessility (e.g. individual plants), through central-place foraging (e.g. colonial breeders), to expansive nomadism (e.g. free-ranging grazers). Additionally, spatial structuring of the landscape may create separation between different types of vital habitats. Therefore, spatial heterogeneity and an organism's mobility determine the availability of habitats experienced from any given position in geographical space. Approaches used to quantify and understand space use (e.g. resource selection functions, Manly et al. 2004) and spatial population dynamics (e.g. Matthiopoulos et al. 2015, 2019) are often formulated in environmental (or niche) spaces. Because such approaches are not explicitly geographic, they are prefaced by an "equal accessibility" assumption, hence ignoring this issue. However, it is becoming increasingly clear that the precise calculation of habitat availability can dramatically affect the inferences and predictions drawn from such models. For example, when analyzing animal usage data, we can be led to infer preference, avoidance or indifference for the same habitats depending on our definition of habitat availability (Beyer et al. 2010). This makes inferences from species distribution models sensitive to habitat availability (Randin et al. 2006, Zurell et al 2009, McLaughlin et al. 2010, Sinclair et al. 2010, Matthiopoulos et al. 2011, Wenger & Olden 2012, Aarts et al. 2013, Northrup et al. 2013).

To account for accessibility, some approaches use expert opinion (e.g. ad-hoc buffers in step selection functions – Thurfjell et al. 2014), simultaneous estimation (e.g. Horne et al. 2008,

50   Avgar et al. 2016), or empirical heuristics (e.g. post-hoc model selection criteria in Paton &

51   Matthiopoulos 2016). Most of these papers describe habitat availability in terms of summaries of

52   samples taken from some spatial domain of relevance. For example, the average temperature

53   prevailing in the neighborhood of a foraging animal can be calculated from a sample of

54   temperatures measured (or remotely sensed) at points selected randomly or systematically from

55   within a circular buffer centered at the position of the forager. Such summaries allow us to

56   incorporate availability into analyses of space use in a particular landscape, but at the expense of

57   analytical tractability and generality across new landscapes with similar properties but limited

58   data. Performing mathematical, rather than sampling-based or numerical, analyses with

59   geographical layers is particularly difficult, because parametric descriptions of heterogeneous

60   landscapes are challenging to construct. Furthermore, not all the details and geographical

61   features of landscapes are necessarily relevant for summaries of habitat availability.

62   An alternative approach is to statistically describe the salient attributes of species mobility

63   and landscape structure and use such statistical summaries to define habitat availability in a

64   compact mathematical form that is an adequate approximation of the neighboring environment

65   from the position of any given individual. This approach is both numerically efficient in

66   describing population processes within a given landscape and generalizable across spatially

67   similar landscapes.

68   The objective of this paper is to formally develop the concept of habitat availability, starting

69   from first principles, and to derive expectations about the environment based on its global

70   statistical properties rather than any particular local configuration of habitats, an approach

71   similar to statistical mechanics in the physics literature (e.g. Sklar 2015). Principally, the ability

72   of an individual to move between two or more habitats will depend on how far apart they are (a

73   distance determined by the spatial autocorrelations of the environmental variables making up

74   these habitats) and how easily the individual can move between them (as determined by various

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75   mobility constraints) (Matthiopoulos 2003). Formalizing these effects of spatial autocorrelation

76   and mobility requires clear conceptual definitions of habitat, and of unconstrained

77   (unconditional) habitat availability. We therefore begin with a brief review of useful notation and

78   terminology (section 2), followed by a mathematical model for conditional habitat availability

79   (section 3), which quantitatively maps accessibility in geographical space (the spatial locations

80   that an organism can access from any given position) to accessibility in environmental space (the

81   habitats that an organism can be expected to access from the habitat corresponding to its given

82   spatial position). Given the rather abstract nature of this framework, we provide three types of

83   intuition-building illustrations. In section 4, we compare measures of habitat availability

84   calculated using our new framework and using a direct sampling approach applied to a buffer

85   zone around a particular location. In section 5, we use our framework to derive an analytical

86   form of the likelihood for step-selection functions (an approach commonly used to quantify

87   habitat selection from fine-scale telemetry data – Thurfjell, Ciuti & Boyce 2014, Hooten et al.

88   2017). In section 6 we use our framework to investigate population fitness for territorial species.

89   This application introduces additional mathematical tools that can allow the formulation of

90   general results connecting habitat accessibility, habitat use and population viability. We

91   conclude by placing this work in its broader context.

92   **2. *G*-spaces, *E*-spaces, habitats and unconditional habitat availability**

93   Models that deal with species-environment interactions frequently differentiate between

94   *geographical space* (*G*-space) and *environmental space* (*E*-space), a distinction historically

95   known as Hutchinson's duality (Hirzel & LeLay 2008, Colwell & Rangel 2009, Elith &

96   Leathwick 2009). *G*-space comprises the three dimensions of latitude, longitude and

97   altitude/depth, often projected onto a Cartesian system of coordinates. In contrast, *E*-space can

98   be high-dimensional, each dimension representing a biotic or abiotic environmental variable, i.e.

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99   a continuous, discrete or qualitative random variable representing a condition (e.g. pH,

100   temperature, sea depth), resource (e.g. soil nutrients, prey, breeding sites) or risk (e.g. predators,

101   pollution). *E*-space can be considered identical to niche-space, as originally conceived by

102   Hutchinson (1957) and MacArthur (1968) although, as extensively argued in the modern

103   literature (Soberón & Nakamura 2009, Peterson et al. 2011, McInerny & Etienne 2013,

104   Matthiopoulos et al. 2015), statistical habitat preference models currently fitted in *E*-space

105   should not be confused with the niche objects as envisaged by these pioneering thinkers.

106   Several papers (Aarts et al 2008, Matthiopoulos et al. 2011, Matthiopoulos et al. 2015 and

107   references therein), conceptualize *habitat* as a point $\mathbf{x}$ in *E*-space, the combination

108   $\mathbf{x} = \{x_1, \ldots, x_K\}$ of specific values for K environmental variables (e.g. geomorphology and

109   climate variables combining into the characteristic makeup of, say, "polar habitat"). Elsewhere,

110   and in colloquial use, "habitat" has been described in a species-dependent way, as the region in

111   geographical space in which an organism lives (e.g. "polar-bear habitat"). The two definitions

112   are not interchangeable (see Hall et al. 1997). We opt for the former definition because it allows

113   objective comparisons between species and quantitative gradations of suitability. Subject to this

114   definition of habitat, we can introduce the *unconditional availability* ($f_\mathbf{x}$) of a particular habitat

115   $\mathbf{x}$ as the relative frequency (i.e. the probability density) with which that habitat occurs across

116   the whole landscape.

117   Data-derived objects recorded in *G*-space are typically complicated and difficult to describe

118   parametrically. For example, describing even a single altitude contour on a map by means of a

119   mathematical formula is a non-trivial task. In contrast, objects in *E*-spaces are generally simpler,

120   as we illustrate in Fig. 1 by visualizing the simple case of a single environmental variable (i.e.,

121   one dimensional *E*-space) measured in a linear region (i.e., one-dimensional *G*-space). The way

122   in which a multimodal variable in *G*-space (Fig. 1b) gives rise to a much simpler (in this case,

123   unimodal) frequency histogram in *E*-space (Fig. 1a) is typical of all landscapes, because multiple

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124 occurrences in *G*-space of the same habitat are condensed into a single habitat frequency in *E*-

125 space. Therefore, most species distribution models (SDMs) are developed and fitted in *E*-space

126 rather than *G*-space (Hooten et al. 2017). That is not to say that a description of habitat

127 availability in *E*-space based on a simple unimodal distribution is always sufficient. Since habitat

128 availability can be a complicated object (Matthiopoulos et al. 2015), a parametric description of

129 the unconditional availability of habitats may be suitably obtained as a mixture of multiple (e.g.

130 Gaussian) components in *K*-dimensional space. For example, Matthiopoulos et al. (2015) used

131 the well-established numerical library **mclust** (Fraley et al. 2005, Fraley et al. 2012) in the R

132 environment (R Core Team, 2016) to approximate unconditional habitat availability in *K*

133 environmental dimensions as a Gaussian mixture of *L* components

$$f_{\mathbf{x}} = \sum_{l=1}^{L} \psi_l f_{l,\mathbf{x}}$$

134
$$= \frac{1}{(2\pi)^{\frac{K}{2}} \prod_{k=1}^{K} \sigma_k} \sum_{l=1}^{L} \psi_l \exp\left(-\frac{1}{2} \sum_{k=1}^{K} \left(\frac{x_k - \mu_{l,k}}{\sigma_k} \right)^2 \right), \tag{1}$$

135 where $f_{l,\mathbf{x}}$ is the lth component (a *K*-dimensional Gaussian probability density function) of the

136 mixture, ψ_l is the weight associated with the lth component (such that $\sum_{l=1}^{L} \psi_l = 1$), $\mu_{l,k}$ is the

137 mean (i.e. the location in *E*-space) of the lth mixture component along the kth environmental

138 dimension and σ_k is the characteristic standard deviation along the kth environmental dimension.

139 Such Gaussian mixtures are universal approximators. Economy in the number *L* of mixture

140 components could be achieved by extending eq. (1) to allow a different standard deviation for

141 each component. However, as in Matthiopoulos et al. (2015), we prioritize mathematical

142 uniformity of the mixture components over parsimony. We therefore allow for a large number of

143 components, but constrain them to have the same standard deviation σ_k.

7

3. Conditional habitat availability

The relative simplicity of E-spaces (compared to G-spaces) comes at a price, because by condensing the environment into the relative frequencies of different habitats, we lose information on the geographical nearness between habitats. Correcting this problem requires an appropriate augmentation of E-space to account for spatial proximity, leading to the notion of *conditional availability*, i.e. the expected availability of habitat **x** to an organism that is currently located in coordinates **s**, characterized by habitat **z**. Importantly, we seek an expression for conditional availability that is not reliant on a neighborhood in G-space defined around a particular location **s**, but rather, on the mixture of habitats typically encountered around a particular habitat **z**. Such an expression would enable us to describe the key patterns in spatially local availability, without the need for models to become spatially explicit.

Fig. 1 shows this concept in one spatial dimension and for one environmental variable. In this low-dimensional illustration, the general notion of a habitat **x** is simply a particular value x of the single environmental variable X and the general location **s** in G-space is the position s on a single spatial axis S. The unconditional availability (i.e., the frequency in E-space) of a particular value x of the environmental variable X is f_x. Collecting such frequencies for all values of the environmental variable forms a probability density function in E-space (Fig. 1a).

Subsequently, we focus on all the spatial locations $s_1,\dots,s_n$ (the dots in Fig. 1b) that are characterized by a particular habitat $z = 30$. An organism with constrained mobility that finds itself in one of these locations will only be able to experience neighboring locations in space. Such localized access to G-space in the neighborhoods of the points $s_1,\dots,s_n$ is illustrated in Fig. 1d using Gaussian kernels, which describe the accessibility of a point at distance r from the current location s_i. These kernels represent the constraints on organism mobility. For example, if we were considering habitat selection by a free-ranging animal over a particular time scale

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168   (say, a year), the kernel could represent Brownian motion over that time scale. Alternatively, if

169   the study organisms are not free-ranging (e.g., because they must provision offspring located at a

170   central place or because they must actively defend a territory), the kernel can be thought of as the

171   result of an Ornstein–Uhlenbeck process (a random walk with a central tendency – Blackwell

172   1997). An isotropic mobility kernel in any number of spatial dimensions can be recast as a

173   function $h(r)$ that describes the probability of an organism reaching a location at distance r

174   away from its current position, over the time period of interest. For data collected infrequently

175   enough that locations can be assumed independent, the kernel can be viewed as determining

176   availability at the home range scale, similar to Horne et al.'s (2008) synoptic model of animal

177   space use. Alternatively, our kernel can be used to model perception range. In particular, Fagan

178   et al. (2017) make the case for mathematical formulations of semi-local perception (an

179   intermediate between the extremes of omniscience and purely local information about habitat)

180   and use Gaussian kernels to describe the diminishing ability of an animal to perceive habitats at

181   greater distances.

182   Since the values of environmental variables in G-space are spatially autocorrelated,

183   neighboring points in E-space (i.e. similar habitats) will tend to be found close to each other in

184   G-space as well. Hence, proximity between locations in G-space must translate to proximity

185   between their corresponding habitats in E-space. This is schematically represented by the single

186   dashed curve in Fig. 1c peaking in the neighborhood of habitat z in environmental space.

187   For those animals viewing the world from the vantage points of habitat z, this localized

188   sampling in G-space (the dots in Fig. 1f) yields a subjective sample of the values of X in E-space

189   (solid black line in Fig. 1e). The comparison between the two curves shown in Fig. 1e represents

190   the main concern of this paper: although, globally, the landscape contains habitats whose

191   frequency is described by the light grey curve (the unconditional availability f_z), an organism

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192   located in a particular habitat z may be surrounded by a considerably different habitat

193   composition as shown by the dark curve (the conditional availability $f_{x|z}$).

194   To write an expression for conditional availability $f_{x|z}$ of habitat x from a position

195   characterized by habitat z, we first consider all pairs of points in G-space separated by a distance

196   r. If the first point is characterized by habitat z, then the probability that the second point is of

197   habitat x is denoted by $g_{x|z}(r)$. If the organism is at the first point, then the probability that it can

198   reach across a distance r is denoted by $h(r)$. Therefore, the product $g_{x|z}(r)h(r)$ represents the

199   probability that habitat x is found at distance r from habitat z, and that it is accessible by the

200   organism located at habitat z. To convert this into a probability density function for conditional

201   availability, irrespective of the distance between two points, we can integrate the product across

202   distances r:

$$f_{x|z} = \frac{1}{C_E} \int_r g_{x|z}(r)h(r) \ dr. \tag{2}$$

203

204   The probability density $g_{x|z}(r)$ encompasses the spatial autocorrelation of habitats, as well as the

205   overall availability of habitat x, and the probability density $h(r)$ represents limitations in

206   accessibility. Since we require $f_{x|z}$ to be a PDF of habitat availability, eq. (2) contains a

207   normalizing constant that integrates over all target habitats x:

$$C_E = \int_E \int_r g_{x|z}(r)h(r) \ dr \, dx. \tag{3}$$

208

209   In one spatial dimension the accessibility kernel can be defined as one-dimensional Gaussian and

210   its associated distance function will then be half-normal:

$$h(r) = \frac{1}{\omega}\left(\frac{2}{\pi}\right)^{\frac{1}{2}} \exp\left(-\frac{r^2}{2\omega^2}\right), \tag{4}$$

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212   where the parameter ω determines the rate at which accessibility decays with distance from the

213   current position. This can be extended to two spatial dimensions by assuming a two-dimensional

214   Gaussian density for the position of the organism. This diffusion-type model implies a Rayleigh

215   distribution (Hughes 1995) for the distance function,

216
$$h(r) = \frac{r}{\omega^2} \exp\left(-\frac{r^2}{2\omega^2}\right). \tag{5}$$

217   Non-Gaussian formulations of the mobility constraint are possible, as long as they are well

218   behaved under integration (for an explanation of this constraint, see eq. (11) below). For

219   example, if we wished to capture the behavior of animals that interspersed localized movement

220   by occasional long-distance forays, we may choose to implement the kernel as a fat-tailed

221   distribution. In that case, a probabilistic model such as the *t*-distribution would be preferable to

222   one whose expectations are pathological, like the Cauchy distribution (Feller 1966).

223   The conditional habitat availability at distance r can be derived from the relationship linking

224   conditional and joint probabilities

225
$$g_{x|z}(r) = \frac{g_{x,z}(r)}{f_z} \ , \tag{6}$$

226   where $g_{x,z}(r)$ is the joint probability density of habitats x and z, quantifying the probability that

227   they can be encountered at distance r from each other. In this expression, f_z is the marginal

228   distribution $f_z(r) = \int_x g_{x,z}(r)\,dx$. Since the destination habitat is integrated out of this expression,

229   the marginal is independent of the distance between x and z, hence $f_z(r) = f_z$. Therefore,

230   irrespective of the particular form of the joint probability distribution of habitats under the

231   requisite distance r, the unconditional availability of habitats is preserved.

232   The joint distribution $g_{x,z}(r)$ must be constructed from the two marginals f_x, f_z (i.e. the

233   unconditional habitat availabilities of habitat x and z, respectively) by introducing a dependence

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234   structure. Dependence structures between any two marginal distributions can be constructed by

235   the method of copulas (Joe 2014), but this is a computationally prohibitive approach because it

236   relies on two inversions of the probability density function (PDF-to-quantile function and back

237   again). Furthermore, in our application, the problem is particularly challenging because the

238   marginal distributions are high-dimensional mixtures (eq. (1)) describing the availability of

239   multiple dimensions in E-space.

240   An alternative proposed by Sawo et al. (2006) for constructing joint PDFs from mixture

241   marginals is to first decompose each marginal f_x, f_z into its L mixture components, and

242   subsequently combine each component from one marginal distribution (following eq. (1), $f_{l,x}$ for

243    $l = 1,..., L$) with every mixture component from the other marginal (which is identical to the first,

244   but specified for another habitat z so, again, following eq. (1), $f_{m,z}$ for $m = 1,..., L$). The

245   weighted sum of these pairwise combinations then yields the joint mixture.

$$g_{x,z}(r) = \sum_{l=1}^{L}\sum_{m=1}^{L}\psi_{l,m}(r)f_{l,x}f_{m,z} \quad , \tag{7}$$

247   where $\psi_{l,m}(r)$ are a new set of weights for the pairwise combinations between $f_{l,x}$ and $f_{m,z}$

248   that, for any given pairwise distance r, must satisfy the following conditions

$$\psi_{l,m}(r) \geq 0, \qquad \sum_{l=1}^{L}\sum_{m=1}^{L}\psi_{l,m}(r) = 1, \qquad \sum_{l=1}^{L}\psi_{l,m}(r) = \psi_m, \qquad \sum_{m=1}^{L}\psi_{l,m}(r) = \psi_l \tag{8}$$

250   Constructing the joint availability function by means of this weighted superposition of products

251   ($f_{l,x}f_{m,z}$) implies independence within the pairwise combinations. For a given number of

252   mixture components, the quality of the approximation of G-space correlations within the joint

253   distribution $g_{x,z}(r)$ could be improved by allowing the covariances of each mixture component

254   to be non-zero. Indeed, it would be possible to allow the variance-covariance structure of each

255   Gaussian component to be unique. These kinds of approaches would lead to efficiencies in the

256   number of Gaussian components needed. At the other extreme, the approach we have used

257   employs large numbers of Gaussian components, all identical and with zero covariances. As the

258   number of components increases, their variances decrease and so does the influence of the

259   assumption of within-component independence. The decision to employ many, identical and

260   simple mixture components was made for analytical tractability. Given that no covariance is

261   assumed within the individual mixture components, the new weights $\psi_{l,m}(r)$ are the only

262   remaining route of generating a covariance in the joint distribution $g_{x,z}(r)$. In other words, we

263   are seeking to construct a covariance structure in $g_{x,z}(r)$ by reweighting radially symmetric

264   Gaussian components. This will introduce some smoothing in the final result (see numerical

265   examples in section 4).

266   To derive the new weights $\psi_{l,m}(r)$, Sawo et al. (2006) propose an algebraic approach, which

267   unfortunately is quite time-consuming for mixtures of multiple components and often fails to

268   satisfy the positivity requirement (the first condition in eq.(8)). We therefore take a more

269   heuristic approach. In Appendix I, we provide an iterative normalization algorithm that

270   constructs a matrix ψ satisfying the conditions in eq. (8) for a given value of *r*. The distance *r*

271   determines the strength of correlation between the two dimensions is. If the distance is small,

272   then the organism will expect to find itself in very similar conditions, which implies that the joint

273   distribution must have high correlation. In contrast, if the organism takes a very large step, then

274   it may find itself in any habitat, with probability proportional to that habitat's global availability.

275   The correlation strength as a function of distance *r* is extracted directly from the environmental

276   data, using an empirical autocorrelation function (ACF – see Appendix I).

277   Placing eqs (7) and (1) into eq. (6) gives

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278

$$g_{x|z}(r) = \frac{\sum_{l=1}^{L}\sum_{m=1}^{L}\psi_{l,m}(r)f_{l,x}f_{m,z}}{\sum_{m=1}^{L}\psi_m f_{m,z}} \ .$$ (9)

279   Replacing into eq. (2) and rearranging the integral produces

280

$$f_{x|z} = \frac{\sum_{l=1}^{L}\sum_{m=1}^{L}f_{l,x}f_{m,z}\int_r \psi_{l,m}(r)h(r)\ dr}{C_E\sum_{m=1}^{L}\psi_m f_{m,z}} \ .$$ (10)

281   In Appendix I, we discuss how the integral in the above expression can be evaluated numerically

282   for a single environmental variable. Henceforth, we replace these integrals by the shorthand

283   notation $\Psi_{l,m}$, defined as

284

$$\Psi_{l,m} = \int_r \psi_{l,m}(r)h(r)\ dr \ .$$ (11)

285   Note that these quantities satisfy the unit-sum requirement (from the second part of eq. (8)),

286

$$\sum_{l=1}^{L}\sum_{m=1}^{L}\Psi_{l,m} = \int_r \left(\sum_{l=1}^{L}\sum_{m=1}^{L}\psi_{l,m}(r)\right)h(r)\ dr = 1 \ ,$$ (12)

287   so they can be thought of as a set of new weights to replace the original quantities $\psi_{l,m}(r)$. This

288   simplifies the overall expression in eq. (10), even after expanding the normalization constant:

289

$$f_{x|z} = \frac{\sum_{l=1}^{L}\sum_{m=1}^{L}f_{l,x}f_{m,z}\Psi_{l,m}}{\int_E\sum_{l=1}^{L}\sum_{m=1}^{L}f_{l,x}f_{m,z}\Psi_{l,m}\ dx} \ .$$ (13)

290   In Appendix II, we show that the denominator in this expression is the marginal distribution of

291   availability, yielding

292

$$f_{x|z} = \frac{\sum_{l=1}^{L}\sum_{m=1}^{L}f_{l,x}f_{m,z}\Psi_{l,m}}{f_z} \ .$$ (14)

14

293　This prompts the identification of the numerator as the joint probability density $f_{x,z}$:

$$f_{x,z} = \sum_{l=1}^{L}\sum_{m=1}^{L} f_{l,x} f_{m,z} \Psi_{l,m} \, . \tag{15}$$

295　Plotting the numerator of eq. (14) for different mobility constraints (Fig. 2) illustrates the

296　operation of the calculations of Appendix I. At low mobility (Fig. 2a) the correlation between

297　different types of habitat is strong, but increasing the mobility of the organism (as shown in Figs

298　2b and 2c, by using higher values of ω), moves the joint distribution closer to the independence

299　scenario $f_{x,z} = f_x f_z$.

300　　The result in eq. (15) is already applicable to one, two or more spatial dimensions (via an

301　appropriate specification of $h(r)$, see examples in eqs (4) and (5)). In principle, eq. (15) is also

302　applicable to multiple environmental dimensions, but this would also require additional

303　methodological work to generalize the algorithm in Appendix I, so as to include any cross-

304　correlations between environmental variables in addition to their auto-correlations. However,

305　using the algorithm of Appendix I in its current form for many environmental variables is also

306　possible if they can plausibly be assumed to be independent of each other. The extensive

307　literature on collinear environmental variables can be used, either to test for non-independence

308　between environmental dimensions, or (e.g. via principal components analysis) to construct a

309　new set of independent environmental variables (Dormann et al. 2013). Given such a set of

310　orthogonal variables, habitat availability in K-dimensional E-spaces can be written as

$$f_{\mathbf{x}|\mathbf{z}} = f_{x_1|z_1} f_{x_2|z_2} \cdots f_{x_K|z_K} \tag{16}$$

312　**4. Illustration using direct sampling of availability from G-space**

313　In the preceding sections, we dealt with the problem of restricted accessibility by extending the

314　mathematical definition of habitat availability. A more direct approach to quantifying availability

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315   in a particular landscape is to sample around different locations in *G*-space (as we did in Fig. 1).

316   It is therefore useful to visualize the outputs of the sampling and analytical approaches on a

317   simple example for a particular simulated landscape, to help with the interpretation of our

318   method and to motivate a discussion of Monte Carlo error.

319   To generate a joint distribution of habitat availability via sampling, the following steps could

320   be adopted:

321   1. Systematically or randomly select a set $\mathbf{S} = \{\mathbf{s}_1,\ldots,\mathbf{s}_n\}$ of points in *G*-space.

322   2. Randomly sample points (in our case, 50) from the vicinity (in *G*-space) of each $\mathbf{s}_i$

323   according to an accessibility kernel with mobility parameter ω. This will generate a set

324   of satellite points $\mathbf{U}_i = \{\mathbf{u}_{i,1},\ldots,\mathbf{u}_{i,50}\}$ reflecting the spatial extent of conditional

325   availability (accounting for both mobility constraint and amount of spatial autocorrelation

326   in the environmental variables).

327   3. For every combination of points $(\mathbf{s}_i, \mathbf{u}_{i,j})$ extract their location $(\mathbf{x}_i, \mathbf{z}_{i,j})$ in joint *E*-space

328   and increment their absolute frequency by one.

329   Using the same simulated landscape throughout this section (see example in Appendix I), we

330   specified two different mobility kernels across the rows of Fig. 3 corresponding to slow-moving

331   animals or short time intervals (Figs 3a, 3b) and fast-moving animals or long time intervals (Figs

332   3c, 3d). The analytical approach in *E*-space derived in section 3 gave the outputs of Figs 3a and

333   3c. We compared these with the corresponding plots (Figs 3b and 3d) obtained via the sampling

334   approach described above. The two approaches give broadly comparable descriptions of the two

335   mobility scenarios, but the model-based approach yielded a smoother description than the

336   sampling algorithm. These differences between the analytical and sampling plots are due to two

337   types of stochasticity. The first relates to Monte Carlo error due to the finite sample sizes taken

338   from each buffer zone. Small sample sizes will tend to introduce stochasticity in the

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339 representation. The second relates to the dependence of the sampling approach on the particular

340 realization of the landscape. Many of its features are essentially a result of chance because they

341 are likely to change if a different landscape with the same statistical properties is sampled. By

342 relying on summaries of spatial autocorrelation, the analytical approach is likely to be more

343 generally applicable to landscapes whose habitat geographies are shaped by similar mechanisms.

344 In general, sampling is more direct, but has three disadvantages: 1) it is computationally

345 expensive (because a large number of focal and satellite points is needed to overcome Monte

346 Carlo error; this increases rapidly with the dimension of E-space); 2) it is specific to the

347 particular realization of the environment presented in the study landscape, inhibiting both

348 understanding about how spatial patterns affect availability and extrapolation to similar

349 landscapes; and 3) it does not yield a compact mathematical expression such as eq. (15) that can

350 allow further applications to make algebraic shortcuts.

351 **5. Applied example: Step selection functions for the analysis of telemetry data**

352 Step selection functions are a method of fitting habitat models to animal telemetry data (Fortin et

353 al. 2005, Thurfjell et al. 2014, Singer et al. 2018). The general step selection model operates in

354 G-space and describes the likelihood that an animal performs a particular relocation from

355 position $\mathbf{s}_{j-1}$ to position $\mathbf{s}_j$ with environmental attributes $\mathbf{x}(\mathbf{s}_j)$. The likelihood $f_u(\mathbf{s}_j | \mathbf{s}_{j-1})$ is

356 described as (see Forester et al. 2009),

357
$$f_u(\mathbf{s}_j | \mathbf{s}_{j-1}) = \frac{w(\mathbf{x}(\mathbf{s}_j)) f_a(\mathbf{s}_j | \mathbf{s}_{j-1})}{\int_{\mathbf{z} \in G} w(\mathbf{x}(\mathbf{u})) f_a(\mathbf{u} | \mathbf{s}_{j-1}) d\mathbf{u}}. \tag{17}$$

358 where $w(\mathbf{x}(\mathbf{s}_j))$ describes habitat preferences and $f_a(\mathbf{s}_j | \mathbf{s}_{j-1})$ expresses mobility (the "resource-

359 independent movement kernel" described in Forester et al. 2009). The selection function $w(\mathbf{x})$ is

360 modeled as a log-linear function of predictor variables. Here, as in Matthiopoulos et al. (2015),

17

361   we employ a curvilinear polynomial form comprising terms up to 2nd order, to allow for the

362   detection of optima in the animal's response to some environmental variables:

$$363 \qquad w(\mathbf{x}) = \exp\left(\sum_{k=1}^{K} \sum_{\eta=1}^{2} \gamma_{\eta,k} x_k^{\eta} \right). \tag{18}$$

364   The objective of statistical inference focuses on the selection coefficients γ. The log-likelihood

365   function corresponding to eq. (17) is

$$366 \qquad l(\mathbf{s}_j \mid \mathbf{s}_{j-1}; \gamma) = \log w(\mathbf{x}(\mathbf{s}_j); \gamma) + \log f_a(\mathbf{s}_j \mid \mathbf{s}_{j-1}) - \log \int_{\mathbf{u} \in G} w(\mathbf{x}(\mathbf{u}); \gamma) f_a(\mathbf{u} \mid \mathbf{s}_{j-1}) d\mathbf{u}. \tag{19}$$

367   The log-likelihood of the entire data set of telemetry data is constructed by combining the

368   individual likelihoods of all the observed relocations in the data,

$$369 \qquad l = \sum_{j=1}^{J} l(\mathbf{s}_j \mid \mathbf{s}_{j-1}; \gamma). \tag{20}$$

370   Employing this log-likelihood within standard estimation approaches, specifically, conditional

371   logistic regression (Fortin et al. 2005), usually involves two simplifying steps (Forester et al.

372   2009). First, the mobility function $f_a(\mathbf{s}_j \mid \mathbf{s}_{j-1})$ is assumed known, and, second, the non-trivial

373   integral of eq. (19) is approximated by point-sampling methods. The first simplifying step allows

374   the term $\log f_a(\mathbf{s}_j \mid \mathbf{s}_{j-1})$ to be dropped from the log-likelihood, since it contains no parameters

375   that need to be estimated from the data. The second step deals with the integral by organizing the

376   telemetry data into strata, each comprising a single focal telemetry location $\mathbf{s}_j$ and a sample (of

377   size V) of control locations $\mathbf{s}_v$. Controls are selected randomly from the geographical vicinity of

378   the telemetry observation $\mathbf{s}_{j-1}$ immediately preceding $\mathbf{s}_j$ so as to represent the habitat options

379   that were available to the animal from that previous position.

380   These two simplifying steps bring the log-likelihood of eq. (19) within the remit of

381   conditional logistic regression, which, for the jth point in a telemetry dataset, is written as

18

382
$$l_{CLL}(\mathbf{s}_j \mid \mathbf{s}_{j-1}; \gamma) = \log(w(\mathbf{x}_j; \gamma)) - \log\left(w(\mathbf{x}_j; \gamma) + \sum_{v=1}^{V} w(\mathbf{z}_v; \gamma) \right), \qquad (21)$$

383 where $\mathbf{x}_j = \{x_1, \ldots, x_K\}_j$ is the habitat at the jth telemetry location and $\mathbf{z}_v$ is the habitat at the vth

384 control location. The likelihood is conditional on the location $\mathbf{s}_{j-1}$ in the sense that the control

385 points are selected from within a neighborhood of that location. The above form of the likelihood

386 is implemented in R, in the form of the clogit() model in the survival library (Therneau &

387 Lumley 2019), and is therefore frequently used for applied analyses (see review in Thurfjell et

388 al. 2014). The estimates of the parameters γ stabilize as the number V of controls selected

389 becomes large, subject to data storage and computational speed capacity. Indeed, if V tends to

390 infinity (e.g. $V > 100$), the likelihood can be replaced by the simpler form

391
$$l_{CLL}(\mathbf{s}_j \mid \mathbf{s}_{j-1}) = \log(w(\mathbf{x}_j)) - \log\left(\sum_{v=1}^{V} w(\mathbf{z}_v) \right). \qquad (22)$$

392 An alternative approach to obtaining a step selection likelihood, without the need to

393 sample control points, is to notice that the sum in eq.(22) is proportional to the expected value of

394 the step selection function in the vicinity of the point $\mathbf{s}_{j-1}$. Therefore, given an exact probability

395 density function of the availability of habitats around the preceding point (i.e. $f_{\mathbf{z} \mid \mathbf{s}_{j-1}}$) we could

396 rewrite eq. (21) as

397
$$l_{CLL}(\mathbf{x}_j \mid \mathbf{s}_{j-1}) = \log(w(\mathbf{x}_j)) - \log\left(\int_E w(\mathbf{z}) f_{\mathbf{z} \mid \mathbf{s}_{j-1}} \, d\mathbf{z} \right). \qquad (23)$$

398 However, in general, an exact form of $f_{\mathbf{z} \mid \mathbf{s}_{j-1}}$ will not be available for any given point $\mathbf{s}_{j-1}$. We

399 can, instead, approximate this function by using the habitat characteristics $\mathbf{x}_{j-1}$ at the point $\mathbf{s}_{j-1}$,

400 so that $f_{\mathbf{z} \mid \mathbf{s}_{j-1}} \cong f_{\mathbf{z} \mid \mathbf{x}_{j-1}}$.

401

19

402

403   This approximation requires knowledge of the unconditional availability of habitats and the

404   spatial autocorrelation in each environmental variable. If these assumptions hold (see below),

405   then the log-likelihood in eq. (23) can be rewritten as

$$l_{CLL}(\mathbf{x}_j \mid \mathbf{x}_{j-1}) = \log(w(\mathbf{x}_j)) - \log\left(\int_E w(\mathbf{z}) f_{\mathbf{z}\mid\mathbf{x}_{j-1}} \, d\mathbf{z} \right). \tag{24}$$

407   Using the results on conditional availability developed in earlier sections, we show in Appendix

408   III that the integral involved in this log-likelihood has a closed form solution. Hence, eq. (20)

409   can be obtained analytically, as

$$l_{CLL} = \sum_{j=1}^{J} \log(w(\mathbf{x}_j)) - \sum_{j=1}^{J} \log\left(\frac{1}{f_{\mathbf{x}_{j-1}}} \prod_{k=1}^{K} \sum_{l=1}^{L} \sum_{m=1}^{L} \Psi_{k,l,m} f_{l,x_k} \Theta(\gamma_{1,k}, \gamma_{2,k}, \mu_{m,k}, \sigma_k) \right), \tag{25}$$

411   where $\Theta(\gamma_{1,k}, \gamma_{2,k}, \mu_{m,k}, \sigma_k)$ is an algebraic function of parameters pertaining to habitat

412   preference and availability. This analytical expression can prove useful in studies with imperfect

413   or irregular environmental data sets. For example, a number of modern telemetry tags,

414   particularly in the marine environment, collect in-situ environmental data in addition to location

415   information (Beringer et al. 2004, Biuw et al. 2007, Hooker et al. 2008, Ericsson et al. 2015). For

416   environmental variables that are only measured at the location of the animal, our model could

417   provide a useful description of habitat availability for locations that were potentially accessible

418   but not visited by the animal. If some representative segments of space have been independently

419   surveyed to allow us to characterize the statistical properties of the distribution of these variables

420   (even if high-resolution covariate layers are not available exactly in the vicinity of the telemetry

421   data) then these can supplement the analysis. In addition, for temporally irregular data, our

422   model's mobility kernel can be used to give a varying degree of accessibility, depending on the

423   time interval between locational fixes (a problem also considered in Johnson et al. 2008,

20

424   Johnson, Hooten & Kuhn 2013). This flexibility can be extended to account for different modes

425   of mobility (e.g. as a result of diurnal activity patterns).

426   Two key assumptions are required to ensure the modelling approximation in E-space provides

427   an adequate approximation to conditional habitat availability:

428   1. **Representativeness assumption.** The data from which the unconditional habitat

429   distribution is derived must be representative of the landscape on which the method is to

430   be applied. Therefore, we require the marginal distributions to be accurate, even if the

431   environmental layers are not known exactly. In a sufficiently large spatial arena, this

432   assumption can be satisfied without the need for high-resolution data. Any large point-

433   sample will suffice as long as it is collected systematically or randomly from the region

434   of interest or a region with similar properties.

435   2. **Stationary autocorrelation function assumption**. The shape of the autocorrelation

436   function must be the same between the regions used for training the approximation and

437   the geographical region of application. This assumption can be satisfied without the need

438   for spatially expansive data. A single high resolution transect that manages to capture the

439   form of autocorrelation will suffice.

440   As a first practical illustration of the above approach, we conducted a comparison between the

441   sampling and modelling approximations (i.e. eqs (21) and (25), respectively) on a real telemetry

442   data set (Fig. 4), collected from individual harbor seals (*Phoca vitulina*), off the north coast of

443   the Netherlands. We used a simple data set of two environmental covariates corresponding to

444   bathymetry (Fig. 4a) and the percentage of silt in the sediment (Fig. 4b). We selected time

445   intervals between the pairs of successive observations in the data set to be less than 24hrs and

446   sub-sampled from the data set (taking 1 out of every 20 consecutive pairs of locations) to ensure

447   that the successive pairs in the data set were serially independent. The value of the parameter of

448   the mobility kernel $\omega = 2.58$ (in units of grid cell lengths) was derived directly from the data, as

        21

449   the standard deviation of the Rayleigh distribution (calculated as $\sqrt{2\,\mathrm{var}(|\Delta\mathbf{s}|)/(4-\pi)}$, where

450    $|\Delta\mathbf{s}|$ were the observed step lengths in the data). The sampling approximation used 200 control

451   points for each stratum (i.e. combined with each pair of successive locations). The controls for

452   the sampling approach were selected using Rayleigh step lengths with a uniformly random

453   direction on the circle. The modelling approximation used the same Rayleigh distribution and

454   covariate information originating either from a box enclosing the telemetry data (the yellow box

455   in Fig. 4c) or from a strip of the sea that was outside the telemetry set (the blue rectangle in Fig.

456   4c). This comparison allowed us to explore the sensitivity of parameter estimates and spatial

457   predictions to changes in habitat structuring (i.e. violations of the two assumptions of

458   representativeness and stationary autocorrelation). The two regions differed in their area, shape

459   and location. The elongated shape of the blue region precluded averaging over the strong

460   anisotropy in the environment. These differences potentially reduced the representativeness of

461   the blue region.

462   To visualize the differences in habitat composition between the two boxes, we plotted the

463   actual frequency of sea depths and sediment values (the black curves in Figs 4d and 4e

464   respectively) against the modeled availability of those two variables within the yellow box (solid

465   brown line for depth in Fig. 4d and solid blue line for sediment in Fig. 4e) and within the blue

466   rectangle (dotted brown line for depth in Fig. 4d and dotted blue line for sediment in Fig. 4e). In

467   addition, we explored differences in spatial autocorrelation between the yellow and blue

468   rectangles (Fig. 4f). We visualized the results of the analysis in geographic as well as parameter

469   space. The geographic visualization for each of the three analyses looked at the value of the step

470   selection function in each of the map's pixels (Figs 4g,h,i). These values can be interpreted as a

471   relative measure of preference in comparison to nearby cells. The parameter space visualization

22

472   examined the estimates and 95% confidence ellipses generated by each of the three methods for

473   the coefficients of the two environmental variables (Figs 4j,k,l).

474   The above comparison leads to the following conclusions. When the training data are

475   obtained from the region of interest, the modelling approximation gives similar spatial results to

476   geographic sampling (compare Fig. 4g with Fig. 4h) and the 95% confidence ellipses overlap

477   (Figs 4j and 4k). Using training data outside the region of interest, so that the assumptions of

478   representativeness and stationary autocorrelation are less faithfully preserved (see diagnostics in

479   Figs 4d,e,f), may result in differences between the two approaches, (compare Fig. 4g with 4h and

480   4i). Yet, the parameter estimates remain within plausible ranges for this particular problem

481   (compare Fig. 4j with 4l). So, while the method gives plausible parameter estimates outside the

482   range of the data we can conclude that there are increasing differences as the training data

483   deviate from the region of interest. Therefore, although the proposed approach of modelling

484   spatial accessibility in E-space is not a substitute for direct sampling of controls in G-space, it is

485   a method that can provide informative results when environmental data are sparse or of limited

486   geographic coverage.

487   We note that the above application only uses the most rudimentary form of step selection

488   estimation. As part of future work, it would be interesting to explore how the above likelihood

489   could be extended to perform simultaneous estimation of movement characteristics and habitat

490   preferences (e.g. Forester et al. 2009, Avgar et al. 2016). Additionally, the approach taken here

491   assumes independence of the conditional availability of the different environmental variables. It

492   is reassuring that the approximation above works reasonably well despite this simplification,

493   given that depth and sediment were moderately cross-correlated (r^2=0.64).

494

6. Theoretical example: The effects of spatial autocorrelation on the fitness of territorial animals

To illustrate how our approach can be used to derive theoretical results, we consider the effects of spatial autocorrelation on the average fitness of populations of animals holding territories of identical size. To derive some useful baseline results, we begin by assuming that space is saturated by territories (i.e. no apparent habitat preference), but relax this assumption later. We consider a habitat described by a single covariate (e.g. a single resource) where z refers to the value of the resource at the territory's centroid and x refers to values of the resource found elsewhere within the territory. The fitness contribution of a habitat (i.e. a particular value of the resource x) is denoted by F_x such that $F_x = a_0 + a_1 x$ for some coefficients a_0, a_1. We require fitness to be negative when the resource x is low, (i.e. $a_0 < 0$) and to have a positive relationship with increasing resource values (i.e. $a_1 > 0$). This example can be extended (with more elaborate algebra, but no loss of analytical tractability) by introducing several covariates, possibly having non-monotonic contributions to fitness (see Matthiopoulos et al. (2015) for more complex extensions).

Fitness in the absence of habitat preference

When a population lives in a landscape of very low spatial autocorrelation (LO), all habitats (i.e. all values of the resource) should, on average, be present within each territory in proportion to their broader availability (f_x). In other words, the composition of each territory, and therefore also the fitness afforded by each territory, will be representative of the broader landscape:

$$F_{LO} = \int_E F_x f_x \, dx . \tag{26}$$

In Appendix IV we show that this simplifies to

24

$$F_{LO} = a_0 + a_1 \sum_{l=1}^{L} \psi_l \mu_l. \qquad (27)$$

518 Thus, the fitness of the organism is derived from a weighted sum of the means of the Gaussian

519 mixture describing habitat availability; this sum is equal to the mean of x. In other words, if $\bar{x}$ is

520 the average value of the resource in the environment, under low spatial autocorrelation, we get

521 the intuitive result, corresponding to perfect mixing,

$$F_{LO} = a_0 + a_1 \bar{x}. \qquad (28)$$

523 More generally, for animals living in more realistic landscapes with some spatial

524 autocorrelation, the expected fitness for a territory centered at habitat z will be

$$F(z) = \int_E F_x f_{x|z}\, dx. \qquad (29)$$

526 In Appendix IV we show that this simplifies to

$$F(z) = a_0 + \frac{a_1}{f_z} \sum_{l=1}^{L} \sum_{k=1}^{L} f_{k,z} \Psi_{l,k} \mu_l. \qquad (30)$$

528 Incidentally, a comparison between eqs (30) and (27) implies that, in the case of perfect mixing,

529 the joint weights of the habitat availability formula take the form

$$\Psi_{l,k} = \psi_l \psi_k. \qquad (31)$$

531 We explore the difference between the average fitness, across the landscape, in the absence and

532 presence of spatial autocorrelation,

$$\bar{F} - \bar{F}_{LO} = \int_z F(z) f_z\, dz - F_{LO}, \qquad (32)$$

534 which rearranges to

$$\bar{F} - \bar{F}_{LO} = a_1 \left(\sum_{l=1}^{L} \sum_{k=1}^{L} \Psi_{l,k} \mu_l - \sum_{l=1}^{L} \psi_l \mu_l \right). \qquad (33)$$

25

536 We note that $\sum_{k=1}^{L} \Psi_{l,k} = \psi_l$ which gives $\bar{F} - \bar{F}_{LO} = 0$. This makes intuitive sense and has been

537 anticipated by previous work (Barraquand & Murrell, 2013, Fig. 1). In an autocorrelated

538 landscape, tessellated by territories, some individuals will benefit from aggregations of high

539 resource while others will lose out by having their territories at resource troughs.

540 *Fitness in the presence of habitat preference*

541 We now relax the assumption of uniform placement of territories by introducing a model of

542 heterogeneity that is affected by an underlying habitat preference function $w(z) = \exp(b_0 + b_1 z)$ to

543 the single resource *z*. We assume for this exploration that habitat preference operates on the

544 selection of the territory centroid, but that the organism uses parts of the territory uniformly. The

545 average fitness afforded by the environment to a population of such animals would therefore be

546
$$\bar{F} = A^{-1} \int_E w(z) f_z F(z) \, dz , \tag{34}$$

547 where $F(z)$ is the fitness associated with a territory centred at habitat *z* (as defined in eq. (30))

548 and $A = \int_E w(z) f_z \, dz$ is a normalizing constant for the preference function. In Appendix V, we

549 show that this expression can be simplified to

550
$$\bar{F} = a_0 + a_1 \frac{\sum_{l=1}^{L} \sum_{k=1}^{L} \Psi_{l,k} \mu_l \exp(b_1 \mu_k)}{\sum_{k=1}^{L} \psi_k \exp(b_1 \mu_k)} . \tag{35}$$

551 This expression describes the average population fitness as a function of unitary fitness

552 parameters (a_0, a_1), marginal resource availability (expressed by the parameters ψ_k, μ_k), spatial

553 autocorrelation (contained in the joint weights $\Psi_{l,k}$) and the selectivity (b_1) in choosing the

554 centroid of a territory. For any particular landscape, the joint weights will generally need to be

555 derived using methods such as the ones presented in Appendix I, but we can simplify our

26

556   investigation by comparing the two extremes of very low and very high spatial autocorrelation.

557   The case of very low spatial autocorrelation is represented by eq. (28). The case of very high

558   spatial autocorrelation can be emulated by setting

559
$$\Psi_{l,k} = \begin{cases} \psi_k & \text{if } l = k \\ 0 & \text{otherwise} \end{cases} . \tag{36}$$

560   Within the expression for joint habitat availability (eq. (15)), this works by accumulating a high

561   probability density close to the line of slope 1 (creating joint PDFs similar to those in Figs. 2a or

562   3a), hence enforcing the probability of encountering similar values of z from an animal's current

563   position. Via this simplification, the fitness equation becomes

564
$$\bar{F} = a_0 + a_1 \frac{\sum_{k=1}^{L} \psi_k \mu_k \exp(b_1 \mu_k)}{\sum_{k=1}^{L} \psi_k \exp(b_1 \mu_k)} . \tag{37}$$

565   Subject to the assumption of high spatial autocorrelation, we proceed to explore the behavior of

566   this function by varying the overall resource richness (related to the mean value of the

567   distribution of the available resource) and heterogeneity (the variability of the distribution of the

568   available resource) of the landscape. To do this in a tractable way, we envisage an environmental

569   space that is constructed of L equally spaced and equally weighted Gaussian components (Fig.

570   4a). The mean value ($\bar{z}$) of the mixture determines overall resource richness and the number (L)

571   of individual components, equally split on either side of the mean, represents heterogeneity. We

572   take the spacing between adjacent Gaussian means μ_k, μ_{k+1} to be equal to σ, the standard

573   deviation of each of the Gaussian components. This assumption tends to give approximately

574   uniform distributions of the resource in E-space (thick grey curve in Fig. 5a). Note however that

575   the distribution of the resource in G-space will be heterogeneous. This simplified representation

576   of the environment yields

27

577
$$\psi_k = \frac{1}{L} \quad \text{and} \quad \mu_k = \bar{x} + \sigma\left(k - \frac{L+1}{2}\right).$$
(38)

578   For fitness (eq. (37)), these simplifications imply that

579
$$\bar{F} = a_0 + a_1\left(\bar{x} - \sigma\frac{L+1}{2} + \sigma\sum_{k=1}^{L} k\theta_k\right),$$
(39)

580   where θ_k are weights driven by the habitat selectivity parameter (b_1):

581
$$\theta_k = \frac{\exp(b_1 k\sigma)}{\sum_{k=1}^{L} \exp(b_1 k\sigma)}.$$
(40)

582   The parameter b_1 represents the ability of an organism to express preference for placing its

583   territory centroid at high-resource locations. In a very small population it is expected that b_1 will

584   be very large, because, when unobstructed by conspecifics, an organism will be able to place its

585   territory at the peak of resource concentration. If the landscape is completely saturated, so that

586   space is covered by territories, apparent selectivity will move towards zero. If the centroid of a

587   territory serves a life-history function that is mutually exclusive to resource acquisition (e.g. a

588   ground nest that needs to be placed within high, but inedible grass), the apparent selectivity for

589   the resource may give negative values of b_1. We therefore consider three scenarios that give rise

590   to important boundaries in the richness/heterogeneity plane (see collected results in Fig. 5b).

591

592   *Scenario 1: Fitness is negative, even when the population displays high selectivity (i.e. very high*

593   *values of b_1).* This corresponds to environments where even small populations, with the ability

594   to concentrate around the best available habitat, become extinct. The scenario of very high

595   selectivity is written

596
$$\lim_{b_1 \to \infty} \sum_{k=1}^{L} k\theta_k = L.$$
(41)

28

597 Using eq. (39), the mathematical condition for negative fitness is

$$\bar{x} < -\frac{a_0}{a_1} - \sigma \frac{L-1}{2} . \tag{42}$$

599 *Scenario 2: Fitness is zero in a saturated population, that has completely filled up space with*

600 *territories, giving the impression of no selectivity ($b_1 = 0$). In this scenario,*

$$\sum_{k=1}^{L} k\theta_k = \frac{L+1}{2} \tag{43}$$

602 Using eq. (39), the mathematical condition for zero fitness is

$$\bar{x} = -\frac{a_0}{a_1} \tag{44}$$

604 *Scenario 3: Fitness is positive even when the organism avoids high concentrations of the*

605 *resource (i.e. for very large negative values of b_1). This scenario implies*

$$\lim_{b_1 \to -\infty} \sum_{k=1}^{L} k\theta_k = 1 \tag{45}$$

607 The mathematical condition for positive fitness is

$$\bar{x} > -\frac{a_0}{a_1} + \sigma \frac{L-1}{2} \tag{46}$$

609 For graphical convenience, we define resource richness in relation to fitness parameters. Further,

610 we define environmental heterogeneity in terms of the number and dispersion of Gaussian

611 components used to describe the range of resource values in environmental space.

$$\text{Richness} = \bar{x} + \frac{a_0}{a_1} \qquad \text{Heterogeneity} = \sigma \frac{L-1}{2} \tag{47}$$

613 These definitions are biologically intuitive. In particular, this index of resource richness takes the

614 value zero, when experiencing the average availability of the resource barely allows an organism

615 to survive. The index of heterogeneity, becomes zero when the minimum number of Gaussian

29

616   components ($L = 1$) is used to describe the environment. Recasting the conditions in eqs (42),

617   (44) and (46) with the aid of these new definitions gives us the combined results in Fig. 5b that

618   enable us to summarize population viability in terms of resource richness and heterogeneity in

619   the case of a highly spatially autocorrelated resource distribution. The figure illustrates that

620   spatial heterogeneity expands the ability of a population to persist and quantifies the thresholds

621   of extinction and persistence in scale-independent coordinates (thanks to the scalings of richness

622   and heterogeneity emerging from this analysis, in the form of eq. (47)).

623   **7. Discussion**

624   Assumptions about habitat accessibility can drastically affect the predictions of population

625   models in space and time. Models that assume either perfectly mixed or completely sessile

626   populations are liable to err for different reasons. We therefore need a theoretical and

627   quantitative framework for describing habitat accessibility. The two basic determinants of habitat

628   accessibility from any given geographical position are the speed with which organisms move and

629   the spatial scales over which the environment varies. Starting from this fact, we have derived a

630   compact expression for conditional habitat availability (eq. (14)) in environmental (or niche)

631   space. This was achieved by describing the availability of all habitats from the vantage point of

632   any given habitat, using functions of distance (reflecting both mobility and spatial

633   autocorrelation). The benefits of this framework are both conceptual and applied. From a

634   conceptual viewpoint, this work can be seen as a contribution to the historical and ongoing

635   discussions about scale in ecology (Wiens 1989, Levin 1992, Schneider 2001, Gurarie &

636   Ovaskainen 2011). Our work offers a quantitative formalization of the interplay between the

637   scale of spatial autocorrelation and the scale of organism mobility over particular time frames. A

638   correctly scaled view of accessibility can quantify relationships that would not have been evident

639   via qualitative arguments alone. The collected findings in Fig. 5b illustrate how the relative

30

640 scales of mobility and environmental heterogeneity can fundamentally alter the fitness that a

641 landscape can afford a population. Regions 2 and 3 in Fig. 5 have a novel biological

642 interpretation, in which habitat selectivity changes the sign of population growth relative to an

643 assumption of no selectivity. Region 3, in particular, is the direct result of animals in the

644 population being able to aggregate at hotspots of resource distribution, and hence experience

645 higher-than-average fitness, compared to a non-spatial model assuming perfect mixing.

646   Many of these insights would be achievable on a particular landscape by means of intensive

647 sampling of space (as we argued in Section 4); however, our framework offers a flexible

648 abstraction of species-habitat interaction based solely on the statistical properties of the system.

649 This allows us to work in environmental spaces and produce generalizable results, applicable to

650 different landscapes with similar landscape compositions. Similar models can be derived through

651 moment equation modeling incorporating at the same time the spatial autocorrelation in

652 environmental variation, the movement processes through kernels – as done here - as well as

653 deriving the environment-organism covariance from the interaction of dispersal, demography

654 and environmental structure (Murrell & Law 2000, Bolker 2003, North et al. 2011). However,

655 these methods require more complex analytical formulas, place their emphasis on population

656 dynamics and do not operate explicitly in E-spaces.

657   A recent review of species range models (Singer et al. 2016) discusses how mechanistic

658 approaches can be used to enhance the predictive ability of correlative models of species'

659 distribution. Hence, the present work can be used to increase the mechanistic content of

660 correlative models, but may also be used for expedient calculation in fully mechanistic

661 approaches. The mechanistic content of our approach can be increased to account for features of

662 movement. For example, the variance of our movement kernel can be assumed to depend on the

663 properties of the local habitat, to account for reductions in mobility due to difficult substrates.

664 Accessibility may also be thought of in larger spatiotemporal scales from the viewpoint of

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dispersal processes. SDMs based on snapshots of species abundance assume that, over many

generations, dispersal events that are hard but not impossible will have been made, at some

point, allowing the species to occupy all the locations that have suitable habitat. Our framework

can accommodate both timescales of dispersal by varying how far out in the tails of the

availability kernel we sample. Indeed, that can become an index of how fast a species can fill up

the landscape, which becomes relevant as we try to figure out whether species will be able to

shift their geographic ranges fast enough to keep up with climate change (Parmesan & Yohe,

2003).

Supplements

Supplementary information is provided for the Appendix derivations as well as an explanation of

the algorithms derived in the paper. Archival files for the R-code and data used in the paper can

be downloaded from https://zenodo.org/record/3479825#.XZ-MDSV7knc.

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825   **Figure 1:** The panels in the left column represent E-space (comprising a single environmental

826   variable) corresponding to the G-space (comprising a single spatial dimension) in the right

827   column. The values plotted in G-space are the local values of the environmental variable X, and

828   E-space summarizes the frequency with which each value of the environmental variable occurs.

829   G-spaces are usually more complicated objects to describe because the same habitat can occur

830   several times. In this example, 7 values in G-space (the dots in b) are condensed to one value in

831   the plot of E-space (a). The accessibility of space around a particular habitat can be represented

832   by symmetric kernels (the dark curves in d). The existence of spatial autocorrelation in the

833   proximity of each of these spatial locations guarantees that similar environmental values will be

834   found within these kernels of accessibility. We represent this by the dashed curve in plate c – an

835   imagined kernel in E-space that represents the correspondence between spatial and

836   environmental proximity. A realization of the sampling process from the kernels (using Gaussian

837   forms) provides a scattering of observations in G-space (shown as dots in f). The resulting plot

838   of frequencies for these localized measurements is shown as the dark curve in (e).

839   **Figure 2:** The joint distribution of habitat availability ($f_{x,z}$), for a given marginal habitat

840   availability (f_z, f_x) under three examples of the mobility constraint ($\omega = 3, 5, 10$). Lighter

841   colors represent higher probability density. The figure explores the case of a single

842   environmental variable X, therefore the axes have identical units and scales, representing the

843   support of that environmental variable in E-space. The marginal distributions shown on the sides

844   of the main plots are identical, representing the fact that the overall habitat availability across the

845   landscape is not affected by mobility.

846   **Figure 3:** Comparison between the analytical and numerical forms of the joint distribution (left

847   and right columns respectively) under scenarios of low and high mobility (top and bottom rows,

848   respectively). The axes represent the variables z (focal habitat) and x (target habitat) for a one-

849   dimensional environmental space. Shading of contours (lighter shades for higher probability) is

850   on the same scale for plots on the same row, for comparison.

851   **Figure 4:** Step selection analysis of harbor seal telemetry data by G-space sampling and E-space

852   approximation. Two environmental variables (a and b) were used to characterize the substrate to

853   movement, observed via satellite telemetry data (c). Step selection by E-space approximation

854   used two different rectangular areas for learning about the environment (shown as yellow and

855   blue in plate c, and giving rise to E-space approximation 1 and 2, respectively). Each variable

856   was summarized in terms of its marginal availability (d and e) and spatial autocorrelation (f). In

857   plots (d,e and f) brown colour is used for depth and blue for sediment. Solid lines correspond to

858   the yellow box in part c and dotted lines correspond to the extrapolation in the blue rectangle in

859   part c. The solid black curves in d and e represent the actual frequency of depth and sediment

860   values in the yellow rectangle. The third row of plots shows the maps of relative preference

861   derived from each step-selection analysis, specifically the G-sampling approach (g), E-space

862   approximation 1, using the yellow rectangle (h) and E-space approximation 2, using the blue

863   rectangle (i). The final row of plots shows the likelihood profiles in 2D parameter space derived

864   from each of the three analyses, G-space sampling (j), E-space approximation 1 (k) and E-space

865   approximation 2 (l). The white cross-hairs indicate maximum likelihood parameter estimates,

866   accompanied by asymptotic 95% confidence ellipses (also drawn in white). The coloration from

867   purple to brown reflects increasing likelihood for different parameter combinations.

868   **Figure 5:** a. Example of a uniform marginal distribution in environmental space in one resource

869   variable constructed from the superposition of equally weighted Gaussian components (each

870   having a standard deviation of σ, which is also used as the placement distance between

40

871 successive components). This arrangement allows us to reduce the description of E-space to the

872 two traits of resource richness (the position of the mixture along the resource axis) and

873 heterogeneity (the dispersion of the mixture, driven here by the number of participating Gaussian

874 components. b. Summary of findings in the graphical plane of resource richness and

875 heterogeneity in the case of a highly autocorrelated resource distribution in G-space. Four

876 regions arise indicating population viability depending on the habitat selectivity displayed by the

877 individuals making up the population.

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Figures
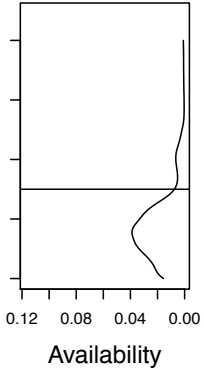
a. E–Space global

b. G–Space global
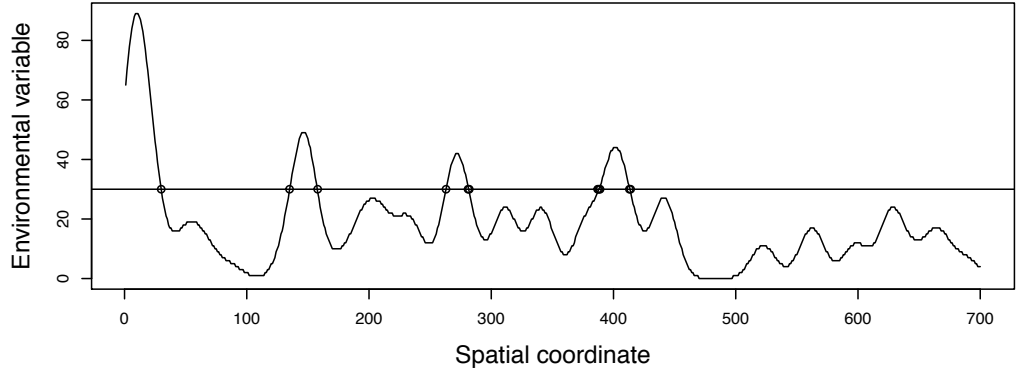
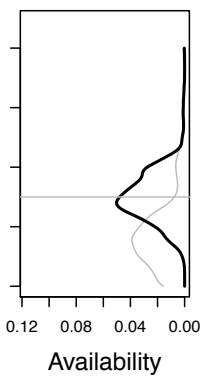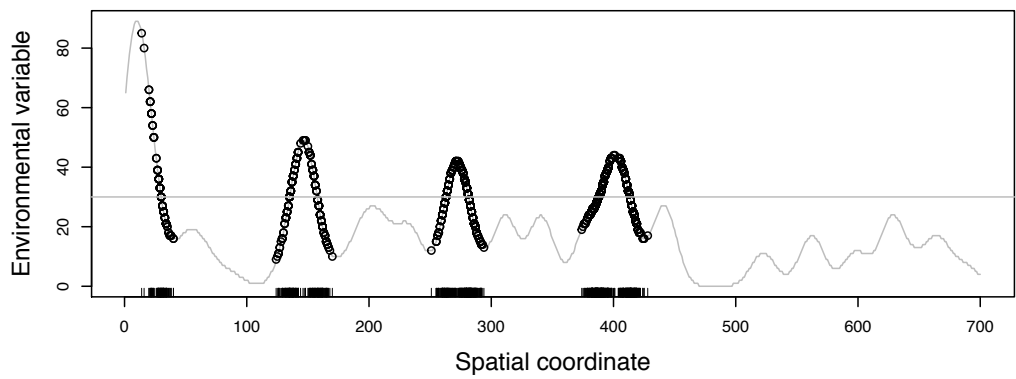**c. E–Space kernel**
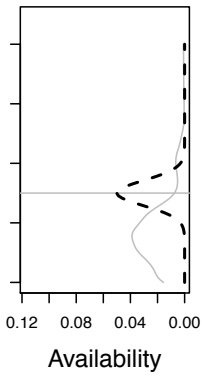
d. G–Space kernel
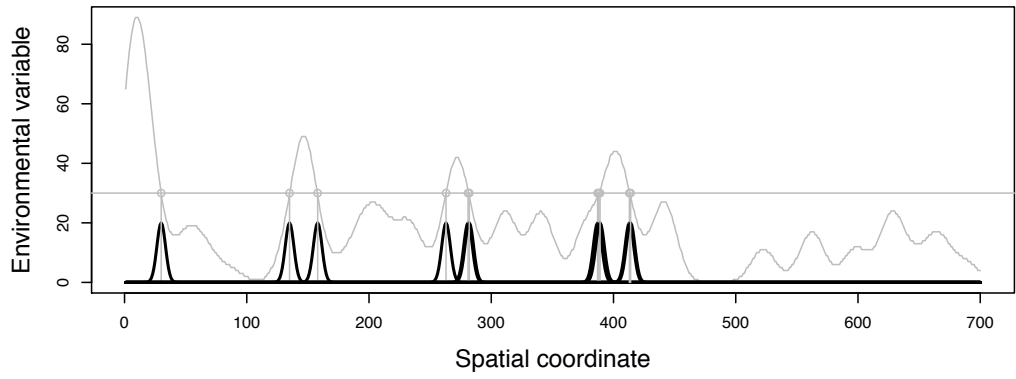
e. E–Space local

f. G–Space local

883   Figure 1

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Figure 2

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Restricted mobility - Model

a

Restricted mobility - Realisation

b

High mobility - Model

c

High mobility - Realisation

d

X (Target habitat)

Z (Focal habitat)
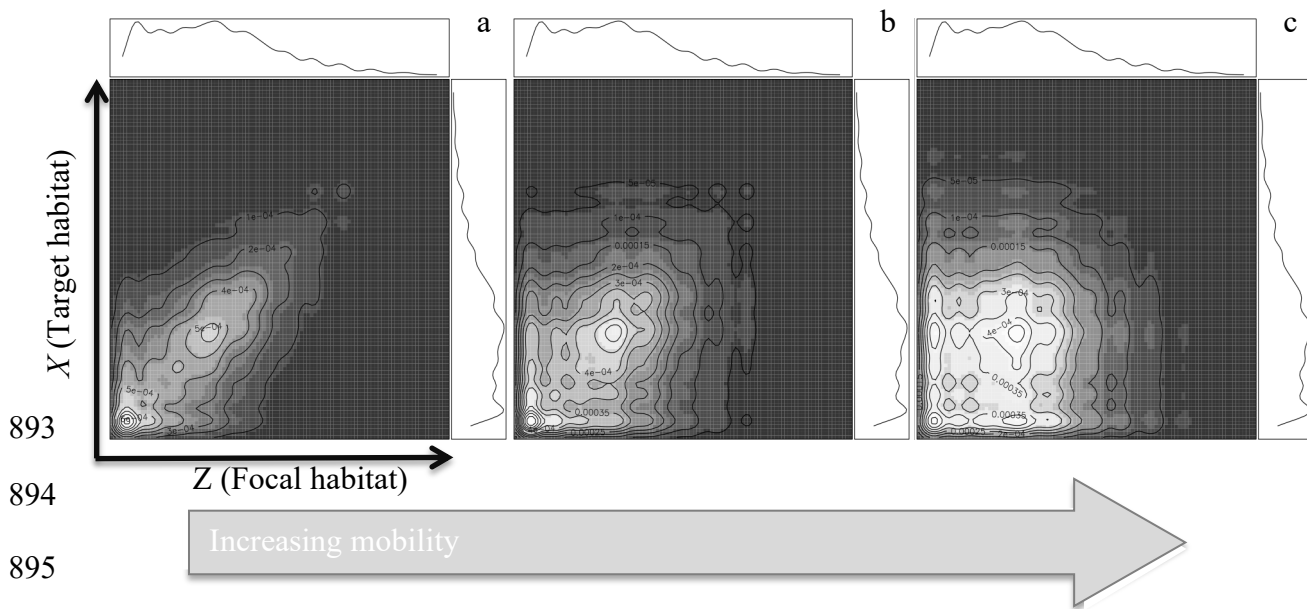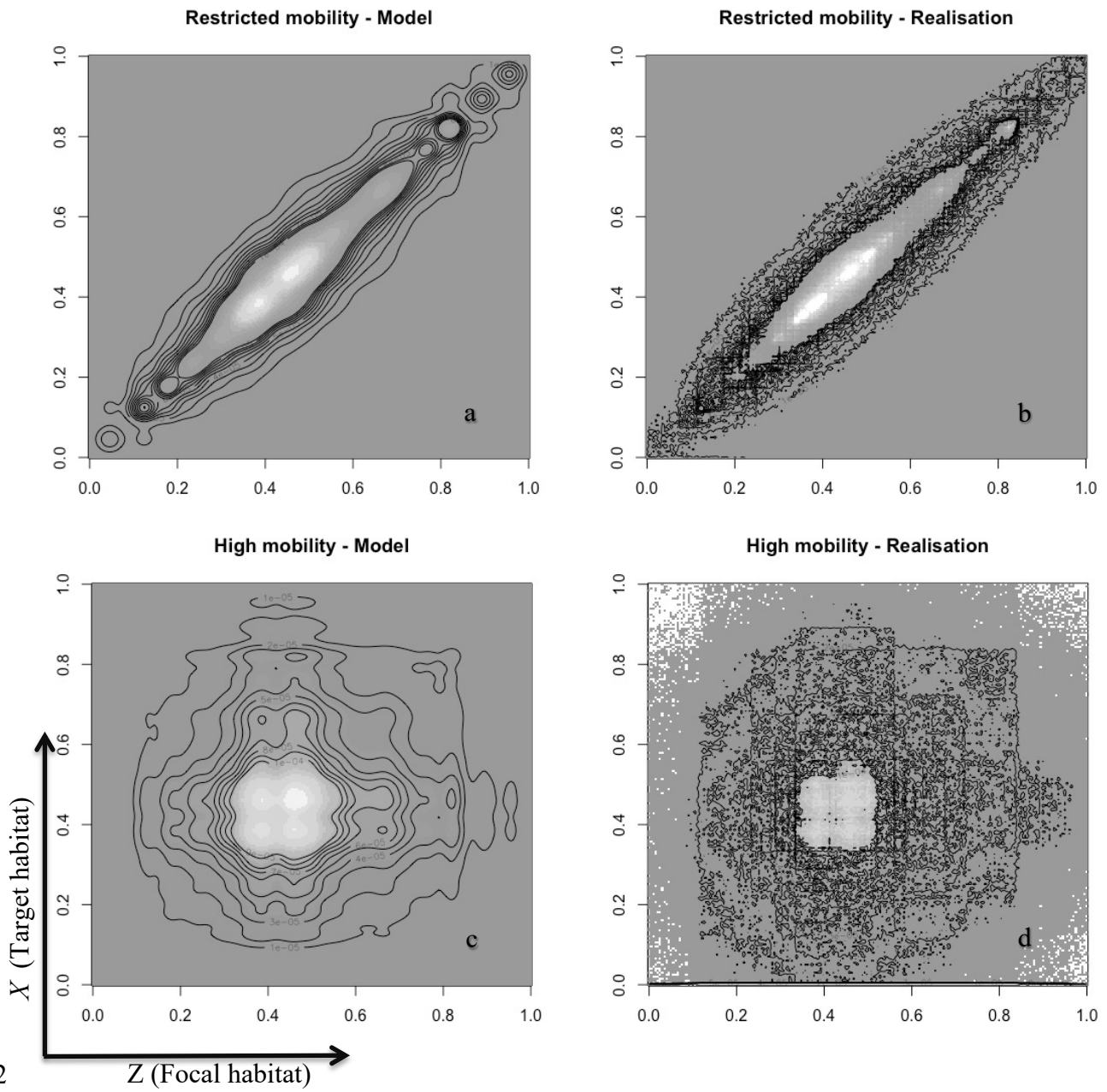
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904

905   Figure 3

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a. Depth

b. Sediment

c. Telemetry

d. Depth marginal availability

e. Sediment marginal availability

f. Autocorrelation

g. SSF by G–space sampling

h. SSF by E–space approx. 1

i. SSF by E–space approx. 2

j. Likelihood by G–space sampling

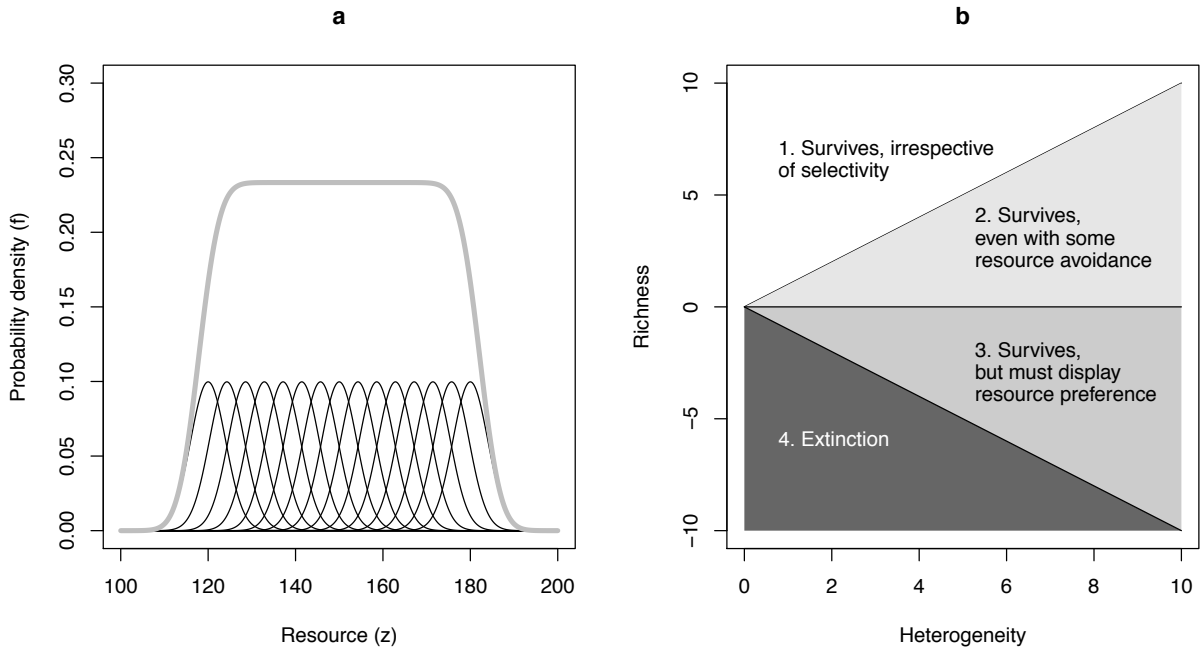**k. Likelihood by E–space approx. 1**

l. Likelihood by E–space approx. 2

907
908   Figure 4

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912   Figure 5

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