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- 1 Downscaling the environmental associations and spatial patterns of species richness
- 2
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- 8
- 9 **Running title:** Downscaling richness-environment associations



10 Abstract

We introduce a method that enables the estimation of richness-environment association and 11 prediction of geographic patterns of species richness at grains finer than the original grain of 12 13 observation. The method is based on a hierarchical model that uses coarse-grain values of 14 species richness and fine-grain environmental data as input. In the model the (unobserved) fine-15 grain species richness is linked to the observed fine-grain environment and upscaled using a 16 simple species-area relationship (SAR). The upscaled values are then stochastically linked to the 17 observed coarse-grain species richness. We tested the method on Southern-African bird atlas 18 data by downscaling richness from 2° to 0.25° (~ 250 km to ~30 km) resolution. When prior 19 knowledge of the SAR slope (average species turnover within coarse-grain cells) was available, the method predicted the fine-grain relationship between richness and environment and provided 20 fine-grain predictions of richness that closely resembled results from native fine-grain models. 21 Without the SAR knowledge the method still accurately quantified the richness-environment 22 23 relationship, but accurately predicted only relative (rank) values of richness. The approach can 24 be easily extended and it is a powerful path for cross-scale statistical modelling of richness-25 environment relationships, and for the provision of high-resolution maps for basic science and 26 conservation.

27

Key words: Bayesian; beta diversity; biodiversity; climate; grid; MCMC; land cover; multilevel;
Poisson; productivity; scale; small area estimation

30 Introduction

The visualization and interpretation of geographic patterns or maps of species richness and their 31 32 association with environment are of pivotal interest to ecology and conservation. Due to the 33 limited accuracy of available species distribution information, the spatial detail of geographic 34 richness patterns is often less than desired. This is in strong contrast with environmental 35 information which is rapidly growing in detail, causing an increasing gap between biodiversity 36 and environmental knowledge (Jetz et al. 2012). For instance, even in well-known terrestrial 37 vertebrates the understanding of species global geographic ranges (based on expert range maps) 38 typically remains coarser than 100 km in resolution (Hurlbert and White 2005, Hurlbert and Jetz 2007) - at finer resolutions range maps over-estimate presences and species richness (Jetz et al. 39 2008). Researchers are sometimes tempted to visualize richness patterns at finer resolution than 40 41 the data may warrant in order to achieve aesthetically pleasing visualizations or convey an unwarranted impression of detail. A broad community would thus benefit from a statistically 42 43 sound method that would allow the mapping of species richness at grains (or resolutions) finer 44 than the grain of the original data.

45 Species richness is often associated with environmental conditions. However, key environmental predictors of species richness vary with spatial grain (Willis and Whittaker 2002, 46 47 Field et al. 2009, Belmaker and Jetz 2011). While the very large grains of regional communities (Ricklefs 2004) or "evolutionary arenas" (Jetz and Fine 2012) tend to be affected by evolutionary 48 49 and regional-historical factors, contemporary climate/productivity and land cover predict species 50 richness at grains around tens to hundreds of km (Field et al. 2009, Belmaker and Jetz 2011), 51 while clade- or species-specific biotic factors and occupancy dynamics are relevant towards even 52 finer grains (Harrison et al. 2006, Soberón and Nakamura 2009, Hortal et al. 2010, White and

Hurlbert 2010, Belmaker and Jetz 2011). To date, the spatial grain of investigations into the 53 54 predictors of species richness has often been limited by the minimum reliable grain of the richness data (e.g. 100 km for expert range maps) rather than the most relevant scale of the 55 56 hypothesized process. Flexible approaches linking diversity to its environmental predictors at finer grains would allow aligning models more closely with the scale of relevant potential 57 58 processes, and ultimately facilitate cross-scale hypothesis testing. Assuming the finer-grain 59 relevance of available environmental factors, they would also enable the mapping of richness over large spatial extents at higher spatial resolutions of greater visual appeal and conservation 60 61 relevance.

In the broader area of *downscaling* of ecological phenomena the past decade has seen 62 several relevant efforts. Specifically, methods have been developed to downscale species 63 occupancy (Kunin 1998, Azaele et al. 2012) and spatial distribution of individual species (Araújo 64 65 et al. 2005, McPherson et al. 2006, Niamir et al. 2011, Bombi and D'Amen 2012, Keil et al. 2013). Araújo et al. 2005, Bombi et al. (2012) and Keil et al. (2013) presented attempts to 66 67 downscale maps of species richness based on stacking of downscaled occurrence maps of 68 individual species. To our knowledge, these efforts have not included a method that would 69 downscale species richness per se. Compared to single-species population densities or 70 probabilities of occurrence values of species richness cannot be added to one another to equal 71 total richness. To get the total richness one requires an additional piece of information: the rate of species turnover between the locations (closely linked to beta diversity or the local slope of 72 73 species-area relationship; Šizling et al. 2011). Hence, any attempt to model species richness at 74 multiple spatial resolutions must explicitly consider species turnover.

Here we introduce a hierarchical modelling approach (Clark and Gelfand 2006) to 75 integrate coarse-grain species richness and species turnover (beta diversity) to predict the 76 patterns of species richness at fine grains. The method assumes that the unobserved fine-grain 77 78 richness is a function of the observed fine-grain environment, and that this unobserved richness can be linked to the observed coarse-grain richness via a simple species-area relationship (whose 79 slope is our measure of beta diversity; Šizling et al. 2011). The posterior marginal probability 80 81 density of parameters of the fine-grain component of the model (given the whole model, the fine-82 grain environment and the coarse-grain richness) are then estimated and used to predict fine-83 grain species richness. The approach offers a general statistical framework for a more scaleflexible evaluation and mapping of geographic patterns of species richness. 84

85

86 Methods

87 *Data*

We collated atlas data on avian breeding distributions for Angola (0.25° grain; Dean 2000), 88 89 Namibia, South Africa, Lesotho, Swaziland, Mozambique, Zimbabwe (0.25° grain; Harrison et 90 al. 1997), Zambia (0.5° grain; Dowsett et al. 2008), Botswana (0.5° grain; Harrison et al. 1997) 91 and Malawi (0.25° grain; Dowsett-Lemaire and Dowsett 2006). For additional data description 92 see McPherson and Jetz (2007). Based on this data we defined a 0.25° prediction grid consisting 93 of 6238 cells (Fig. 1). We then aggregated the existing atlas datasets to generate a gridded 94 coarse-grain 2° map of species richness over the southern part of the African continent, consisting of 107 cells (Fig. 1A). The 2° resolution was chosen as it gives congruent values of 95 96 richness no matter if survey data (our case) or range-map data are used (Hurlbert and Jetz 2007, 97 Hawkins et al. 2008). For the purpose of model validation we then created a *reference dataset* by

98 manually selecting a subset of 600 grid cells at the original 0.25° fine-grain that met minimum 99 100 records in Namibia and Angola (regions with slightly less available data), and minimum of 100 200 records in South Africa, Zimbabwe, Malawi, Swaziland and Lesotho (blue grid cells in Fig. 101 1A). We manually chose the locations of the reference grid cells to be as minimally clumped as 102 possible (blue cells in Fig. 1A). 103 For each of the 6238 fine-grain (0.25°) cells we selected environmental variables that 104 have been hypothesized to influence species richness (Field et al. 2009, Belmaker and Jetz 105 2011). These were MODIS-derived net primary productivity (NPP: Mu et al. 2007), Shannon 106 index of diversity of GlobCover land-cover categories (LC; Bontemps et al. 2010), WorldClim-107 based mean precipitation in wettest month (PW), mean annual temperature (T), precipitation seasonality (PS) (Hijmans et al. 2005), and the human footprint index (HFP; 108 109 Trombulak et al. 2010). We standardized all of these variables to zero mean and unit variance (see Appendix A for their pair-wise correlations). 110

111

112 *Models*

113 In order to fully appreciate the model structure we recommend to study the description presented

here, together with Fig. 2 and Table 1, and also BUGS code provided in Supplemental material.

115 We built three models which all follow the same spatial indexing: there is N coarse-grain (2°)

116 grid cells indexed by $i (i \in 1: N)$ and within each *i*-th coarse-grain cell there is n_i fine-grain

117 (0.25°) grid cells indexed by j ($j \in 1: n_i$) (Fig. 2). The models are described as:

Reference model. - To validate the accuracy of our downscaling exercise we first
produced a fine-grain *Reference model* that used only the subset of 600 well-sampled fine-grain
grid cells to predict richness at the same grain (Fig. 1). We used Poisson log-linear regression

121 (Kutner et al. 2005) to link the mean species richness λ_{ij} within a fine-grain cell *ij* to the cell's 122 environmental conditions:

123
$$\log \lambda_{ij} = \beta_0 + \beta_1 NPP_{ij} + \beta_2 LC_{ij} + \beta_3 PW_{ij} + \beta_4 HFP_{ij} + \beta_5 PS_{ij} + \beta_6 T_{ij}$$
(1)

124 where $\beta_{0...}\beta_{6}$ are coefficients to be estimated. The observed number of species, alias fine-grain

125 richness (s_{ij}) , is modelled as an outcome of a Poisson-distributed random process with mean λ_{ij} :

(2)

126
$$s_{ij} \sim Poisson(\lambda_{ij})$$

Note that although the model uses the *ij* indexing there is no actual 2° coarse-grain component in
the *Reference model* (see also Fig. 2 and Table 1).

129 Downscaling models 1 and 2. - These models operate simultaneously at both the fine and 130 the coarse grain but there are no actual fine-grain data on richness used to fit them (Table 1). For 131 the two downscaling models the fine-grain link between the observed fine-grain environment and 132 mean fine-grain richness λ_{ij} (an unobserved or "latent" variable) is identical to Eq. 1. However,

133 we added a simple link between λ_{ij} and mean coarse-grain richness Λ_i :

134
$$\Lambda_i = \beta_{\rm w} \times \widehat{\lambda}_i$$
 where $\widehat{\lambda}_i = \frac{\sum_{j=1}^{n_i} \lambda_{ij}}{n_i}$ (3)

135 β_{w} is the ratio of the mean coarse-grain richness (Λ_{i}) and *averaged* mean fine-grain richness ($\hat{\lambda}_{i}$). 136 β_{w} is generally known as Whittaker's index of beta diversity (Koleff et al. 2003a) or ratio of local 137 and regional diversity. Eq. 3 can be interpreted as a simple species-area relationship which has a 138 constant slope (i.e. constant β_{w}) over the whole set of *N* coarse-grain cells. The observed coarse-139 grain richness S_{i} is modelled as an outcome of a Poisson-distributed random process with mean 140 Λ_{i} :

141
$$S_i \sim Poisson(\Lambda_i)$$
 (4)

142	The difference between the two downscaling models is (see also Table 1): In
143	<i>Downscaling Model 1</i> we use strong prior information on $\beta_w = 1.8$ which was obtained by
144	"cheating" - we estimated it by using the 600 well-surveyed fine-grain grid cells (Appendix B
145	gives details on this estimation). The model explores the hypothetical possibility that we had
146	some prior (and correct) information about species turnover in the region. In reality, however, we
147	may not have such information on β_{w} . That is why we built <i>Downscaling model 2</i> which used
148	only a very weak information on β_w . In order to at least realistically bound β_W we reviewed
149	published works on species-area relationship and beta diversity at comparable extents and grains
150	(Drakare et al. 2006, Keil et al. 2012). We found that species richness in 2° grid cells was
151	unlikely to be more than 5 times the mean richness in the 0.25° cells. Hence, we set the prior
152	distribution to be $\beta_w \sim Uniform(1,5)$ (this is only approximate; see Supplement for details).
153	We fitted all models using MCMC sampler in JAGS (Plummer 2003). For each model we
154	run 3 MCMC chains of 200,000 iterations, discarded 100,000 as burn-in, and saved every 100th
155	iteration for inference. We also monitored all values of fine-grain λ_{ij} (in order to calculate their
156	prediction intervals). We found good convergence of $\beta_1\beta_6$ using visual inspection and the
157	Gelman-Rubin diagnostic (Gelman and Rubin 1992). The R and BUGS language representations
158	of the models together with the data are provided in Supplement.
159	Our performance criteria for the Downscaling models were: (1) how close are their
160	predictions to the <i>absolute</i> species richness in the 600 well-sampled fine-grain cells; (2) how
161	well do they predict <i>relative</i> species richness in the 600 well-sampled fine-grain cells; (3) do

162 they give model coefficients similar to those of the *Reference model*?

163 **Results**

164

165 richness that were indistinguishable among another (Fig. 3), with the exception of NPP (β_l)

All models led to estimates of the effects of the environmental variables $(\beta_1...\beta_6)$ on species

- 166 which had a significantly lower effect in the *Reference model* (Fig. 3). The strongest positive
- 167 predictor of richness at the fine grain was land-cover heterogeneity (LC), while the weakest was
- 168 mean annual temperature (T) (Fig. 3). Particularly striking is the result that the parameters $\beta_1...\beta_6$
- 169 were almost identical in both *Downscaling models*. This means that, for this region and range of
- 170 grains, we uncovered the same richness-environment association (i.e. the same relative
- 171 importance of various environmental variables) regardless of the exact values of β_w in the model.
- 172 Differences between *Downscaling models* 1 and 2 were mostly in their intercepts (β_0) and in the

173 values of beta diversity (β_w), which both acted as scaling parameters and did not influence the

174 richness-environment relationship (i.e. $\beta_1 \dots \beta_6$). β_0 and β_w were also the main source of

175 uncertainty in the predictions of *Downscaling model 2* (pink bars in Fig. 4A), as the inclusion of

176 informative β_{w} in *Downscaling model 1* dramatically reduced the uncertainty (light blue bars in

177 Fig. 4A) and improved model predictions. *Downscaling model 2* only poorly estimated β_{W}

(median 2.96, C.I._{2.5%} =1.1, C.I._{97.5%}=4.88) and gave no improvement over our non-informative
prior distribution.

180 Medians of the posterior distribution of R^2 values of the *Reference model* and

181 *Downscaling model 1* (calculated using the observed richness in the 600 well-surveyed cells)

182 were 0.453 (C.I._{2.5%} =0.451, C.I._{97.5%}=0.454) and 0.418 (C.I._{2.5%} =0.402, C.I._{97.5%}=0.431),

183 respectively, which is in line with other recent large-extent studies at this grain (e.g. Belmaker 184 and Jetz 2011). The fine-grain richness-environment association represented by the *Reference*

185 *model* also gave relatively good out-of-sample predictions (cross-validated R^2 of 0.44; 10-fold

186 crossvalidation). *Downscaling Model* 1 that used strong prior information on species turnover 187 (β_w =1.8) matched the predictions of *Reference model* very well (R^2 of the 1:1 line is 0.94; Fig. 188 3B), although there is a slight over-prediction (Fig. 4B). The strong concordance of the 189 *Reference model* and *Downscaling model 1* is also obvious from their mapped predictions (Fig. 190 5). In contrary, median predictions of *Downscaling model 2* were so far below the observed 191 richness that calculation of meaningful R^2 was not possible (residual variance higher than 192 variance in the data) (Fig. 4).

Although the *Downscaling model 2* yielded poor absolute estimates of the fine grain richness and these had great uncertainty (caused by the absence of information on β_w), there was an excellent concordance between the ranked (that means relative) richness predicted by each of the models (maps in Fig. 5, and Fig. 4C-D).

197

198 **Discussion**

199 We showed that models associating species richness with environmental conditions can be fitted 200 at grains finer then the grain of the original richness data, and that predictions of these models 201 can be used to map patterns of species richness and identify high biodiversity areas at finer 202 spatial grains. Our approach is especially suitable for poorly surveyed areas and taxa (such as 203 plants and invertebrates) for which the richness data come in the form of raw and large-scale 204 expert range estimates (e.g. Jetz and Fine 2012) or regional checklists (e.g. Keil and Hawkins 205 2009). While for this introduction we used equal-sized and -shaped coarse-grain data, we note 206 that the approach is equally suited for unevenly shaped survey areas (e.g. administrative areas) 207 and enables the harmonization of spatially disparate biodiversity data to a standard grid.

208	The case study we present here is simplified in order to clearly demonstrate the novel
209	concept of multi-scale hierarchical modelling of species richness. We contend that future
210	research should focus on incorporating spatial autocorrelation into the model (Fortin and Dale
211	2005) and relaxing our assumption that β_w is constant across all coarse-grained cells (see
212	Appendix B and Lennon et al. 2001, Koleff et al. 2003b, Drakare et al. 2006, Hurlbert and Jetz
213	2010; see also Appendix B). Our method can incorporate both geographically structured and
214	environmentally driven species turnover. Hence, future development of the method will not only
215	greatly benefit from better understanding of what drives beta diversity across scales (e.g. Keil et
216	al. 2011), the method can actually be used to estimate the drivers of beta diversity by simply
217	making $\beta_{\rm w}$ a function of environment within the hierarchical model.
218	Irrespective, the proposed method may reach its limits for very large ranges of grains and
219	toward finer resolutions where the associations between species richness and environment can be
220	weak (Field et al. 2009, Belmaker and Jetz 2011) and where biotic interactions as well as
221	environmental and demographic stochasticity may be increasingly dominant drivers of richness.
222	These together can explain the relatively moderate ($R^2=0.45$) amount of explained variability of
223	our environmentally deterministic models at the 0.25° grain; when we additionally measured the
224	richness-environment association of well-surveyed cells at 0.5° grain (instead of 0.25°) and used
225	the same set of environmental variables and the same model, the R^2 increased to ca. 0.67 (results
226	not shown here).
227	Unsurprisingly, we found that when weak prior information on beta diversity is used the

Unsurprisingly, we found that when weak prior information on beta diversity is used the method is unable to predict absolute values of species richness. If in such a case absolute richness values were of key interest, a simple heuristic approach is to apply as prior a turnover value (and its variance) from a (regionally, taxonomically and scale-wise) appropriate empirical

231 study or meta-analysis (Drakare et al. 2006, Soininen et al. 2007, Keil et al. 2012, Storch et al. 232 2012). These constraints notwithstanding, even as lack of informative priors on turnover 233 compromised the estimation of absolute richness estimates, the presented approach provided 234 reliable regression coefficients of the fine-grain richness-environment associations and, 235 subsequently, reliable maps of richness gradients. Thus, a statistically rigorous tool now exists to 236 explore richness-environment associations at, for instance, intermediate grains, from 150 km 237 down to 20 km or even 5 km or finer, the grains that are usually too difficult to survey 238 comprehensively over large extents, yet too fine for expert range maps to correctly represent 239 (Hurlbert and Jetz 2007, Hawkins et al. 2008). The same statistical framework also facilitates the 240 identification of richness "hotspots" at fine grains. Both these advances create exciting new possibilities for a more rigorous and general way to understand and map biodiversity at finer 241 242 spatial grains, especially for regions and taxa with limited data yet high basic or applied 243 ecological significance.

244

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- 363

- 364 Supplemental material
- 365
- 366 Appendix A Correlations between the environmental variables.
- 367
- **368** Appendix **B** Estimation of β_W and spatial variation of β_W .
- 369
- 370 Supplement Commented R and JAGS codes of the models and the complete dataset used in
- this study.



- **Table 1.** Comparison of the components and outcomes of the three models used in our study.
- 373 Note that the distinction between variables and parameters is somewhat arbitrary in Bayesian
- 374 framework (parameters can be random variables).

Model	Grains at	Latent variables	Model	Informative	Observed variables		
	which the		parameters	priors	(data)		
	model						
	operates						
Reference	fine-grain	λ_{ij} - fine-grain mean	$\beta_0\beta_6$	None	<i>s_{ij}</i> - observed fine-grain		
model	only	richness in cell ij			richness in cell <i>ij</i> ;		
					$NPP_{ij}, LC_{ij}, PW_{ij}, HFP_{ij},$		
					PS_{ij}, T_{ij} - observed fine-		
					grain environmental		
					variables		
Downscalin	fine-grain and	λ_{ij} - fine-grain mean	$eta_{0}eta_{6,}$	Strong prior	S_i - observed richness in		
g model 1	coarse-grain	richness in cell <i>ij</i> ;	$eta_{ m W}$	$\beta_{\rm W} = 1.8$	coarse-grain cell <i>i</i> ;		
		Λ_i - coarse-grain			$NPP_{ij}, LC_{ij}, PW_{ij}, HFP_{ij},$		
		mean richness in			PS_{ij} ; T_{ij} - observed fine-		
		cell <i>i</i>			grain environmental		
					variables		
Downscalin	fine-grain and	λ_{ij} - fine-grain mean	$eta_{0}eta_{6,}$	Weak prior	S_i - observed richness in		
g model 2	coarse-grain	richness in cell <i>ij</i> ;	$eta_{ m W}$	$1 < \beta_{\rm W} < 5$	coarse-grain cell <i>i</i> ;		
		Λ_i - coarse-grain			$NPP_{ij}, LC_{ij}, PW_{ij}, HFP_{ij},$		
		mean richness in			PS_{ij} ; T_{ij} - observed fine-		

cell *i*

375

grain environmental

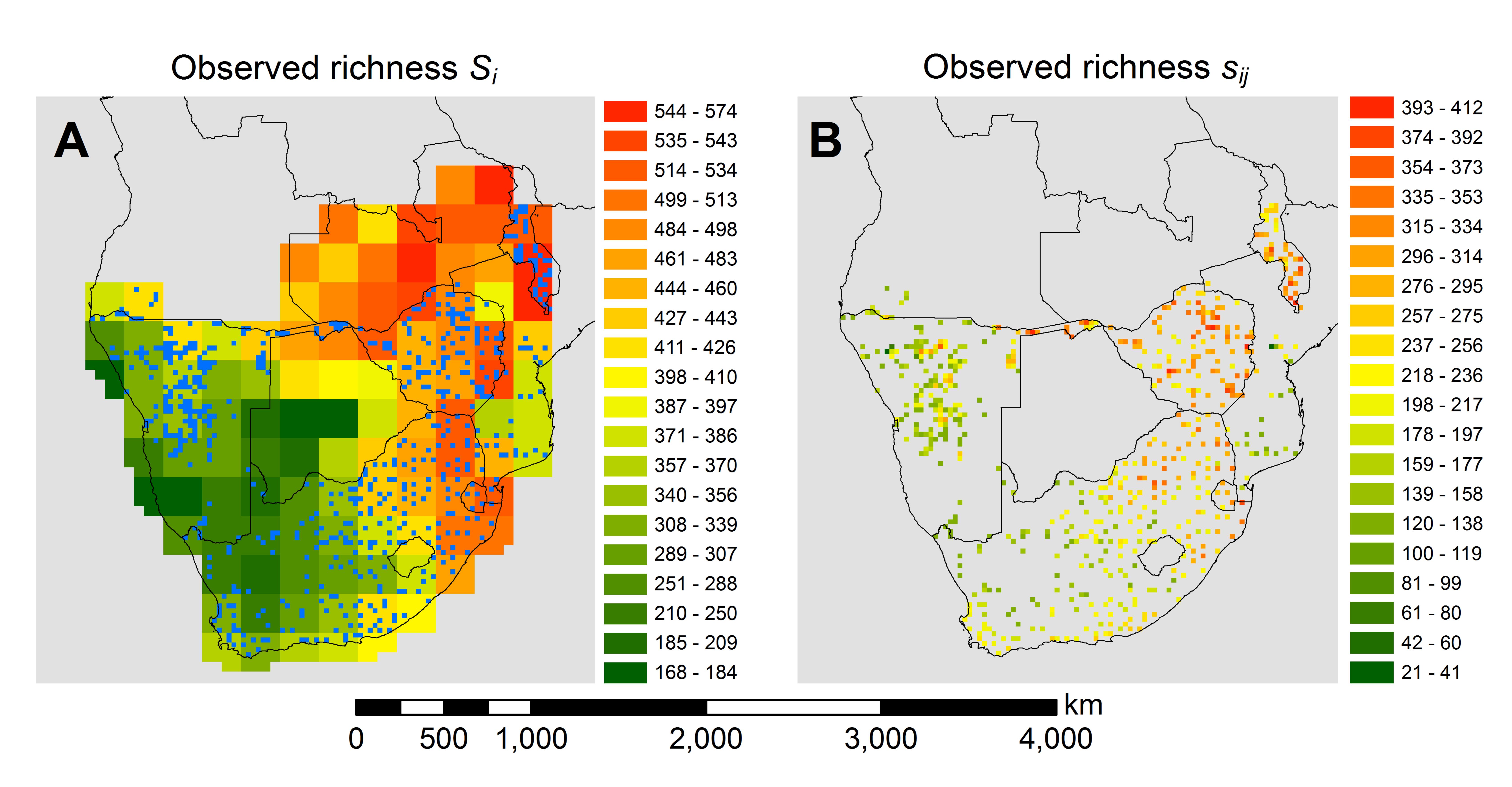
variables

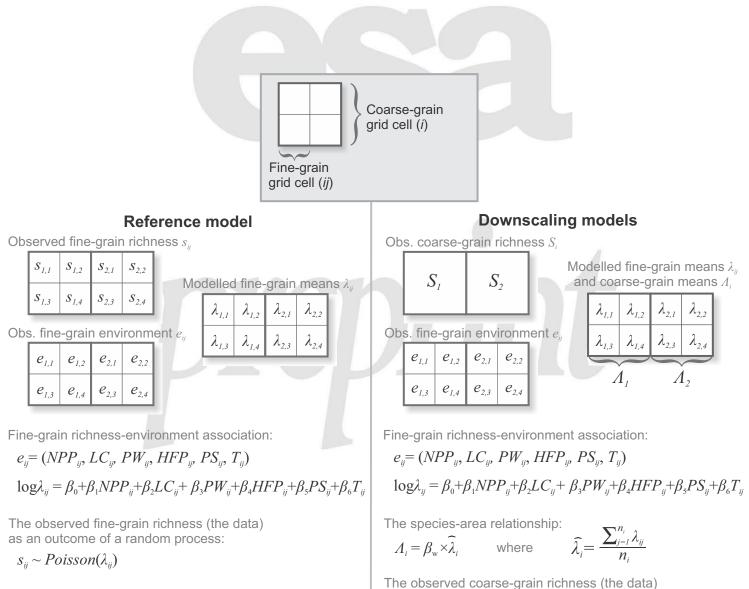


376	Figure legends
377	
378	Figure 1 Maps of observed species richness of birds at the 2° grain (A) and observed species
379	richness in the 600 well-surveyed locations at the 0.25° grain (B) in South Africa. Blue color in
380	A depicts the same grid cells that are showed in B. All panels use "equal interval" classification
381	of colors.
382	
383	Figure 2 A graphical illustration of our models. Here we provide all of the equations and spatial
384	structures together. For more precise definitions of the symbols see Methods and Table 1.
385	
386	Figure 3 Posterior parameter values (see Eq. 1 and 3) of <i>Reference model</i> and <i>Downscaling</i>
387	models 1 and 2. Shown are medians (dots), 75% (thick bars) and 95% (thin bars) credible
388	intervals of posterior distributions. All predictors were standardized and centered so that the
389	coefficients are comparable. We did not standardize species richness (the response variable). The
390	abbreviations are: NPP - net primary productivity, LC - Shannon index of diversity of land cover
391	types, PW - precipitation in wettest month, HFP - human footprint index, PS - precipitation
392	seasonality, T - mean annual temperature.
393	

Figure 4 Performance of *Downscaling models 1* and 2 in the 600 well-surveyed fine-grain 394 395 0.25° grid cells: (A) Observed and predicted values of absolute species richness. (B) The match 396 between the Reference model and the Downscaling models. (C and D) Similar axes as in A and B, but the ranks of the values are used. Kendall's τ rank-rank correlations of relationships in C 397 and D are 0.48 and 0.94 respectively. Solid diagonal lines are lines of identity. The dots are 398

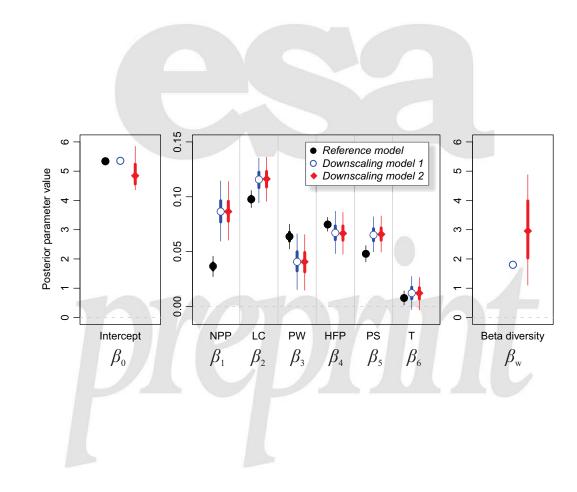
- medians of model predictions (as in Fig. 5), light-blue and pink bars in A and B are 95%
 prediction intervals of *Downscaling models 1* and 2 respectively.
- 401
- Figure 5 Maps of predicted bird species richness λ_{ii} at 0.25° grain in Southern Africa from our 402 three models. In the right column all panels use the same ("equal interval") color classification, 403 404 as opposed to the left column where each panel uses its own color classification. This was done in order to highlight both the similarities (left column) and the differences (right column) 405 406 between the predictions. There is an excellent match between predictions of the *Reference model* 407 (A) and the *Downscaling model 1* (B) which uses a highly informative prior on beta diversity. 408 Downscaling model 2 (C) uses weak prior on beta diversity; it underestimates absolute values of richness (right column) but accurately represents spatial patterns and thus relative richness 409 410 gradients (left column; see also Fig 4).

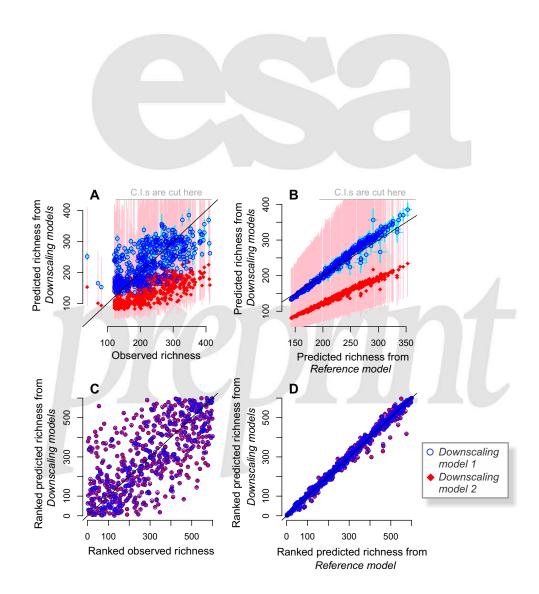




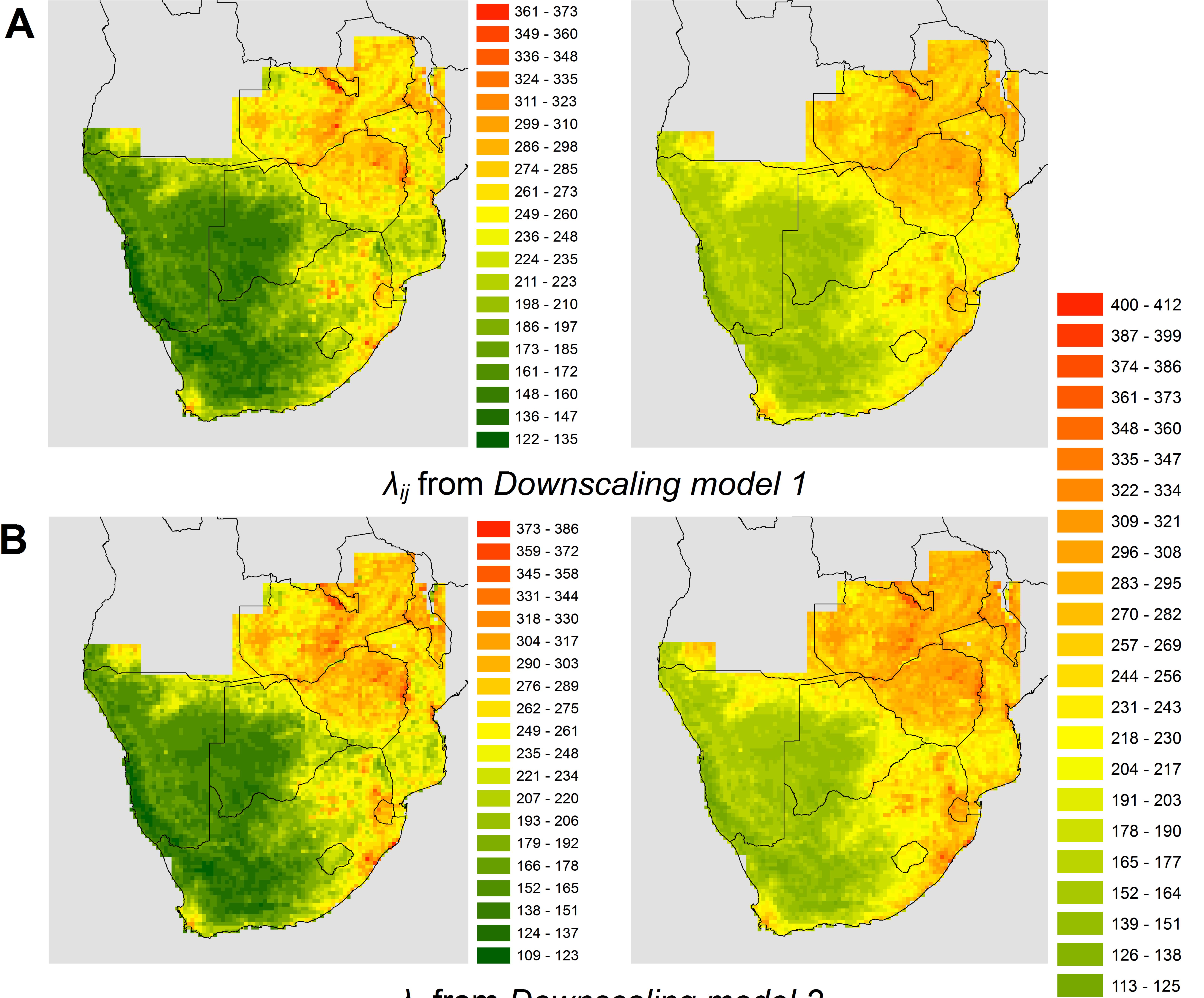
as an outcome of a random process:

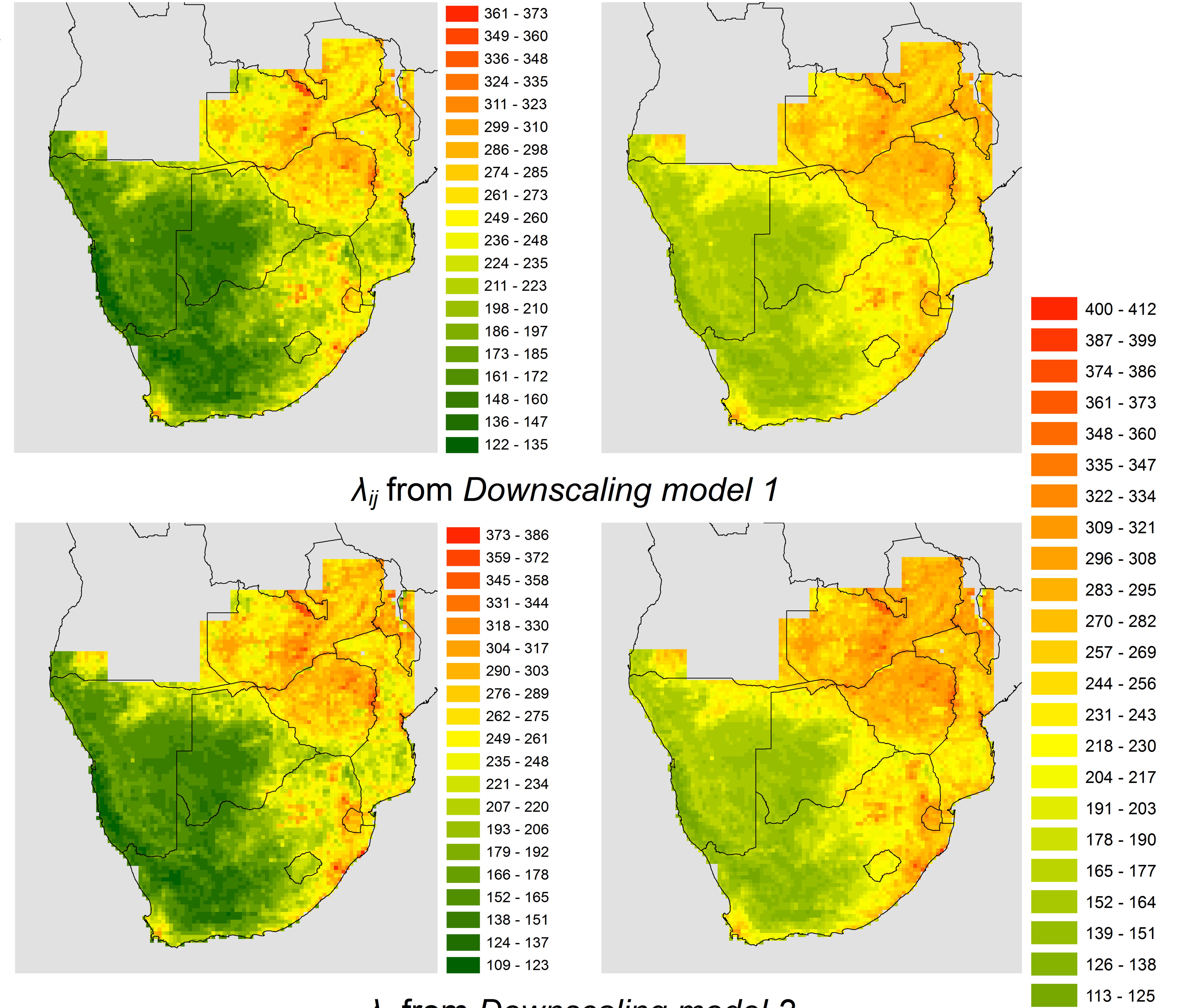
 $S_i \sim Poisson(\Lambda_i)$





λ_{ii} from Reference model





λ_{ii} from Downscaling model 2

