1 **Title:**

2 Integrating over uncertainty in spatial scale of response within multispecies occupancy

3 models yields more accurate assessments of community composition

4

5 **Running title:** Spatial-scale selection in occupancy models

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17 habitat conversion, joint community model, focal-site multi-scale

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Abstract:

20

21 1. Species abundance and community composition are affected not only by the local

22 environment, but also by broader landscape and regional context. Yet determining the

23 spatial scale at which landscapes affect species remains a persistent challenge that hinders

24 ecologists' abilities to understand how environmental gradients influence species

25 presence and shape entire communities, especially in the face of data deficient species

26 and imperfect species detection.

27 2. Here we present a Bayesian framework that allows uncertainty surrounding the 'true'

28 spatial scale of species' responses (*i.e.,* changes in presence/absence) to be integrated

29 directly into a community hierarchical model.

30 3. This scale selecting multi-species occupancy model (ssMSOM) estimates the scale of

31 response, and shows high accuracy and correct type I error rates across a broad range of

32 simulation conditions. In contrast, ensembles of single species GLMs frequently fail to

33 detect the correct spatial scale of response, and are often falsely confident in favoring the

34 incorrect spatial scale, especially as species' detection probabilities deviate from perfect.

35 4. Integrating spatial scale selection directly into hierarchical community models

36 provides a means of formally testing hypotheses regarding spatial scales of response, and

37 more accurately determining the environmental drivers that shape communities.

38

39

Introduction

Features of the landscape beyond the local scale often affect the processes that give rise

to patterns of community composition (Wiens 1989; Levin 1992; Kneitel & Chase 2004;

Dray *et al.* 2012; Fortin *et al.* 2012; McGarigal *et al.* 2016). As a result, ecologists have

sought to quantify what landscape features, in what contexts, and at what spatial scales

explain the presence and abundance of species. Yet determining how species respond to

the landscape has been challenging, in part because the relevant spatial scale(s) at which

environmental conditions affect species and communities are rarely known *a priori*. This

difficulty has led to uncertainty regarding the conclusions of many landscape level

studies (Jackson & Fahrig 2015). The development of statistical methods that more

robustly incorporating scales of responses within the statistical analysis of communities

(Borcard & Legendre 2002; Jombart *et al.* 2009; Matthiopoulos *et al.* 2011; Dray *et al.*

2012; Warton *et al.* 2015; Ovaskainen *et al.* 2016, 2017), and more accurately convey

uncertainty regarding these scales (Chandler & Hepinstall-Cymerman 2016), have the

potential to accelerate basic and applied ecological research.

When considering landscape level effects on species presence, abundance, or

biomass, two properties of the species are generally of interest. First, at what spatial scale

does the species respond to the environment (Desrochers *et al.* 2010), and second, how

do they respond (positively or negatively)? The most commonly used approach for

determining spatial scale of response (*i.e.,* the spatial context, spatial contingency; Fortin

et al. 2012) quantifies the average environmental value within buffers of various radii

(Holland *et al.* 2004; Weaver *et al.* 2012; Zuckerberg *et al.* 2012; McGarigal *et al.* 2016),

and then repeats a statistical analysis using the environmental covariate at each spatial

3

63   scale (Figure 1). For each species in turn, or for some community-level index like species

64   richness or diversity (*e.g.*, Shannon Index), the most likely spatial scale (as quantified by

65   AICc, correlation coefficient, or slope parameter value) is selected to represent the best

66   match of a species' response to landscape heterogeneity.

67   This multi-scale analysis approach has been successful in elucidating species and

68   community responses (McGarigal *et al.* 2016). By considering landscapes as a whole it

69   has helped quantify the benefits of small forest fragments to biological communities, and

70   related ecosystem services (Karp *et al.* 2013; Mendenhall *et al.* 2016). More generally it

71   has highlighted that species respond to different environmental conditions at different

72   spatial scales, and that species distribution models possess greater predictive power when

73   these multiple scales are directly incorporated (Desrochers *et al.* 2010; Weaver *et al.*

74   2012). However, the current multi-scale approach does present a number of problems

75   related to estimating the spatial scale of response, exacerbating uncertainty by treating

76   species individually rather than the community as an integrated whole, and ignoring

77   issues with species detectability. All of these will inflate error in estimating the true

78   spatial scale of response, and quantifying how species respond to the environment.

79   First, single species model comparison approaches that select a single best model

80   typically neither quantify nor integrate over uncertainty regarding scale selection. This

81   means that other parameters may be biased if the 'most likely' scale is not the true scale.

82   Relatedly, the set of scales analyzed is often quite small (Desrochers *et al.* 2010; Jackson

83   & Fahrig 2015), and as a result is unlikely to even include the true spatial scale. Meta-

84   analysis has shown that the most likely spatial scale is often at one of the extremes of

85   those analyzed—suggesting that the true spatial scale is even more extreme (Jackson &

86   Fahrig 2015). Recently, Chandler & Hepinstall-Cymerman (2016) proposed a modeling

87   approach that internalizes spatial scale estimation within a single species model by using

88   smoothing kernels to average landscape variables around focal sites. This single-species

89   model addresses these two problems by maximizing likelihood over the spatial scale

90   parameter, and also allows confidence intervals to be calculated around it. Further,

91   because spatial scale is a continuous (albeit bounded) parameter, it eliminates the

92   problem of not including the true spatial scale among the scales assessed (provided an

93   appropriate range of scales is investigated).

94   The second major problem with the standard approach is that it makes

95   assessments of multiple species in a species-by-species fashion. In the study of entire

96   communities, however, this approach is often inadequate, because it ignores rare species

97   (which are both typically of greatest conservation concern, and may be trophically

98   influential). This problem is especially true in tropical communities, which are

99   particularly under threat from land-use change, and where species rarity is common

100   (MacArthur 1969; Hubbell 2001). Further, a species by species approach is prone to

101   estimation bias and loss of power (Ovaskainen & Soininnen 2011; Banks-Leite *et al.*

102   2014). Hierarchical joint community models have been proposed to move beyond

103   piecemeal assessments (Ovaskainen & Soininnen 2011; Warton *et al.* 2015; Ovaskainen

104   *et al.* 2017). By assuming that species parameters come from common distributions,

105   overall community error is minimized and rare species can be included in analyses.

106   Finally, imperfect detection of species is a problem for animal communities

107   generally, especially when species traits, site characteristics, or the time or conditions of

108   observation influence detectability. Multi-species occupancy models (MSOMs) are a

109   commonly adopted solution to account for imperfect and variable detection within

110   communities (Iknayan *et al.* 2013). MSOMs are typically implemented in a Bayesian

111   framework (relying on MCMC to overcome challenges in maximizing likelihoods when

112   numerous random effects exist). Yet, model comparison and selection is still difficult to

113   implement with Bayesian models (*e.g.*, Hooten & Hobbs, 2015; but see Lele *et al.* 2007).

114   Together this means that comparing models across a large range of spatial scales would

115   be both time extremely time consuming (because MCMCs are relatively slow), and non-

116   trivial to implement. Because MSOMs are not easily amenable to adequate testing at

117   multiple spatial scales, the scale of response has generally not been incorporated into

118   community analyses that incorporate imperfect detection. Consequently, their power has

119   not been sufficiently directed to understand how landscape features structure community-

120   level processes.

121   Fortunately scale selection can be integrated directly into MSOMs by establishing

122   a parameter that allows the spatial scale at which species respond to be estimated (*e.g.*,

123   Chandler & Hepinstall-Cymerman, 2016). When extended to the community as a whole,

124   incorporating scale selection into the model should result in the appropriate spatial

125   scale(s) being estimated directly from the data within a single model run, and also ensure

126   that other parameter estimates are not biased because they were analyzed at the wrong

127   spatial scale. One of us (LOF) recently developed the foundations of the approach

128   presented here in an attempt to internalize scale selection within hierarchical multispecies

129   models to overcome uncertainty about what spatial scale to analyze data for two specific

130   empirical studies (Frank et al. In Press; Karp et al, In review). However, this technique

131   was not fully developed in those works, and it remains unclear whether this approach has

132   correct type I error rates, and whether it does indeed increase power and accuracy over

133   more traditional approaches. Here we fully describe, and demonstrate the use of, a multi

134   spatial scale selection multi-species occupancy model (hereafter; ssMSOM), and test its

135   performance in estimating both spatial scale of response, and species' strengths of

136   response to the environment (*i.e.*, a landscape-level covariate). We compare this approach

137   to the standard method of analysis: a series of species-by-species GLMs. While the

138   approach here is demonstrated with a simple single season occupancy model for multiple

139   species, the internalized scale selection is generalizable. For example, it could be directly

140   integrated into abundance models, or combined with flexible hierarchical modeling

141   approaches to query population dynamics through times, or the effects of species traits,

142   phylogenetic relatedness, or interspecific competition on community structure (Yackulic

143   *et al.* 2014; Frishkoff *et al.* 2017).

144

145   **Methods**

146   *Model overview:*

147   The scale selecting multi-species occupancy model (ssMSOM) estimates parameters

148   related to occupancy and detection probabilities in communities containing multiple

149   species (indexed by *i*), across multiple sites (*j*), with multiple site visits (*k*). The observed

150   detection histories ($Y_{i,j,k}$) are assumed to derive from unobserved (latent) occupancy states

151   ($Z_{i,j}$, where $Z_{i,j} = 1$ for presence, and 0 for absence) and detection probabilities determined

152   by species, and site ($P_{i,j}$; visit based variability in detection is ignored for simulations and

153   models, but could be incorporated if desired). Specifically:

$$Y_{i,j,k} \sim Bern(Z_{i,j} * P_{i,j}).$$

154   The occupancy state ($Z_{i,j}$) in turn was assumed to come from some underlying occupancy

155   probability according to:

156    $$Z_{i,j} \sim Bern(\psi_{i,j}).$$

157   The detection process was modeled according to:

$$\text{logit}(P_{i,j}) = \alpha 0_i + \alpha 1_i * Env_{j,1}.$$

158   And the occupancy probability ($\psi_{i,j}$) according to:

$$\text{logit}(\psi_{i,j}) = \beta 0_i + \beta 1_i * Env_{j,s} + \gamma 0_j.$$

159   Here $Env_{j,s}$ is a site-by-scale matrix of some landscape level environmental variable

160   (centered and scaled within each column). All parameters in the α and β groups are

161   estimated for each species, with species terms drawn from a normal distribution of mean

162   (μ) and variance (σ^2) estimated from the data. γ terms were random intercepts for each

163   site (variance estimated from data around a mean of 0) designed to incorporate consistent

164   differences in occupancy probabilities in all species across sites that are not accounted for

165   by Env. The indexing value s (representing columns of the $Env_{j,s}$ matrix) spans multiple

166   spatial scales, and the parameter value of s that best fits the data is estimated from the

167   model. Because models are implemented using MCMC, this process results in a posterior

168   distribution for values of s, which fully integrates over the uncertainly regarding the

169   proper spatial scale, and which further can be used to select the most appropriate spatial

170   scale (*e.g.,* posterior mean or mode) or an interval of spatial scales that well describe the

171   data. This formulation is conceptually similar to generalized linear models that integrate

172   over phylogenetic uncertainty in tree topology (de Villemereuil *et al.* 2012). For

173   simplicity, the environmental effect of a species' detection probability is assumed to

174   come from the environmental conditions at the finest (*i.e.*, most local) spatial scale. This

175   assumption could be relaxed if there is reason to expect that more distant environmental

176   conditions somehow affect detection probability.

177   For demonstration and testing purposes, we here assume that a single

178   environmental gradient affects community composition. However, the ssMSOM could be

179   generalized to include multiple environmental conditions (multiple site-by-scale

180   environment matrixes, e.g., $Env1_{j,s}$ $Env2_{j,t}$ $Env3_{j,u}$, etc.), each affecting communities at

181   different spatial scales (with scale parameters $s,\ t,\ u$, etc., each independently estimated

182   from the data).

183

184   *Simulation conditions*

185   In order to test the performance of the ssMSOM, we simulated communities, using an

186   *Env* matrix based on empirical landscape forest cover. Spatial forest cover data for

187   simulation and analysis came from northwestern Costa Rica, used as part of a study of

188   how local and landscape level habitat conversion affects community composition (Karp

189   et. al. In review). In that study, sites were selected to ensure that local forest cover varied

190   independently from landscape level forest cover. To measure surrounding forest cover,

191   all tree cover within 1.5km of sites was classified using high-resolution Google Earth

192   images obtained from 2013-2016. The resulting 5m-resolution tree cover map was

193   verified based on ground-truthed data collected in the field. For analysis, site level forest

194   cover proportion was calculated in radii from 50m to 1500m, in 50m increments,

195   resulting in an *Env* matrix with 30 columns. For the ssMSOM it would be most appealing

196   to use the smallest increments possible to generate the largest number of spatial scales

197   possible, since using few spatial scales makes it likely that the true scale will not be

198   among the analyzed set. We settled on 50m increments because of a balance of

199   computational efficiency in model runs, and increments that approximate a continuous

200   stretch from our smallest to largest spatial scale.

201   To test the performance of ssMSOM under a variety of conditions, we simulated

202   120 communities (four at each of the 30 spatial scales), each with 16 species (N_{sp}), across

203   50 sites (N_{site}), with three site visits per site (N_{visit}). All species parameters were drawn

204   from normal distributions, generating diversity in species' commonness (simulations

205   included both common and rare species), and species' responses to tree cover (some

206   responded negatively and others responded positively to 'deforestation'). This diversity

207   of overall commonness and responses to the environment mimics patterns observed in

208   many empirical systems. We repeated these simulations under five alternative detection

209   scenarios:

210   1. Perfect detection, where the probability of detecting a species at a site if the site

211   is occupied is 1.

212   2. High detection probability: average detectability equals ~ 0.5.

213   3. Low detection probability: average detectability equals ~ 0.25.

214   4. Low detection with detection affected by local environment: average

215   detectability equals ~ 0.25, but rising to ~0.5 under high local values of *Env* and dropping

216   to ~0.1 under low local values of *Env*.

217   5. Low detection with species-specific variation in detectability by local

218   environment: Same as 4, but some species increase in detectability with increasing values

219   of local *Env*, while others decrease in detectability.

220   For an overview of all simulation parameters see Table 1.

221

Model comparison

223 To examine ssMSOM performance, versus a typical analysis strategy for this type of

224 data, we compared it to a series of single species models fit using maximum likelihood

225 across all 30 spatial scales. These models are referred to as piecemeal GLMs throughout

226 and are described by standard binomial GLM functions of the form:

$$\text{logit}(\psi_j) = \beta 0 + \beta 1 * Env_j$$

$$Y_j \sim bern(\psi_j)$$

227 where ψ_j is the naïve occupancy probability of the focal species at the focal spatial scale,

228 and Y_j is the naïve occupancy state (*i.e.*, whether a species was detected at a site across all

229 site visits or not). To match the approach taken by empirical analyses species with

230 observations at fewer than 10% of all sites were excluded from analysis (because data

231 would presumably be insufficient for precise parameter estimates; *e.g.*, Desrochers *et al.*

232 2010; Zuckerberg *et al.* 2012). We then used AICc to choose the optimal spatial scale for

233 each species in turn.

234   We focus on two core questions when evaluating the ssMSOM versus standard

235 GLM approaches. First, does using an integrated community analysis provide more

236 accurate estimates of the correct spatial scale (*s*) than a piecemeal approach? For species

237 for which *β1* is close to 0, the spatial scale of response cannot be evaluated in the

238 piecemeal GLMs because the scale of response is undefined if the species does not

239 respond to the environment. For this set of analyses we therefore additionally excluded

240 all species for which *β1* was not significantly different from 0 in the most likely GLM, as

241 estimation of true spatial scale should be more accurate for the remaining species.

242   Second, even when estimating spatial scale is not the primary goal and is

243   therefore considered a nuisance variable, does integrating over uncertainty regarding the

244   correct spatial scale result in more accurate estimates of how species respond to the

245   environment ($\beta 1$) than a piecemeal approach? To answer this question we additionally

246   compared parameter estimates with GLMs using the true spatial scale under which

247   simulations were conducted. While for empirical data the true spatial scale is never

248   known without error, using it here represents the 'best-case scenario' for community

249   level analyses of landscape level responses to the environment.

250   To quantify the accuracy of the ssMSOM versus a piecemeal GLM approach, we

251   calculated the root mean square error (RMSE) across the entire community of the family

252   of parameter estimates from the true simulated value. With regards to 's', we consider the

253   posterior mode in the case of the ssMSOM, where as for the GLMs we consider the

254   spatial scale that minimizes AICc for each species. To ensure the results are comparable

255   in both approaches we calculate RMSE for each species in turn, even though in the case

256   of the ssMSOM the parameter s is estimated for all species simultaneously, and is

257   therefore identical for all species.

258   We also examine coverage probability of the posterior estimates (*i.e.*, the inverse

259   of type I error). If models are behaving as expected, the 95% CIs of the parameter

260   estimates should contain the true value 95% of the time. For ssMSOMs and GLMs the

261   coverage probabilities for $\beta 1$ can be calculated directly from species-specific parameter

262   estimates. Similarly coverage probabilities around 's' for the ssMSOMs can be calculated

263   using equal tail Bayesian credible intervals around the posterior of s. To calculate a value

264   equivalent to coverage probabilities of the spatial scale in the case of the piecemeal

265   GLMs we first calculated the AICc weight for all spatial scales for a given species, and

266   then asked whether the true spatial scale was within the top 95% of the cumulative model

267   weights.

268

269   *Model Fitting*

270   Models were fit using JAGS through the R environment. Simulation code in R and JAGS

271   model code is available in the supplement. For MCMC analyses diffuse priors were used

272   throughout, with a flat prior placed on '*s'*.

273

274   **Results**

275   *Inferring spatial scale*

276   The posterior mode of spatial scales from the ssMSOM tended to accurately estimate the

277   true spatial scale of response, and had relatively low error, typically off by less than

278   100m under the conditions simulated (Figures 2 and 3). In contrast, piecemeal GLMs

279   failed to consistently recover the true spatial scale for the majority of species in the

280   community, even when detection was perfect. The degree of error was lower when

281   restricting analysis to only those species for which the lowest AICc GLM showed a

282   significant relationship with the environmental gradient, though RMSE across the entire

283   community was still >3X that of the ssMSOM (Figure 3a). Further, when detection itself

284   varied along the environmental gradient at local scales in a species-specific manner,

285   using a standard GLM approach resulted in error in estimating species response scales

286   that is no better (and sometime worse) than guessing a scale at random (Figure 3a). Not

287   surprisingly, error in estimating the scale of response within piecemeal GLMs was

288   greatest for both species that were detected in a small number of sites, as well as species

289   detected in the majority of sites (Figure 3b).

290   The ssMSOM demonstrated correct type I error rates when estimating *s*,

291   regardless of detection regime. In contrast, piecemeal GLMs showed inflated type I error

292   when estimating the true spatial scale, which was exacerbated as detection probability

293   deviated from perfect (Figure 4). This behavior was further accentuated when excluding

294   species that did not have a significant response to the environmental gradient at its most

295   likely spatial scale, such that nearly 20% of all species assessments did not include the

296   true spatial scale model in the top 95% Akaike weighted models under a low-detection

297   regime with specific-specific variation in detectability by environment.

298

299   *Estimating species responses to the environment*

300   Estimates of species responses to the environment ($\beta 1$) were more accurate in the

301   ssMSOM than in piecemeal GLMs, even when GLMs were run using the true spatial

302   scale (Figure 5). These patterns were not strongly affected by detection regime, though in

303   general estimates are more accurate when detection probabilities are high. Type I error

304   does however strongly shift with detection. If detection is perfect, and the true spatial

305   scale in known *a priori*, then a piecemeal GLM approach performs as well as the

306   ssMSOM (Figure 6). However, when the spatial scale must be inferred from the data

307   GLMs generate falsely confident results, with the true values of species responses

308   excluded from the 95% confidence intervals up to 30% of the time under some simulated

309   conditions (*i.e.* 6X the nominal type I error rate). In contrast the ssMSOM possess 95%

310   CIs that behave has expected, regardless of detection regime.

311

Discussion

313 Here we described and tested the statistical properties of the ssMSOM against the

314 standard method for ascertaining species' and communities' scales of response. We find

315 that internalizing scale selection into the model results in greater community wide

316 accuracy for key parameter estimates, and reduces the probability of making incorrect

317 inferences. The key strength of the ssMSOM is that it does not rely on setting the spatial

318 scale *a priori*. Like the approach of Chandler & Hepinstall-Cymerman (2016), the

319 ssMSOM avoids the problem of researchers selecting only a few scales to investigate,

320 which are too narrow to include the true scale of response (Jackson & Fahrig 2015). This

321 of course requires that researchers first extract landscape data from as broad a range of

322 scales as possible, ideally in the finest increments possible. This allows spatial scale to be

323 treated as nearly continuous, such that 95% CIs can be created, and inferences made as

324 with any other continuous parameter in the model. When taking a flexible scale

325 estimation approach it is essential to use as fine scale environmental data as possible. If

326 environmental data are coarse with respect to the resolution at which species interact with

327 the environment then the estimated spatial scale of response will be strongly upwardly

328 biased and overall model performance will suffer (Mendenhall *et al.* 2011).

329

330 *Examples of empirical use*

331 Two recent studies have demonstrated the power of using the scale selection routine from

332 the ssMSOM (*i.e.*, indexing the *Env* matrix by scale) when analyzing empirical datasets.

333 Frank et al. (in press) used a phylogenetic occupancy model (Frishkoff *et al.* 2017) with

334   the internalized spatial scale selection method presented here, finding that bat responses

335   to deforestation are strongly phylogenetically conserved. Similarly, Karp et al (in review)

336   used Bayesian spatial scale selection embedded within an *N*-mixture model to examine

337   how bird communities responded to habitat conversion while accounting for imperfect

338   detection in order to understand how β-diversity was structured along land-use and

339   climate gradients. In both cases spatial scale selection strongly supported deforestation

340   affecting the communities at fairly small spatial scales. While in both cases scales at over

341   a kilometer away from focal sites were queried, for bats the posterior distribution peaked

342   at 50m, and excluded all scales above 100m, while for birds scales below 300m were

343   favored. Because of the ssMSOM framework, these studies were able to analyze both

344   common and rare species. Had these studies relied on individual GLMs (or species-by-

345   species occupancy models) the uncertainty around the scale of response would likely

346   have been extremely high, and un-estimatable for the majority of rare species. This was

347   particularly important in the case of Neotropical bats for which rare and hard to detect

348   species tended to be found in natural forests. Indeed, if imperfect detection were not

349   taken into account species richness would have appeared to have been unaffected by

350   forest loss, when in fact it declined sharply (Frank *et al. In press*). These early examples

351   of embedding spatial scale selection into hierarchical models highlight the broad

352   applicability of the method. The ssMSOM approach is easily extended to abundance

353   models (i.e., *N*-mixture or recapture models), or indeed any Bayesian implementation of

354   multispecies models with or without detection for which the true spatial scale of response

355   is unknown could benefit from the general approach.

356

357 *Assumptions, limitations, and future directions*

358 Critically, for the simulations presented (and within the ssMSOM itself) there is the

359 assumption that a single, true spatial scale exists at which all species respond to the

360 environment. This may or may not be true for a given assemblage in nature. Empirical

361 studies have shown that different species respond to different spatial scales (*e.g.*,

362 Chambers *et al.* 2016), and theoretical approaches suggest that some species traits may

363 modulate the scale of response (Jackson & Fahrig 2012). However, we show in our

364 simulations that empirical analyses conducted on a species by species basis (as past

365 studies have been) are often unable to recover the true spatial scale at which species

366 respond, and show high heterogeneity in the scale of response even if all species are

367 simulated to respond at the same spatial scale. While many species likely do respond at

368 different scales, this finding casts some doubt on the specific estimates of scales of

369 response presented in past empirical studies. The high degree of inaccuracy inherent in

370 the piecemeal GLM approach may be partially responsible for the lack of correlation

371 between empirically estimated scales of response, and species traits thought to modulate

372 these scales (Jackson & Fahrig 2015).

373 Future development of the ssMSOM and similar community wide approaches

374 should be able to relax the assumption that all species have the same scale of response,

375 although doing so may diminish the ability to precisely estimate response scales for rare

376 species. One path would be to estimate spatial scale separately for two or more groups of

377 species, delimited based on natural history knowledge, functional guild placement, or

378 other *a priori* expectations (Pacifici *et al.* 2014). An *a priori* grouping based approach,

379 however, is at best an imperfect solution. Ideally individual species' scales of response

380   would be allowed to vary from one another—using random effect structures within the

381   scale selection component of the model would be one logical way to do so. Allowing

382   random variation among species could additionally allow species' level covariates to

383   affect the scale of response, thereby facilitating testing the hypothesis that some species'

384   traits correlate with scale of response that both maintains high power, and is minimally

385   afflicted by type I error.

386   In real communities, species' responses to the broader landscape might be

387   predicated on conditions at the local scale (*i.e.*, an interaction between local and

388   landscape scales). For example, a farm-land bird species might benefit from landscape

389   level tree cover when the local habitat is agriculture, but might only exist in forest when

390   there are low amounts of landscape level tree cover because it uses forest edge habitat.

391   Allowing interaction terms between landscape and local effects (*e.g.*, forest cover as

392   estimated within a point count radius) will allow these types of species interactions with

393   the environment to be tested (Matthiopoulos *et al.* 2011; Paton & Matthiopoulos 2016).

394   Chandler and Hepinstall-Cyberman (2016) pointed out that the step function used

395   to calculate proportion of focal habitat within a given radius has no theoretical basis, and

396   instead favor a Gaussian weighting function. This approach could be easily implemented

397   with the Bayesian framework presented here, by indexing the *Env* matrix based on the

398   output of the weighting function over incremental changes in its key parameter. While,

399   alternatives to the commonly used step functions are certainly appealing on theoretical

400   grounds, at least one study that examined Gaussian weighting versus a step function

401   radius method found that models performed roughly equivalently (Timm *et al.* 2016).

402

403 *Conclusion*

404 Humans are altering landscapes across the globe, such that the remaining extent of

405 natural habitats are often much diminished and severely fragmented (Haddad *et al.* 2015).

406 Such complex, heterogeneous landscapes challenge ecologists' abilities to discern the

407 underlying environmental drivers of community composition. Yet achieving successful

408 conservation strategies in these landscapes requires simultaneously describing and

409 predicting how these spatially heterogeneous environments affect not just individual

410 species, but entire communities. Internalizing spatial scale selection within community

411 models offers one approach to uncover the environmental drivers behind such community

412 change while accommodating the unavoidable uncertainty in the 'true' scale of species'

413 responses. The ssMSOM possess high accuracy and correct type I error rates when both

414 identifying the spatial scale of response, and the direction and magnitude with which

415 individual species respond to environmental gradients. This approach represents a

416 promising path forward for understanding the ecological drivers of community

417 composition, and the consequences of ongoing environmental change.

418

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536 **Figures and Tables**

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538 Table 1: Simulation conditions of communities.

		Detection Regime				
Component	Parameter	Perfect	High	Low	Low-Env	Low-Env Variable
Detection	$\mu_{\alpha 0}$	100	0	-1	-1	-1
	$\sigma_{\alpha 0}$	0	1	1	1	1
	$\mu_{\alpha 1}$	0	0	0	1	1
	$\sigma_{\alpha 1}$	0	0	0	0	1
Occupancy	$\mu_{\beta 0}$	-1	-1	-1	-1	-1
	$\sigma_{\beta 0}$	1	1	1	1	1
	$\mu_{\beta 1}$	0.5	0.5	0.5	0.5	0.5
	$\sigma_{\beta 1}$	1	1	1	1	1
	$\sigma_{\gamma 0}$	0.1	0.1	0.1	0.1	0.1
	s	variable	variable	variable	variable	variable
Sample Size	Nsp	16	16	16	16	16
	Nsite	50	50	50	50	50
	Nvisit	3	3	3	3	3

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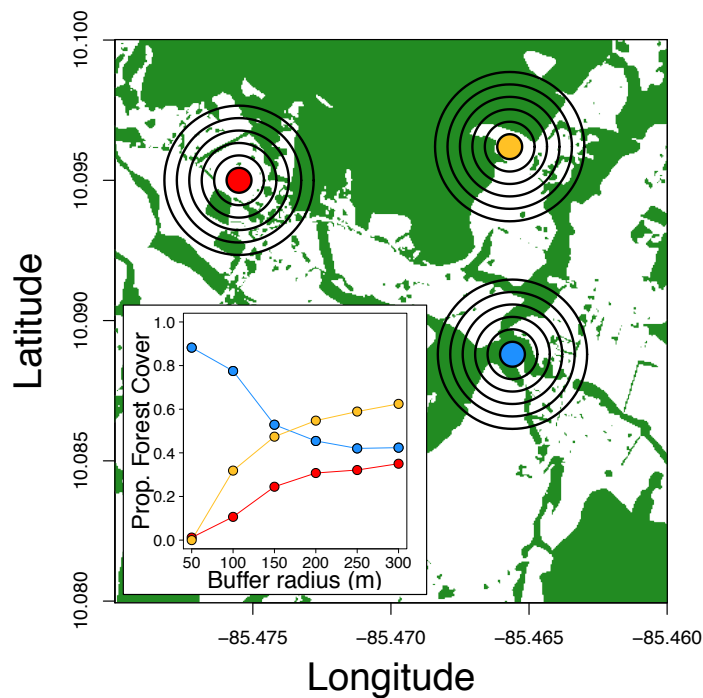
Figure 1. Map of empirical 5m-resolution subsection of forest cover landscape in northwestern Costa Rica with three fictitious sampling points that break the correlation structure between local and broader landscape forest cover. Colored points represent 50m-point count radii, and each successive buffer represents an increase in radius of 50m. Only 50-300m radii are shown, though for simulation analyses radii extended to 1500m.
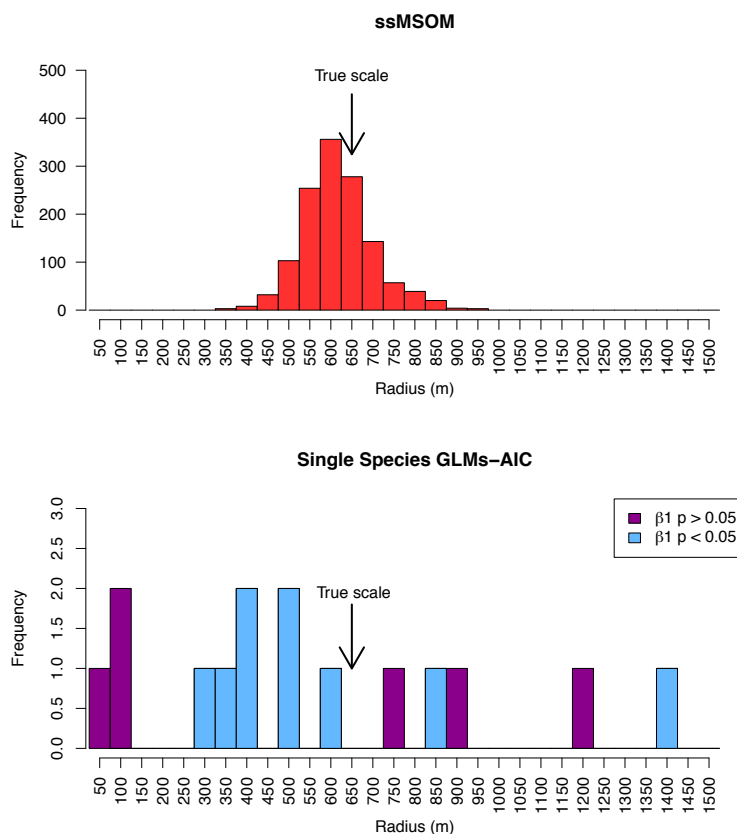
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553 **Figure 2.** Example histograms of single species GLMs, and the ssMSOM. Example
554 comes from low detection case (mean detection = ~0.25). Upper panel depicts posterior
555 distribution of the spatial scale that describes species responses to the environment from
556 the ssMSOM. Lower panel depicts the spatial scale that minimizes AICc for each single-
557 species GLM, after removing one species that was observed in fewer than 10% of sites
558 (*i.e.* 15 species remaining). Purple bars are species for which the response to the
559 environment does not differ significantly from 0, at the 'best' spatial scale, whereas blue
560 species have significantly positive or negative responses to the environment at the 'best'
561 spatial scale.
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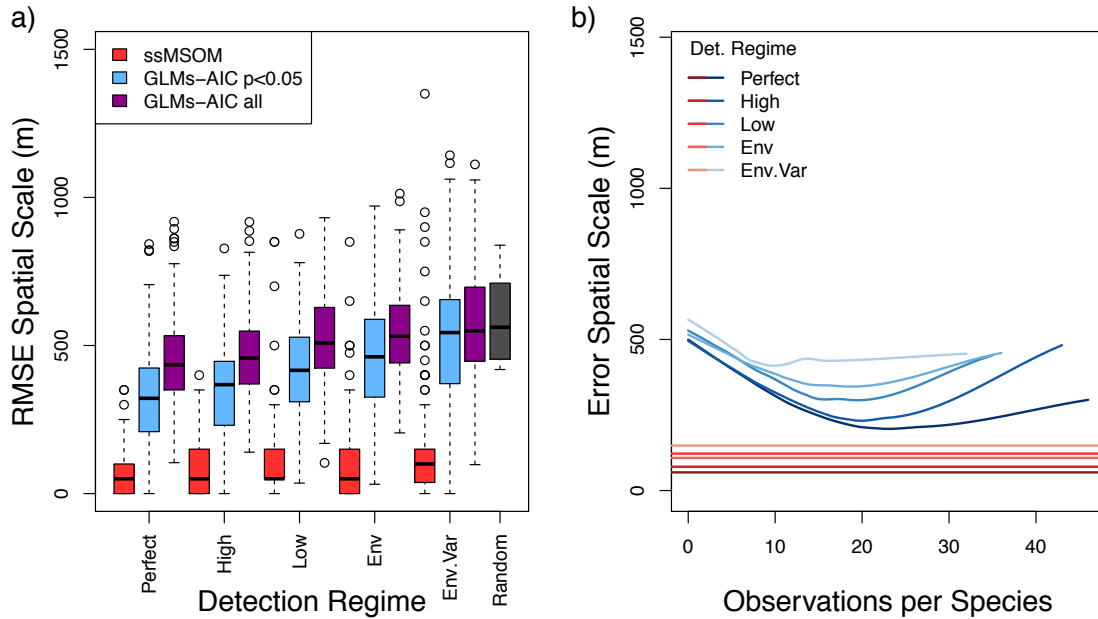
Figure 3. (a) General comparison of root mean square error for spatial scale across 120 simulations per detection regime, comparing posterior mode from ssMSOM, and AICc selected spatial scale for each species in single cases (splitting off only species with statistically significant responses to the environment [in blue], from all species [in purple]). 'Random' indicates the distribution of RMSEs that one would obtain if selecting spatial scales randomly along the uniform range from 50m to 1500m. (b) Blue lines in right panel depict lowess smoothers through all individual species' error in spatial scale estimation from piecemeal GLMs (across all simulated communities), as a function of the number of individuals observed. Red lines show mean error across all ssMSOMs (all species in the community are assumed to respond at the same scale, so species' level error is invariant to number of observations). Ability to estimate a species' scale of response suffers when species are either too rare, or too common, when using piecemeal GLMs.
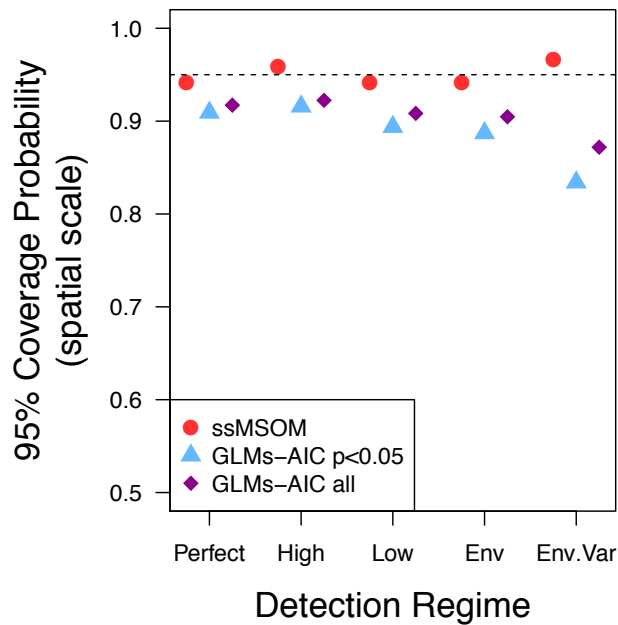
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Figure 4. Quality of inference of true spatial scale declines for single species cases
declines as detection becomes lower confounded with environment. For ssMSOM
coverage probability indicates the proportion of simulations ($n = 120$ per regime) for
which the true spatial scale was within the 95% CIs of the spatial scale posterior. For
GLMs coverage probability indicates the proportion of species across simulations for
which the true spatial scale was within the top 95% of Akaike weighted models.
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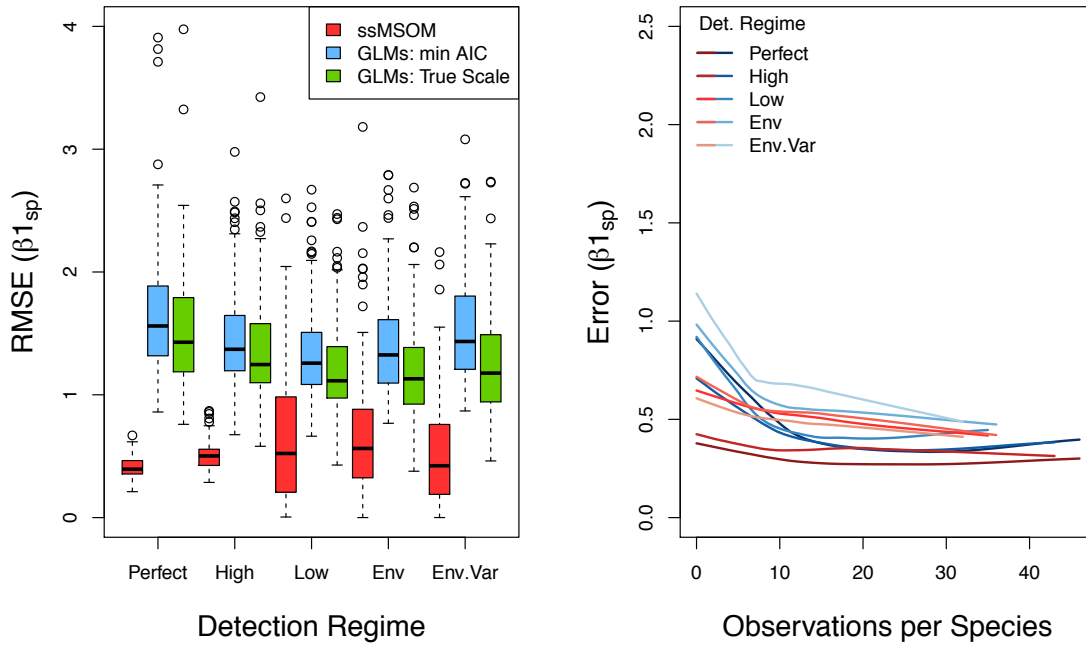
Figure 5. Accuracy of estimates of species responses to the environment ($\beta1_{sp}$). Left panel depicts boxplots of community level RMSE of $\beta1_{sp}$ values for each of 120 simulations per detection regime. Species observed in fewer than 10% of sites were removed from GLM estimates in left panel. Right panel depicts lowess smoothers through individual species' error in $\beta1_{sp}$ (across all simulated communities), as a function of the number of individuals observed. Here blue lines represent estimates from piecemeal GLMs (using min. AICc), whereas red lines represent estimates from ssMSOMs.
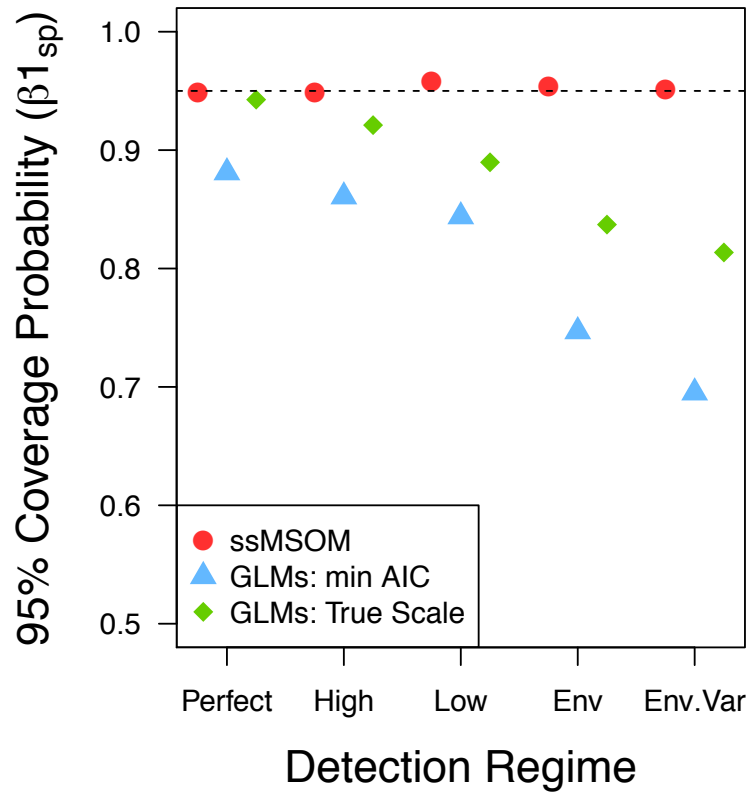
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Figure 6. Coverage probabilities around true value of response to the environment ($\beta 1_{sp}$). Each point represents the proportion of species across all simulations for which the true value fell within the 95% CIs of the estimate. For GLMs all species observed in fewer than 10% of sites were excluded from the analysis. GLMs min AICc indicates each species' GLM at the 'best' spatial scale. GLM True scale is the GLM from at the spatial scale that the responses were simulated at, regardless of whether this GLM possessed the lowest AICc.