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9 **Title:** Do joint species distribution models reliably detect interspecific interactions from

10 co-occurrence data in homogenous environments?

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Abstract:

Whether species interactions influence species response to environment and species ranges has always been a central question in ecology. Joint species distribution models (JSDMs) simultaneously model the species-environment relationships of multiple species and the residual correlation between these species. These residual correlations are assumed to depict whether species co-occur less or more often than expected by the modelled species-environment relationships, which could ultimately be attributed to species interactions, or hidden environmental information. Here, we propose to specifically test the capacity of JSDMs to detect species interactions from co-occurrence data, at different scales of data aggregation. Using a recently published point-process model, we simulated equilibrium co-occurrence patterns of species pairs by varying the strength and type of interactions (e.g. competition, predator-prey, mutualism) as well as the prevalence of the interacting species in homogeneous environments (assuming the environment does not influence the species responses and co-occurrence). Then, we fitted JSDMs without environmental predictors, and compared the estimated residual correlations against the known interaction coefficients. JSDMs detected competition and mutualism well, but failed with predator-prey interactions. For the latter, JSDMs predicted both negative and positive residual correlations for these kinds of interactions, depending on the prevalence of the interacting species. Interestingly, the estimated residual correlation was strongly influenced by species' prevalence and can thus not be translated to interaction strength. At increasingly coarser data resolution, the signals of negative and positive interactions became indiscernible by JSDMs, but – reassuringly –were rarely confounded. The underlying point-process model simulates the consequences rather than the mechanisms of interspecific interactions, and thus is

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47 better at corroborating rather than discrediting JSDMs. Nevertheless, our simple

48 theoretical exercise pinpoints important limitations of JSDMs. In conclusion, we caution

49 against interpreting residual correlations from JSDMs as interaction strength and

50 against comparing these across different species and communities.

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Introduction

54   Determining the factors that influence species' ranges is a prerequisite for deriving

55   reliable biodiversity scenarios (Urban et al. 2016). The importance of abiotic factors has

56   long been recognized (Pulliam 2000, Chase and Leibold 2003, Soberón and Nakamura

57   2009), and correlative species distribution models (SDMs) that relate species'

58   occurrence to prevailing environmental factors have become the most widely used tools

59   in biogeography (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and

60   Leathwick 2009). However, it is now generally accepted that interspecific interactions

61   likely influence species' distributions at larger spatial and temporal scales than

62   previously thought (Blois et al. 2013, Svenning et al. 2014). Ignoring these interactions

63   could thus hamper the ability of SDMs to predict current and future species ranges and

64   communities (Leathwick and Austin 2001, Meier et al. 2010, Zurell et al. 2016a). Hence,

65   over the last couple of years, several approaches have been discussed or proposed to

66   incorporate interspecific interactions between multiple species into distribution models

67   (Kissling et al. 2012, Pellissier et al. 2013, Thuiller et al. 2013, Wisz et al. 2013).

68   Aided by computational advances, methods have been introduced that combine species

69   distribution modelling with co-occurrence analyses that originate from community

70   ecology (Ovaskainen et al. 2017). These joint species distribution models (JSDMs)

71   decompose species co-occurrence patterns into shared environmental responses and

72   residual correlation (Ovaskainen et al. 2010, Clark et al. 2014, Pollock et al. 2014,

73   Warton et al. 2015, Hui 2016, Ovaskainen et al. 2016). The latter correlation relates to

74   the patterns of co-occurrence that are unexplained by the environmental information

75   given to the model. The temptation is then to attribute this residual correlation to biotic

76   interactions, such as competition and facilitation. Although this residual correlation can

77   reflect intuitive ecological (Latimer et al. 2009, Ovaskainen et al. 2010) or evolutionary

78   processes (Pollock et al. 2015), there could also be many non-biological explanations

79   such as missing environmental variables or poor model fit. Theoretically, JSDMs should

80   predict positive residual correlation between a pair of species if these co-occur more

81   often than expected given the environment (or by chance in a homogenous

82   environment) and predict negative residual correlation when the species co-occur less

83   often than expected given the environment (or by chance in a homogenous

84   environment).

85   To date, no study exists that explicitly tests JSDM's ability to identify the signal and the

86   strength of species interactions and the effects of complicating factors such as species'

87   prevalence and spatial scale. Also, the limits of JSDMs to detect asymmetric (positive-

88   negative) interactions such as predator-prey relationships have not been tested. As

89   JSDMs basically evaluate whether (residual) co-occurrence deviates from the null

90   expectation (given by environmental overlap), they can *per definitionem* only capture

91   symmetric interactions. However, a recent study by Araújo and Rozenfeld (2014)

92   showed that range overlaps of species pairs resulting from predator-prey relationships

93   could resemble both co-occurrence patterns of competition (-/-) and mutualism (+/+).

94   It is thus an important question whether JSDMs could possibly distinguish asymmetric

95   interactions such predator-prey relationships (+/-) from symmetric interactions (-/-

96   and +/+).

97   Here, we build on the point-process model of Araújo and Rozenfeld (2014) that

98   simulates co-occurrence of species pairs at steady state across all interspecific

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99   interaction types (-/-, +/-, +/+) and across all possible combinations of interspecific

100   interaction strength ($0 \leq I \leq 1$). We use this point-process model to generate co-

101   occurrence data of species pairs in homogeneous environments, and then use these data

102   to fit JSDMs. Other models could be used to simulate the distribution of interacting

103   species, for example spatially explicit population models such as Lotka-Volterra-type

104   models, coupled map-lattice models (Zurell et al. 2009) or individual-based models

105   (Travis et al. 2005). However, by using data from the steady-state point-process model

106   and from homogeneous environments, we ensure that species co-occurrence patterns

107   are not confounded by other factors such as history, missing environmental variables or

108   demographic stochasticity. We thus provide a simple proof-of-concept and ask whether

109   JSDMs can detect the signal of interspecific interactions from co-occurrence data under

110   idealised conditions, which we regard as prerequisite for applying these models in

111   complex real-world applications. Specifically, we test whether JSDMs can detect

112   different interspecific interactions ranging from negative to positive, how JSDMs cope

113   with positive-negative interactions such as predator-prey relationships, and how the

114   ability to detect interactions is influenced by the resolution of the data used for

115   modelling (i.e. scale-dependence).

116   **Methods**

117   **Simulating co-occurrence patterns**

118   We used the point-process model developed by Araújo and Rozenfeld (2014) to simulate

119   co-occurrence of species at steady state across all possible interaction types (+/+, +/-, -

120   /-, +/0, -/0) and all possible combinations of interaction strengths ($0 \leq |I_x| \leq 1$). If there

121   is no interaction between species, then the expected probability of co-occurrence P(A

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122   and B) of a species pair is simply given by the product of their prevalence P(A) x P(B).

123   This corresponds to the null expectation of co-occurrence. With interspecific interaction

124   present, the probability of co-occurrence is a function of species' prevalence and the

125   strength of their interaction, which could be repulsive or attractive. Mutualistic

126   interactions (+/+) will cause the species to co-occur more often than expected under the

127   null model, whereas competitive interactions (-/-) will cause them to co-occur less often

128   than expected. In case of predator-prey relationships (+/-), both positive and negative

129   interactions will cause deviation from the null model. Whether this results in higher or

130   lower co-occurrence than expected by the null model, depends on both the relative

131   strength of positive and negative interactions and on the prevalence of the species. Thus,

132   the resulting co-occurrence (relative repulsion and attraction of species pairs) is

133   deterministic while the spatial distribution of the species is stochastic. For a more

134   detailed description of the model formulation, please see Araújo and Rozenfeld (2014).

135   For simplicity, the environment is assumed homogenous and does not influence species'

136   ranges and prevalence.

137   Here, we simulated co-occurrence patterns of two species A and B in homogeneous

138   environments of 100x100 cells for all combinations of potential interactions. Species'

139   occurrence in space was random without any spatial autocorrelation. Araújo and

140   Rozenfeld (2014) showed that the co-occurrence patterns and their scale dependence

141   were comparable between spatially correlated and spatially uncorrelated landscapes.

142   We varied the interaction coefficients *I* from -1 to 1 in 0.1 increments. This resulted in

143   441 simulations per prevalence level. As an extension to previous results (Araújo and

144   Rozenfeld 2014), we systematically varied prevalence levels. Specifically, in the first set

145   of five scenarios, species A and B had equal prevalence of varying magnitude [0.1, 0.2,

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146   0.3, 0.4, 0.5]. In a second set of two scenarios, species A and B had unequal prevalence

147   [A=0.1 and B=0.5; A=0.2 and B=0.4].

148   For all scenarios, we calculated the co-occurrence index and the null expectation of co-

149   occurrence, to evaluate whether species co-occurred more or less often than expected

150   by chance. The co-occurrence index was defined as the number of cells where both

151   species occur together divided by the total number of occupied cells. As the null

152   probability of co-occurrence P(A and B) is given by the product of species' prevalence

153   P(A) x P(B), the co-occurrence value corresponding to the null expectation is given by (

154   P(A) x P(B)) / ((P(A) + P(B) – P(A) x P(B)) where the dividend is the proportion of cells

155   occupied by both species together and the divisor is the overall proportion of occupied

156   cells. Hence, the exact co-occurrence value corresponding to the null expectation, where

157   both species co-occur simply by chance, varies with prevalence (Fig. 1a-f).

158   To test for scale dependence in co-occurrence patterns and in the estimation of JSDMs,

159   we aggregated the original landscape grid to two increasingly coarser resolutions by

160   aggregating 2x2 cells and 4x4 cells, respectively. In these cases, species interactions

161   (repulsion and attraction) are still modelled at the initial resolutions, but JSDMs are

162   fitted at coarser resolution mimicking large scale and coarse resolution data such as

163   atlas data (Gotelli et al. 2010, Zurell et al. 2016b), or continental and global datasets

164   (McGill 2010, Jetz et al. 2012).

165   All simulations were carried out in R (R Core Team 2015), and the code is provided in

166   the Supplementary Material Appendix 1.

Estimating joint species distribution models

168 The spatial distributions of species A and B as simulated by the point-process model

169 over the full biotic interaction space served as input for JSDMs. We thus assumed perfect

170 detection of the species and ideal sample sizes, meaning that the entire space was

171 sampled although we also tested for sample size effects (Appendix 1). We fitted JSDMs

172 using the code provided by Pollock et al. (2014). These jointly estimate the occurrence

173 probability of multiple species with a hierarchical multivariate probit regression, and

174 the residual correlation between those species' presences by means of an unstructured

175 covariance matrix. As we were mainly interested in the ability of JSDMs to detect

176 underlying interactions, we assumed homogeneous environments and fitted the

177 environmental response with an intercept only model that controls for prevalence. The

178 JSDMs were run with JAGS from within R (R Core Team 2015) with 3 chains. As the

179 simulated data were very simple and without noise (meaning no sampling error was

180 included), for most combinations of interaction strengths ($-1 < I < +1$) a comparably low

181 number of 10000 iterations with a burn-in of 5000 and a thinning rate of 20, were

182 sufficient for reaching convergence with rhat values below 1.1 for all parameters. For

183 extreme interactions strengths (with an interaction coefficient I of -1 or +1),

184 convergence was not achieved under 10000 iterations and we subsequently tested

185 stability of parameters values for increasing numbers of iterations. The residual

186 correlation between species' presences was given by the mean of the posterior

187 distribution and was judged as significant when the range between the 5% and 95%

188 posterior quantiles did not include zero.

Results

190 Different prevalence levels produced different co-occurrence patterns across the biotic

191 interaction space (Fig. 1a-f). Co-occurrence was always lower than the null expectation

192 for competitive interactions (-/-) and for amensalism (-/0) and always higher than the

193 null expectation for mutualism (+/+) and commensalism (+/0). However, the exact

194 asymmetric interaction coefficients (+/-), at which co-occurrence was not different from

195 the null expectation, strongly depended on prevalence (of the more common species of

196 the species pair). When prevalence was low in both species, then co-occurrence was

197 higher than the null expectation for most combinations of positive-negative (+/-)

198 interactions (Fig. 1b), while co-occurrence was mostly lower than the null expectation if

199 at least one species in the predator-prey relationship was more common (Fig. 1f;

200 Supplementary material Appendix 1, Fig. A1).

201 JSDMs correctly assigned negative residual correlations to competitive interactions, and

202 correctly assigned positive residual correlations to mutualistic interactions. More

203 broadly, the difference between observed co-occurrence and the null expectation

204 determined the residual correlation estimated by JSDMs. Negative residual correlations

205 were estimated when species co-occurred less often than the null expectation (meaning

206 the co-occurrence value corresponding to the case when both species co-occur only by

207 chance), and positive residual correlations when the species co-occurred more often

208 than the null expectation. However, the magnitude of residual correlations varied across

209 scenarios with different prevalence of the interacting species (Fig. 1g-k). For example,

210 for two species A and B with an intermediate and symmetric negative interaction ($I_A = I_B$

211 = -0.5), JSDMs estimated a residual correlation of approx. -0.19 if both species had a

212 prevalence of 0.1, and a residual correlation of approx. -0.71 if both species had a

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213   prevalence of 0.5. These results were robust, as we obtained convergence with rhat

214   values below 1.1 for most combinations of interaction strengths except for the extreme

215   interaction coefficients of $|I|=1.0$ (Fig. A2). For these extreme cases, convergence was

216   achieved for larger numbers of iterations, whereby the model parameters were stable

217   across different numbers of iterations (Fig. A3). Also, prevalence levels were correctly

218   predicted in all cases. All these results correspond to ideal sampling without detection

219   error and very large sample sizes. Reduced sample sizes will increase type II errors but

220   the general patterns reported above remain unchanged (Fig. A4).

221   JSDMs were not able to separate predator-prey relationships from competitive or

222   mutualistic interactions, and assigned both negative and positive residual correlations

223   to such asymmetric (+/-) interactions (Fig. 1). Here, residual correlations from JSDMs

224   exhibited the same sensitivity to prevalence as co-occurrence patterns, meaning that the

225   exact asymmetric interactions coefficients (+/-) that divided positive from negative

226   residual correlations estimated by JSDMs depended on prevalence (Fig. 1g-k; Fig. A1).

227   Last, JSDMs had difficulties at depicting the underlying co-variation between species at

228   increasingly coarser resolution of the data (Fig. 2a-f). In line with Araújo and Rozenfeld

229   (2014) co-occurrence patterns were highly scale dependent, which led to more

230   insignificant residual correlation estimates in JSDMs (meaning that the parameters

231   credible interval between the 5% and 95% quantiles of the posterior distribution

232   included zero; Fig. 2 g-j). Thereby, chains mixed well and parameter convergence was

233   well achieved. Generally, for competitive interactions, increasingly coarser data

234   resolution led to lower estimates of absolute residual correlation than at the original

235   resolution (at which the interaction outcome was being modelled). This scaling effect

236   was much less pronounced for facilitative interactions (Figs. 2-3). Signals of interspecific

237   interactions were lost most readily for more prevalent species (Fig. 3). The probability

238   of confounding negative and positive residual correlations seemed to increase with

239   decreasing prevalence and with increasingly coarser resolution of the data (Fig. 3). The

240   insignificant residual correlations were only partially explained by the reduced sample

241   sizes when aggregating data. When repeating the data aggregation for larger sample

242   sizes, the type II errors were slightly smaller but the general patterns reported above

243   remained unchanged (Fig. A5).

244   **Discussion**

245   In this paper, we propose to systematically test the capacity of JSDMs to retrieve species

246   interactions from co-occurrence patterns in the case of simple bi-partite interactions

247   within a homogenous environment, and test whether this capacity was influenced by the

248   resolution at which species were modelled. The key results are that (i) JSDMs reliably

249   predict negative residual correlations for competitive interactions and positive residual

250   correlations for mutualistic interactions. However, the magnitude of residual correlation

251   does not directly relate to interaction strength because it is mostly driven by species

252   prevalence. (ii) Positive-negative interactions such as predator-prey relationships can

253   be problematic for model interpretation because JSDMs cannot disentangle these from

254   competitive and mutualistic interactions. (iii) At increasingly coarser spatial resolution

255   of the data, both the signals of negative and positive interactions become indiscernible

256   by JSDMs, but reassuringly the signals rarely were confounded. Overall, our results have

257   important implications for the interpretation of JSDMs, and pinpoint important aspects

258   that will need further model development. At the same time, we want to stress that

259   these results were obtained under idealised conditions, and real-world applications will

260   be complicated by even more factors. If JSDMs fail to detect interspecific interactions in

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261   very simple cases such as the one used here, there is no reason why they should work

262   better at detecting interactions (occurring within local communities) in more complex

263   real world applications.

264   First, we tested JSDMs' ability to detect negative and positive interactions from co-

265   occurrence data. And indeed, JSDMs reliably detected competitive and mutualistic

266   interactions in our simulated data, which is promising. However, interpretation of model

267   residuals as interaction coefficients proved non-trivial. Importantly, prevalence strongly

268   affected the magnitude of residual correlations estimated by JSDMs. This implies that

269   residual correlations from JSDMs do not directly relate to nor can be interpreted as

270   interaction strength, and also they cannot be compared across different species (with

271   different prevalence levels). In real-world applications, this may be further confounded

272   by the species' environmental response, detection bias, and by (direct and indirect)

273   interactions between multiple species, which should be further tested.

274   Second, we asked how JSDMs deal with competitive and mutualistic interactions from

275   asymmetric interactions such as predator-prey relationships. Per definition, JSDMs will

276   model symmetric correlations and should not be able to detect asymmetric interactions.

277   Nevertheless, it is important to understand whether and how residual correlations

278   estimated from JSDMs differ between symmetric and asymmetric interactions especially

279   when applying JSDMs to taxa from multiple trophic levels (such as birds and mammals).

280   As has been discussed earlier (Araújo and Rozenfeld 2014, Cazelles et al. 2015),

281   asymmetric positive-negative interactions can result in co-occurrence patterns that

282   could be either higher or lower than expected by chance, meaning in both positive and

283   negative net associations between pairs of species. Here, we showed that this also

284   depends on interaction strength between species A and B and their prevalence.

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285 Specifically, predator-prey relationships are more likely to produce positive residual

286 correlations when prevalence of both species is low. By contrast, when prevalence of at

287 least one species is high, then predator-prey relationships are more likely to produce

288 negative residual correlations in JSDMs. As a consequence, the problem that JSDMs are

289 not able to tease apart predator-prey relationships from competitive or mutualistic

290 interactions using co-occurrence data is exacerbated by the fact that asymmetric

291 interactions could show up both as positive and negative residual correlations, which

292 has been discussed previously but never been shown explicitly (Cazelles et al. 2015,

293 Morales-Castilla et al. 2015, Warton et al. 2015). These results suggest that a useful next

294 step would be to incorporate directional conditionality into future joint species

295 distribution modelling, extending their capacity beyond pairwise symmetric

296 correlations (Pollock et al. 2014, Warton et al. 2015, Hui 2016). Recent examples are

297 beginning to consider more complex (direct and indirect) interactions for small datasets

298 (e.g. Harris 2016, with up to 20 species). Schliep et al. (2017) recently introduced a

299 method for incorporating temporal processes into JSDMs that allows inferring

300 directionality from temporal co-abundance data. These advances would be extremely

301 useful not only for distinguishing predator-prey relationships but also for detecting

302 asymmetric interaction strengths between competing and facilitating species (Kissling

303 et al. 2012, Harris 2016). Still, it remains to be tested in how far co-occurrence data will

304 allow estimation of asymmetric residual correlation or under which circumstances co-

305 abundance data will be needed (Cazelles et al. 2015, Gallien et al. 2018). Also additional

306 information could be used to distinguish competitive and mutualistic interactions from

307 predator-prey relationships, for example trait information may aid simple plausibility

308 checks (Morales-Castilla et al. 2015), and behavioural observations and manipulative

309   experiments could help informing prior distributions (Harris 2016, Staniczenko et al.

310   2017).

311   Last, we tested for scale dependence of JSDM estimates by analysing the co-occurrence

312   data at increasingly coarse resolution while the interactions took place at the original,

313   fine spatial resolution. We found that with increasingly coarser resolution, both the

314   signals of positive and negative interactions became indiscernible by JSDMs, whereby

315   the signal of negative interactions was more sensitive to scale. This is in line with

316   previous findings that co-occurrence patterns are highly scale-dependent (Araújo and

317   Rozenfeld 2014) and also that the effects of local interspecific interactions vanish at

318   coarser spatial scales (Thuiller et al. 2015). Thus, JSDMs are unlikely to give any insight

319   on the potential interactions between species if the scale of the data does not match the

320   process scale. At best, they might give better and more reliable models and the residual

321   correlation might shed light on missing environmental variables and historical factors.

322   Also, the species lists from monitoring schemes or atlas data are often at comparably

323   coarse resolution, for example for many animals, such that the signal of interspecific

324   interactions and sub-scale environmental heterogeneity can get easily confounded

325   (Zurell et al. 2016b). When we apply JSDMs to vegetation plots, the analysis of the

326   residual correlation in respect to interspecific interactions might thus be more

327   meaningful since the interactions between species, for instance for light competition,

328   might here be at the right scale (e.g. a 10x10m plot). Empirical analyses testing whether

329   the residual correlations from JSDMs are related to known interactions between species

330   might thus be of particular interest. Furthermore, our results showed that less prevalent

331   species are less sensitive to mismatches between process scale and data scale. At the

332   same time, at increasingly coarse resolution negative and positive interactions were

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333   confounded easier. Thus, we recommend interpreting JSDMs cautiously when modelling

334   rare species.

335   We deliberately chose to use the steady-state point process model from Araújo and

336   Rozenfeld (2014) to simulate spatial co-occurrence patterns. In contrast to spatially

337   explicit population models (Kot 2001, Travis et al. 2005), this model does not explicitly

338   simulate the spatial dynamics of interacting species, but directly generates non-random

339   co-occurrence patterns that represent the spatial effects of interspecific interactions at

340   equilibrium. The point-process model characterises the consequences rather than the

341   mechanisms of interspecific interactions. Similarly, JSDMs are phenomenological and

342   thus model the consequences of interspecific interactions on species co-occurrence

343   (while accounting for environment). Therefore, we expect this set-up to corroborate

344   rather than discredit JSDMs. This was mostly the case, except for some important

345   limitations of JSDMs when trained on co-occurrence data. Although this is a basic test,

346   such proof-of-concept is still worthwhile because if a model fails in simple virtual

347   examples, chances are that it will also fail in the real world (Zurell et al. 2010). In the

348   future, JSDMs and their extensions (e.g. to incorporate directional conditionality) should

349   be tested using more complex and spatially explicit population models.

350   In summary, our simulation study indicates that JSDMs might be reliable in inferring

351   simple symmetric species interactions if the species are modelled at the resolution of

352   the interactions. However, even in our idealised and error-free data, JSDMs could easily

353   confound predator-prey relationships with either competitive or mutualistic

354   interactions, they do not give an estimate of interactions strengths, they are not easily

355   comparable across species, they are affected by prevalence and by scale. Thus, we

356   should be very cautious when interpreting JSDM results as interactions (Clark et al.

357   2014, Pollock et al. 2014). Nevertheless, they have the ability of enhancing our analyses

358   and allow us to form hypotheses about potential interspecific interactions when used

359   cautiously (Ovaskainen et al. 2010). Our results provide a first test of potentially

360   important or confounding factors in JSDM analyses. In the future, more efforts are

361   needed to test JSDMs in more complicated settings, for example to test their ability to

362   disentangle environmental response and residual correlation for multiple interacting

363   species, for cases when species interact directly and indirectly, and for other

364   confounding factors such as detection bias and missing environmental covariates.

365   Thereby, further theoretical tests under controlled conditions could be useful, but we

366   also emphasise the need for more empirical tests, for example comparing JSDM

367   estimates against known interactions (e.g. from experiments). Hence, JSDMs constitute

368   an important step forward for testing hypotheses of how interspecific interactions affect

369   species distributions. Nevertheless, there are important limits to their capability of

370   detecting interspecific interactions, for example for trophic and indirect interactions,

371   highlighting the need for further model improvements in this respect.

380   **References**

381   Araújo, M. B. and Rozenfeld, A. 2014. The geographic scaling of biotic interactions. -

382   Ecography 37: 406-415.

383   Blois, J. L. et al. 2013. Climate change and the past, present, and future of biotic

384   interactions. - Science 341: 499-504.

385   Cazelles, K. et al. 2015. A theory for species co-occurrence in interaction networks. –

386   Theor. Ecol. 9: 39-48.

387   Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and

388   contemporary approaches. – Univ. Chicago Press.

389   Clark, J. S. et al. 2014. Competition-interaction landscapes for the joint response of

390   forests to climate change. – Glob. Change Biol. 20: 1979-1991.

391   Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation

392   and prediction across space and time. – Annu. Rev. Ecol. Evol. Syst. 40: 677-697.

393   Gallien, L. et al. 2018. Frequency and intensity of facilitation reveal opposing patterns

394   along a stress gradient. – Ecol. Evol. 8: 2171-2181.

395   Gotelli, N. J. et al. 2010. Macroecological signals of species interactions in the Danish

396   avifauna. – Proc. Natl. Acad. Sci. U. S. A. 107: 5030-5035.

397   Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than

398   simple habitat models. – Ecol. Lett. 8: 993-1009.

399   Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in

400   ecology. – Ecol. Model. 135: 147-186.

401   Harris, D. J. 2016. Inferring species interactions from co-occurrence data with Markov

402   networks. - Ecology 97: 3308-3314.

403   Hui, F. K. C. 2016. boral – Bayesian ordination and regression analysis of multivariate

404   abundance data in R. - Methods Ecol. Evol. 7: 744-750.

405   Jetz, W. et al. 2012. Integrating biodiversity distribution knowledge: toward a global

406   map of life. - Trends Ecol. Evol. 27: 151-159.

407   Kissling, W. D. et al. 2012. Towards novel approaches to modelling biotic interactions in

408   multispecies assemblages at large spatial extents. – J. Biogeogr. 39: 2163-2178.

409   Kot, M. 2001. Elements of Mathematical Ecology. - Cambride Univ. Press.

410   Latimer, A. M. et al. 2009. Hierarchical models facilitate spatial analysis of large data

411   sets: a case study on invasive plant species in the northeastern United States. –

412   Ecol. Lett. 12: 144-154.

413   Leathwick, J. R. and Austin, M. P. 2001. Competitive interactions between tree species in

414   New Zealand's old-growth indigenous forests. - Ecology 82: 2560-2573.

415   McGill, B. 2010. Matters of scale. - Science 328: 575-576.

416   Meier, E. S. et al. 2010. Biotic and abiotic variables show little redundancy in explaining

417   tree species distributions. - Ecography 33: 1038-1048.

418   Morales-Castilla, I. et al. 2015. Inferring biotic interactions from proxies. - Trends Ecol.

419   Evol. 30: 347-356.

420   Ovaskainen, O. et al. 2010. Modeling species co-occurrence by multivariate logistic

421   regression generates new hypotheses on fungal interactions. - Ecology 91: 2514-

422   2521.

423   Ovaskainen, O. et al. 2016. Uncovering hidden spatial structure in species communities

424   with spatially explicit joint species distribution models. - Methods Ecol. Evol. 7:

425   428-436.

426   Ovaskainen, O. et al. 2017. How to make more out of community data? A conceptual

427   framework and its implementation as models and software. – Ecol. Lett. 20: 561-

428   576.

429   Pellissier, L. et al. 2013. Combining food web and species distribution models for

430   improved community projections. – Ecol. Evol. 3: 4572-4583.

431   Pollock, L. J. et al. 2015. The roles of ecological and evolutionary processes in plant

432   community assembly: the environment, hybridization, and introgression

433   influence co-occurrence of Eucalyptus. – Am. Nat. 185: 784-796.

434   Pollock, L. J. et al. 2014. Understanding co-occurrence by modelling species

435   simultaneously with a Joint Species Distribution Model (JSDM). - Methods Ecol.

436   Evol. 5: 397-406.

437   Pulliam, H. R. 2000. On the relationship between niche and distribution. – Ecol. Lett. 3:

438   349-361.

439   R Core Team. 2015. R: A language and environment for statistical computing. - R

440   Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-

441   project.org/.

442   Schliep, E. M. et al. 2017. Joint species distribution modelling for spatio-temporal

443   occurrence and ordinal abundance data. – Glob. Ecol. Biogeogr. 27: 142-155.

444   Soberón, J. and Nakamura, M. 2009. Niches and distributional areas: concepts, methods,

445   and assumptions. – Proc. Natl. Acad. Sci. U. S. A .106: 19644-19650.

446   Staniczenko, P. P. A. et al. 2017. Linking macroecology and community ecology: refining

447   predictions of species distributions using biotic interaction networks. – Ecol. Lett.

448   20: 693-707.

449   Svenning, J.-C. et al. 2014. The influence of interspecific interactions on species range

450   expansion rates. - Ecography 37: 1198-1209.

451   Thuiller, W. et al. 2013. A road map for integrating eco-evolutionary processes into

452   biodiversity models. – Ecol. Lett. 16: 94-105.

453   Thuiller, W. et al. 2015. From species distributions to meta-communities. – Ecol. Lett.

454   18: 1321-1328.

455   Travis, J. M. J. et al. 2005. The interplay of positive and negative species interactions

456   across an environmental gradient: insights from an individual-based simulation

457   model. – Biol. Lett. 1: 5-8.

458   Urban, M. C. et al. 2016. Improving the forecast for biodiversity under climate change. -

459   Science 353: aad8466.

460   Warton, D. I. et al. 2015. So Many Variables: Joint Modeling in Community Ecology. -

461   Trends Ecol. Evol. 30: 766-779.

462   Wisz, M. S. et al. 2013. The role of biotic interactions in shaping distributions and

463   realised assemblages of species: implications for species distribution modelling. –

464   Biol. Rev. 88: 15-30.

465   Zurell, D. et al. 2010. The virtual ecologist approach: simulating data and observers. -

466   Oikos 119: 622-635.

467   Zurell, D. et al. 2009. Static species distribution models in dynamically changing

468   systems: how good can predictions really be? - Ecography 32: 733-744.

469   Zurell, D. et al. 2016a. Benchmarking novel approaches for modelling species range

470   dynamics. – Glob. Change Biol. 22: 2651-2664.

471   Zurell, D. et al. 2016b. Effects of functional traits on the prediction accuracy of species

472   richness models. – Div. Distrib. 22: 905-917.

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474

475 Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).

476 Appendix 1.

477

Figure captions

479 Figure 1. Expected co-occurrence (A-F) and residual correlation (estimated by JSDM; G-

480 K) across the biotic interaction space of two species A and B and for different prevalence

481 levels. (A) Species A and B can have negative to positive effects on each other. The co-

482 occurrence index is defined as the number of cells where species A and B occur together

483 divided by the total number of occupied cells. The null probability of co-occurrence P(A

484 and B) is given by the product of species' prevalence P(A) x P(B), and the corresponding

485 co-occurrence value is given by (P(A) x P(B)) / ((P(A) + P(B) – P(A) x P(B)) (white

486 line). (B-F) show the co-occurrence values obtained at different prevalence levels (0.1,

487 0.2, 0.3, 0.4, 0.5) with equal prevalence for both species. Again the null expectation of co-

488 occurrence is shown in white. (G-K) show the corresponding residual correlations

489 estimated by JSDMs, with grey areas indicating non-significant residual correlations.

490

491 Figure 2. Scale dependence of co-occurrence patterns and corresponding residual

492 correlations estimated by JSDMs. Both species A and B have prevalence of 0.3. (A-C)

493 show the spatial distribution of species at increasingly coarser resolution resulting from

494 intermediate competition and intermediate mutualism (species A in black, species B in

495 grey, species A and B co-occurring in red). (D-F) show the resulting co-occurrences

496 across the biotic interaction space of species A and B, and (G-I) the corresponding

497 residual correlations estimated by JSDMs (please refer to Fig. 1 for legend description).

498 (J) shows the relationship between (significant) residual correlations estimated at the

499 original resolution and at coarser resolution.

500

501   Figure 3. Scale dependence of JSDMs for different prevalence levels. Shown is the

502   significant residual correlation estimated by JSDMs at the original scale against

503   significant residual correlation estimated at coarser resolution (block size 2x2 in black,

504   block size 4x4 in red) across biotic interaction space. Scale dependence of JSDMs

505   increases with prevalence from left to right such that no significant residual correlations

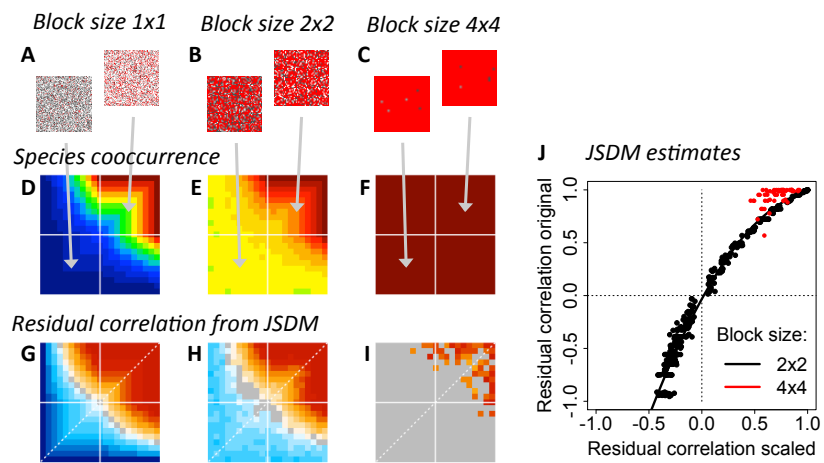506   were estimated for the 4x4 block size in (E).

507

508 **Figures**
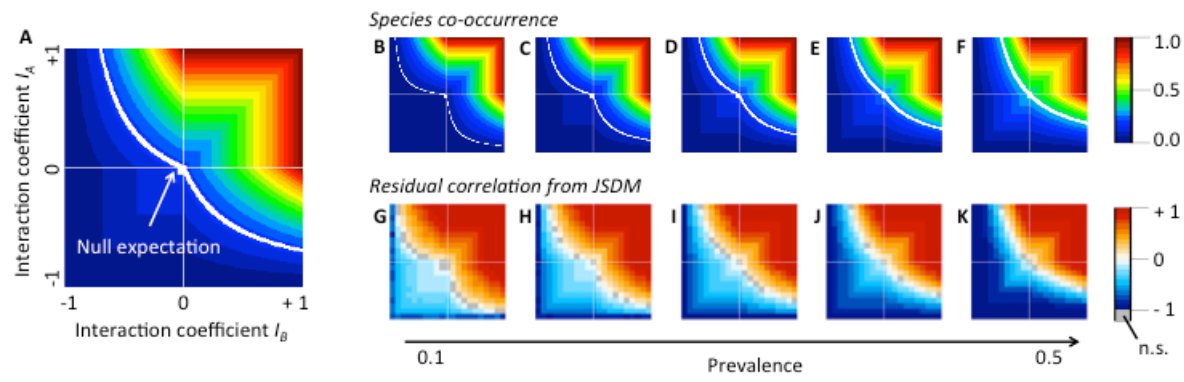
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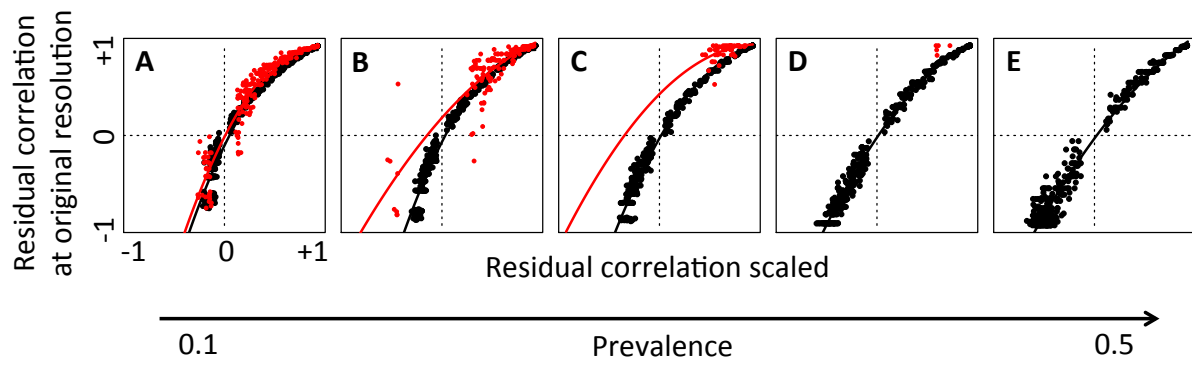510   Figure 1

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Figure 2

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516   Figure 3

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