

1 **Fauxcurrence: simulating multi-species occurrences for null models in species
2 distribution modelling and biogeography**

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33 ABSTRACT

34 Defining appropriate null expectations for species distribution hypotheses is important
35 because sampling bias and spatial autocorrelation can produce realistic, but ecologically
36 meaningless, geographic patterns. Generating null species occurrences with similar spatial
37 structure to observed data can help overcome these problems, but existing methods focus on
38 single or pairs of species and do not incorporate between-species spatial structure that may
39 occlude comparative biogeographic analyses. Here, we describe an algorithm for generating
40 randomised species occurrence points that mimic the within- and between-species spatial
41 structure of real datasets and implement it in a new R package - *fauxcurrence*. The algorithm
42 can be implemented on any geographic domain for any number of species, limited only by
43 computing power. To demonstrate its utility, we apply the algorithm to two common
44 analysis-types: testing the fit of species distribution models (SDMs) and evaluating niche-
45 overlap. The method works well on all tested datasets within reasonable timescales. We
46 found that many SDMs, despite a good fit to the data, were not significantly better than null
47 expectations and identified only two cases (out of a possible 32) of significantly higher niche
48 divergence than expected by chance. The package is user-friendly, flexible and has many
49 potential applications beyond those tested here, such as joint SDM evaluation and species
50 co-occurrence analysis, spanning the areas of ecology, evolutionary biology and
51 biogeography.

52 KEYWORDS

53 Environmental niche model; Joint species distribution modelling; Niche conservatism; Niche
54 divergence; Niche overlap; Null biogeographical model; Species distribution model

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58 **1 INTRODUCTION**

59 Eco-geographical hypothesis testing using species occurrence data can be hampered by
60 spatial autocorrelation and the difficulty of defining appropriate null expectations (Bahn &
61 McGill, 2007; Beale, Lennon, & Gimona, 2008; Chapman, 2010; Fourcade, Besnard, &
62 Secondi, 2018; Moore, Bagchi, Aiello-Lammens, & Schlichting, 2018). A major issue is that
63 spatial clustering of conspecific, or separation of heterospecific, occurrence records can be
64 affected by multiple factors, which are often difficult to disentangle. These include: i) habitat
65 suitability (Phillips, Anderson, & Schapire, 2006), ii) dispersal limitation (Glor & Warren,
66 2010), iii) interactions between individuals of the same or different species such as
67 conspecific attraction, competitive exclusion or mutualism (Mielke et al., 2020), or iv)
68 sampling bias, where occurrence records are more likely to be collected from more easily
69 accessible or intensively studied areas (Phillips et al., 2009).

70

71 One approach to overcome these issues has been to use null species occurrences to define the
72 expectations if only the inherent spatial structure within species has shaped their distributions
73 (Beale et al., 2008; Algar, Mahler, Glor, & Losos, 2013). To define the null expectation,
74 these approaches use an iterative procedure to produce null species distributions with similar
75 spatial structure to observed occurrences, excluding any consideration of environment or
76 specific geographic location. While these methods are well-suited to testing habitat-suitability
77 hypotheses for single species, they do not take spatial structure between species into account,
78 making them unsuitable for testing multispecies hypotheses involving, for example, niche
79 overlap or range boundaries. Some methods designed to test niche overlap hypotheses
80 employ null models for pairs of species, but these either do not take spatial structure into
81 account (Warren, Glor, & Turelli, 2008), or simply translocate the entire set of occurrence

82 points. This preserves spatial structure but limits their application to species which are range-
83 restricted relative to the study region (Nunes & Pearson, 2017).

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85 Here, we present a method to fill this gap, which is implemented in a new *R* package –
86 *fauxcurrence* version 1.0 (available at <https://github.com/ogosborne/fauxcurrence>). The
87 package can produce null species occurrences which preserve the spatial structure within and
88 between an arbitrary number of species, and provides many options to tailor these
89 occurrences to the user’s needs. We demonstrate the utility of the package using a dataset of
90 22 species of plants, vertebrates and arthropods. We use the resulting null occurrence points
91 to test the significance of species distribution models (SDMs) and to test for significant
92 deviations from null expectations of niche overlap between species.

93

94 **2 MATERIALS AND METHODS**

95 **2.1 Method description**

96 Our method (Fig. 1a) has three main modes of operation, distinguished by how inter-point
97 distances are used to define spatial structure. Within-species distances (divided into one
98 subset per species) are always included and can also be used alone (which we refer to here as
99 the “*Intra*” null model; Fig. 1b). The total set of between-species distances can be divided
100 into subsets in two ways: either as sets of general between-species distances per species (i.e.,
101 the distances from a species’ occurrence points to all heterospecific occurrence points; the
102 “*Inter*” null model; Fig. 1b) or as a separate set of distances between each pair of species in
103 the dataset (the “*Inter-sep*” model; Fig. 1b; Appendix 1.1).

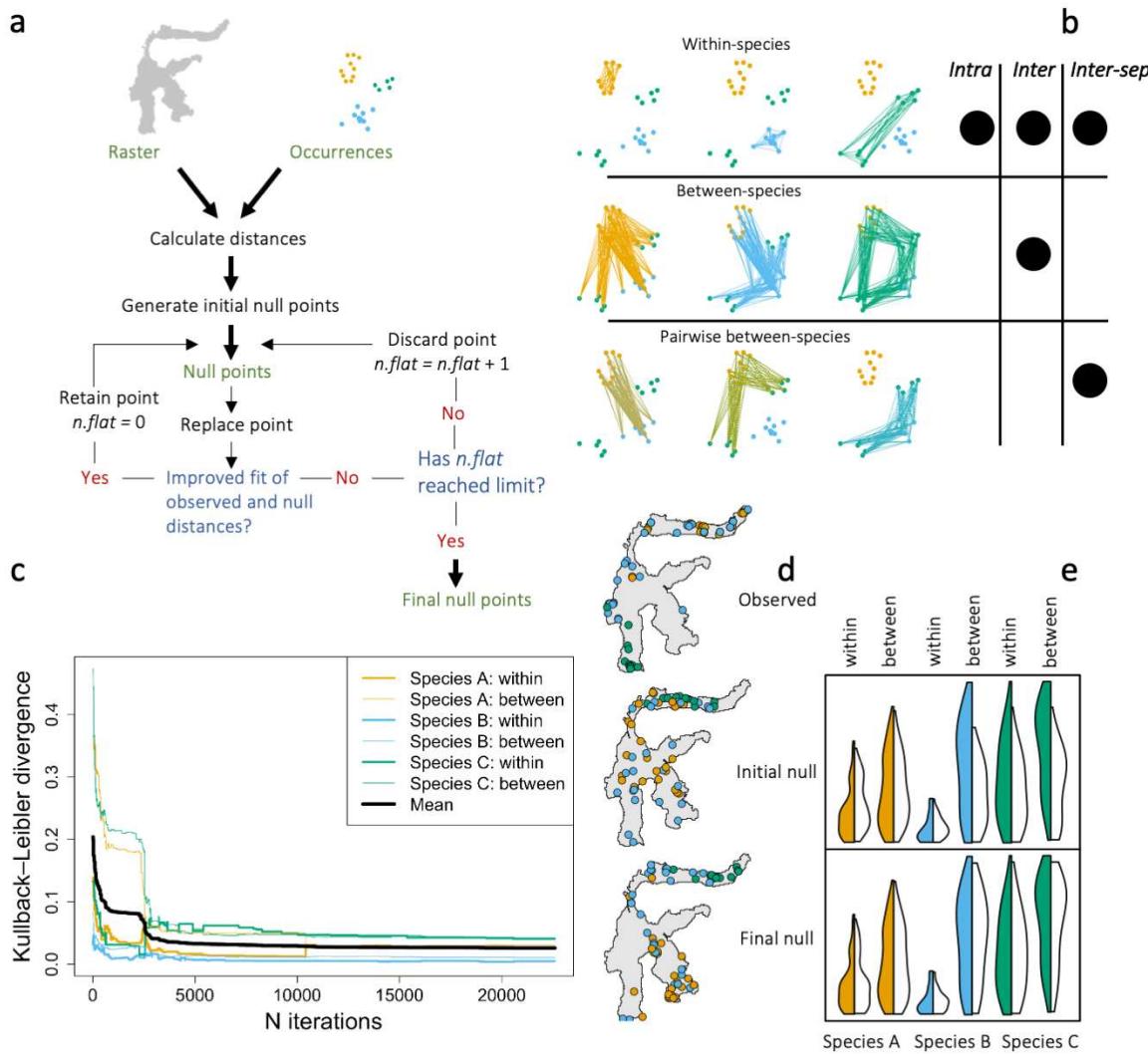
104

105 The user provides a set of species occurrence points and a raster defining the study area. The
106 algorithm begins by randomly generating one simulated occurrence point per species. It then

107 adds occurrence points for each species by drawing each new point D distance away from a
108 random existing conspecific point (where D is sampled from the empirical distribution
109 function of observed within-species distances) until each species has the same number of
110 occurrences as in the observed dataset (Appendix 1.7).

111
112 Once the initial set of simulated points are generated, the fit of their spatial structure to that of
113 the observed points is iteratively improved. For each iteration, one point is replaced and the
114 match between null and observed interpoint distances is evaluated using discrete Kullback-
115 Leibler (KL) divergence (Kullback & Leibler, 1951), where smaller values indicate a better
116 match between the simulated and observed points. Since there are multiple interpoint distance
117 distributions (i.e., within- and between-species distances for multiple species or pairs of
118 species), a weighted mean of KL-divergence across all distributions is used, weighted such
119 that within- and between-species distances contribute equally. The point replacement is only
120 retained if it improves the match, and this procedure is repeated until either no improvement
121 has been made for a set number of iterations or a maximum iteration limit has reached (Fig.
122 1c-e; see Appendix 1 for full details).

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131 Figure 1. Overview of the method. A flowchart (a) shows the basic functioning of the
 132 algorithm: initial null points are generated based on observed inter-point distances, these are
 133 then iteratively improved. The algorithm finishes when the number of iterations with no
 134 improvement ($n.flat$) reaches a user-defined limit. There are three classes of inter-point
 135 distance sets in the algorithm (b), within-species (used in all models), general between-
 136 species (used in the *Inter* model) and pairwise between-species (used in the *Inter-sep* model).
 137 The circles to the right of each indicate which null models they are used in. Panels (c-e) show
 138 an example run of the *Inter* model. Kullback-Leibler divergence decreases across iterations
 139 (c) and this improvement can be clearly seen when comparing the initial and final null
 140 occurrence points (d; map panels). The left of each split violin plot (e) shows the density of

141 observed interpoint distances for each of the distance sets in the model and the right shows
142 those of the null, which are more similar to the observed distances in the final null (bottom)
143 than the initial null (top).

144

145 **2.2 Test data**

146 We tested the method on seven species occurrence datasets from Sulawesi, Indonesia each
147 containing between one and six species from a single genus (Fig. S1a; Appendix 2). We ran
148 the *Intra* model on all datasets, and the *Inter* model on all datasets with over one species.
149 Since the *Inter* and *Inter-sep* models are identical for species pairs, we only ran the *Inter-sep*
150 model for datasets with over two species. The iterative improvement was continued until
151 there had been no improvement for 10,000 iterations. For each dataset/model combination,
152 we produced 1,000 independent, null occurrence replicates, each with similar spatial
153 structure, but differing in the final locations selected by the algorithm.

154

155 **2.3 SDM model-fitting and niche overlap**

156 We used *Maxent* v. 3.4.1 (Phillips et al., 2006) to build Species Distribution Models (SDMs)
157 for all species using the 19 *BIOCLIM* climate variables and altitude from the *WorldClim1*
158 database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). To determine if SDMs for the
159 observed data had a significantly better fit than the null models, we calculated P-values by
160 comparison of area under the receiver operating characteristic curve (AUC) in SDMs built
161 from observed data to those from all null model replicates. For datasets with more than one
162 species, we compared null and observed niche overlap using Schoener's *D* (Schoener, 1968)
163 and Warren's *I* (Warren et al., 2008), between all pairs of congeneric species (See Appendix
164 3 for full details).

165

166 **3 RESULTS**

167 **3.1 Method performance**

168 Average time per iteration ranged from 3.2 milliseconds (ms) to 21.5 ms and the mean
169 number of iterations ranged from 48,155 to 341,610 (Fig. S1). Number of occurrences was
170 the best predictor of number of iterations to model completion, although number of species
171 also had an effect (Table S1). Plotting KL divergence across iterations suggested that 10,000
172 iterations without improvement was more than sufficient to minimise the KL-divergence
173 statistic for most datasets (Fig. S2-S4).

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175 **3.2 Application to SDM model-fitting and niche overlap**

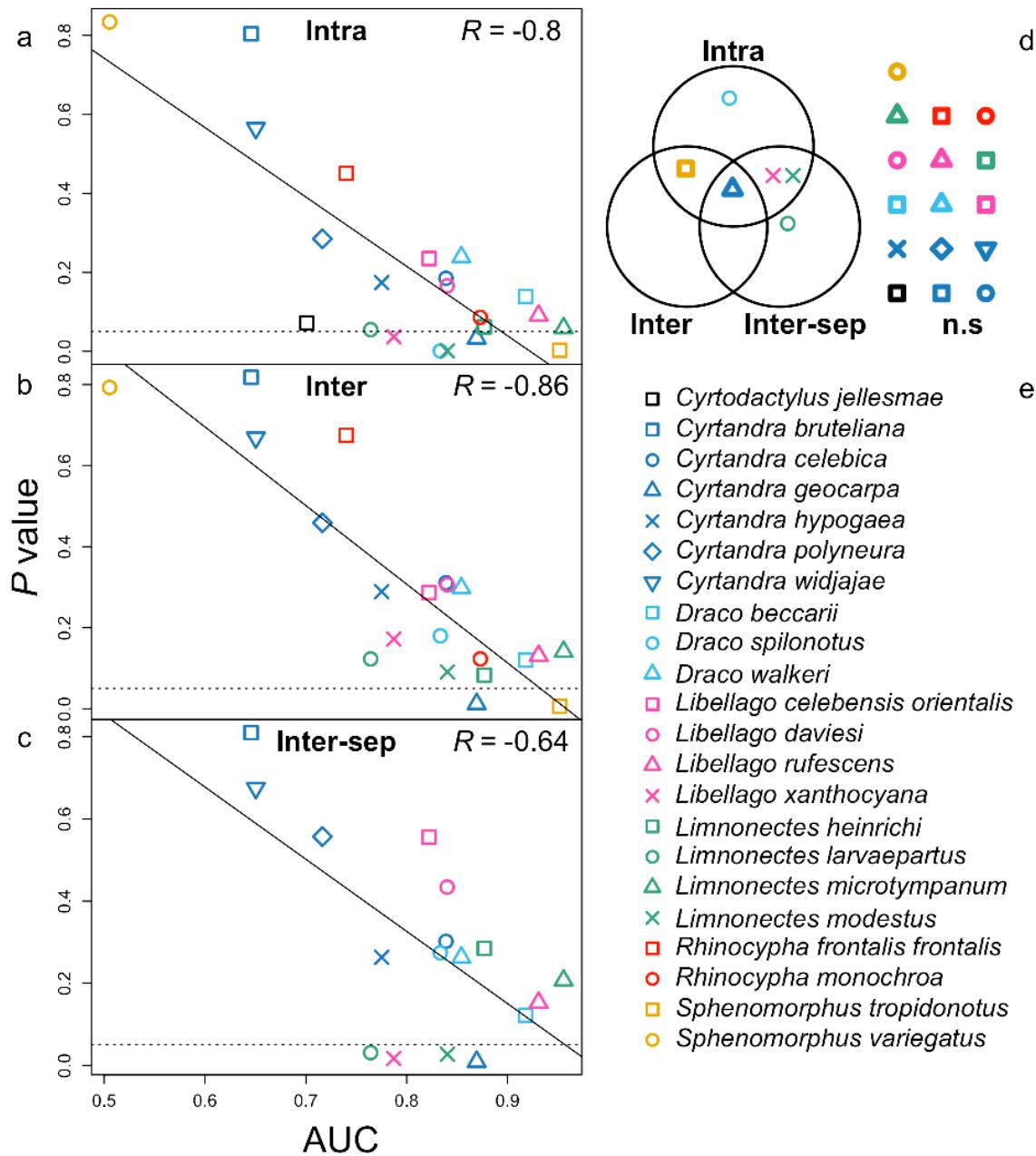
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177 The AUC values were over 0.8 for 13 of 22 species and over 0.9 for four species, values
178 typically interpreted as “excellent” or “outstanding” discrimination, respectively (Hosmer,
179 Lemeshow, & Sturdivant, 2013). Nevertheless, just six of these were significantly greater
180 than null expectations according to at least one of our null model types (Fig. 2a-c) and where
181 they were significantly greater than those of one null model type, they were often not
182 significantly different to those of the others (Fig. 2a-d). In fact, SDMs for only two species
183 had a significantly better AUC than all applied null models (Fig. 2d).

184

185 Observed niche divergence differed from null expectations in only two species pairs, both of
186 which showed significant niche divergence (Fig. S5-S8). Both of these involved *Cyrtandra*
187 *geocarpa*, which was also one of only two species whose SDM fit significantly better than
188 those from all the null models (Fig. 2). Both *Inter* and *Inter-sep* null models, and both niche
189 overlap statistics found the same two species pairs to be significant (Figs. S5-S8).

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192 Figure 2. The relationship between Area Under Curve (AUC) of the Species Distribution
 193 Models (SDMs) for observed occurrences, and the *P*-values for comparison to AUC of each
 194 null model type (a-c). Dotted lines mark 0.05 on the *P*-value axis, the solid line is a linear
 195 regression line and Pearson's correlation is shown in the top-right of each plot. A Venn
 196 diagram (d) shows the overlap in significance ($P < 0.05$) between the three models. Each
 197 labelled circle contains species with significantly higher observed AUC than those of

198 simulated data of each null model type and those which were significantly higher than
199 simulated data from multiple null models are shown in the appropriate intersection (those
200 outside the circles were not significant: “n.s”). Where all implemented models agree, symbols
201 are in bold. Species symbols are shown in the legend (e).

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203

204 **4 DISCUSSION**

205 Here, we describe a new tool to help overcome the difficulties of defining null expectations
206 when working with multi-species occurrence data. Our case study demonstrates the utility of
207 the method. Although SDMs were calculated individually for each species, the between-
208 species distances used in the null model had a major effect on their significance. For
209 example, *Draco spilonotus* had a significantly better fit than the *Intra* null model ($P = 0.001$),
210 but was not significantly different from either the *Inter* or *Inter-sep* models ($P = 0.18$ and $P =$
211 0.27, respectively). Such a pattern may be expected if, for example, competitive exclusion
212 between species, rather than climate suitability, was responsible for the geographical
213 separation of species into ranges that happen to have distinct climates (Godsoe, Franklin, &
214 Blanchet, 2017). While AUC and P -values were highly correlated, many species with very
215 high AUC scores did not have a significantly better fit than the null models. The lowest AUC
216 score which was significantly higher than any of the null models was 0.76, underlining that
217 SDMs with low AUC scores (e.g., < 0.75) should be treated with great caution. Using our
218 method to demonstrate that SDMs fit significantly better than null expectations will provide
219 much greater certainty than simple inspection of AUC.

220

221 We also demonstrated the applicability of our method to identify significant niche divergence
222 (or niche conservatism). Our method has advantages over existing approaches. The approach

223 of Nunes & Pearson (2017) creates null replicates by translocating and rotating observed
224 species occurrences. This would clearly be inappropriate for a study region such as Sulawesi,
225 since most rotations and translocations would result in a large proportion of occurrences
226 being translocated to the sea, leading to a high number of similar replicates, as noted by the
227 authors (Nunes & Pearson, 2017). The contorted geography of Sulawesi is not unique, and
228 many intensely studied locations such as Isabela Island in the Galápagos archipelago and
229 Lord Howe Island, Australia, also fall into this category. It is possible our model could have
230 similar issues in extreme cases, where dense occurrence points cover a very large proportion
231 of the study region. However, we expect it to work on a wider range of datasets due to our
232 use of “as similar as possible” rather than identical spatial structure and the capability to
233 include overland distances.

234

235 Aside from the two applications shown here, there are many other potential uses for the
236 package. For example, the performance of joint species distribution models (Pollock et al.,
237 2014), which jointly model environmental and community effects on species distributions,
238 could be assessed with our approach in a similar way to our tests of SDM fit. Other potential
239 applications include identifying significant effects of biotic factors (other species) on a focal
240 species' distribution (Algar et al., 2013; Giannini, Chapman, Saraiva, Alves-dos-Santos, &
241 Biesmeijer, 2013) where the comparison of different null models can give insight into the
242 relevance of pairwise and complex biotic interactions, and testing for significant co-
243 occurrence of range-boundaries across clades (Swenson & Howard, 2005). More generally,
244 *fauxcurrence*-generated occurrences could be used in any theoretical biogeographical
245 application where realistic occurrences of species and clades are required. Overall, the
246 method is easy to use, flexible, and can add rigour and insight into investigations of a wide
247 range of problems in ecology, evolution and biogeography.

248

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254

255 **AUTHOR CONTRIBUTIONS**

256 Ideas for the study were conceived by ACA, OGO, HGF and ASTP. OGO wrote the package
257 based partly on earlier code by ACA and HGF. HA, JvT and DP collated the species
258 occurrence data. HGF and OGO ran the species distribution modelling and niche overlap
259 analyses. ASTP and ACA supervised the project. OGO drafted the first version of the
260 manuscript and all authors contributed to and approved the final version of the manuscript.

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