

# 1 Co-occurrence is not evidence of ecological interactions

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## 6 **Authorship Statement**

7 All authors made a significant contribution to this review article. Each author brings  
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9 audience.

## 10 **Data Statement**

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## 24 **Abstract**

25 There is a rich amount of information in co-occurrence data that could be used to un-  
26 derstand community assembly. This proposition first envisioned by Forbes (1907) and  
27 then Diamond (1975) prompted the development of numerous modelling approaches (e.g.  
28 null model analysis, co-occurrence networks and, more recently, joint species distribu-  
29 tion models). Both theory and experimental evidence support the idea that ecological  
30 interactions may affect co-occurrence, but it remains unclear to what extent the signal  
31 of interaction can be captured in observational data. The time is now ripe to step back  
32 from the statistical developments and critically assess whether co-occurrence data really  
33 is a proxy for ecological interactions. In this paper we present a series of arguments based  
34 on probability, sampling, food web and coexistence theories supporting that significant  
35 spatial associations between species (or the lack of) is a poor proxy for ecological inter-  
36 actions. We discuss appropriate interpretations of co-occurrence, along with potential  
37 avenues to extract as much information as possible from such data. Finally, we propose  
38 various avenues to better describe, understand and predict ecological interactions.

## 39 **Introduction**

40 Co-occurrence analysis is the study of interactions between species distributions, and as  
41 such, it has been at the centre of community ecology for more than 100 years. Throughout  
42 this paper, we assumed an interaction occurs when the presence of a species has some form  
43 of influence on another. With the arrival of new statistical methods and the accumulation  
44 of observational data co-occurrence analysis recently attracted a lot of attention from  
45 different fields (e.g. ecology and microbiology) and for various systems (e.g. boreal forests  
46 and gut microbiome). We believe there is a rich amount of information in co-occurrence  
47 data but its interpretation should be done with care. There are several theoretical and  
48 statistical reasons explaining why there is only a weak relationship between co-occurrence  
49 and interactions. Here, we first review the rich literature on co-occurrence and then  
50 propose a set of arguments using probability, sampling, food-web and coexistence theories  
51 to support our claim that spatial associations (or lack of) between species should not be  
52 considered as a proxy for ecological interactions.

## 53 **A rich and long debate**

54 It is a truism of ecology that species must co-occur to directly interact. It is also a  
55 truism of population biology that interactions impact demography, which in turn must  
56 affect co-occurrence. This explains why early on ecologists have proposed and discussed  
57 statistical methods to infer relationships among species based on presence-absence data  
58 (Forbes, 1907; Michael, 1920; Pielou & Pielou, 1967, 1968; Diamond, 1975). As early as  
59 1907, Forbes proposed a systematic analysis of pairwise co-occurrences using the ratio  
60 between the number of observed and expected co-occurrences to determine the degree  
61 of association among pairs of fishes (Forbes, 1907; Alroy, 2015). Some 13 years later,  
62 in a modern "plea in behalf of quantitative biology", Michael (1920) highlighted several  
63 drawbacks of Forbes's coefficient, notably he pointed out the importance of the spatial  
64 scale of sampling units to draw meaningful conclusion about the underlying ecological

65 relationship inferred from it. Hence, Forbes (1907) was likely the first ecologist to quantify  
66 ecological relationships with an index based on an incidence matrix, while Michael (1920)  
67 was among the first biologists to point out potential drawbacks of such indices.

68 Forbes coefficient was forgotten for years and similar approaches, grounded on the  
69 same rationale, have been developed independently (Alroy, 2015; Arita, 2016). In 1967  
70 and 1968, Pielou and Pielou developed two statistical methods to discriminate mecha-  
71 nisms of co-existence among Diptera species on a bracket fungus by determining whether  
72 the frequencies of certain assemblages departed from random expectations (Pielou &  
73 Pielou, 1967, 1968). A few years later, Diamond (1975) introduced his assembly rules to  
74 explain the checkerboard distributions of bird communities on archipelagos. Diamond's  
75 assembly rules were quickly challenged by Connor & Simberloff (1979) who criticized the  
76 lack of random expectations thereof. This marked the beginning of a still ongoing debate  
77 about the link between co-occurrence data and species interactions (Gotelli & McCabe,  
78 2002; Connor *et al.*, 2013; Diamond *et al.*, 2015) and, as a side contribution, generated  
79 a number of new techniques aimed at improving the extraction of ecological information  
80 from co-occurrence data (e.g. Whittam & Siegel-Causey, 1981).

81 The current array of methods available can be classified into three different categories.  
82 First, the matrix-level approaches aim at determining the main drivers of species' distri-  
83 bution for a given community based on the entire incidence matrix properties (Stone &  
84 Roberts, 1990; Gotelli & Ellison, 2002; Sfenthourakis *et al.*, 2006; Cardillo & Meijaard,  
85 2010; Arita *et al.*, 2012; Ulrich & Gotelli, 2013). To do so, one or several indices are  
86 computed based on the observation data and compared to random expectations derived  
87 from null models. For instance, Patterson & Atmar (1986) used nestedness to support the  
88 hypothesis that selective extinctions occurred in the mammal community of the southern  
89 Rocky Mountains. More recently, following Leibold & Mikkelsen (2002), Presley *et al.*  
90 (2010) proposed a hierarchical approach based on coherence, species turnover and clump-  
91 ing to characterize the spatial structure of the community and hence determine the role  
92 played by colonization and niche partitioning (D'Amen *et al.*, 2018). The development of  
93 these techniques led to more sophisticated null models, and the successful inclusion of en-

94 vironmental variables (Gotelli & Ulrich, 2010) spurred enthusiasm for methods originating  
95 from research in species distribution modelling.

96 The second category originates from developments in species distribution models  
97 (SDMs) that predict the geographic repatriation of species from abiotic variables (Elith  
98 *et al.*, 2006). Indeed SDMs, developed in the 90' and early 2000' were criticized for  
99 neglecting biotic interactions (Wisz *et al.*, 2013) whereas it has been repeatedly shown  
100 that biotic interactions improve the accuracy of predictions (Leathwick & Austin, 2001;  
101 Heikkinen *et al.*, 2007; Meier *et al.*, 2010; Leach *et al.*, 2016; Barbaro *et al.*, 2019). Conse-  
102 quently, the now so-called joint species distribution models (JSDMs; Pollock *et al.*, 2014)  
103 were developed and can predict the distribution of set of species that are potentially inter-  
104 dependent based on abiotic factors using the entire incidence matrix (Özesmi & Özesmi,  
105 1999; Latimer *et al.*, 2009; Clark *et al.*, 2014; Kaldhusdal *et al.*, 2015; Warton *et al.*, 2015;  
106 Ovaskainen *et al.*, 2010, 2016, 2017; Hui, 2016; Clark *et al.*, 2017; Staniczenko *et al.*,  
107 2017). In most cases, these models provide individual species responses to the abiotic  
108 environment together with a covariance matrix whose elements capture the correlations  
109 in the incidence matrix that are not explained by the abiotic factors. Based on its math-  
110 ematical definition, this matrix has been suggested as a robust way of finding significant  
111 association in co-occurrence data while accounting for environment filtering (D'Amen  
112 *et al.*, 2018) and hence JSDMs are now used to infer interactions from ecological data  
113 (Morales-Castilla *et al.*, 2015; D'Amen *et al.*, 2018; Barner *et al.*, 2018).

114 The methods in the last category directly infer ecological relationships based on the  
115 incidence matrix: for each pair of species, the two vectors of occurrence and an optional set  
116 of covariates (e.g. abiotic factors, species abundances) are combined to compute statistical  
117 associations (Veech, 2014; Morueta-Holme *et al.*, 2016; Mandakovic *et al.*, 2018). Several  
118 techniques have been used to obtain those scores, including Fisher's tests (Veech, 2013;  
119 Arita, 2016), odd ratios (Lane *et al.*, 2014), correlations (Steele *et al.*, 2011; Faust & Raes,  
120 2012) and Markov networks (Harris, 2016; Clark *et al.*, 2018; Popovic *et al.*, 2019). In  
121 essence, those approaches are close to Forbes (1907) coefficient proposed a century ago  
122 (Veech, 2013; Arita, 2016, and some are actually very similar, e.g.), but recent approaches

123 are now focusing on the entire set of the significant co-occurrence associations, i.e. the  
124 co-occurrence network (Araújo *et al.*, 2011; Tulloch *et al.*, 2016; Kay *et al.*, 2017). Among  
125 these methods, a dividing line must be drawn: while some approaches interpret variations  
126 in co-occurrence networks as evidence for changes in ecological interactions (Araújo *et al.*,  
127 2011; Tulloch *et al.*, 2016; Kay *et al.*, 2017), other treat them as a direct proxy for  
128 interactions (Zelezniak *et al.*, 2015; Harris, 2016).

129 From the first to the third category of methods, there is a major conceptual shift from  
130 the interpretation of significant spatial associations in co-occurrence data as a potential  
131 sign of biotic interactions towards the reconstruction of entire ecological networks derived  
132 from large presence absence datasets (Wisz *et al.*, 2013; Faust & Raes, 2012; Berry &  
133 Widder, 2014; Zelezniak *et al.*, 2015; Mandakovic *et al.*, 2018). Although inferring eco-  
134 logical interactions from the easiest data to acquire (presence-absence data) holds a great  
135 appeal, one should bear in mind that this is feasible only if ecological interactions leave a  
136 signal in the presence-absence data that is regular enough to be detected and interpreted  
137 by adequate statistical methods. While some recent studies have unveiled such a regu-  
138 lar signal (e.g. Gotelli *et al.*, 2010; Cardillo, 2011), other have shown that the signal is  
139 blurred and diluted in complex networks (Cazelles *et al.*, 2016) or even absent (Brazeau &  
140 Schamp, 2019) and thus, the existence of a signal and properties thereof are still debated.

141 In the past two years, no less than three examinations have been proposed of re-  
142 cent statistical approaches used to infer species associations from presence-absence data  
143 (Barner *et al.*, 2018; Freilich *et al.*, 2018; Thurman *et al.*, 2019). Those studies focused on  
144 a specific set of species that met two criteria: (1) regional scale species presence-absence  
145 data were available and (2) biotic interactions among the species considered were docu-  
146 mented *a priori*. Using this information, the ability of existing statistical techniques to  
147 detect real interactions (covering the three categories described above) were evaluated.  
148 Interestingly, the three studies reached similar conclusions: current methods are gener-  
149 ally inaccurate, and thus, the spatial associations detected are poor proxies for biotic  
150 interactions. Even though these papers “cast doubts on studies that equate species co-  
151 occurrences to species interactions” (Barner *et al.*, 2018), there are two major limits that

152 preclude general conclusions to be drawn from them. First, as these investigations were  
153 carried out on specific systems, the reasons behind the poor performances observed could  
154 be idiosyncratic. Second, it could be argued that the results obtained merely pinpoint  
155 shortcomings in statistical approaches employed that could be addressed by future techni-  
156 cal advances. Therefore, there is still a need for a critical examination of the assumptions  
157 under which (1) ecological interactions actually leave a signal in presence-absence data  
158 and (2) whether it is feasible to detect and interpret this signal properly; this is especially  
159 true given the enthusiasm around the promise of detecting interactions from presence-  
160 absence data, which may lead to infer ecological processes where there is none (Warren  
161 *et al.*, 2014). In the following lines, we propose such an examination and develop seven  
162 arguments based on probability, sampling, food web and coexistence theories supporting  
163 that significant spatial associations between species (or lack thereof) is a poor proxy for  
164 ecological interactions.

## 165 **Interpretation of co-occurrences using conditional prob-** 166 **abilities**

167 Through the eyeglass of probability theory, the distribution of each species can be under-  
168 stood as a stochastic variable (referred to as  $X$ ) where the probability of occurrence of  
169 species A and B are respectively defined as probability events  $P(X_A, X_B)$ . This can then  
170 be compared to the expectation assuming the two species were occurring independently  
171 from each other, i.e.  $P(X_A) \times P(X_B)$ , often obtained through randomization (Gotelli  
172 & Graves, 1996; Ulrich & Gotelli, 2013; Presley *et al.*, 2010). In this respect, it is com-  
173 mon for observations significantly larger or smaller than the random expectation to be  
174 interpreted as evidence of an ecological interaction. This is the rationale behind classical  
175 approaches such as the C-score (Stone & Roberts, 1990; Gotelli *et al.*, 2010); we refer to  
176 this departure from a random expectation as ‘co-occurrence signal’.

177 An interaction is inferred when the presence of a species at a given location has

178 an influence (regardless of its nature) on the probability of observing another species  
179 at that same location. This can be presented formally by stating that the conditional  
180 probability  $P(X_A|X_B = 1)$  is significantly different from  $P(X_A|X_B = 0)$  (see section I  
181 of Supplementary Information for further details). This definition of interaction differs  
182 from the conventional definition of interactions used in community ecology, which states  
183 that an interaction is the effect of a species on the *per capita* growth rate of another one  
184 (Berlow *et al.*, 2004). In the following lines, we present arguments explaining in detail  
185 why co-occurrences does not imply interactions using the conditional and joint probability  
186 formalism.

## 187 **Argument 1 – Species occurrences depend on the environment**

### 188 **Rationale**

189 Let's assume that the occurrence of species A and B are both conditional on an environ-  
190 mental variable E. In other words, the occurrence probability of A and B varies along an  
191 environmental gradient. Assuming that neither species interact, we may still observe a  
192 strong signal in their co-occurrence profile due to the similarity (or dissimilarity) in their  
193 environmental requirements. Figure 1a illustrates an example of how such situations  
194 occur in nature (on Mont Mégantic, Canada).

195 From a mathematical standpoint, this argument is based on the fundamental difference  
196 between the probability of co-occurrence of A and B over the entire environmental gradient

$$P(X_A, X_B) \tag{1}$$

197 and the expected co-occurrence of the two species for a given environmental condition

$$P(X_A, X_B|E). \tag{2}$$

198 Note that equation 2 could also have been written  $P(X_B, X_A|E)$ .

199 In the context of SDMs, independence among species is assumed, and the general

200 interpretation is that ecological interactions do not influence species distribution (Jeschke  
201 & Strayer, 2008). In this respect, independence should be mathematically defined as

$$P(X_A, X_B|E) = P(X_A|E)P(X_B|E), \quad (3)$$

202 where  $P(X_A|E)$  and  $P(X_B|E)$  explicitly state that the probability of occurrence of each  
203 species is conditional on the environment. Graphically, Figure 1bc depicts conceptually  
204 how typical deciduous and conifer species co-occur along an elevation gradient. However,  
205 the assumption of independence is often treated in the absence of environmental pressure,  
206 thus defined as:

$$P(X_A, X_B) = P(X_A)P(X_B). \quad (4)$$

207 The critical issue here is that Equation (3) does not imply Equation (4) (we explain  
208 why in the “The problem of abiotic factors” section of SI). If interactions are inferred  
209 from spatial associations over an environmental gradient, the variation in the probability  
210 of presence for one (or both) species along the gradient could generate false positives and  
211 more rarely false negatives. We illustrated such a situation in Figure 1 where we show  
212 how the distribution of the environment  $E$  (Panel d) dramatically influences the observed  
213 co-occurrence (Panel e) even though the species are independent (Panel c).

## 214 **Conclusion**

215 This argument suggests that any environmental condition influencing the distribution of  
216 two species may cause a strong co-occurrence signal that could be misinterpreted as eco-  
217 logical interactions. Further, the sampling design could lead to different interpretations.  
218 Although it could make the use of multivariate models that accounts for environmen-  
219 tal filtering (e.g. JSDMs, Ovaskainen *et al.*, 2010; Warton *et al.*, 2015; D’Amen *et al.*,  
220 2018) appropriate, this is not the case. The co-occurrence signals (e.g. a significant  
221 positive or negative correlation value) estimated from these models could originate from  
222 any abiotic factors that impact species differently. Therefore, this correlation *cannot* be

223 systematically interpreted as a signal of biotic interactions, as it could rather express  
224 potential non-measured environmental drivers (or combinations of them) that influence  
225 species distribution and co-distribution.

226 A potentially interesting way to approach this problem is to use latent variable mod-  
227 els (e.g., Warton *et al.*, 2015; Ovaskainen *et al.*, 2017) because latent variables may be  
228 able to capture some unmeasured environmental variables. However, no distinctions are  
229 made about the type of information captured by latent variables making the use of such  
230 technique far from optimal. This difficulty of discriminating between interaction and  
231 environment using species distribution data has been shown by Godsoe *et al.* (2017) for  
232 simple interactions using simulations.

## 233 **Argument 2 – The detection of the interaction between two** 234 **species vanishes if either of these species interact with other** 235 **species**

### 236 **Rationale**

237 We focus here on the interaction among three species and assume that no other factors  
238 (biotic, environmental or others) influence their occurrence. What we show through this  
239 argument is that ecological interactions can influence the presence of a species in a specific  
240 location in unexpected ways. As species are embedded in complex networks, it becomes  
241 problematic to define a specific association without accounting for other ones. Cazelles  
242 *et al.* (2016) have already discussed this issue and showed that the higher the degree of a  
243 species (i.e. the number of interactions between this species and any other) the weaker is  
244 its statistical association with them. In other words, if an interaction between two species  
245 exists, the existence of another interaction hampers the detection of the former.

246 This problem is illustrated in Figure 2 with an artificial system of three species (a  
247 predator (P) and two consumers (C1 and C2)). We assumed here that the two consumers  
248 occur independently and that the conditional co-occurrences of the predator with the two  
249 consumers reflect interaction strengths. Based on these assumptions, we examine how

250 increasing the interaction strength between P and C2 while keeping the strength of the  
251 interaction between P and C1 constant affects the perceived relationship between P and  
252 C1 (see SI section “Simulations” for computational details).

253 In mathematical terms, the problem highlighted in this argument is that  $P(X_P)$  de-  
254 pends on both  $P(X_{C1})$  and  $P(X_{C2})$ :

$$P(X_P) = P(X_P|X_{C1})P(X_{C1}) + P(X_P|X_{C2})P(X_{C2}) \quad (5)$$

255 but the detection of the signal in the co-occurrence data of P and one of the consumers,  
256 say C1, based on the departure from random expectation:  $P(X_P, X_{C1}) - P(X_P)P(X_{C1})$   
257 does not account for the third species. As a consequence, the association profile between  
258 P and C1 changes markedly (Figure 2a-d). This argument also highlights the necessity of  
259 having accurate knowledge of the probability of occurrence of all species considered as well  
260 as the strength of interaction between P and C1 in the absence of C2, to correctly interpret  
261 the values of the association. Even for well-known species, gathering this information can  
262 be challenging.

## 263 **Conclusion**

264 Even though two species may interact strongly, the corresponding association values may  
265 be very low because of the interactions with other species (Cazelles *et al.*, 2016). It thus  
266 becomes important to find adequate approaches to characterize independent interactions  
267 while controlling for all the other interactions a species may have. A way to overcome  
268 this issue would be to keep exploring partial correlations using Bayesian (Staniczenko  
269 *et al.*, 2017) and Markov networks (Harris, 2016; Clark *et al.*, 2018). Paradoxically,  
270 to benefit from such tools and accurately detect interactions (e.g. to meaningfully use  
271 partial correlations), the full topology of the network needs to be known beforehand. In  
272 a recent study, Popovic *et al.* (2019) proposed a generalization of the ideas proposed  
273 by Harris (2016) that can combine different data types (e.g. presence-absence, count,  
274 biomass, ordinal, etc.) in a single model using Gaussian copula. This is an interesting

275 development because it focuses on studying relations among species using data more  
 276 informative than presence-absence data. However, the ideas proposed by Popovic *et al.*  
 277 (2019) and Harris (2016) suffer from the same pitfalls when used on co-occurrence data.

### 278 **Argument 3 – Species associations could arise indirectly**

#### 279 **Rationale**

280 In ecological networks, indirect interactions may generate non-random associations among  
 281 species. For instance, if a top predator feeds on a predator that in turn feeds on a  
 282 consumer, the top predator and the consumer may co-occur more frequently than expected  
 283 even though they do not interact directly. Using simulated (co-)occurrence data, Cazelles  
 284 *et al.* (2016) have shown a decrease of the co-occurrence signal with an increase of the  
 285 shortest path between two species within the same ecological network.

286 In order to illustrate how indirect association can emerge from a chain of direct in-  
 287 teractions, we consider a chain of four trophic levels where each species feeds solely on  
 288 the one directly below it in the chain (Figure 3b). Using conditional probabilities and  
 289 assuming that a predator cannot survive without its prey, we obtain

$$P(X_C) = P(X_C|X_R)P(X_R) \tag{6}$$

$$P(X_P) = P(X_P|X_C)P(X_C) = P(X_P|X_C)P(X_C|X_R)P(X_R) \tag{7}$$

$$P(X_T) = P(X_T|X_P)P(X_P) = P(X_T|X_P)P(X_P|X_C)P(X_C|X_R)P(X_R). \tag{8}$$

290 With this example, we examined how increasing the strength of association between C  
 291 and R affects the co-occurrence signal between R and the other species. In this case, the  
 292 signal is computed as the difference between the observed co-occurrence and the expected  
 293 one under the assumption that species are independent (see section “Simulation” in SI  
 294 for further details).

295 Figure 3a shows an increase in the co-occurrence signal for R-P and R-T as the

296 association strength between R and C increases, meaning that the signal propagates  
297 through the network. On the other hand, this illustration also shows that the signal  
298 weakens along the chain. While the results are direct consequences of the assumption  
299 and the equations above, it also points out the difficulty to interpret the co-occurrence  
300 signal without prior knowledge of the network (which we have in our illustration, Figure  
301 3b). Indeed, the sole examination of the co-occurrence signal would not allow us to  
302 determine whether the interactions T-R and P-R are direct but weak, or indirect.

### 303 **Conclusion**

304 Indirect interactions can generate non-random associations that can be interpreted sim-  
305 ilarly to the ones resulting from direct interactions. While in some cases, revealing the  
306 presence of an interaction, be it direct or indirect, is enough (e.g. to predict species distri-  
307 butions in the case of JSDM), this argument constitutes a major obstacle to the accurate  
308 inference of complex networks based on co-occurrence data alone. Also, because it is  
309 rarely obvious whether a particular association is direct or indirect from co-occurrence  
310 studies, such interactions could be misinterpreted. To further confound us, species may  
311 modify their interactions solely in the presence of another particular species. Study on  
312 invasive species are rich in examples of this particularity of nature (Zavaleta *et al.*, 2001,  
313 for a review). That being said, graphical models (Popovic *et al.*, 2019) may be an inter-  
314 esting starting point to approach this problem because they were shown to be efficient  
315 in capturing direct association among species. However, the associations measured by  
316 Popovic *et al.* (2019) are not, and have never been considered, interactions.

### 317 **Sampling is a key to making correct inference**

318 In this section, we focus on the role played by different characteristics of the sampling  
319 design in the inference of species interactions from presence-absence data. To assess  
320 whether a co-occurrence is not spurious, it is important to sample enough, to sample  
321 properly and to integrate the metadata pertaining to it (e.g. size of the sampling unit,

322 spatial location, etc.) Assuming that the data gathered is well sampled and in large  
323 enough quantities, one can then give an interpretation to the estimated co-occurrence.  
324 In particular, the choice of the spatial scale at which to sample and the sampling effort  
325 have important impacts on the co-occurrence computed signal.

## 326 **Argument 4 – Sampling scale influences measures of co-occurrence**

### 327 **Rationale**

328 It has repeatedly been argued that interactions must be a major determinant of the  
329 broad geographic distribution of species (Holt & Barfield, 2009; Benning *et al.*, 2019),  
330 but also that, as a local process (acting at the individuals scale), their impact may not be  
331 discernible at coarser spatial scales (Pearson & Dawson, 2003; Russell *et al.*, 2006; McGill,  
332 2010). While the problem of sampling scale in co-occurrence studies has been raised early  
333 in the literature (Michael, 1920), biogeographers still investigate this technical but central  
334 topic (Araújo & Rozenfeld, 2014; Bar-Massada *et al.*, 2018; Thuiller *et al.*, 2015; Belmaker  
335 *et al.*, 2015). For instance, using simulations, Araújo & Rozenfeld (2014) demonstrated  
336 that while negative interactions quickly vanish as the spatial extent of sampling unit  
337 increases, the imprint of positive interactions scales up. Such findings emphasize that  
338 sampling resolution needs to be carefully chosen so that the true underlying co-occurrence  
339 signal can be extracted from the data.

340 To illustrate this aspect of the sampling design, we considered two independent species  
341 A and B, that either poorly overlap (Fig. 4a) or strongly overlap (Fig. 4b). For these  
342 two scenarios, we simulated sampling and then computed co-occurrence signals along the  
343 gradient for a moving window increasing in size (see section “Simulation” in the SI for  
344 more details). What is striking about the results obtained is that for two negatively  
345 associated species (Figure 4a,c), a sampling area that encompasses most (but not all) of  
346 the distributional range of both species tends to overemphasize the negative association  
347 between the species. Conversely, when two species are positively associated (Figure 4b,d),  
348 the co-occurrence signal varies widely, especially for a sampling area that includes between

349 roughly 30% and 50% of the distributional range of both species. Thus, the associations  
350 detected highly depend on the portion of the environmental gradient considered.

## 351 **Conclusion**

352 In addition to the crucial importance of sampling resolution (Araújo & Rozenfeld, 2014;  
353 Bar-Massada *et al.*, 2018; Thuiller *et al.*, 2015), the portion of the environmental gradient  
354 sampled should also be carefully examined to avoid erroneous conclusions (Bar-Massada  
355 & Belmaker, 2017). To infer ecological interactions from co-occurrence data, the full  
356 distributional range of both species needs to be considered. In more colloquial terms,  
357 there are no free lunches when assessing co-occurrence through observational data.

## 358 **Argument 5 – Appropriate statistical inference requires a very** 359 **large sample size**

### 360 **Rationale**

361 Species co-occurrence is a relatively rare phenomenon to document. To contextualize,  
362 it is already challenging to gather a large enough number of samples to estimate how  
363 a single species relates to the environment. Although there is no specific sample size  
364 prescription for species distribution models, studying model significance (e.g. through  
365 the use of confidence intervals), we generally have a good idea of whether a sample was  
366 large enough to obtain reliable results. However, to estimate a co-occurrence, many  
367 samples are required, much more than what is typically used to measure co-occurrence  
368 structure.

### 369 **How many samples is enough samples?**

370 Let's consider a simple situation with two relatively common species. If we assume that  
371 species A occurs in 40% ( $P(X_A) = 0.4$ ) of samples and species B in 60% ( $P(X_B) = 0.6$ ),  
372 probability theory tells us that the null expectation of co-occurrence between the two  
373 species will be  $P(X_A) \times P(X_B) = 0.24$ . Of course, this probability will increase (decrease)

374 as the co-occurrence signal between the two species also increases (decreases). However,  
375 it is not readily obvious how many samples would be required to assess whether the  
376 association between species A and B is different from a null expectation or to evaluate  
377 if both species co-occur with a particular correlation level, say, 0.9, 0.5, -0.5, -0.9. This  
378 question can be approached using the multivariate Bernoulli distribution (Teugels, 1990)  
379 and binomial confidence intervals (DasGupta *et al.*, 2001, compares different techniques  
380 to calculate confidence intervals on binomial data).

381 The results in Figure 5 show that in the best case scenario, over 500 samples are  
382 required to reach a 95% confidence limit. Note that this example is actually conservative  
383 because when the probability of occurrence of each pair of species is either higher or lower,  
384 the number of samples increases to many thousands of samples.

385 What is even more worrying is that the results presented in Figure 5 assume that  
386 the pair of species are solely influencing each other, a rare case in nature. Species often  
387 interact with a group of other species which will, in most cases, reduce the probability of  
388 co-occurrence on the considered species pair (see *Argument 2*) and in turn require that  
389 an even larger number of samples be gathered to efficiently measure the co-occurrence  
390 between the two species.

## 391 **Conclusion**

392 The number of samples required to accurately measure co-occurrence among species is  
393 impractical for most studies. As a comparison, it is common for studies in ecology focusing  
394 on co-occurrence to have a small sample size compared to what is discussed in this section.  
395 For example, of the 294 datasets gathered in Atmar & Patterson (1995), only four had  
396 more than 100 samples, the largest having 202 samples. This is not unique to ecology,  
397 environmental microbiology (Rocca *et al.*, 2019) and microbiome research (e.g. Levy &  
398 Borenstein, 2013) suffers from the same problem. Granted, in the last twenty years larger  
399 datasets are becoming increasingly available (see, e.g. the datasets used by Ovaskainen  
400 *et al.*, 2017). That being said, studies with a sample size that meet the requirements  
401 highlighted in this argument are still extremely rare.

402 The results of this section suggest that no statistical approach, regardless of its level  
403 of sophistication, can be used to assess spatial associations between species accurately  
404 and this even for reasonably large sample size.

## 405 **The imprint of ecological interactions on co-occurrence** 406 **data**

407 In this section we discuss the relationships we should expect from co-occurrence data  
408 based on current ecological theory. Whether it is from foodweb or coexistence theories,  
409 we have learned that there are different types of interactions with different strengths.  
410 In this section, we discuss how what we know of ecological interactions is expressed in  
411 co-occurrence data.

### 412 **Argument 6 – Asymmetry of associations between species can** 413 **blur co-occurrence signal**

#### 414 **Rationale**

415 Different types of interactions do not result in the same co-occurrence signal (Araújo  
416 & Rozenfeld, 2014). Most co-occurrence analyses are, however, derived from the joint  
417 species distribution (as defined above), which is a symmetric measure of spatial associa-  
418 tion. There is, however, no reason why two species should have exactly the same effect on  
419 each other and we should therefore expect species-specific variation in the co-occurrence  
420 signal. Further, some interactions such as predation, herbivory or parasitism could even  
421 lead to opposing signals, making the expectation for the joint species distribution in-  
422 determinable. This is noteworthy because these types of interactions have traditionally  
423 been the most studied ones in community ecology and are now increasingly inferred from  
424 proxies (Morales-Castilla *et al.*, 2015), including co-occurrence.

425 This argument is best understood with a decomposition of the joint probability of  
426 occurrence. Using the product rule (and ignoring the effect of the environment  $E$ ), we

427 find that the joint distribution of species A and B can be decomposed into the product  
428 of conditional and marginal probabilities

$$P(X_A, X_B) = P(X_A|X_B)P(X_B) \quad (9)$$

429 and inversely

$$P(X_A, X_B) = P(X_B|X_A)P(X_A). \quad (10)$$

430 In the previous equations, the conditional occurrence probability  $P(X_A|X_B)$  is the mea-  
431 sure of the effect of species  $B$  on the occurrence of species  $A$ . Unless the marginal prob-  
432 abilities are exactly the same, the conditional occurrence probabilities must absolutely  
433 differ from each other to equal the joint occurrence probability. This means that the  
434 joint occurrence probability masks the variability in the strength of associations between  
435 species.

436 The decomposition presented above may have unexpected and far-reaching impact.  
437 For example, strong negative and positive associations, such as between a predator and a  
438 prey, may cancel each other and result in a joint occurrence probability not different from  
439 the null expectation. A numerical example best illustrates this point. Let's consider a  
440 predator  $A$  with marginal occurrence  $P(X_A) = 0.2$  and a prey with marginal occurrence  
441  $P(X_B) = 0.5$ . We know from probability theory that their random expectation is  $P(X_A) \times$   
442  $P(X_B) = 0.1$ . Let's further assume that their realization is  $P(X_A, X_B) = 0.15$ , so slightly  
443 above the expectation. Using these values and equations 9 and 10, we can calculate the  
444 probability of finding the predator given the presence of the prey  $P(X_A = 1|X_B = 1) = 0.3$   
445 or its absence  $P(X_A = 1|X_B = 0) = 0.167$ . These results states that it is almost twice as  
446 probable for a predator and a prey to be found together then separated. Conversely, using  
447 the same approach, we find the conditional occurrence of the prey in the predator's  
448 absence to be  $P(X_B = 1|X_A = 0) = 0.5625$ , which is more than two times larger than in  
449 the presence of the predator,  $P(X_B = 1|X_A = 1) = 0.25$ . This simplistic example shows  
450 how variable the conditional probabilities can be and how they can have opposite effects,

451 even if the joint occurrence is not much different from the null expectation.

## 452 **Conclusion**

453 Analysis of joint distribution of presence-absence data is not appropriate to assess in-  
454 teractions because not all asymmetric interactions can be identified. This particularity  
455 of co-occurrence data may lead to bias interpretation of interactions towards symmetric  
456 interactions. In this respect, conditional probabilities are more relevant to document vari-  
457 ance in association strength as well as asymmetric associations. There are four conditional  
458 probabilities associated with a pair of co-occurring species and their comparison reveals  
459 the direction and strength of effects of one species on another. While conditional prob-  
460 abilities are very promising and could be extended to an entire network using Bayesian  
461 networks (Staniczenko *et al.*, 2017), they may be challenging to solve, especially when  
462 cycles are present in the network.

## 463 **Argument 7 – Coexistence theory predicts that strong interac-** 464 **tions may lead to exclusion before leaving a significant signal**

### 465 **Rationale**

466 In a competition system, stable coexistence, whether it is at the local or regional scale,  
467 requires interspecific interactions to be weaker than intraspecific interactions (Chesson,  
468 2000). The weaker competitor tends to get excluded when interaction strength increases.  
469 This narrows down the range where interactions can actually be detected using co-  
470 occurrence data: if interactions are too weak, the imprint left in co-occurrence data  
471 may be undetectable but if interactions are strong it may prevent coexistence to happen.

472 This assertion can be explored using a multi-species adaptation of the Levins (1969)  
473 metapopulation model. Such a model was presented by Hanski (1983) to illustrate the  
474 patch dynamics between a strong (species A) and a weak (species B) competitor as well  
475 as to quantify the proportion of patches occupied solely by either or both of the two  
476 species. Using this model, we can vary colonization competition (corresponding to pre-

477 emptive competition) or extinction competition (corresponding to competitive exclusion),  
478 (Gravel & Massol, 2019). In doing so, we can investigate the proportion of patches where  
479 species co-occurrences vary while interaction strength increases. Intuitively, the stronger  
480 pre-emptive competition and competitive exclusion are, the smaller the co-occurrence  
481 will be relative to marginal occurrence (species will avoid each other). This is indeed  
482 what the model predicts. In addition, it also shows that marginal occurrences of the  
483 weak competitor rapidly decline when the interaction strength increases, resulting in  
484 very small absolute co-occurrence (Figure 6). Given *Argument 5*, based on this result,  
485 we would need a very large sample size to document such rare phenomena. As such, it is  
486 unlikely that spatial repulsion may be detected when interaction strength is strong.

## 487 **Conclusion**

488 Strong negative interspecific interactions are incompatible with coexistence. Species may  
489 be excluded by competition before the interaction signal can be captured in co-occurrence  
490 data. In other words, a species absent regionally cannot generate any interaction signal  
491 because it will never be sampled. Although this may not be for all types of interactions,  
492 if not opposite for positive interactions (see Gravel & Massol, 2019), it nonetheless leads  
493 to the paradox that the strong interactions we want to document with co-occurrence may  
494 be impossible to measure.

## 495 **Concluding Remarks**

496 The seven arguments we present paint a rather grim picture of the problems related to  
497 the inference of interactions from co-occurrence data. There are two broad conclusions  
498 to be drawn from them. First, the various layers of complexity inherent to ecological  
499 systems (e.g. environmental variability, diversity of biotic interactions, etc.) blur the  
500 link between interactions and co-occurrence. This is not even accounting other more  
501 specific aspects of ecological systems that can generate additional complications. For  
502 example, it is inherently challenging to measure interactions among rare or transient

503 species, regardless of the approach used. Similarly, particular species may interact only  
504 in specific situations, making their assessment difficult because the context influencing  
505 these interactions may be difficult to evaluate. Also, most co-occurrence analysis considers  
506 species distribution to be at equilibrium, which could be dynamic (e.g. metapopulation)  
507 or not, a constraining assumptions especially in the context of environmental changes  
508 (e.g. climate change). Second, because the relationship between interactions and co-  
509 occurrence is rarely clear, there are several technical and theoretical challenges to infer  
510 ecological interactions from co-occurrence data that still remain to be tackled.

511 One aspect of ecological interactions that was not discussed in this paper was the  
512 importance of temporal variations and its impact on species and their interactions. Ac-  
513 counting for time when assessing ecological interactions is undoubtedly important and has  
514 potentially far-reaching consequences. For example, hibernation, migration, phenology  
515 are all temporal drivers of change for ecological interactions. However, assessing interac-  
516 tions from temporal co-occurrence raises a number of additional issues that are outside  
517 the scope of this paper.

518 Independently and together, the arguments we developed illustrate the diversity of  
519 those challenges. Even if statistical/sampling/theoretical solutions can be found for some,  
520 it is difficult to contemplate a solution that would solve all problems raised, while still  
521 using presence-absence data. The minimal amount of information these data carry is  
522 indeed at the core of most of the challenges we pointed out in this study. Even JSDMs,  
523 which have been seen by some as an appealing new modelling framework to efficiently  
524 study ecological interactions, are not able to tackle most of the arguments we presented  
525 above. The correlation matrix (estimated from JSDMs) describing the association among  
526 pairs of species, now often used as illustration to represent species association, is likely  
527 what triggered the interest of using JSDMs to infer species interactions. Using such a  
528 representation, it is extremely tempting to make the intellectual jump to infer ecological  
529 interactions. In this respect, we advocate that such representation should never be used  
530 when the underlying data used to construct the model is presence-absence data.

531 Our perspective of the problems related to co-occurrences and its use to study inter-

532 actions has far-reaching implications for some historical debates in community ecology.  
533 Among others, it suggests the importance of revisiting the long-standing debates on null  
534 models initiated by Diamond (1975) and Connor & Simberloff (1979). The arguments  
535 we raised have implications for the ability to detect significant signal with null models.  
536 Scale and sampling effort problems have been debated for a while in this ‘null model  
537 war’. Yet, the other arguments also need considerations. For example, even the most  
538 recent developments to analyse co-occurrence data using null models (e.g. D’Amen *et al.*,  
539 2018) still assume species influence each other the same way. More fundamentally, all  
540 the arguments we present show that the observation of spatial associations (or the lack  
541 thereof) may be impossible to accurately assess and interpret. We do not suggest here  
542 that the whole field pertaining to null models should be discarded. Rather, researchers  
543 should be more critical of the limits of their tools when interpreting their results. With  
544 null models, what is tested is whether pairs of species are spatially associated or not, this  
545 is what is tested with null models.

546 Presence-absence data undoubtedly remain central to ecology and ecologists must cer-  
547 tainly keep collecting them in order to broaden our knowledge on species distributions  
548 and our understanding of the factors that determine the presence of a specific community  
549 in a particular area. But it is also crucial to identify what can be inferred from such data  
550 and what cannot. Some avenues deserve to be explored bearing that in mind. A con-  
551 ceptually simple but technically challenging solution would be to derive interactions from  
552 abundance (count) data instead of presence-absence data. From a modelling perspective,  
553 tools exist that can be used to assess relationships among species using abundance data  
554 and infer interactions (Poisot *et al.*, 2015; Faisal *et al.*, 2010; Popovic *et al.*, 2019). From  
555 an empirical perspective, a few studies have used different ways to infer interactions from  
556 abundance (or plant cover) data both in ecology (le Roux *et al.*, 2013) and microbiology  
557 (Levy & Borenstein, 2013). Hopefully, using ecological data carrying more information  
558 that presence-absence data (such as abundance data) would provide reliable proxies for  
559 biotic interactions.

560 Another direction worth investigating is to study interactions through the eyeglass of

561 conditional probabilities. Through this approach, we can get a much more direct interpre-  
562 tation of how a species react in the presence of other species by being more mathematically  
563 explicit about how species relate to each other. Networks of conditional probabilities may  
564 directly solve some of the above arguments (e.g. 1,2,3 and 6), especially if accounting  
565 for covarying environmental variables. From a statistical perspective, Bayesian networks  
566 and Markov networks offer appealing avenues to investigate. There are, however, several  
567 technical challenges that will need to be solved before these could be used. Among them,  
568 the presence of cycles (species A affect species B and vice-versa) is a fundamental prob-  
569 lem, large sample size cannot be avoided and some prior knowledge of interactions is also  
570 required. Yet another way to study species interactions is with mechanistic models where  
571 the known (or hypothesized) mechanisms of interactions are explicitly accounted for. By  
572 testing how close these mechanistic models represent data on species associations, we can  
573 then infer the underlying processes structuring species.

574 Experiments are one avenue that needs to be further explored to understand how  
575 biotic interactions impact distribution. Although they are often time consuming and  
576 costly, they can increase our knowledge on interactions while remaining in the world of  
577 co-occurrences. As an example, Brazeau & Schamp (2019) have recently shown it is pos-  
578 sible to experimentally link competition and negative co-occurrence for flowering plants.  
579 Similarly, Kopelke *et al.* (2017) gathered a large dataset directly recording the interaction  
580 between willow tree species and sawflies, a group of parasites feeding on willow leaves.  
581 These studies are particularly interesting because they focus explicitly on interactions. A  
582 way forward would be to pursue the development of modelling approaches that can make  
583 full use of these datasets but also of theoretical ideas that can advance our understanding  
584 of ecological interaction.

585 Early on ecologists recognized there is a large amount of unexplored information in  
586 co-occurrence data. New and powerful statistical tools are becoming available that allows  
587 ecologists to gain new insights from co-occurrence data and efforts should continue in that  
588 way. That said, although very tempting at first, with our current knowledge, interpreting  
589 significant co-occurrence signals between species as evidence of ecological interactions

590 should be avoided.

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### 597 **Box 1: Outstanding Questions**

- 598 • Is it possible to infer ecological interactions from distribution data? There  
599 may not be a clear answer, there may be situations where it is possible and  
600 other where it is not. Discriminating the former situation from the latter  
601 would represent a major step forward and the relevant question will then be :  
602 under which assumptions are co-occurrence signals good proxies for ecological  
603 interactions?
- 604 • How to interpret co-occurrence networks? Even though such networks are  
605 more frequently used in the literature, from a theoretical point of view, it  
606 remains unclear how they relate to ecological interaction networks.
- 607 • What are the relevant covariates required to infer ecological interactions from  
608 species distributions? In case where distribution data are not enough to  
609 conclude, is it possible to provide additional information to infer interactions?
- 610 • How strong are interaction signals in abundance data? This can be assessed  
611 using data gathered on species known to interact. Statistically, many of the  
612 methods currently available and applied on co-occurrence data can be used  
613 (and compared) to approach this question.
- How important are detection errors when assessing interactions? There are a

621

614

615 growing number of models that accounts for detection errors they were never  
616 used to study the influence of detection error when measuring interactions.

- 617 • How can we account for cycles in network models? Currently, network models  
618 cannot account for cycles which are an inherent part of trophic networks.
- 619 • How can we design experiments and data collection to better assess interac-  
620 tions?

622

## 623 **References**

624 Alroy, J. (2015). A new twist on a very old binary similarity coefficient. *Ecology*, 96,  
625 575–586.

626 Araújo, M.B. & Rozenfeld, A. (2014). The geographic scaling of biotic interactions.  
627 *Ecography*, 37, 001–010.

628 Araújo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011). Using species co-  
629 occurrence networks to assess the impacts of climate change. *Ecography*, 34, 897–908.

630 Arita, H.T. (2016). Species co-occurrence analysis: pairwise versus matrix-level ap-  
631 proaches: Correspondence. *Global Ecology and Biogeography*, 25, 1397–1400.

632 Arita, H.T., Christen, A., Rodríguez, P. & Soberón, J. (2012). The presence-absence  
633 matrix reloaded: the use and interpretation of range-diversity plots: Range-diversity  
634 plots. *Global Ecology and Biogeography*, 21, 282–292.

635 Atmar, W. & Patterson, B.D. (1995). *The nestedness temperature calculator: a visual*  
636 *basic program, including 294 presence-absence matrices*. Aics research, inc. edn. Uni-  
637 versity Park, NM, and The Field Museum, Chicago.

- 638 Bar-Massada, A. & Belmaker, J. (2017). Non-stationarity in the co-occurrence patterns  
639 of species across environmental gradients. *Journal of Ecology*, 105, 391–399.
- 640 Bar-Massada, A., Yang, Q., Shen, G. & Wang, X. (2018). Tree species co-occurrence  
641 patterns change across grains: insights from a subtropical forest. *Ecosphere*, 9, e02213.
- 642 Barbaro, L., Allan, E., Ampoorter, E., Castagneyrol, B., Charbonnier, Y., De Wandeler,  
643 H., Kerbiriou, C., Milligan, H.T., Vialatte, A., Carnol, M., Deconchat, M., De Smedt,  
644 P., Jactel, H., Koricheva, J., Le Viol, I., Muys, B., Scherer-Lorenzen, M., Verheyen,  
645 K. & van der Plas, F. (2019). Biotic predictors complement models of bat and bird  
646 responses to climate and tree diversity in European forests. *Proceedings of the Royal  
647 Society B: Biological Sciences*, 286, 20182193.
- 648 Barner, A.K., Coblenz, K.E., Hacker, S.D. & Menge, B.A. (2018). Fundamental contra-  
649 dictions among observational and experimental estimates of non-trophic species inter-  
650 actions. *Ecology*, 99, 557–566.
- 651 Belmaker, J., Zarnetske, P., Tuanmu, M.N., Zonneveld, S., Record, S., Strecker, A. &  
652 Beaudrot, L. (2015). Empirical evidence for the scale dependence of biotic interactions:  
653 Scaling of biotic interactions. *Global Ecology and Biogeography*, 24, 750–761.
- 654 Benning, J.W., Eckhart, V.M., Geber, M.A. & Moeller, D.A. (2019). Biotic interactions  
655 contribute to the geographic range limit of an annual plant: herbivory and phenology  
656 mediate fitness beyond a range margin. *The American Naturalist*, p. 703187.
- 657 Berlow, E.L., Neutel, A.M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M.,  
658 Fox, J.W., Jansen, V.A.A., Iwan Jones, J., Kokkoris, G.D., Logofet, D.O., McKane,  
659 A.J., Montoya, J.M. & Petchey, O. (2004). Interaction strengths in food webs: Issues  
660 and opportunities. *Journal of Animal Ecology*, 73, 585–598.
- 661 Berry, D. & Widder, S. (2014). Deciphering microbial interactions and detecting keystone  
662 species with co-occurrence networks. *Frontiers in Microbiology*, 5.

- 663 Brazeau, H.A. & Schamp, B.S. (2019). Examining the link between competition and  
664 negative co-occurrence patterns. *Oikos*.
- 665 Cardillo, M. (2011). Phylogenetic structure of mammal assemblages at large geograph-  
666 ical scales: linking phylogenetic community ecology with macroecology. *Philosophical*  
667 *Transactions of the Royal Society B: Biological Sciences*, 366, 2545–2553.
- 668 Cardillo, M. & Meijaard, E. (2010). Phylogeny and co-occurrence of mammal species on  
669 Southeast Asian islands. *Global Ecology and Biogeography*.
- 670 Cazelles, K., Araújo, M.B., Mouquet, N. & Gravel, D. (2016). A theory for species  
671 co-occurrence in interaction networks. *Theoretical Ecology*, 9, 39–48.
- 672 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of*  
673 *Ecology and Systematics*, 31, 343–366.
- 674 Clark, J.S., Gelfand, A.E., Woodall, C.W. & Zhu, K. (2014). More than the sum of  
675 the parts: forest climate response from joint species distribution models. *Ecological*  
676 *Applications*, 24, 990–999.
- 677 Clark, J.S., Nemergut, D., Seyednasrollah, B., Turner, P.J. & Zhang, S. (2017). Gen-  
678 eralized joint attribute modeling for biodiversity analysis: median-zero, multivariate,  
679 multifarious data. *Ecological Monographs*, 87, 34–56.
- 680 Clark, N.J., Wells, K. & Lindberg, O. (2018). Unravelling changing interspecific in-  
681 teractions across environmental gradients using Markov random fields. *Ecology*, 99,  
682 1277–1283.
- 683 Connor, E.F., Collins, M.D. & Simberloff, D. (2013). The checkered history of checker-  
684 board distributions. *Ecology*, 94, 2403–2414.
- 685 Connor, E.F. & Simberloff, D. (1979). The assembly of species communities: Chance or  
686 competition? *Ecology*, 60, 1132.

- 687 D’Amen, M., Mod, H.K., Gotelli, N.J. & Guisan, A. (2018). Disentangling biotic interac-  
688 tions, environmental filters, and dispersal limitation as drivers of species co-occurrence.  
689 *Ecography*, 41, 1233–1244.
- 690 DasGupta, A., Cai, T.T. & Brown, L.D. (2001). Interval Estimation for a Binomial  
691 Proportion. *Statistical Science*, 16, 101–133.
- 692 Diamond, J., Pimm, S.L. & Sanderson, J.G. (2015). The checkered history of checkerboard  
693 distributions: comment. *Ecology*, 96, 3386–3388.
- 694 Diamond, J.M. (1975). Assembly of species communities. In: *Ecology and Evolution of*  
695 *Communities* (eds. Cody, M.L. & Diamond, J.M.). Harvard Univ Press, Cambridge,  
696 Mass, pp. 342–444.
- 697 Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hi-  
698 jmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L.,  
699 A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Over-  
700 ton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R.,  
701 E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M. & E. Zimmermann, N. (2006).  
702 Novel methods improve prediction of species’ distributions from occurrence data. *Ecog-*  
703 *raphy*, 29, 129–151.
- 704 Faisal, A., Dondelinger, F., Husmeier, D. & Beale, C.M. (2010). Inferring species in-  
705 teraction networks from species abundance data: A comparative evaluation of various  
706 statistical and machine learning methods. *Ecological Informatics*, 5, 451–464.
- 707 Faust, K. & Raes, J. (2012). Microbial interactions: From networks to models. *Nature*  
708 *Reviews Microbiology*, 10, 538–550.
- 709 Forbes, S. (1907). *On the Local Distribution of Certain Illinois Fishes: An Essay in*  
710 *Statistical Ecology*. No. v. 7, no. 8 in Bulletin of the Illinois State Laboratory of Natural  
711 History. Illinois State Laboratory of Natural History.

- 712 Freilich, M.A., Wieters, E., Broitman, B.R., Marquet, P.A. & Navarrete, S.A. (2018).  
713 Species co-occurrence networks: Can they reveal trophic and non-trophic interactions  
714 in ecological communities? *Ecology*, 99, 690–699.
- 715 Godsoe, W., Franklin, J. & Blanchet, F.G. (2017). Effects of biotic interactions on  
716 modeled species' distribution can be masked by environmental gradients. *Ecology and*  
717 *Evolution*, 7, 654–664.
- 718 Gotelli, N.J. & Ellison, A.M. (2002). Assembly rules for New England ant assemblages.  
719 *Oikos*, 99, 591–599.
- 720 Gotelli, N.J. & Graves, G.R. (1996). *Null models in ecology*. Smithsonian Institution  
721 Press, Washington.
- 722 Gotelli, N.J., Graves, G.R. & Rahbek, C. (2010). Macroecological signals of species  
723 interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences*,  
724 107, 5030–5035.
- 725 Gotelli, N.J. & McCabe, D.J. (2002). Species co-occurrence: A meta-analysis of JM  
726 Diamond's assembly rules model. *Ecology*, 83, 2091–2096.
- 727 Gotelli, N.J. & Ulrich, W. (2010). The empirical Bayes approach as a tool to identify  
728 non-random species associations. *Oecologia*, 162, 463–477.
- 729 Gravel, D. & Massol, F. (2019). Toward a general theory of metacommunity ecology. *in*  
730 *review*.
- 731 Hanski, I. (1983). Coexistence of competitors in patchy environment. *Ecology*, 64, 493–  
732 500.
- 733 Harris, D.J. (2016). Inferring species interactions from co-occurrence data with Markov  
734 networks. *Ecology*, 97, 3308–3314.

- 735 Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G. & Körber, J.H. (2007). Biotic  
736 interactions improve prediction of boreal bird distributions at macro-scales. *Global*  
737 *Ecology and Biogeography*, 16, 754–763.
- 738 Holt, R.D. & Barfield, M. (2009). Trophic interactions and range limits: the diverse roles  
739 of predation. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1435–1442.
- 740 Hui, F.K. (2016). Boreal- Bayesian Ordination and Regression Analysis of Multivariate  
741 Abundance Data in R. *Methods in Ecology and Evolution*, 7, 744–750.
- 742 Jeschke, J.M. & Strayer, D.L. (2008). Usefulness of Bioclimatic Models for Studying  
743 Climate Change and Invasive Species. *Annals of the New York Academy of Sciences*,  
744 1134, 1–24.
- 745 Kaldhusdal, A., Brandl, R., Müller, J., Möst, L. & Hothorn, T. (2015). Spatio-  
746 phylogenetic multispecies distribution models. *Methods in Ecology and Evolution*, 6,  
747 187–197.
- 748 Kay, G.M., Tulloch, A., Barton, P.S., Cunningham, S.A., Driscoll, D.A. & Lindenmayer,  
749 D.B. (2017). Species co-occurrence networks show reptile community reorganization  
750 under agricultural transformation. *Ecography*.
- 751 Kopelke, J.P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S. & Roslin, T. (2017).  
752 Food-web structure of willow-galling sawflies and their natural enemies across Europe.  
753 *Ecology*, 98, 1730–1730.
- 754 Lane, P.W., Lindenmayer, D.B., Barton, P.S., Blanchard, W. & Westgate, M.J. (2014).  
755 Visualization of species pairwise associations: a case study of surrogacy in bird assem-  
756 blages. *Ecology and Evolution*, 4, 3279–3289.
- 757 Latimer, A.M., Banerjee, S., Sang, H., Mosher, E.S. & Silander, J.A. (2009). Hierarchical  
758 models facilitate spatial analysis of large data sets: a case study on invasive plant  
759 species in the northeastern United States. *Ecology Letters*, 12, 144–154.

- 760 Leach, K., Montgomery, W.I. & Reid, N. (2016). Modelling the influence of biotic factors  
761 on species distribution patterns. *Ecological Modelling*, 337, 96–106.
- 762 Leathwick, J.R. & Austin, M.P. (2001). Competitive interactions between tree species in  
763 New Zealand’s old-growth indigenous forests. *Ecology*, 82, 2560–2573.
- 764 Leibold, M.A. & Mikkelsen, G.M. (2002). Coherence, species turnover, and boundary  
765 clumping: elements of meta-community structure. *Oikos*, 97, 237–250.
- 766 Levins, R. (1969). Some demographic and genetic consequences of environmental het-  
767 erogeneity for biological control. *Bulletin of the Entomological Society of America*, 15,  
768 237–240.
- 769 Levy, R. & Borenstein, E. (2013). Metabolic modeling of species interaction in the human  
770 microbiome elucidates community-level assembly rules. *Proceedings of the National*  
771 *Academy of Sciences*, 110, 12804–12809.
- 772 Mandakovic, D., Rojas, C., Maldonado, J., Latorre, M., Travisany, D., Delage, E., Bi-  
773 houée, A., Jean, G., Díaz, F.P., Fernández-Gómez, B., Cabrera, P., Gaete, A., La-  
774 torre, C., Gutiérrez, R.A., Maass, A., Cambiazo, V., Navarrete, S.A., Eveillard, D. &  
775 González, M. (2018). Structure and co-occurrence patterns in microbial communities  
776 under acute environmental stress reveal ecological factors fostering resilience. *Scientific*  
777 *Reports*, 8.
- 778 McGill, B.J. (2010). Matters of Scale. *Science*, 328, 575–576.
- 779 Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.C., Thuiller, W., Araújo, M.B.,  
780 Guisan, A. & Zimmermann, N.E. (2010). Biotic and abiotic variables show little re-  
781 dundancy in explaining tree species distributions. *Ecography*, 33, 1038–1048.
- 782 Michael, E.L. (1920). Marine Ecology and the Coefficient of Association: A Plea in Behalf  
783 of Quantitative Biology. *The Journal of Ecology*, 8, 54.

- 784 Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic  
785 interactions from proxies. *Trends in Ecology & Evolution*, 30, 347–356.
- 786 Morueta-Holme, N., Blonder, B., Sandel, B., McGill, B.J., Peet, R.K., Ott, J.E., Violle,  
787 C., Enquist, B.J., Jørgensen, P.M. & Svenning, J.C. (2016). A network approach for  
788 inferring species associations from co-occurrence data. *Ecography*, 39, 1139–1150.
- 789 Ovaskainen, O., Abrego, N., Halme, P. & Dunson, D. (2016). Using latent variable models  
790 to identify large networks of species-to-species associations at different spatial scales.  
791 *Methods in Ecology and Evolution*, 7, 549–555.
- 792 Ovaskainen, O., Hottola, J. & Siitonen, J. (2010). Modeling species co-occurrence by mul-  
793 tivariate logistic regression generates new hypotheses on fungal interactions. *Ecology*,  
794 91, 2514–2521.
- 795 Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson,  
796 D., Roslin, T. & Abrego, N. (2017). How to make more out of community data? A  
797 conceptual framework and its implementation as models and software. *Ecology Letters*,  
798 20, 561–576.
- 799 Patterson, B.D. & Atmar, W. (1986). Nested subsets and the structure of insular mam-  
800 malian faunas and archipelagos. *Biological Journal of the Linnean Society*, 28, 65–82.
- 801 Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the  
802 distribution of species: are bioclimate envelope models useful? *Global Ecology and*  
803 *Biogeography*, 12, 361–371.
- 804 Pielou, D. & Pielou, E. (1967). The detection of different degrees of coexistence. *Journal*  
805 *of Theoretical Biology*, 16, 427–437.
- 806 Pielou, D.P. & Pielou, E.C. (1968). Association among species of infrequent occurrence:  
807 the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *Journal of Theo-*  
808 *retical Biology*, 21, 202–216.

- 809 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: why ecological interaction  
810 networks vary through space and time. *Oikos*, 124, 243–251.
- 811 Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O’Hara, R.B., Parris, K.M., Vesk,  
812 P.A. & McCarthy, M.A. (2014). Understanding co-occurrence by modelling species  
813 simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology  
814 and Evolution*, 5, 397–406.
- 815 Popovic, G.C., Warton, D.I., Thomson, F.J., Hui, F.K.C. & Moles, A.T. (2019). Untan-  
816 gling direct species associations from indirect mediator species effects with graphical  
817 models. *Methods in Ecology and Evolution*, 10, 1571–1583.
- 818 Presley, S.J., Higgins, C.L. & Willig, M.R. (2010). A comprehensive framework for the  
819 evaluation of metacommunity structure. *Oikos*, 119, 908–917.
- 820 Rocca, J.D., Simonin, M., Blaszczyk, J.R., Ernakovich, J.G., Gibbons, S.M., Midani,  
821 F.S. & Washburne, A.D. (2019). The Microbiome Stress Project: Toward a Global  
822 Meta-Analysis of Environmental Stressors and Their Effects on Microbial Communities.  
823 *Frontiers in Microbiology*, 9.
- 824 le Roux, P.C., Lenoir, J., Pellissier, L., Wisz, M.S. & Luoto, M. (2013). Horizontal,  
825 but not vertical, biotic interactions affect fine-scale plant distribution patterns in a  
826 low-energy system. *Ecology*, 94, 671–682.
- 827 Russell, R., Wood, S., Allison, G. & Menge, B. (2006). Scale, Environment, and Trophic  
828 Status: The Context Dependency of Community Saturation in Rocky Intertidal Com-  
829 munities. *The American Naturalist*, 167, E158–E170.
- 830 Savage, J. & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags  
831 in vegetation change during 40 years of climate warming. *Ecography*, 38, 546–555.
- 832 Sfenthourakis, S., Tzanatos, E. & Giokas, S. (2006). Species co-occurrence: the case of  
833 congeneric species and a causal approach to patterns of species association. *Global  
834 Ecology and Biogeography*, 15, 39–49.

- 835 Staniczenko, P.P., Sivasubramaniam, P., Suttle, K.B. & Pearson, R.G. (2017). Link-  
836 ing macroecology and community ecology: refining predictions of species distributions  
837 using biotic interaction networks. *Ecology Letters*, 20, 693–707.
- 838 Steele, J.A., Countway, P.D., Xia, L., Vigil, P.D., Beman, J.M., Kim, D.Y., Chow, C.E.T.,  
839 Sachdeva, R., Jones, A.C., Schwalbach, M.S., Rose, J.M., Hewson, I., Patel, A., Sun,  
840 F., Caron, D.A. & Fuhrman, J.A. (2011). Marine bacterial, archaeal and protistan  
841 association networks reveal ecological linkages. *The ISME Journal*, 5, 1414–1425.
- 842 Stone, L. & Roberts, A. (1990). The checkerboard score and species distributions. *Oe-*  
843 *cologia*, 85, 74–79.
- 844 Teugels, J.L. (1990). Some representations of the multivariate Bernoulli and binomial  
845 distributions. *Journal of Multivariate Analysis*, 32, 256–268.
- 846 Thuiller, W., Pollock, L.J., Gueguen, M. & Münkemüller, T. (2015). From species distri-  
847 butions to meta-communities. *Ecology Letters*, 18, 1321–1328.
- 848 Thurman, L.L., Barner, A.K., Garcia, T.S. & Chestnut, T. (2019). Testing the link  
849 between species interactions and species co-occurrence in a trophic network. *Ecography*,  
850 42, 1658–1670.
- 851 Tulloch, A.I.T., Chadès, I., Dujardin, Y., Westgate, M.J., Lane, P.W. & Lindenmayer,  
852 D. (2016). Dynamic species co-occurrence networks require dynamic biodiversity sur-  
853 rogates. *Ecography*, 39, 1185–1196.
- 854 Ulrich, W. & Gotelli, N.J. (2013). Pattern detection in null model analysis. *Oikos*, 122,  
855 2–18.
- 856 Veech, J.A. (2013). A probabilistic model for analysing species co-occurrence: Probabilis-  
857 tic model. *Global Ecology and Biogeography*, 22, 252–260.
- 858 Veech, J.A. (2014). The pairwise approach to analysing species co-occurrence. *Journal*  
859 *of Biogeography*, 41, 1029–1035.

- 860 Warren, D.L., Cardillo, M., Rosauer, D.F. & Bolnick, D.I. (2014). Mistaking geography for  
861 biology: inferring processes from species distributions. *Trends in Ecology & Evolution*,  
862 29, 572–580.
- 863 Warton, D.I., Blanchet, F.G., O’Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C. &  
864 Hui, F.K. (2015). So Many Variables: Joint Modeling in Community Ecology. *Trends*  
865 *in Ecology & Evolution*, 30, 766–779.
- 866 Whittam, T.S. & Siegel-Causey, D. (1981). Species Interactions and Community Structure  
867 in Alaskan Seabird Colonies. *Ecology*, 62, 1515–1524.
- 868 Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dor-  
869 mann, C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A., Heikkinen, R.K., Høye,  
870 T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.C., Normand, S., Öckinger, E.,  
871 Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P. & Sven-  
872 ning, J.C. (2013). The role of biotic interactions in shaping distributions and realised  
873 assemblages of species: implications for species distribution modelling. *Biological Re-*  
874 *views*, 88, 15–30.
- 875 Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001). Viewing invasive species removal in  
876 a whole-ecosystem context. *Trends in Ecology & Evolution*, 16, 454–459.
- 877 Zelezniak, A., Andrejev, S., Ponomarova, O., Mende, D.R., Bork, P. & Patil, K.R. (2015).  
878 Metabolic dependencies drive species co-occurrence in diverse microbial communities.  
879 *Proceedings of the National Academy of Sciences*, 112, 6449–6454.
- 880 Özesmi, S.L. & Özesmi, U. (1999). An artificial neural network approach to spatial  
881 habitat modelling with interspecific interaction. *Ecological Modelling*, 116, 15–31.
- 882 Šidák, Z. (1967). Rectangular Confidence Regions for the Means of Multivariate Normal  
883 Distributions. *Journal of the American Statistical Association*, 62, 626–633.



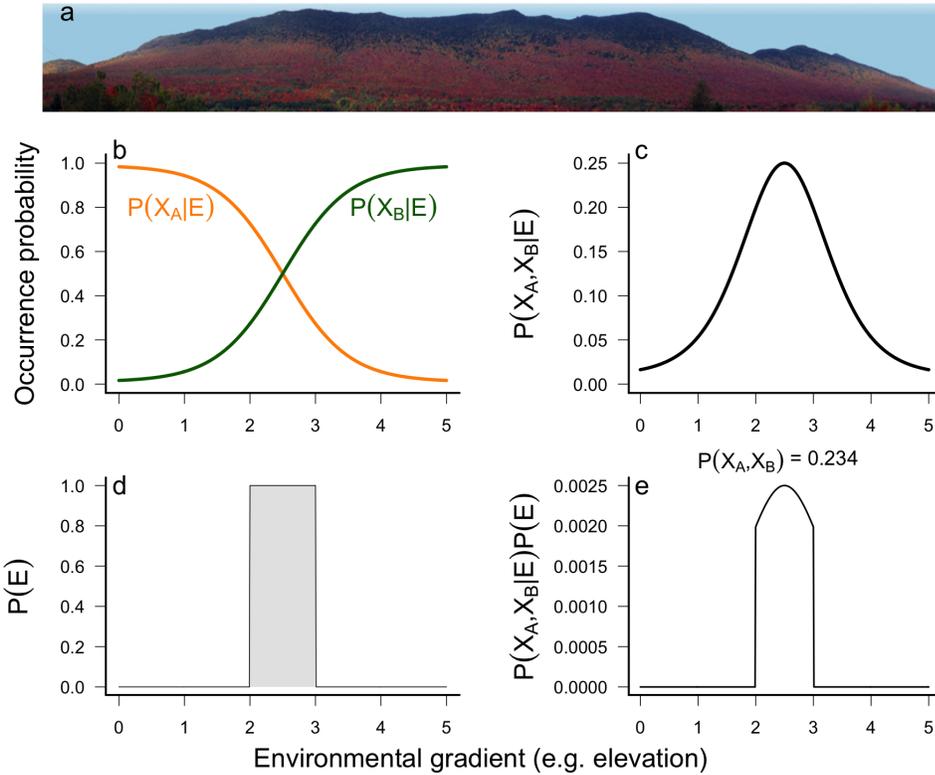


Figure 1: Species co-occurrences may depend on the abiotic environment. (a) Picture of Mont Mégantic taken in fall showing spatial repulsion between conifers (dark green) and deciduous (red, orange and yellow) trees. The zone where tree species co-occurrence is caused by the elevation gradient and does not represent interaction among species *per se* Savage & Vellend (2015). (b) Occurrence probability of species A (orange) and B (green) along an environmental gradient (abscissa). Assuming the environmental gradient presents the full elevation of Mont Mégantic, A is a typical deciduous species while B is a typical coniferous species, then panel b conceptually depicts an elevation transect of the picture in panel a. (c) Co-occurrence probability of finding both A and B along the elevation gradient. Recall that species A and B are assumed independent and as such this is the conditional probability resulting from Equation (3). (d-f) Three contrasting environmental gradients. (g-i) Product of the scenarios in panels d-f with the conditional probability of co-occurrence presented in panel c for the two species of panel b. The marginal probability of co-occurrence for A and B is at the top of each respective panel.

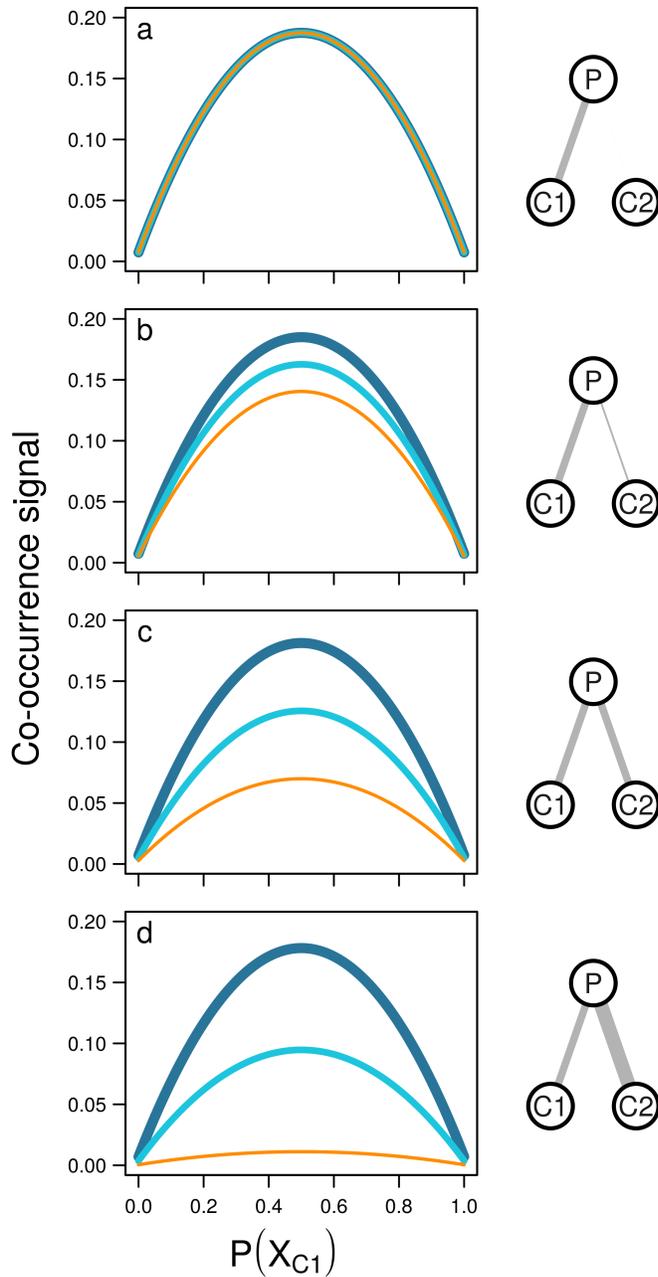


Figure 2: Co-occurrence signal between a predator (P) and two consumers (C1 and C2). The co-occurrence signal is the departure of the co-occurrence from random expectations, i.e.  $P(X_P, X_{C1}) - P(X_P)P(X_{C1})$ . It is computed along the gradient made by the occurrence probabilities of consumer C1 ( $P(X_{C1})$ ) while the occurrence probabilities of consumer C2 remain constant at  $P(X_{C2}) = 0.05$  (dark blue),  $P(X_{C2}) = 0.5$  (light blue) and  $P(X_{C2}) = 0.95$  (orange). In (a) P and C2 are independent and thus  $P(P|C2) = P(P)P(C2)$ , for the three other panels, this probability increases: 0.2 (b), 0.75 (c) and 0.95 (d). The interaction between P and C1 remains constant with a value of 0.75 for all panels.

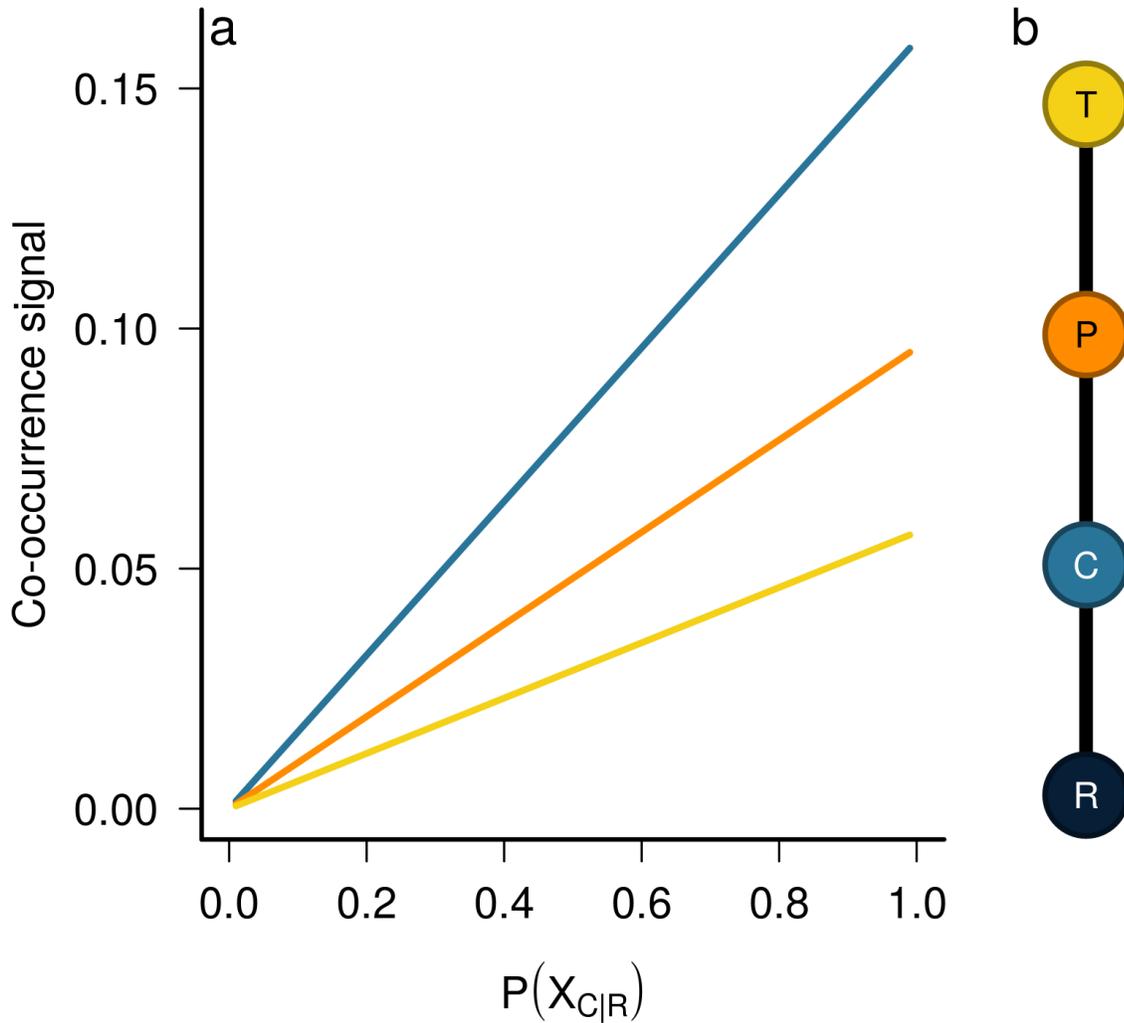


Figure 3: Significant spatial associations can emerge from indirect interactions. Three co-occurrence signals quantifying the association between species in the food chain and the resource species are computed for an increasing association between a resource and its consumer for a linear chain of four species (b) including a resource R, a consumer C, a predator P and a top predator T. The co-occurrence signals are calculated as follows:  $P(X_{R,C}) - P(X_R)P(X_C)$  (blue line),  $P(X_{R,P}) - P(X_R)P(X_P)$  (orange line) and  $P(X_{R,T}) - P(X_R)P(X_T)$  (yellow line).

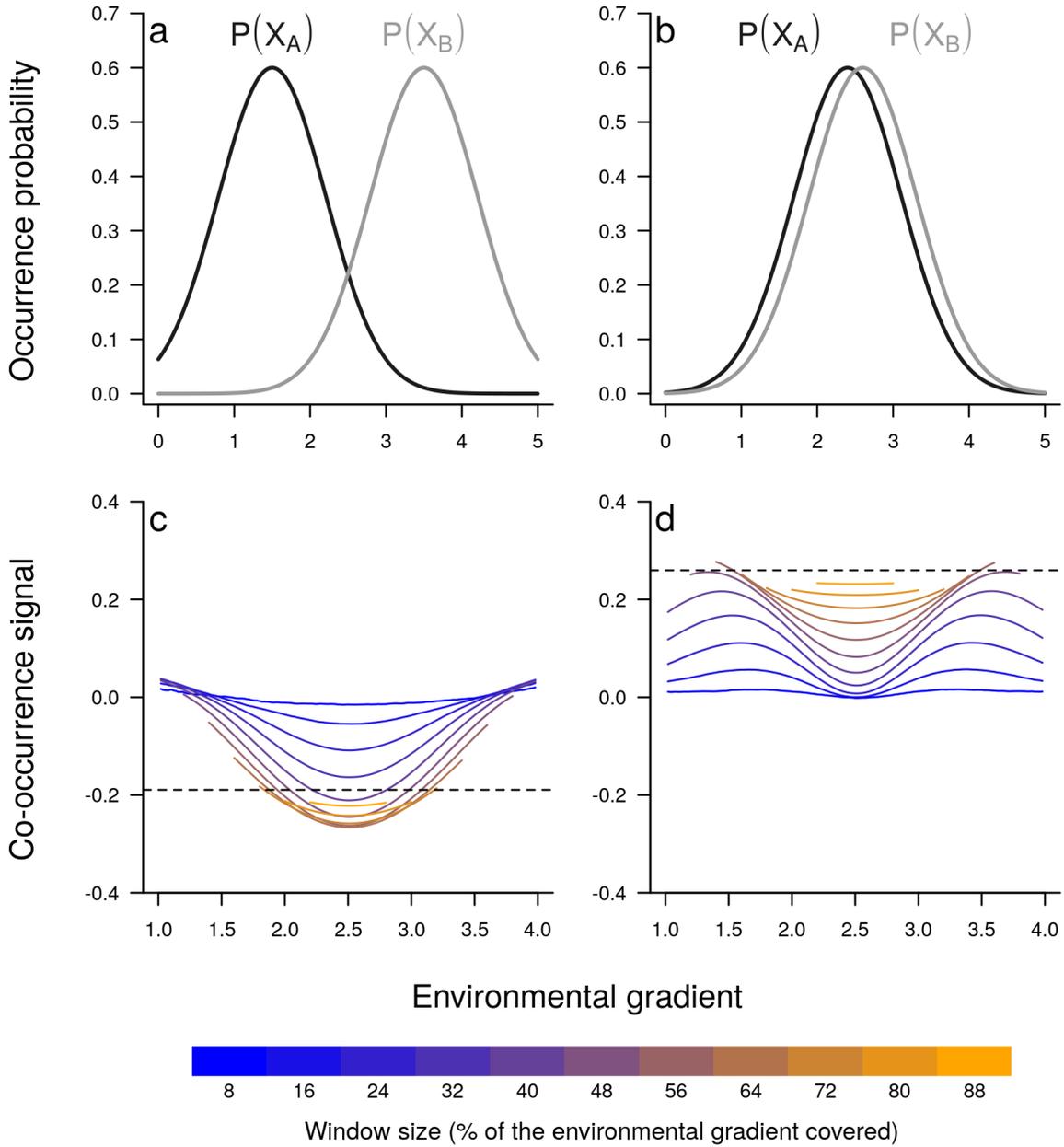


Figure 4: Co-occurrence signal and sampling scale. Top panels describe the occurrence probabilities along an environmental gradient of the independent species A and B in two contrasting scenarios. In (a) species occur in different abiotic conditions whereas in (b) they share very similar environmental requirements. The corresponding bottom panels represent co-occurrence signals (measured as a correlation between simulated occurrences) along the environmental gradient using moving windows of different sizes as the sampling area considered to assess co-occurrence structure. Dotted lines represent the correlation computed over the entire gradient. Note that correlations are used to measure co-occurrence signals.

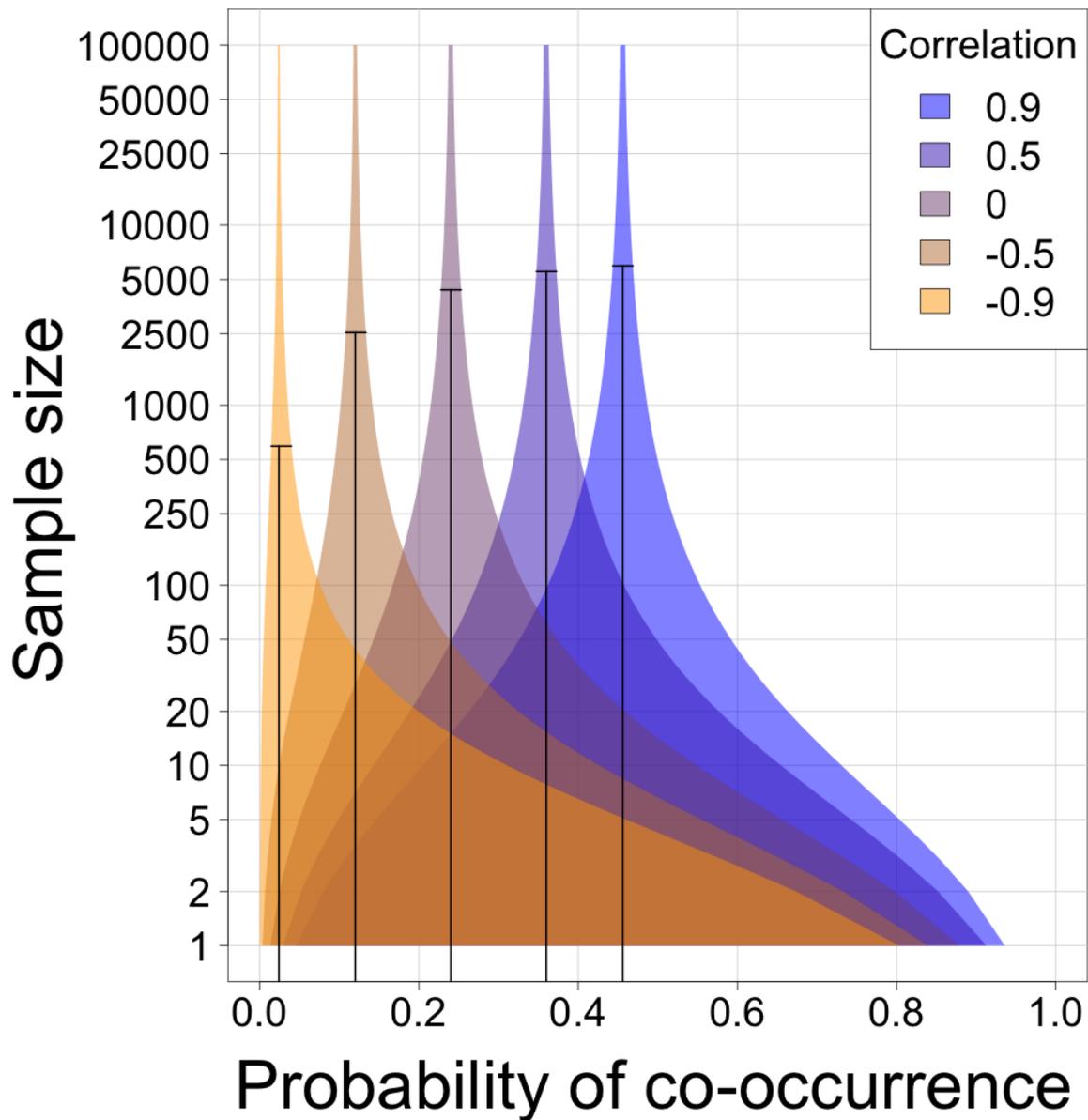


Figure 5: Co-occurrence signal and sample size. Estimated confidence intervals (coloured envelopes) given a specific sample size for a pair of species presenting different levels of correlation. The probability of occurrence for the two species is 0.4 and 0.6. As such, the probabilities of co-occurrence varied depending on the correlation levels. The true probabilities of co-occurrence are illustrated by black vertical lines. The short horizontal black lines in each envelope highlight the number of samples required to reach a 95% level of confidence in the estimated co-occurrence. The calculation of the confidence intervals were performed using the Wilson scores intervals, which have been shown to be accurate and robust (DasGupta *et al.*, 2001). To calculate the number of samples required to reach a 95% level of confidence, we applied a Dunn-Sidak correction (Šidák, 1967) because two species were used to compute the co-occurrence probability.

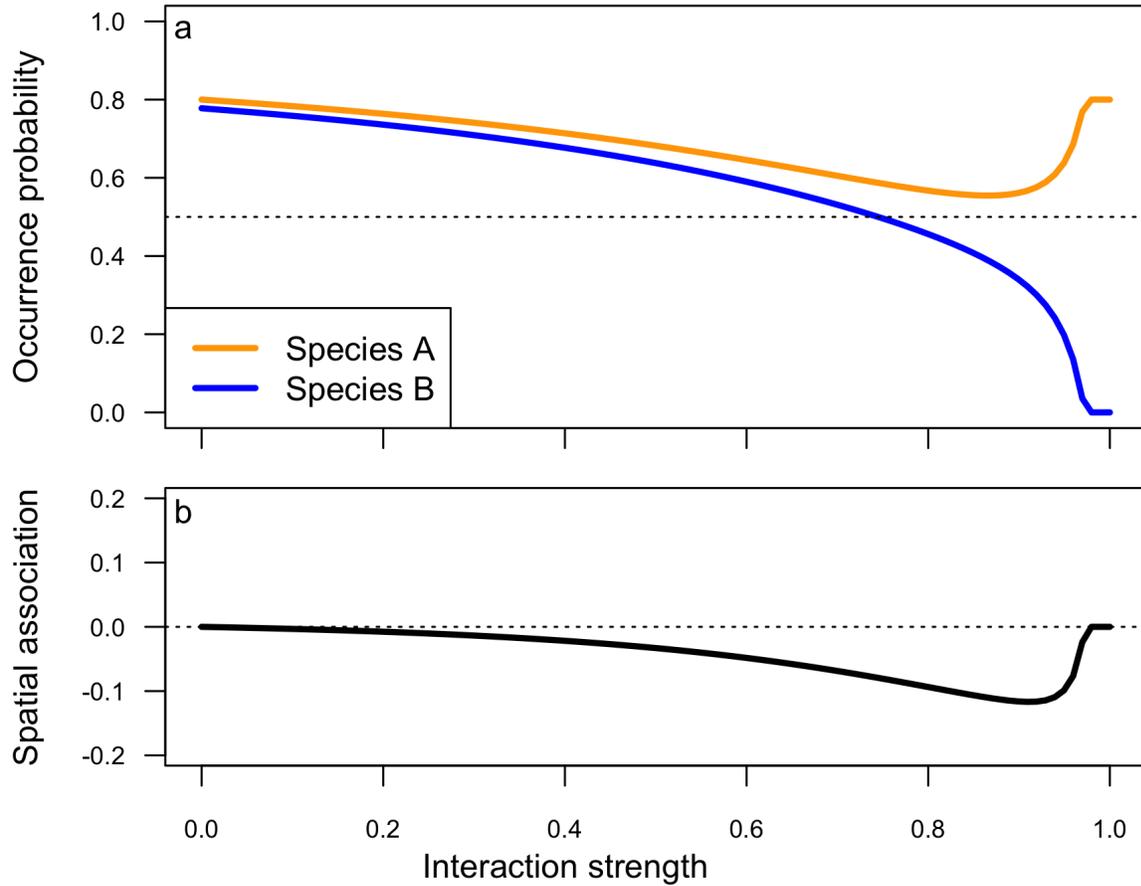


Figure 6: Co-occurrence signal and interaction strength in a metacommunity model (see Gravel & Massol (2019) for model specification). Competition for space between two species in a metacommunity impact regional occurrence (a) and co-occurrence (b). Increasing interaction strength reduces the occurrence of both species, up to the point where the weak competitor (species B, blue) is regionally extinct and the strong competitor (species A, orange) reaches its regional capacity. The strength of co-occurrence relative to the random expectation increases with interaction strength, but is hardly detectable because of a coincident reduction in the frequency of co-occurrence.