

1 *Running head:* Species interactions in Markov networks

2 **Title:** Estimating species interactions from observational data with Markov
3 networks

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5 **Abstract**

6 Inferring species interactions from observational data is one of the most controversial tasks in
7 community ecology. One difficulty is that a single pairwise interaction can ripple through an
8 ecological network and produce surprising indirect consequences. For example, two
9 competing species would ordinarily correlate negatively in space, but this effect can be
10 reversed in the presence of a third species that is capable of outcompeting both of them
11 when it is present. Here, I apply models from statistical physics, called Markov networks or
12 Markov random fields, that can predict the direct and indirect consequences of any possible
13 species interaction matrix. Interactions in these models can be estimated from observational
14 data via maximum likelihood. Using simulated landscapes with known pairwise interaction
15 strengths, I evaluated Markov networks and several existing approaches. The Markov
16 networks consistently outperformed other methods, correctly isolating direct interactions
17 between species pairs even when indirect interactions or abiotic environmental effects largely
18 overpowered them. A linear approximation, based on partial covariances, also performed well
19 as long as the number of sampled locations exceeded the number of species in the data.
20 Indirect effects reliably caused a common null modeling approach to produce incorrect
21 inferences, however.

22 **Key words:** Ecological interactions; Occurrence data; Species associations; Markov network;
23 Markov random field; Ising model; Biogeography; Presence–absence matrix; Null model

24 ***Introduction***

25 If nontrophic species interactions, such as competition, are important drivers of community
26 assembly, then ecologists might expect to see their influence in our data sets (MacArthur
27 1958, Diamond 1975). Despite decades of work and several major controversies, however
28 (Lewin 1983, Strong et al. 1984, Gotelli and Entsminger 2003, Connor et al. 2013), existing
29 methods for detecting competition's effects on community structure are unreliable (Gotelli
30 and Ulrich 2009), and thus important ecological processes remain poorly understood. More
31 generally, it can be difficult to reason about the complex web of direct and indirect species
32 interactions in real assemblages, especially when these interactions occur against a
33 background of other ecological processes such as dispersal limitation and environmental
34 filtering (Connor et al. 2013). For this reason, it isn't always clear what kinds of patterns
35 would even constitute evidence of competition, as opposed to some other biological process
36 or random sampling error (Lewin 1983, Roughgarden 1983).

37 Most existing methods in this field compare the frequency with which two putative
38 competitors are observed to co-occur, versus the frequency that would be expected if *all*
39 species on the landscape were independent (Strong et al. 1984, Gotelli and Ulrich 2009).
40 Examining a species pair against such a "null" background, however, rules out the possibility
41 that the overall association between two species could be driven by an outside force. For
42 example, even though the two shrub species in Figure 1 compete with one another for
43 resources at a mechanistic level, they end up clustering together on the landscape because
44 they both grow best in areas that are not overshadowed by trees. If this sort of effect is
45 common, then significant deviations from independence will not generally provide convincing
46 evidence of species' direct effects on one another.

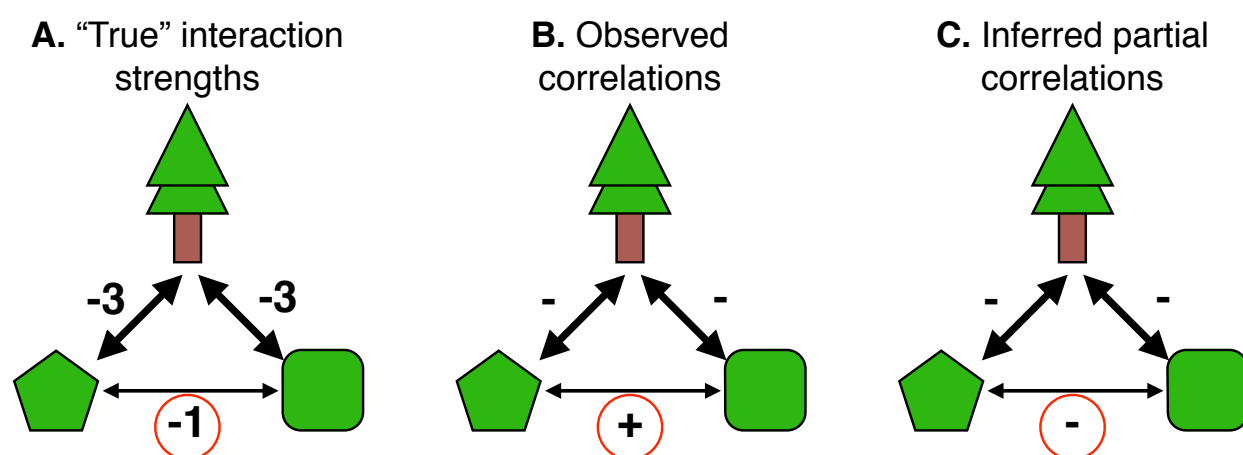


Figure 1: **A.** A small network of three competing species. The tree (top) tends not to co-occur with either of the two shrub species, as indicated by the strongly negative coefficient linking them. The two shrub species also compete with one another, as indicated by their negative coefficient (circled), but this effect is substantially weaker. **B.** In spite of the competitive interactions between the two shrub species, their shared tendency to occur in locations without trees makes their occurrence vectors positively correlated (circled). **C.** Controlling for the tree species' presence with a conditional method such as a partial covariance or a Markov network allows us to correctly identify the negative interaction between these two species (circled).

47 While competition between the two shrubs in the previous example does not leave the
48 commonly-expected pattern in community structure (negative association at the landscape
49 level), it nevertheless does leave a signal in the data (Figure 1C). Specifically, *among shaded*
50 *sites*, there will be a deficit of co-occurrences, and *among unshaded sites*, there will also be
51 such a deficit.

52 In this paper, I introduce Markov networks (undirected graphical models also known as
53 Markov random fields; Murphy 2012) as a framework for understanding the landscape-level
54 consequences of pairwise species interactions, and for detecting them with observational data.
55 Markov networks, which generalize partial correlations to non-Gaussian data (Lee and Hastie
56 2012, Loh and Wainwright 2013), have been used in many scientific fields for decades to
57 model associations between various kinds of “particles”. For example, a well-studied network
58 named the Ising model has played an important role in our understanding of physics (where
59 nearby particles tend to align magnetically with one another; Cibra 1987). In spatial
60 contexts, these models have been used to describe interactions between adjacent grid cells
61 (Harris 1974, Gelfand et al. 2005). In neurobiology, they have helped researchers determine
62 which neurons are connected to one another by modeling the structure in their firing
63 patterns (Schneidman et al. 2006). Following recent work by Azaele et al. (2010) and Fort
64 (2013), I suggest that ecologists could similarly treat species as the interacting particles in
65 the same modeling framework. Doing so would allow ecologists to simulate and study the
66 landscape-level consequences of arbitrary species interaction matrices, even when our
67 observations are not Gaussian. While ecologists explored some related approaches in the
68 1980’s (Whittam and Siegel-Causey 1981), computational limitations had previously imposed
69 severe approximations that produced unintelligible results (e.g. “probabilities” greater than

70 one; Gilpin and Diamond 1982). Now that it is computationally feasible to fit these models
71 exactly, the approach has become worth a second look.

72 The rest of the paper proceeds as follows. First, I discuss how Markov networks operate and
73 how they can be used to simulate landscape-level data or to predict the direct and indirect
74 consequences of possible interaction matrices. Then, using simulated data sets where the
75 “true” ecological structure is known, I compare this approach with several existing methods
76 for detecting species interactions. Finally, I discuss opportunities for extending the approach
77 presented here to larger problems in community ecology.

78 ***Methods***

79 ***Conditional relationships and Markov networks.*** Ecologists are often interested in
80 inferring direct interactions between species, controlling for the indirect influence of other
81 species. In statistical terms, this implies that ecologists want to estimate *conditional*
82 (“all-else-equal”) relationships, rather than *marginal* (“overall”) relationships. The most
83 familiar conditional relationship is the partial correlation, which indicates the portion of the
84 sample correlation between two species that remains after controlling for other variables in
85 the data set (Albrecht and Gotelli 2001). The example with the shrubs and trees in Figure 1
86 shows how the two correlation measures can have opposite signs, and suggests that the
87 partial correlation is more relevant for drawing inferences about species interactions
88 (e.g. competition). Markov networks extend this approach to non-Gaussian data, much as
89 generalized linear models do for linear regression (Lee and Hastie 2012).

90 Markov networks give a probability value for every possible combination of presences and
91 absences in communities. For example, given a network with binary outcomes (i.e. 0 for
92 absence and 1 for presence), the relative probability of observing a given presence-absence

93 vector, \vec{y} , is given by

$$p(\vec{y}; \alpha, \beta) \propto \exp\left(\sum_i \alpha_i y_i + \sum_{i \neq j} \beta_{ij} y_i y_j\right).$$

94 Here, α_i is an intercept term determining the amount that the presence of species i
95 contributes to the log-probability of \vec{y} ; it directly controls the prevalence of species i .
96 Similarly, β_{ij} is the amount that the co-occurrence of species i and species j contributes to
97 the log-probability; it controls the probability that the two species will be found together
98 (Figure 2A, Figure 2B). β thus acts as an analog of the partial covariance, but for
99 non-Gaussian networks. Because the relative probability of a presence-absence vector
100 increases when positively-associated species co-occur and decreases when
101 negatively-associated species co-occur, the model tends to produce assemblages that have
102 many pairs of positively-associated species and relatively few pairs of negatively-associated
103 species (exactly as an ecologist might expect).

104 A major benefit of Markov networks is the fact that the conditional relationships between
105 species can be read directly off the matrix of β coefficients (Murphy 2012). For example, if
106 the coefficient linking two mutualist species is $+2$, then—all else equal—the odds of
107 observing either species increase by a factor of e^2 when its partner is present (Murphy 2012).
108 Of course, if all else is *not* equal (e.g. Figure 1, where the presence of one competitor is
109 associated with release from another competitor), then species' marginal association rates
110 can differ from this expectation. For this reason, it is important to consider how coefficients'
111 effects propagate through the network, as discussed below.

112 Estimating the marginal relationships predicted by a Markov network is more difficult than

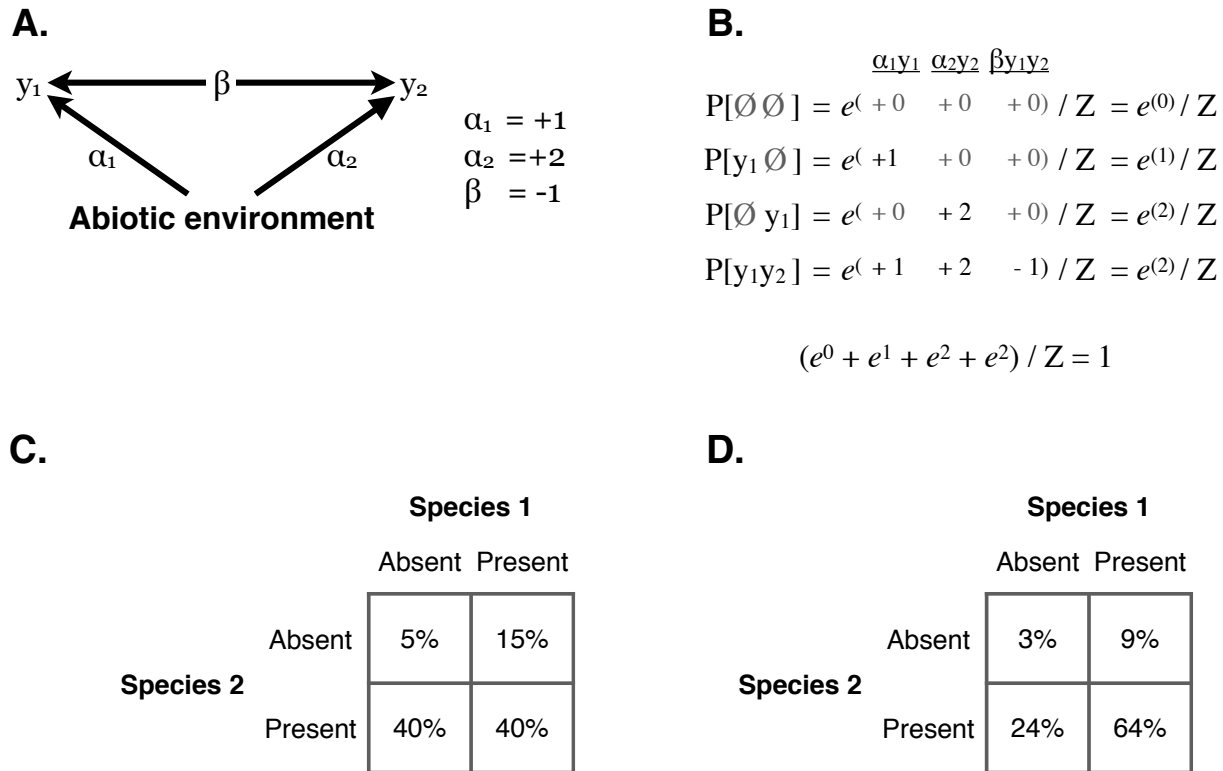


Figure 2: **A.** A small Markov network with two species. The depicted abiotic environment favors the occurrence of both species ($\alpha > 0$), particularly species 2 ($\alpha_2 > \alpha_1$). The negative β coefficient linking these two species implies that they co-occur less than expected under independence. **B.** Relative probabilities of all four possible presence-absence combinations for Species 1 and Species 2. The exponent includes α_1 whenever Species 1 is present ($y_1 = 1$), but not when it is absent ($y_1 = 0$). Similarly, the exponent includes α_2 only when species 2 is present ($y_2 = 1$), and β only when both are present ($y_1 y_2 = 1$). The normalizing constant Z , ensures that the four relative probabilities sum to 1. In this case, Z is about 18.5. **C.** Using the probabilities, we can find the expected frequencies of all possible co-occurrence patterns between the two species of interest. **D.** If β equaled zero (e.g. if the species no longer competed for the same resources), then the reduction in competition would allow each species to increase its occurrence rate and the deficit of co-occurrences would be eliminated.

113 estimating conditional relationships, because doing so requires absolute probability estimates.
114 Turning the relative probability given by Equation 1 into an absolute probability entails
115 scaling by a *partition function*, $Z(\alpha, \beta)$, which is defined so that that the probabilities of all
116 possible assemblages that could be produced by the model sum to one (bottom of Figure
117 2B). Calculating $Z(\alpha, \beta)$ exactly, as is done in this paper, quickly becomes infeasible as the
118 number of species increases: with 2^N possible assemblages of N species, the number of
119 bookkeeping operations required for exact inference spirals exponentially into the billions
120 and beyond. Numerous techniques are available for working with Markov networks that keep
121 the computations tractable, e.g. via analytic approximations (Lee and Hastie 2012) or Monte
122 Carlo sampling (Salakhutdinov 2008), but they are beyond the scope of this paper.

123 ***Simulations.*** In order to compare different methods for drawing inferences from
124 observational data, I simulated two sets of landscapes using known parameters.
125 The first set of simulated landscapes included the three competing species shown in Figure 1.
126 For each of 1000 replicates, I generated a landscape with 100 sites by sampling exactly from
127 a probability distribution defined by the interaction coefficients in that figure (Appendix A).
128 Each of the methods described below (a Markov network, two correlation-based methods and
129 a null model) was then evaluated on its ability to correctly infer that the two shrub species
130 competed with one another, despite their frequent co-occurrence.

131 I also simulated a second set of landscapes with five, ten, or twenty potentially-interacting
132 species on landscapes composed of 20, 100, 500, or 2500 observed communities (24 replicate
133 simulations for each combination; Appendix B). These simulated data sets span the range
134 from small, single-observer data sets to large collaborative efforts such as the North
135 American Breeding Bird Survey. As described in Appendix B, I randomly drew the “true”

136 coefficient values for each replicate so that most species pairs interacted negligibly, a few
137 pairs interacted very strongly, and competition was three times more common than
138 facilitation. I then used Gibbs sampling to randomly generate replicate landscapes with
139 varying numbers of species and sites (Appendix B). For half of the simulated landscapes, I
140 treated each species' α coefficient as a constant, as described above. For the other half, I
141 treated the α coefficients as linear functions of two abiotic environmental factors that varied
142 from location to location across the landscape (Appendix B). The latter set of simulated
143 landscapes provide an important test of the methods' ability to distinguish co-occurrence
144 patterns that were generated from pairwise biotic interactions from those that were generated
145 by external forces like abiotic environmental filtering. This task was made especially difficult
146 because—as with most analyses of presence-absence data for co-occurrence patterns—the
147 inference procedure did not have access to any information about the environmental or
148 spatial variables that helped shape the landscape (cf Connor et al. 2013, Blois et al. 2014).

149 ***Inferring α and β coefficients from presence-absence data.*** In the previous two
150 sections, the values of α and β were known. In practice, however, ecologists will often need
151 to estimate these parameters from co-occurrence data. When the number of species is
152 reasonably small, one can compute exact maximum likelihood estimates for all of the α and
153 β coefficients by optimizing $p(\vec{y}; \alpha, \beta)$. Fully-observed Markov networks like the ones
154 considered here have unimodal likelihood surfaces (Murphy 2012), ensuring that this
155 procedure will always converge on the global maximum. This maximum is the unique
156 combination of α and β coefficients that would be expected to produce exactly the observed
157 co-occurrence frequencies. For the analyses in this paper, I used the *rosalia* package (Harris
158 2015a) for the R programming language (R Core Team 2015) to define the objective function

159 and gradient as R code. The *rosalia* package then uses the BFGS method in R's `optim`
160 function to find the best values for α and β .

161 For analyses with 5 or more species, I made a small modification to the maximum likelihood
162 procedure described above. Given the large number of parameters associated with some of
163 the networks to be estimated, I regularized the likelihood using a logistic prior distribution
164 (Gelman et al. 2008) with a scale of 1 on the α and β terms.

165 ***Other inference techniques for comparison.*** After fitting Markov networks to the
166 simulated landscapes described above, I used several other techniques for inferring the sign
167 and strength of marginal associations between pairs of species (Appendix B).

168 The first two alternative interaction measures were the sample covariances and the partial
169 covariances between each pair of species' data vectors on the landscape (Albrecht and Gotelli
170 2001). Because partial covariances are undefined for landscapes with perfectly-correlated
171 species pairs, I used a regularized estimate based on ridge regression [Wieringen and Peeters
172 (2014); i.e. linear regression with a Gaussian prior]. For these analyses, I set the ridge
173 parameter to 0.2 divided by the number of sites on the landscape.

174 The third alternative method, described in Gotelli and Ulrich (2009), involved simulating
175 possible landscapes from a null model that retains the row and column sums of the original
176 matrix (Strong et al. 1984). Using the default options in the Pairs software described in
177 Gotelli and Ulrich (2009), I simulated the null distribution of scaled C-scores (a test statistic
178 describing the number of *non-co-occurrences* between two species). The software then
179 calculated a Z statistic for each species pair using this null distribution. After multiplying
180 this statistic by -1 so that positive values corresponded to facilitation and negative values
181 corresponded to competition, I used it as another estimate of species interactions.

182 **Method evaluation.** For the simulated landscapes based on Figure 1, method evaluation
183 was fairly qualitative: any method whose test statistic for the two shrubs indicated a
184 negative relationship passed; other methods failed.

185 For the larger landscapes, I rescaled the four methods' estimates using linear regression
186 through the origin so that they all had a consistent interpretation. In each method, I
187 regressed the "true" β coefficient for each species pair against the model's estimate,
188 re-weighting the pairs so that each landscape contributed equally to the rescaled estimate.
189 These regressions yielded squared errors for each of the 23,140 simulated species pairs, across
190 all conditions and replicates. I then partitioned these errors into groups defined by the
191 properties of the simulated landscapes (i.e. species richness, number of observed
192 communities, and the presence/absence of environmental filtering). Within each partition,
193 the mean squared error was used to calculate the proportion of variance explained
194 (compared with a baseline model that assumed all interaction strengths to be zero).

195 **Results**

196 **Three species.** As shown in Figure 1, the marginal relationship between the two shrub
197 species was positive—despite their competition for space at a mechanistic level—due to
198 indirect effects of the dominant tree species. As a result, the covariance method falsely
199 reported positive associations for 94% of the simulated landscapes, and the
200 randomization-based null model falsely reported such associations 100% of the time. The two
201 methods for evaluating conditional relationships (Markov networks and partial covariances),
202 however, successfully controlled for the indirect pathway via the tree species and each
203 correctly identified the direct negative interaction between the shrubs 94% of the time.

204 **Larger landscapes.** The accuracy of the four evaluated methods varied substantially,

205 depending on the parameters that produced the simulated communities (Figure 3). In
206 general, however, there was a consistent ordering: overall, the Markov network explained
207 54% of the “true” parameters’ squared deviations from zero, followed by partial covariances
208 (33%), and sample covariances (22%). The null model scores initially explained only 12%.
209 After manually reducing the value of one especially strong outlier ($Z = 1004$, implying
210 $p < 10^{-1000000}$), this increased to 17% (Appendix B). Figure 3 reflects the adjusted version of
211 the results.

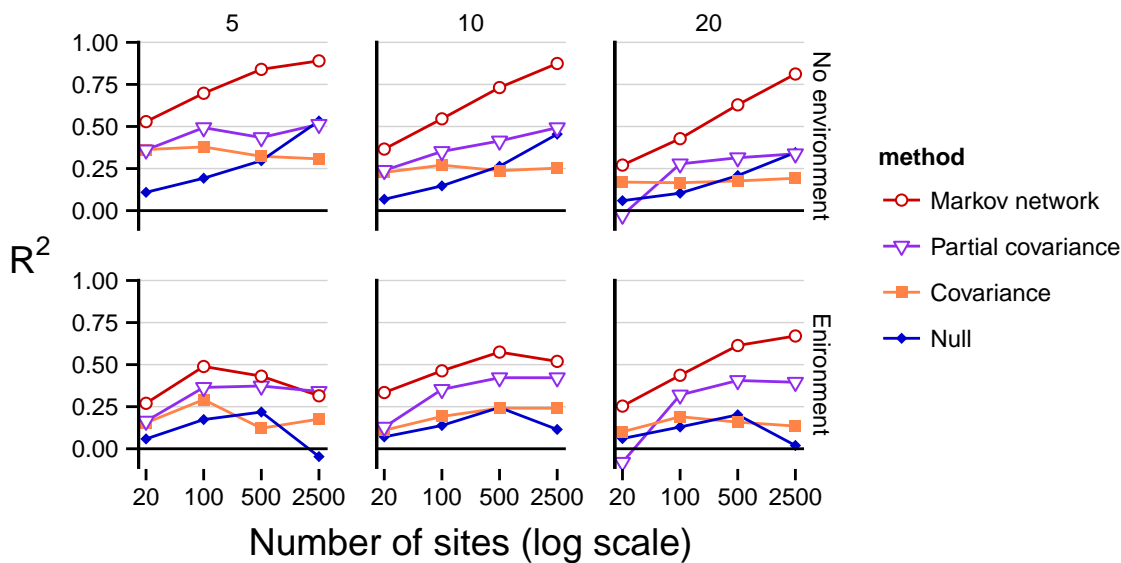


Figure 3: Proportion of variance in interaction coefficients explained by each method with 5, 10, or 20 species arrayed across varying numbers of sampled locations when environmental filtering was absent (top row) or present (bottom row). A negative R^2 values implies that the squared error associated with the corresponding subset of the predictions was larger than the error one would get from assuming that all coefficients equalled zero.

212 *Discussion*

213 The results presented above show that Markov networks can reliably recover species’ pairwise
214 interactions from observational data, even for cases where a common null modeling technique
215 reliably fails. Specifically, Markov networks were successful even when direct interactions
216 were largely overwhelmed by indirect effects (Figure 1) or environmental effects (lower panels

217 of Figure 3). For cases where fitting a Markov network is computationally infeasible, these
218 results also indicate that partial covariances—which can be computed straightforwardly by
219 linear regression—can often provide a surprisingly useful approximation. The partial
220 correlations’ success on simulated data may not carry over to real data sets, however; Loh
221 and Wainwright (2013) show that the linear approximations can be less reliable in cases
222 where the true interaction matrix contains more structure (e.g. guilds or trophic levels). On
223 the other hand, if ecologists are familiar enough with the natural history of their study
224 systems to describe this kind of structure as a prior distribution on the parameters or as a
225 penalty on the likelihood, then this information could reduce the effective degrees of freedom
226 to estimate and real-world results might be even better than those shown in Figure 3.

227 Ecologists will also need natural history to pin down the exact nature of the interactions
228 identified by a network model (e.g. which species in a positively-associated pair is facilitating
229 the other), particularly when real pairs of species can reciprocally influence one another in
230 multiple ways simultaneously (Bruno et al. 2003); the β coefficients in Markov networks
231 have to reduce this complexity to a single number. In short, partial correlations and Markov
232 networks both help prevent us from mistaking marginal associations for conditional ones, but
233 they can’t tell us the underlying biological mechanisms at work.

234 Despite these limitations, Markov networks have enormous potential to improve ecological
235 inferences. For example, Markov networks provide a simple answer to the question of how
236 competition should affect a species’ overall prevalence, which was a major flash point for the
237 null model debates in the 1980’s (Roughgarden 1983, Strong et al. 1984). Equation 1 can be
238 used to calculate the expected prevalence of a species in the absence of biotic influences
239 ($\frac{1}{1+e^{-\alpha}}$; Lee and Hastie 2012). Competition’s effect on prevalence in a Markov network can

240 then be calculated by subtracting this value and the observed prevalence (cf Figure 2D).

241 Markov networks—particularly the Ising model for binary networks—have been studied in
242 statistical physics for nearly a century (Cipra 1987), and the models’ properties, capabilities,
243 and limits are well-understood in a huge range of applications, from spatial statistics
244 (Gelfand et al. 2005) to neuroscience (Schneidman et al. 2006) to models of human behavior
245 (Lee et al. 2013). Modeling species interactions using the same framework would thus allow
246 ecologists to tap into an enormous set of existing discoveries and techniques for dealing with
247 indirect effects, stability, and alternative stable states (i.e. phase transitions; Cipra (1987)).

248 This modeling approach is also highly extensible, even when it is inconvenient to compute
249 the likelihood exactly. For example, the *mistnet* software package for joint species
250 distribution modeling (Harris 2015b) can fit *approximate* Markov networks to large species
251 assemblages (>300 species) while simultaneously modeling each species’ nonlinear response
252 to the abiotic environment. Combining multiple ecological processes into a common model
253 could help ecologists to disentangle different factors that can confound simpler co-occurrence
254 analyses (cf Connor et al. 2013). Numerous other extensions are possible: Markov networks
255 can be fit with a mix of discrete and continuous variables, for example (Lee and Hastie 2012).
256 There are even methods (Whittam and Siegel-Causey 1981, Tjelmeland and Besag 1998)
257 that would allow the coefficient linking two species in an interaction matrix to vary as a
258 function of the abiotic environment or of third-party species that tip the balance between
259 facilitation and exploitation (Bruno et al. 2003).

260 Finally, the results presented here have important implications for ecologists’ continued use
261 of null models to draw inferences about species interactions. Null and neutral models can be
262 very useful for clarifying our thinking about the numerical consequences of species’ richness

263 and abundance patterns (Harris et al. 2011, Xiao et al. 2015), but deviations from a null
264 model must be interpreted with care (Roughgarden 1983). In complex networks of ecological
265 interactions (and even in small networks with three species), it may simply not be possible
266 to implicate individual species pairs or specific ecological processes like competition by
267 rejecting a general-purpose null (Gotelli and Ulrich 2009). Estimating pairwise coefficients
268 directly seems like a much more promising approach: to the extent that the models' relative
269 performance on real data sets is similar to the range of results shown in Figure 3, scientists
270 in this field could easily double their explanatory power by switching from null models to
271 linear regression and partial covariances, or triple it by switching to a Markov network.

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277 ***References:***

278 Albrecht, M., and N. J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland
279 ants. *Oecologia* 126:134–141.

280 Azaele, S., R. Muneeppeerakul, A. Rinaldo, and I. Rodriguez-Iturbe. 2010. Inferring plant
281 ecosystem organization from species occurrences. *Journal of theoretical biology* 262:323–329.

282 Blois, J. L., N. J. Gotelli, A. K. Behrensmeier, J. T. Faith, S. K. Lyons, J. W. Williams, K.
283 L. Amatangelo, A. Bercovici, A. Du, J. T. Eronen, and others. 2014. A framework for
284 evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil
285 pollen associations across the late Quaternary. *Ecography* 37:1095–1108.

- 286 Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into
287 ecological theory. *Trends in Ecology & Evolution* 18:119–125.
- 288 Cipra, B. A. 1987. An introduction to the Ising model. *American Mathematical Monthly*
289 94:937–959.
- 290 Connor, E. F., M. D. Collins, and D. Simberloff. 2013. The checkered history of
291 checkerboard distributions. *Ecology* 94:2403–2414.
- 292 Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the
293 design of natural reserves. *Biological conservation* 7:129–146.
- 294 Fort, H. 2013. Statistical Mechanics Ideas and Techniques Applied to Selected Problems in
295 Ecology. *Entropy* 15:5237–5276.
- 296 Gelfand, A. E., A. M. Schmidt, S. Wu, J. A. Silander, A. Latimer, and A. G. Rebelo. 2005.
297 Modelling species diversity through species level hierarchical modelling. *Journal of the Royal*
298 *Statistical Society: Series C (Applied Statistics)* 54:1–20.
- 299 Gelman, A., A. Jakulin, M. G. Pittau, and Y.-S. Su. 2008. A Weakly Informative Default
300 Prior Distribution for Logistic and Other Regression Models. *The Annals of Applied*
301 *Statistics* 2:1360–1383.
- 302 Gilpin, M. E., and J. M. Diamond. 1982. Factors contributing to non-randomness in species
303 Co-occurrences on Islands. *Oecologia* 52:75–84.
- 304 Gotelli, N. J., and G. L. Entsminger. 2003. Swap algorithms in null model analysis.
305 *Ecology*:532–535.
- 306 Gotelli, N. J., and W. Ulrich. 2009. The empirical Bayes approach as a tool to identify
307 non-random species associations. *Oecologia* 162:463–477.

- 308 Harris, D. J. 2015a. Rosalia: Exact inference for small binary Markov networks. R package
309 version 0.1.0. Zenodo. <http://dx.doi.org/10.5281/zenodo.17808>.
- 310 Harris, D. J. 2015b. Generating realistic assemblages with a Joint Species Distribution
311 Model. *Methods in Ecology and Evolution*.
- 312 Harris, D. J., K. G. Smith, and P. J. Hanly. 2011. Occupancy is nine-tenths of the law:
313 Occupancy rates determine the homogenizing and differentiating effects of exotic species.
314 *The American naturalist* 177:535.
- 315 Harris, T. E. 1974. Contact Interactions on a Lattice. *The Annals of Probability* 2:969–988.
- 316 Lee, E. D., C. P. Broedersz, and W. Bialek. 2013. Statistical mechanics of the US Supreme
317 Court. arXiv:1306.5004 [cond-mat, physics:physics, q-bio].
- 318 Lee, J. D., and T. J. Hastie. 2012, May. Learning Mixed Graphical Models.
- 319 Lewin, R. 1983. Santa Rosalia Was a Goat. *Science* 221:636–639.
- 320 Loh, P.-L., and M. J. Wainwright. 2013. Structure estimation for discrete graphical models:
321 Generalized covariance matrices and their inverses. *The Annals of Statistics* 41:3022–3049.
- 322 MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous
323 forests. *Ecology* 39:599–619.
- 324 Murphy, K. P. 2012. *Machine Learning: A Probabilistic Perspective*. The MIT Press.
- 325 R Core Team. 2015. *R: A Language and Environment for Statistical Computing*. R
326 Foundation for Statistical Computing, Vienna, Austria.
- 327 Roughgarden, J. 1983. *Competition and Theory in Community Ecology*. The American
328 *Naturalist* 122:583–601.

- 329 Salakhutdinov, R. 2008. Learning and evaluating Boltzmann machines. Technical Report
330 UTML TR 2008-002, Department of Computer Science, University of Toronto, Dept. of
331 Computer Science, University of Toronto.
- 332 Schneidman, E., M. J. Berry, R. Segev, and W. Bialek. 2006. Weak pairwise correlations
333 imply strongly correlated network states in a neural population. *Nature* 440:1007–1012.
- 334 Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984. *Ecological communities:
335 Conceptual issues and the evidence*. Princeton University Press.
- 336 Tjelmeland, H., and J. Besag. 1998. Markov Random Fields with Higher-order Interactions.
337 *Scandinavian Journal of Statistics* 25:415–433.
- 338 Whittam, T. S., and D. Siegel-Causey. 1981. Species Interactions and Community Structure
339 in Alaskan Seabird Colonies. *Ecology* 62:1515–1524.
- 340 Wieringen, W. N. van, and C. F. Peeters. 2014. Ridge Estimation of Inverse Covariance
341 Matrices from High-Dimensional Data. arXiv preprint arXiv:1403.0904.
- 342 Xiao, X., D. J. McGlinn, and E. P. White. 2015. A strong test of the Maximum Entropy
343 Theory of Ecology. *The American Naturalist* 185:E70–E80.