

Running head: Species interactions in Markov networks

Title: Estimating species interactions from observational data with Markov networks

Author: David J. Harris: Population Biology; 1 Shields Avenue, Davis CA, 95616

Abstract: Estimating species interactions from observational data is one of the most controversial tasks in community ecology. One difficulty is that a single pairwise interaction can ripple through an ecological network and produce surprising indirect consequences. For example, two competing species would ordinarily correlate negatively in space, but this effect can be reversed in the presence of a third species that is capable of outcompeting both of them when it is present. Here, I apply models from statistical physics, called Markov networks or Markov random fields, that can predict the direct and indirect consequences of any possible species interaction matrix. Interactions in these models can be estimated from observational data via maximum likelihood. Using simulated landscapes with known pairwise interaction strengths, I evaluated Markov networks and several existing approaches. The Markov networks consistently outperformed other methods, correctly isolating direct interactions between species pairs even when indirect interactions or abiotic environmental effects largely overpowered them. Two computationally efficient approximations, based on linear and generalized linear models, also performed well. Indirect effects reliably caused a common null modeling approach to produce incorrect inferences, however.

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

22 Introduction

23 If nontrophic species interactions, such as competition, are important drivers of community
24 assembly, then ecologists might expect to see their influence in our data sets (MacArthur
25 1958, Diamond 1975). Despite decades of work and several major controversies, however
26 (Lewin 1983, Strong et al. 1984, Gotelli and Entsminger 2003, Connor et al. 2013), existing
27 methods for detecting competition's effects on community structure are unreliable (Gotelli
28 and Ulrich 2009). In particular, species' effects on one another can become lost in the
29 complex web of direct and indirect interactions in real assemblages. For example, the
30 competitive interaction between the two shrub species in Figure 1A can become obscured by
31 their shared tendency to occur in unshaded areas (Figure 1B). If this sort of effect is common,
32 then the vast majority of ecologists' methods, which rely on test statistics describing the
33 total number of co-occurrences or overall correlation between putatively interacting species
34 (Diamond 1975, Strong et al. 1984, Gotelli and Ulrich 2009, Veech 2013, Pollock et al. 2014)
35 will not generally provide much evidence regarding species' direct effects on one another.

36 While competition doesn't reliably leave the expected pattern in community structure
37 (a low co-occurrence rate at the landscape level), it nevertheless does leave a signal in the
38 data (Figure 1C). Specifically, *among shaded sites*, there will be a deficit of co-occurrences
39 between the competing shrub species, and *among unshaded sites*, there will also be such a
40 deficit. More generally, we can obtain much better estimates of the association between two
41 species from their conditional relationships (i.e. by controlling for other species in the
42 network) than we could get from their overall co-occurrence rates. This kind of precision is
43 difficult to obtain from null models, which begin with the assumptions that all the pairwise
44 interactions are zero and thus don't need to be controlled for. Nevertheless, null models have

dominated this field for more than three decades (Diamond 1975, Strong et al. 1984, Gotelli and Ulrich 2009).

In this paper, following recent work by Azaele et al. (2010) and Fort (2013), I show that Markov networks (undirected graphical models also known as Markov random fields; Murphy 2012) can provide a framework for understanding the landscape-level consequences of pairwise species interactions, and for detecting them from observed presence-absence matrices. Markov networks have been used in many scientific fields for decades in similar contexts, from physics (where nearby particles interact magnetically with one another; Cipra 1987) to spatial statistics (where adjacent grid cells interact with one another; Harris 1974, Gelfand et al. 2005). While community ecologists explored some related approaches in the 1980's (Whittam and Siegel-Causey 1981), computational limitations had previously imposed severe approximations that produced unintelligible results (e.g. “probabilities” greater than one; Gilpin and Diamond 1982). Now that it is computationally feasible to fit these models exactly, this kind of approach is worth a second look.

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

Methods

Conditional relationships and Markov networks. Ecologists are often interested in learning about direct interactions between species, controlling for the indirect influence of other species. In statistical terms, this implies that ecologists want to estimate *conditional* (“all-else-equal”) relationships, rather than *marginal* (“overall”) relationships. The example with the shrubs and trees in Figure 1 shows how the two measures can have opposite signs, and suggests that conditional relationships are more relevant for drawing inferences about species interactions (e.g. competition).

Markov networks define species interactions in conditional terms, and use these conditional relationships to determine whether a given combination of co-occurring species is consistent with their interactions. Given a set of binary outcomes for each species (i.e. 0 for absence and 1 for presence), the Markov network defines the relative probability of observing a given presence-absence vector, \vec{y} , as

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

Here, α_i is an intercept term determining the amount that the presence of species i contributes to the log-probability of \vec{y} ; it directly controls the prevalence of species i . Similarly, β_{ij} is the amount that the co-occurrence of species i and species j contributes to the log-probability; it controls the probability that the two species will be found together (Figure 2A, Figure 2B). Because the relative probability of a presence-absence vector increases when positively-associated species co-occur and decreases when negatively-associated species co-occur, the model tends to produce assemblages that have many pairs of positively-associated species and relatively few pairs of negatively-associated species (exactly as an ecologist might expect).

A major benefit of Markov networks is the fact that the conditional relationships between

species can be read directly off the matrix of β coefficients (Murphy 2012). For example, if the coefficient linking two mutualist species is +2, then—all else equal—the odds of observing either species increase by a factor of e^2 when its partner is present (Murphy 2012). In this way, the β coefficients behave very similarly to the coefficients in a logistic regression model (Lee and Hastie 2012).

Of course, if all else is *not* equal (e.g. Figure 1, where the presence of one competitor is associated with release from another competitor), then species’ marginal association rates can differ from this expectation. For this reason, it is important to consider how coefficients’ effects propagate through the network, as discussed below.

Estimating the marginal relationships predicted by a Markov network is more difficult than estimating conditional relationships, because doing so requires absolute probability estimates. Turning the relative probability given by Equation 1 into an absolute probability entails scaling by a normalizing constant, Z , so that the probabilities of all possible assemblages will sum to one (bottom of Figure 2B). Calculating Z exactly, as is done in these analyses, quickly becomes infeasible as the number of species increases: with 2^N possible assemblages of N species, the number of bookkeeping operations required spirals exponentially into the billions and beyond. Numerous techniques are available for keeping the calculations tractable, e.g. via analytic approximations (Lee and Hastie 2012) or Monte Carlo sampling (Salakhutdinov 2008), but they are beyond the scope of this paper. Alternatively, as noted below, some common linear and generalized linear methods can also be used as computationally efficient approximations to the full network.

Estimating α and β coefficients from presence-absence data. In the previous two sections, the values of α and β were known. In practice, however, ecologists will often need

to estimate these parameters from co-occurrence data (i.e. from a matrix of ones and zeros indicating which species are present at which sites). When the number of species is reasonably small, one can compute exact maximum likelihood estimates for all of the α and β coefficients given a presence-absence matrix by optimizing $p(\vec{y}; \alpha, \beta)$. Fully-observed Markov networks like the ones considered here have unimodal likelihood surfaces (Murphy 2012), ensuring that this procedure will always converge on the global maximum. This maximum represents the unique combination of α and β coefficients that would be expected to produce exactly the observed co-occurrence frequencies (i.e. it matches the sufficient statistics of the model distribution to the sufficient statistics of the data). For the analyses in this paper, I used the *rosalia* package (Harris 2015a) for the R programming language (R Core Team 2015) to define the objective function and gradient in R code and then find the optimum.

Simulated landscapes. In order to compare different methods, I simulated two sets of landscapes using known parameters.

The first set of simulated landscapes included the three competing species shown in Figure 1. For each of 1000 replicates, I generated a landscape with 100 sites by sampling exactly from a probability distribution defined by the interaction coefficients in that figure (Appendix A). Each of the methods described below was then evaluated on its ability to correctly infer that the two shrub species competed with one another, despite their frequent co-occurrence.

I also simulated a second set of landscapes using a stochastic community model based on generalized Lotka-Volterra dynamics, as described in the Appendix. In these simulations, each species pair was randomly assigned to either compete for a portion of the available carrying capacity (negative interaction) or to act as mutualists (positive interaction). In these simulations, mutualism operated by mitigating the effects of intraspecific competition

on each partner’s death rate. For these analyses, I simulated landscapes with up to 20 species and 25, 200, or 1600 sites (50 replicates per landscape size; see Appendix).

Recovering species interactions from simulated data. I used Markov networks and several other techniques for determining the sign and strength of the associations between pairs of species (Appendix B).

For the Markov networks, I used the *rosalia* package (Harris 2015a), as described above. Given the large number of parameters associated with some of the networks to be estimated, I regularized the likelihood using a logistic prior distribution with a scale of 2 on the α and β terms. This convex prior distribution has a similar shape to the Laplace distribution used in LASSO regularization (especially in the tails), but does not force the estimates to be exactly zero.

I also evaluated five alternative methods from the existing literature to calibrate the performance of the Markov network as a method for estimating species interactions. The first two alternative interaction measures were the sample correlations and the partial correlations between each pair of species’ data vectors on the landscape (Albrecht and Gotelli 2001, Faisal et al. 2010). Because partial correlations are undefined for landscapes with perfectly-correlated species pairs, I used a regularized estimate based on James-Stein shrinkage, as implemented in the *corpcor* package’s `pcor.shrink` function with the default settings (??). In the context of non-Gaussian data, the partial correlation can be thought of as a computationally efficient approximation to the full Markov network model (Loh and Wainwright 2013).

The third alternative, generalized linear models (GLMs), can also be thought of as a computationally efficient approximation to the Markov network (Lee and Hastie 2012).

Following Faisal et al. (2010), I fit regularized logistic regression models for each species, using the other species on the landscape as predictors. [[Observational presence-absence data does not have enough degrees of freedom to estimate this many parameters, so I symmetrized the pairwise correlations by averaging the coefficient for predicting species i 's status from species j and vice versa.]]

The fourth alternative method, described in Gotelli and Ulrich (2009), involved simulating possible landscapes from a null model that retains the row and column sums of the original matrix (Strong et al. 1984). Using the default options in the Pairs software described in Gotelli and Ulrich (2009), I simulated the null distribution of scaled C-scores (a test statistic describing the number of *non*-co-occurrences between two species). The software then calculated a Z statistic for each species pair using this null distribution, which I used as its estimator of species interactions.

The last two methods used the latent correlation matrix estimated by the BayesComm package (???) to evaluate the claim from recent papers that the correlation coefficients estimated by “joint species distribution models” provide an accurate assessment of species’ pairwise interactions (Pollock et al. 2014, see also Harris 2015b). I reported both the average correlation between each pair of species’ latent variables across 1000 Monte Carlo samples, as well as the average *partial* correlation.

Evaluating model performance. For the simulated landscapes based on Figure 1, method evaluation was fairly qualitative: any method whose test statistic for the two shrubs indicated a negative relationship passed; other methods failed. For methods that provide confidence intervals or other inferential statistics (Appendix), I also reported how often they rejected the null hypothesis of no interaction.

Because the different methods mostly describe species interactions on different scales (e.g. correlations versus Z scores versus regression coefficients), I used linear regression through the origin to rescale the different estimates produced by each method so that they had a consistent interpretation. After rescaling each method’s estimates, I calculated squared errors between the scaled interaction estimates and “true” interaction values for each of the $[[N]]$ species pairs across all the simulated data sets. These squared errors determined the proportion of variance explained for different combinations of method and landscape size (compared with a baseline model that assumed all interaction strengths to be zero).

Results

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

Twenty species. The accuracy of the evaluated methods varied substantially, depending on the parameters that produced the simulated communities (Figure 3a). In general, however, there was a consistent ordering. The Markov network explained the largest portion of the variance (34.6% overall), followed by the generalized linear models (29.9%), partial

correlations from the raw presence-absence data (27.5%), and partial correlations from BayesComm, the joint species distribution model (26.1). The three methods that did not attempt to control for indirect interactions all explained less than 20% of the variance. Of these, the sample correlation matrix based on the raw data performed the best (18.6%), followed by the null model (15.4) and BayesComm’s correlation matrix (11.6).

Although these last three methods had very different R^2 values, there was a very close mapping between their estimates (after controlling for the size of the simulated landscapes; Figure 3b). This suggests that the correlation matrices from joint species distribution models and especially the effect sizes from null models contain essentially the same information that could be obtained more easily by calculating correlation coefficients between species’ presence-absence vectors. This, in turn, demonstrates that these methods do not effectively control for any indirect effects in the network.

Discussion

The results presented above show that Markov networks can reliably recover species’ pairwise interactions from observational data, even for cases where a common null modeling technique reliably fails. Specifically, Markov networks were successful even when direct interactions were largely overwhelmed by indirect effects (Figure 1). For cases where fitting a Markov network is computationally infeasible, these results also indicate that partial covariances and generalized linear models (the two methods that estimated conditional relationships rather than marginal ones) can both provide useful approximations. The partial correlations’ success on simulated data may not carry over to real data sets, however; Loh and Wainwright (2013) show that the linear approximations can be less reliable in cases where the true interaction matrix contains more structure (e.g. guilds or trophic levels).

226 Similarly, the approximation involved in using separate generalized linear models for each
 227 species can occasionally lead to catastrophic overfitting with small-to-moderate sample sizes
 228 (Lee and Hastie 2012). For these reasons, it will usually be best to fit a Markov network
 229 rather than one of the alternative methods when one’s computational resources allow it.

230 It’s important to note that none of these methods can identify the exact nature of the
 231 pairwise interactions (e.g. which species in a positively-associated pair is facilitating the
 232 other), particularly when real pairs of species can reciprocally influence one another in
 233 multiple ways simultaneously (Bruno et al. 2003); with compositional data, there is only
 234 enough information to provide a single number describing each species pair.

235 On the other hand, if ecologists are familiar enough with the natural history of their study
 236 systems that they can augment the likelihood function with a prior distribution or a suitable
 237 penalty, then this information could reduce the effective degrees of freedom to estimate and
 238 real-world results might be even better than those shown in Figure 3.

239 Despite these limitations, Markov networks have enormous potential to improve ecological
 240 understanding. For example, Markov networks provide a simple answer to the question of
 241 how competition should affect a species’ overall prevalence, which was a major flashpoint for
 242 the null model debates in the 1980’s (Roughgarden 1983, Strong et al. 1984). Equation 1 can
 243 be used to calculate the expected prevalence of a species in the absence of biotic influences
 244 ($\frac{1}{1+e^{-\alpha}}$; Lee and Hastie 2012). Competition’s effect on prevalence in a Markov network can
 245 then be calculated by subtracting this value and the observed prevalence (cf Figure 2D).

246 Markov networks—particularly the Ising model for binary networks—have been studied in
 247 statistical physics for nearly a century (Cipra 1987), and the models’ properties, capabilities,
 248 and limits are well-understood in a huge range of applications. Modeling species interactions

249 using the same framework would thus allow ecologists to tap into an enormous set of existing
250 discoveries and techniques for dealing with indirect effects, stability, and alternative stable
251 states. Numerous other extensions are possible: Markov networks can be fit with a mix of
252 discrete and continuous variables, for example (Lee and Hastie 2012). There are even
253 methods (Whittam and Siegel-Causey 1981, Tjelmeland and Besag 1998) that would allow
254 the coefficient linking two species in an interaction matrix to vary as a function of the abiotic
255 environment or of third-party species that tip the balance between facilitation and
256 exploitation (Bruno et al. 2003).

257 Finally, the results presented here have important implications for ecologists' continued use
258 of null models to draw inferences about species interactions. Null and neutral models can be
259 very useful for clarifying our thinking about the numerical consequences of species' richness
260 and abundance patterns (Harris et al. 2011, Xiao et al. 2015), but deviations from a null
261 model must be interpreted with care (Roughgarden 1983). In complex networks of ecological
262 interactions (and even in small networks with three species), it may simply not be possible
263 to implicate individual species pairs or specific ecological processes like competition by
264 rejecting a general-purpose null (Gotelli and Ulrich 2009). Moreover, the null model's
265 estimates were extremely similar to what could be obtained from a simple correlation matrix,
266 which raises questions about how much additional value the null model adds. Estimating
267 pairwise coefficients directly seems like a much more promising approach: to the extent that
268 the models' relative performance on real data sets is similar to the range of results shown in
269 Figure 3, scientists in this field could [[easily double their explanatory power by switching
270 from null models to partial correlations or generalized linear models, or triple it by switching
271 to a Markov network]]. Regardless of the specific methods ecologists ultimately choose, the

most important consideration is clearly that we need to control for indirect effects and estimate conditional relationships between species, rather than marginal ones.

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References:

Figure captions

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).

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.

Figure 3. A. Proportion of variance in interaction coefficients explained by each method across varying numbers of sampled locations. **B.** The Z -scores produced by the null model (i.e. the Pairs software) for each pair of species are very predictable from the correlation between the presence-absence vectors of those same species and from the number of sites on the landscape.

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