

Discerning true from false negatives in ecological interactions

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Abstract: Species interactions and the networks that emerge from them structure ecosystem processes and enable biodiversity to persist through time. Still a robust understanding of interactions between species, how human activity is effecting these interactions, and how these change will effect Earth's ecosystems in the future remains elusive. This knowledge-gap is largely driven by a shortfall of data—although species occurrence data has rapidly increased in the last decade, species interaction data has lagged behind, largely due to the intrinsic difficulty of sampling interactions. These sampling challenges bias data. Here, we demonstrate that the realized false-negative rate can be quite highly biased toward species with high relative abundance. We then simulate observation on both 243 empirical food webs and generated models to estimate the sampling effort required to reduce the false-negative rate to less than 10%. We then assess how false negatives effect measurements of network properties and models of network prediction. We conclude by discussing how understanding of false-negatives can inform how we design sampling of species interactions and the networks they form.

Keywords:
ecological networks
sampling effort
biogeography

1 Introduction

It may, therefore, be a subject worthy of curiosity, to enquire what is the nature of that evidence which assures us of any real existence and matter of fact, beyond the present testimony of our senses, or the records of our memory.

David Hume, *An Enquiry Concerning Human Understanding*

Understanding how different species interact is a fundamental question of community ecology and an increasing imperative both to mitigate the effects of human activity on Earth's biodiversity (Makiola et al. 2020; Jordano 2016a) and to predict potential spillover of zoonotic disease (Becker et al. 2020). Over the past decade biodiversity data has become increasingly available due to improved sensing technology (Stephenson 2020) and increased adoption of open data sharing practices (Kenall, Harold, and Foote 2014). Modern remote-sensing has enabled collection of data on spatial scales and resolutions previously unimaginable, and in-situ sensors in the form of both camera-traps and environmental sensors have substantially increased the amount of

in-situ data available to ecologists. Yet widespread data about species interactions has remained illusive as detection of an interaction between two species often requires human sampling, as although remote methods can be used to detect cooccurrence, this itself is not necessarily indicative of interaction (Blanchet, Cazelles, and Gravel 2020). This limitation induces constraints on sampling of interactions based on the spatial and temporal scales feasible to human sampling.

These sampling constraints go on to bias species interaction data in several ways: we only observe a small fraction of the variation of species interactions in space and time, sampling of species interactions is geographically biased toward the usual suspects (Poisot, Bergeron, et al. 2021), and these observations themselves are reflect the distribution of abundance within communities (Poisot, Stouffer, and Gravel 2015). These biases have practical consequences for answering questions about species interactions (de Aguiar et al. 2019). The data we collect is **noisy** and likely contains many *false-negatives*, where there is not an observation of two species interacting even though they actually interact in some capacity (Young, Valdovinos, and Newman 2021; Stock et al. 2017).

Here we seek to understand how false negatives in ecological interaction data impact the analysis and prediction of ecological networks, and also to understand how a better understanding of the relationship between sampling effort and likelihood of a “true negative” can guide how we design surveys of ecological interactions (Jordano 2016b). The questions we pose and attempt to answer are: 1) How many times do you have to observe a non-interaction between two species to be confident in saying that is a true negative? 2) How “wrong” are the measurements of network structure modularity as a function of false-negative probability? and lastly 3) How do false-negatives impact our ability to make reliable predictions about interactions? We conclude by suggesting use of null models like those presented here as a tool for guiding design of surveys of species interactions, and increased adoption of modeling detection error in predictive ecological models.

2 How many observations of a non-interaction do we need to classify it as a true negative?

To answer the titular question of this section, we present a naive model of interaction detection: we assume that every true interaction between two species is incorrectly observed as a non-interaction with an independent and fixed probability, which we denote p_{fn} and subsequently refer to as the False-Negative Rate (FNR). If we observe the same species not-interacting N times the probability of a true negative (denoted p_{tn}) is given by $p_{tn} = 1 - (p_{fn})^N$. This relation is shown in fig. 1 for varying values of the false negative rate p_{fn} . This illustrates a fundamental link between our ability to reliably say an interaction doesn’t exist— p_{tn} —and our sampling effort N . Further, within this model there is no non-zero p_{fn} for which we can ever *prove* that an interaction does not exist.

From fig. 1 (and general intuition) it is clear that the more times we see two species *occurring*, but **not interacting**, the more likely the interaction is a true negative. But how does one decide what this threshold of number of observations should be when planning to sample a given system? If false-negative rates presented in fig. 1 seem unrealistically high, consider that species are not observed independent of their relative abundance. In the next section we demonstrate the distribution of biomass in ecosystems can lead to high realized values of p_{fn} for species with low relative abundance. We suggest using neutral models of species abundances to design the number of observations sufficient to say an interaction doesn’t exist.

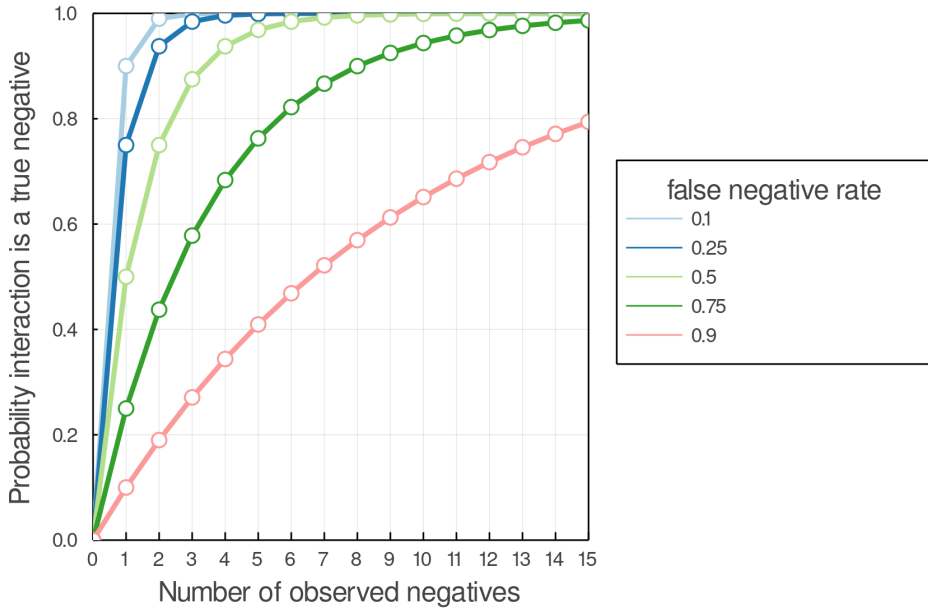


Figure 1 The probability an observed interaction is a “true negative” (y-axis) given how many times it has been sampled as a non-interaction (x-axis). Each color reflects a different value of p_{fn} , the false-negative rate (FNR). It’s the birthday paradox, but backwards.

2.1 False-negatives as a product of relative abundance

In this section we demonstrate the realized false-negative rate (FNR) changes drastically with sampling effort, largely due to the intrinsic variation of abundances within a community. We do this by simulating the process of observation of species interactions, applied both to 243 empirical food webs from the Mangal database (Banville, Vissault, and Poisot 2021) as well as random food-webs generated using the niche model (Williams and Martinez 2000). Our neutral model of observation assumes each observed species is drawn from the distribution of those species’ abundances at that place and time. Although there is no shortage of debate as to the processes the govern the general shape of this distribution, across communities the abundance distribution can be reasonably-well described by a log-normal distribution (Volkov et al. 2003). Controversies around theory of species abundance distributions aside, the practical consequence of skewed distribution of biomass in communities is seeing two low biomass species interacting requires two low probability events, which is observing two species of low relative biomass.

For each ecological network A with S species, we simulate abundances from S independent draws from a standard-log-normal distribution. For each true interaction $A_{ij} = 1$ we estimate the probability of observing both species i and j at given place and time by simulating a distribution of O individual observations, where the species observed at the $s = 1, 2, \dots, O$ -th observation is drawn from the generated log-normal distribution of abundances. For each pair of species (i, j) , if both i and j are observed within the s observations, the interaction is tallied as a true positive if $A_{ij} = 1$ and a false positive otherwise. Similarly, if i and j are *not* observed in these s observations, but $A_{ij} = 1$, this is counted as a false-negative, and a true-negative otherwise. fig. 2 shows this model applied to 243 food-webs from the Mangal database on the right, and niche model (Williams and Martinez 2000) across varying levels of species richness on the left. All simulations were done with 500 replicates of per unique number of observations s , and analyses presented here are done in Julia v1.6 (Bezanson et al. 2015) using both EcologicalNetworks.jl v0.5 and Mangal.jl v0.4 (Banville, Vissault, and Poisot 2021). Note that the empirical data also is, due to the phenomena described here, very likely to *already* have many false negatives, which is why we are interested in prediction of networks in the first place—we’ll revisit this in the final section.

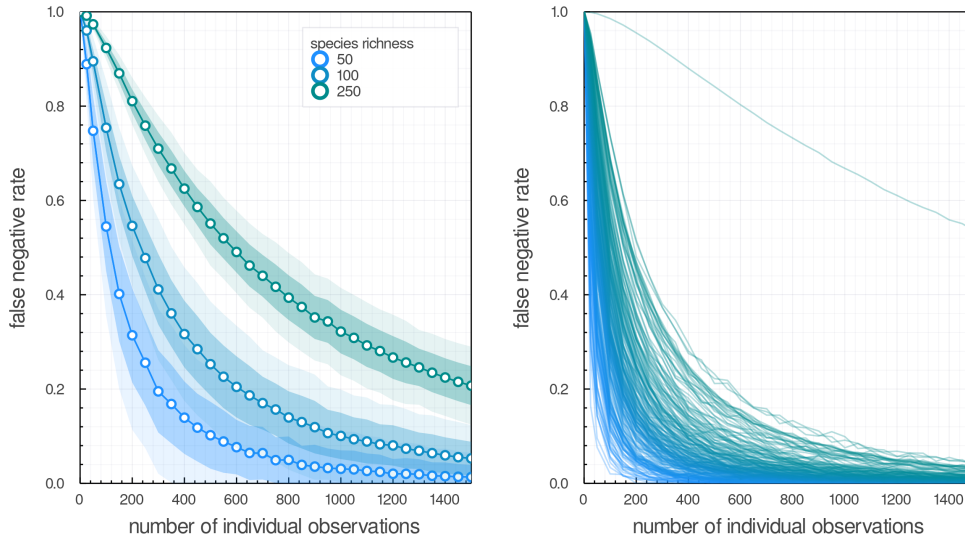


Figure 2 False negative rate (y-axis) as a function of sampling effort (x-axis) and network size, computed using the method described above. Left panel: this relation for 500 independent draws from the niche model (Williams and Martinez 2000) at varying levels of species richness (colors) with connectance $C = 0.1$. For each draw from the niche model, 200 sets of 1500 observations are simulated, for which each the mean false negative rate at each observation-step is computed. Means denoted with points, with 1σ in the first shade and 2σ in the second Right panel: empirical food webs from Mangal database in teal, applied to the same process as the left The outlier on panel B is a 714 species food-web.

Empirical data on interactions, limited by the practical realities of funding and human-work hours, tend to fall on the order on 100s or 1000s observations of individuals per site Schwarz et al. (2020), although clear aggregation of this data has proven difficult to find and a meta-analysis of network data and sampling effort seems both pertinent and necessary. Further, from fig. 2 it is evident that the number of species considered in a study is inseparable from the false-negative rate in that study, and this effect should be taken into account when designing samples of ecological networks in the future.

2.2 Positive associations can increase the probability of false-negatives

This model above doesn't consider the possibility that there are positive or negative associations which shift the realized probability of observing two species together as a consequence of their interaction. However, here we demonstrate that the probability of observing a false negative can be *higher* if there is some positive association between occurrence of species A and B . If we denote the probability that we observe an existing interaction between A and B as $P(AB)$, and if there is *no* association between the marginal probabilities of observing A and observing B , denoted $P(A)$ and $P(B)$ respectfully, then the probability of observing the interaction $P(AB) = P(A)P(B)$.

In the other case where there *is* some positive strength of association between observing both A and B because this interaction is “important” for each species, then the probability of observation both A and B , $P(AB)$, is greater than $P(A)P(B)$ as $P(A)$ and $P(B)$ are not independent and instead are positively correlated, *i.e.* $P(AB) > P(A)P(B)$. In this case, the probability of observing a false negative in our naive model from before is $p_{fn} = 1 - P(AB)$ which due to the above inequality implies $p_{fn} \geq 1 - P(A)P(B)$ which indicates increasingly greater probability of a false negative as $P(AB) \rightarrow P(AB) \gg P(A)P(B)$. This should be noted with the caveat that this does not consider variation in species abundance in space and time. If positive or negative associations between species structure variation in the distribution of $P(AB)$ across space/time, then the spatial and temporal biases induced by data collection would further impact the realized false negative rate, as in this case the probability of false negative would not be constant for each pair of species across sites.

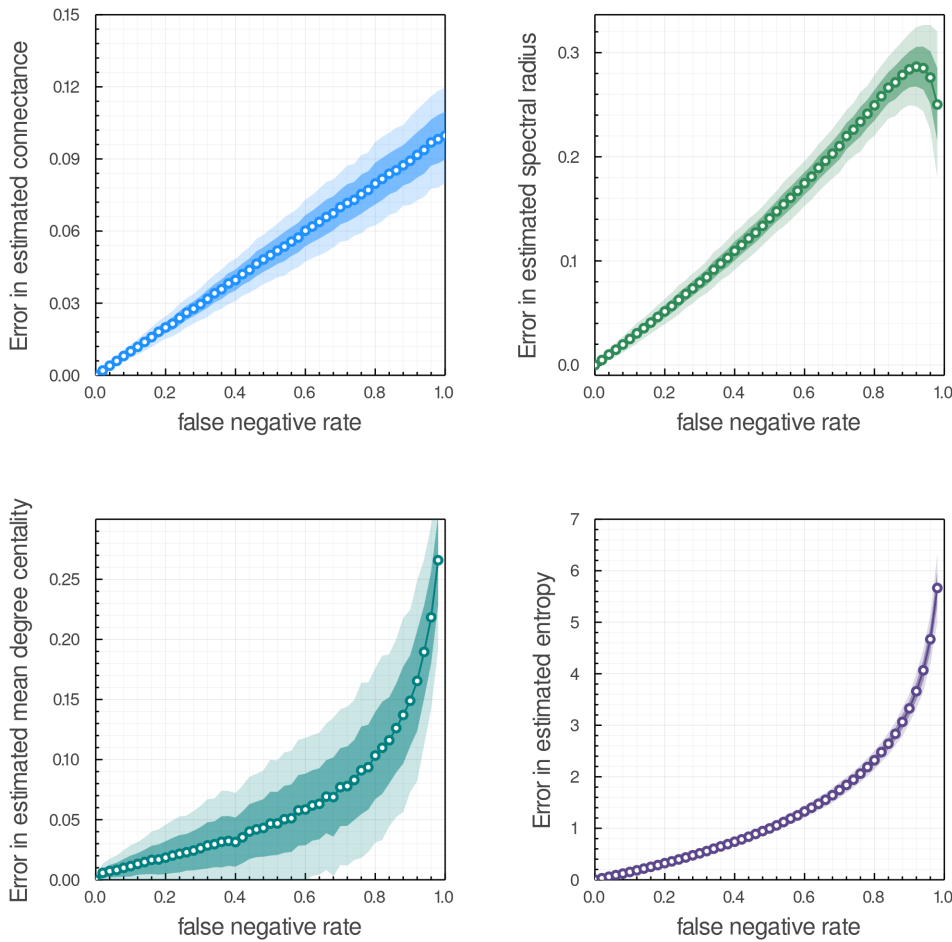


Figure 3 The mean-squared error (y-axis) of various network properties (different panels) across various simulated false-negative rates (x-axis). Means denoted with points, with 1σ in the first shade and 2σ in the second.

3 The impact of false-negatives on network analysis and prediction

We now transition toward assessing the effects of false negatives in data on the properties of ecological networks which we derive from interaction data, and their effect on models for predicting interactions in the future.

3.1 Effects of false-negatives on network properties

Here we simulate the effects of observation error to generate synthetic data with a known proportion of false negatives to compare the computed network properties of the original “true” network to the computed properties of the “observed” network with added false-negatives. In fig. 3 we show four properties (connectance, spectral radius, mean degree-centrality, and entropy) computed across 200 replicates at each value of the false negative rate p_{fn} . Each replicate uses a random food-web simulated using the niche model (Williams and Martinez 2000) with 100 species and true connectance $C = 0.1$.

The primary information to be gained from fig. 3 is that properties vary in their response to num-

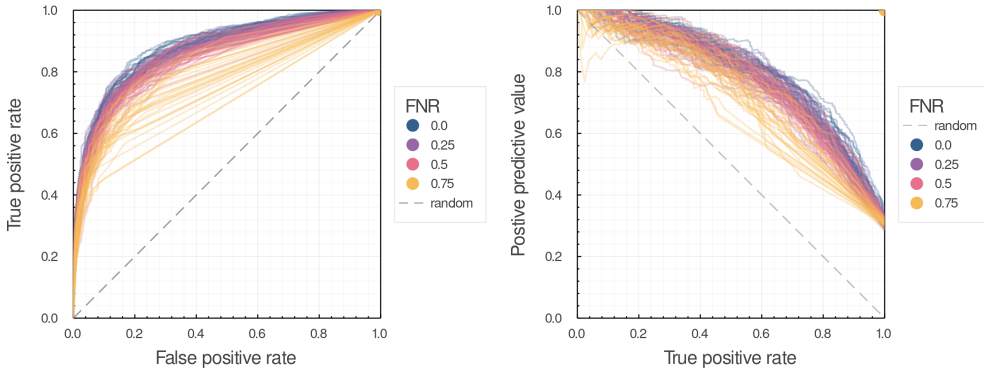


Figure 4 Receiver-operating-characteristic (left) and precision-recall (right) curves for the model on varying levels of false-negatives in the data (colors). For each value of FNR, we run 30 random training/test splits on 80/20 percent of the data. Replica of figure 1 in Strydom et al. (2021)

ber of false negatives in a sample—spectral radius (generally a measure of global structure) and connectance show roughly linear responses to false negatives, whereas mean degree centrality and entropy are decisively non-linear. We propose that simulating the effects of false negatives in data in this way can serve as an additional validation tool when aiming to detect structural properties of networks using generative null models (Connor, Barberán, and Clauset 2017).

3.2 Effects of false negatives on ability to make predictions

In this section, we assess the effect of false negatives in data on our ability to make predictions about interactions. The prevalence of false-negatives in data is the catalyst for interaction prediction in the first place, and as a result methods have been proposed to counteract this bias (Poisot, Ouellet, et al. 2021; Stock et al. 2017). However, if the number of false-negatives in a dataset becomes too overwhelming, it is feasible this could induce too much noise for a interaction prediction model to detect the signal of interaction due to the latent properties of each species derived from the empirical network.

To test this, we use the same predictive model and dataset as in Strydom et al. (2021) to predict a metaweb from various empirical slices of the species pool observed across space. This dataset from Hadfield et al. (2014) describes host-parasite interaction networks sampled across 51 sites. We partition the data into 80-20 training-test split, and then seed the training data with false negatives varying rates, but crucially do nothing to the test data. We use the same model, a neural-network with 3 layers to predict outputs based on features extracted from cooccurrence, see Strydom et al. (2021) for more details. In fig. 4, we show receiving-operating-characteristic (ROC) and precision-recall (PR) curves for the model with varying levels of synthetic false-negatives added to the data.

Interestingly, the performance of the model from Strydom et al. (2021) changes little with many added false-negatives, which is good evidence in favor neural-networks as a class of model for interaction detection. Again, similar to our caveat in the previous section, this data is *already* likely to have many false-negatives, so the effects of adding more as we do in this illustration might be mitigated because there are already non-simulated false-negatives in the original data which impact the models performance, even in the $p_{fn} = 0$ case.

4 Conclusion

In this paper we have demonstrated that expect a certain number of false negatives in species interaction datasets purely due to the distribution of abundances within a community. Positive associations between species occurrence due to interactions can increase the false-negative rate if the sample is spatially biased. We have also shown that these false negatives can cause varying responses in our measurements of network properties and further could impact our ability to reliably predict interactions, which highlights the need for further research into methods for correcting this bias in existing data, e.g. (Stock et al. 2017). A brief caveat here is that we do not consider the rate of false positives—in large part false positives can be explained by misidentification of species, although this could be a relevant consideration in some cases.

What then does the elucidate about how to design samples of interactions (Jordano 2016b)? The primary takeaway is that when planning the sampling effort across sites, it is necessary to take both the species richness of the metaweb into account. Further simulating the process of observation can be a powerful tool for planing study design which takes relative abundance into account, and provide a null baseline for detection of interaction strength. A model similar to that here can and should be used to provide a neutral expectation of true-negative probability given a number of observations of individuals at a given place and time.

What does the future hold for this research? A better understanding of how false-negatives impact our analyses and prediction of ecological networks is a practical necessity. In general, building models that explicitly account for observation error is a necessary step forward for predictive ecological models (Young, Valdovinos, and Newman 2021; Johnson and Larremore 2021). Neural networks, like the one used to predict interactions in the above section, have been used to reflect hidden states which account for detection error in occupancy modeling (Joseph 2020), and could be integrated in the predictive models of the future. Incorporating a better understanding of sampling effects and bias on both the future design of biodiversity monitoring systems, and the predictive models we wish to apply to this data, is imperative in making actionable predictions about the future of ecological interactions on our planet.

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