

The missing link: discerning true from false negatives when sampling species interaction networks

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1 Introduction

2 Species interactions drive many processes in evolutionary biology and community ecology. A better
3 understanding of interactions among species is an imperative to both mitigate the potentially harmful
4 impacts of anthropogenic change on Earth's biodiversity (Makiola *et al.* 2020) and to predict zoonotic
5 spillover of disease to prevent future pandemics (Becker *et al.* 2021). However, meeting these challenges is
6 difficult because interactions are intrinsically hard to sample (Jordano 2016). Over the past few decades
7 biodiversity data has become increasingly available—for example, remote-sensing has enabled collection
8 of data on spatial scales and resolutions previously unimaginable (Stephenson 2020), while the adoption
9 of open data practices (Kenall *et al.* 2014) have substantially increased the amount of data available to
10 ecologists. Still, widespread data about species interactions remains elusive (Poisot *et al.* 2021). Observing
11 an interaction between two species often requires human observation because remote sampling methods
12 can primarily detect co-occurrence (but see Niedballa *et al.* (2019)), and this itself is not necessarily
13 indicative of an interaction (Blanchet *et al.* 2020). This constraint induces biases on species interaction
14 data subject to the spatial and temporal scales that current observation methods can feasibly sample. This
15 is further compounded by semantic confusion around the word “interaction”—for example one might
16 consider competition a type of species interaction, even though it is marked by a lack of co-occurrence
17 between species, unlike other types of interactions, like trophism or pollination, which require both
18 species to be together at the same place and time. We define interaction in the latter sense, where two
19 species have fitness consequences on one-another if they are in the sample place at the same time. In
20 addition, here we only consider direct (not higher-order) interactions.

21 The importance of *sampling effort* and its impact on resulting ecological data has produced a rich body of
22 literature. The recorded number of species in a dataset or sample depends on the total number of
23 observations (Walther *et al.* 1995; Willott 2001)—as do estimates of population abundance (Griffiths
24 1998)—in addition to spatial coverage and species detectability. This has motivated more quantitatively
25 robust approaches to account for error in sampling data in many contexts: to determine if a given species
26 is extinct (Boakes *et al.* 2015), to determine sampling design (Moore & McCarthy 2016), and to measure
27 species richness across large scales (Carlson *et al.* 2020). In the context of interactions, an initial concern
28 was the compounding effects of limited sampling effort combined with the amalgamation of data (across
29 both study sites, time of year, and taxonomic scales) could lead any empirical set of observations to

30 inadequately reflect the reality of how species interact (Paine 1988) or the structure of the network as a
31 whole (McLeod *et al.* 2021). Martinez *et al.* (1999) showed that in a plant-endophyte trophic network,
32 network connectance is robust to sampling effort, but this was done in the context of a system for which
33 observation of 62,000 total interactions derived from 164,000 plant-stems was feasible. In some systems
34 (e.g. megafauna food-webs) this many observations is either impractical or infeasible due to the absolute
35 abundance of the species in question.

36 We cannot feasibly observe all (or even most) of the direct interactions that occur in an ecosystem. This
37 means we can be confident two species actually interact if we have a record of it (given an estimate of
38 species misidentification probability), but not at all confident that a pair of species *do not* interact if we
39 have no record of those species observed together. In other words, it is difficult to distinguish
40 *true-negatives* (two species never interact) from *false-negatives* (two species interact sometimes, but we do
41 not have a record of it). For a concrete example of a false-negative in a food web, see fig. 1. Because even
42 the most highly sampled systems will still contain missing interactions, there is increasing interest in
43 combining species-level data (e.g. traits, abundance, range, phylogenetic relatedness, etc.) to build models
44 to predict interactions between species we haven't observed together before (Strydom *et al.* 2021).
45 However, the noise of false-negatives could impact the efficacy of our predictive models and have practical
46 consequences for answering questions about interactions (de Aguiar *et al.* 2019). This data constraint is
47 amplified as the interaction data we have is geographically biased toward the usual suspects (Poisot *et al.*
48 2021). We therefore need a systematic approach to assessing these biases in the observation process and
49 the consequences this has for our understanding of interaction networks.

50 The intrinsic properties of ecological communities create several challenges for sampling: first, species are
51 not observed with equal probability—we are much more likely to observe a species of high abundance
52 than one of very low abundance (Poisot *et al.* 2015). Canard *et al.* (2012) presents a null model of food-web
53 structure where species encounter one-another directly in proportion to each species' relative-abundance.
54 This assumes that there are no associations in species co-occurrence due to an interaction (perhaps
55 because this interaction is “important” for both species; Cazelles *et al.* (2016)), but in this paper we later
56 show increasing strength of associations leads to increasing probability of false-negatives in interaction
57 data, and that these positive associations are rampant in existing network data. Second, observed
58 co-occurrence is often equated with meaningful interaction strength, but this is not necessarily the case
59 (Blanchet *et al.* 2020)—a true “non-interaction” would require that neither of two species, regardless of

60 whether they co-occur, exhibit any meaningful effect on the fitness of the other. So, although
61 co-occurrence is not directly indicative of an interaction, it is a precondition for an interaction. Therefore
62 observations of “non-interactions” between pairs of species that are outside of the union of both species
63 ranges do not provide any information about that interaction, i.e. they should be excluded from
64 consideration.

65 Here, we illustrate how our confidence that a pair of species we believe to not interact highly depends on
66 sampling effort, and suggest that surveys of species interactions can benefit from simulation modeling of
67 detection probability. We demonstrate that the realized false-negative rate of interactions is directly
68 related to the relative abundance of the species involved, and demonstrate how simulation can be used to
69 produce a null estimate of the false-negative rate as a function of total sampling effort (the total count of
70 all individuals of all species seen). We show that positive associations in co-occurrence data can increase
71 realized probability of false-negatives, and demonstrate these positive associations are ubiquitous in
72 network datasets. We conclude by recommending that the simulation of sampling effort and species
73 occurrence can and should be used to help design surveys of species interaction diversity (Moore &
74 McCarthy 2016), and by advocating use of null models like those presented here as a tool for both guiding
75 design of surveys of species interactions and for modeling detection error in predictive models.

76 [Figure 1 about here.]

77 **How many observations of a non-interaction do we need to be confident** 78 **it's a true negative?**

79 We start with a naive model of interaction detection: we assume that every interacting pair of species is
80 incorrectly observed as not-interacting with an independent and fixed probability, which we denote p_{fn}
81 and subsequently refer to as the False-Negative Rate (FNR). If we observe the same species not-interacting
82 N times, then the probability of a true-negative (denoted p_{tn}) is given by $p_{tn} = 1 - (p_{fn})^N$. This relation
83 (the probability-mass-function of geometric distribution, a special case of the negative-binomial
84 distribution) is shown in Figure 1(A) for varying values of p_{fn} and illustrates a fundamental link between
85 our ability to reliably say an interaction doesn't exist— p_{tn} —and the number of times we have observed a
86 given species. In addition, note that also there is no non-zero p_{fn} for which we can ever prove that an

interaction does not exist—no matter how many observations of non-interactions N we have, $p_{tn} < 1$.

From fig. 2(A) it is clear that the more often we see two species co-occurring, but not interacting, the more likely the interaction is a true negative. This has several practical consequences: first it means negatives taken outside the overlap of the range of each species aren't informative. Second, we can use this relation to compute the expected number of total observations needed to obtain a “goal” number of observations of a particular pair of species (fig. 2(B)). As an example, if we hypothesize that A and B do not interact, and we want to see species A and B both co-occurring and not interacting 10 times to be confident this is a true negative, then we need an expected 1000 observations of all species if the relative abundances of A and B are both 0.1.

Because the true FNR is latent, we can never actually be sure what the actual number of false negatives in our data—however, we can use simulation to estimate it for datasets of a given size using neutral models of observation. If some of the “worst-case” FNRs presented in fig. 2(A) seem unrealistically high, consider that species are observed in proportion to their relative abundance. In the next section we demonstrate that the distribution of abundance in ecosystems can lead to very high realized values of FNR (p_{fn}) simply as an artifact of sampling effort.

[Figure 2 about here.]

False-negatives as a product of relative abundance

We now show that the realized FNR changes drastically with sampling effort due to the intrinsic variation of the abundance of individuals of each species 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 *et al.* 2021) and random food-webs generated using the niche model (Williams & Martinez 2000), a simple generative model of food-web structure. Our neutral model of observation assumes each observed species is drawn from the distribution in proportion to each species' abundance at that place and time. The abundance distribution of a community can be reasonably well described by a log-normal distribution (Volkov *et al.* 2003). In addition to the log-normal distribution, we also tested the case where the abundance distribution is derived from power-law scaling $Z^{(\log(T_i)-1)}$ where T_i is the trophic level of species i and Z is a scaling coefficient (Savage *et al.* 2004), which yields the same qualitative behavior. The

114 practical consequence of abundance distributions spanning many orders of magnitude of abundance is
115 that observing two “rare” species interacting requires two low probability events: observing two rare
116 species at the same time.

117 To simulate the process of observation, for an ecological network M with S species, we sample abundances
118 for each species from a standard-log-normal distribution. For each true interaction in the adjacency
119 matrix M (i.e. $M_{ij} = 1$) we estimate the probability of observing both species i and j at a given place and
120 time by simulating n observations of all individuals of any species, where the species of the individual
121 observed at the $\{1, 2, \dots, n\}$ -th observation is drawn from the generated log-normal distribution of
122 abundances. For each pair of species (i, j) , if both i and j are observed within the n -observations, the
123 interaction is tallied as a true positive if $M_{ij} = 1$. If only one of i or j are observed—but not both—in these
124 n observations, but $M_{ij} = 1$, this is counted as a false-negative, and a true-negative otherwise.

125 In fig. 2(C) we see this model of observation applied to niche model networks across varying levels of
126 species richness, and in fig. 2(D) the observation model applied to Mangal food webs. For all niche model
127 simulations in this manuscript, for a given number of species S the number of interactions is drawn from
128 the flexible-links model fit to Mangal data (MacDonald *et al.* 2020), effectively drawing the number of
129 interactions L for a random niche model food-web as

$$L \sim \text{BetaBinomial}(S^2 - S + 1, \mu\phi, 1 - \mu\phi)$$

130 where the MAP estimate of (μ, ϕ) applied to Mangal data from (MacDonald *et al.* 2020) is
131 $(\mu = 0.086, \phi = 24.3)$. All simulations were done with 500 independent replicates per unique number of
132 observations n . All analyses presented here are done in Julia v1.8 (Bezanson *et al.* 2015) using both
133 EcologicalNetworks.jl v0.5 and Mangal.jl v0.4 (Banville *et al.* 2021) and are hosted at
134 (GITHUB_LINK_TODO). Note that the empirical data, for the reasons described above, very likely
135 already contains many false negatives, we’ll revisit this issue in the final section.

136 From fig. 2(C) it is evident that the number of species considered in a study is inseparable from the
137 false-negative rate in that study, and this effect should be taken into account when designing samples of
138 ecological networks in the future. We see a similar qualitative pattern in fig. 2(D) where the FNR drops off
139 quickly as a function of observation effort, mediated by total richness. The practical consequence of the
140 bottom row of Figure 1 is whether the total number of observations of all species (the x-axis) for the range

of possible FNR we deem acceptable (the y-axis) is feasible. This raises two points: first, empirical data on interactions are subject to the practical limitations of funding and human-work hours, and therefore existing data tend to fall on the order of hundreds or thousands observations of individuals per site. Clear aggregation of data on sampling effort has proven difficult to find and a meta-analysis of network data and sampling effort seems both pertinent and necessary, in addition to the effects of aggregation of interactions across taxonomic scales (Gauzens *et al.* 2013; Giacomuzzo & Jordán 2021). This inherent limitation on in-situ sampling means we should optimize where we sample across space so that for a given number of samples, we obtain the maximum information possible. Second, what is meant by “acceptable” FNR? This raises the question: does a shifting FNR lead to rapid transitions in our ability inference and predictions about the structure and dynamics of networks, or does it produce a roughly linear decay in model efficacy? We explore this in the next section.

We conclude this section by advocating for the use of neutral models similar to above to generate expectations about the number of false-negatives in a data set of a given size. This could prove fruitful both for designing surveys of interactions but also because we may want to incorporate models of imperfect detection error into predictive interactions models, as Joseph (2020) does for species occurrence modeling. Additionally, we emphasize that one must consider the context for sampling—is the goal to detect a particular species (as in fig. 2(C)), or to get a representative sample of interactions across the species pool? This argument is well-considered when sampling individual species (Willott 2001), but has not yet been adopted for designing samples of communities.

Positive associations increase the false-negative rate

This model above doesn’t consider the possibility that there are positive or negative associations which shift the probability of observing two species together due to their interaction (Cazelles *et al.* 2016). However, here we demonstrate that the probability of observing a false negative can be higher if there is some positive association in the occurrence of species *A* and *B*. If we denote the probability that we observe the co-occurrence of two species *A* and *B* that we know interact as $P(AB)$ and if there is no association between the marginal probabilities of observing *A* and observing *B*, denoted $P(A)$ and $P(B)$ respectively, then the probability of observing their co-occurrence $P(AB) = P(A)P(B)$. In the other case where there is some positive strength of association between observing both *A* and *B* because this

169 interaction is “important” for each species, then the probability of observation both A and B , $P(AB)$, is
 170 greater than $P(A)P(B)$ as $P(A)$ and $P(B)$ are not independent and instead are positively correlated,
 171 i.e. $P(AB) > P(A)P(B)$. In this case, the probability of observing a false negative in our naive model from
 172 fig. 2(A) is $p_{fn} = 1 - P(AB)$, which due to the above inequality implies $p_{fn} > 1 - P(A)P(B)$. This indicates
 173 an increasingly greater probability of a false negative as $P(AB) \rightarrow P(AB) \gg P(A)P(B)$. However, this still
 174 does not consider variation in species abundance in space and time (Poisot *et al.* 2015). If positive or
 175 negative associations between species structure variation in the distribution of $P(AB)$ across space/time,
 176 then the spatial/temporal biases induced by data collection would further impact the realized false
 177 negative rate, as the probability of false negative would not be constant for each pair of species across sites.
 178 To test for this association in data we scoured Mangal for datasets with many spatial or temporal replicates
 179 of the same system. For each dataset, we compute the marginal probability $P(A)$ of occurrence of each
 180 species A across all networks in the dataset. For each pair of interacting species A and B , we then compute
 181 and compare the probability of co-occurrence if each species occurs independently, $P(A)P(B)$, to the
 182 empirical joint probability of co-occurrence, $P(AB)$. Following our analysis above, if $P(AB)$ is greater than
 183 $P(A)P(B)$, then we expect our neutral estimates of the FNR above to underestimate the realized FNR. In
 184 fig. 3, we see the difference between $P(AB)$ and $P(A)P(B)$ for the seven suitable datasets with enough
 185 spatio-temporal replicates and a shared taxonomic backbone (meaning all individual networks use
 186 common species identifiers) found on Mangal to perform this analysis. Further details about each dataset
 187 are reported in tbl. 1.

188 [Figure 3 about here.]

Table 1: This table describes the datasets used in the above analysis (Fig 2). The table reports the type of
 each dataset, the total number of networks in each dataset (N), the total species richness in each dataset (S),
 the connectance of each metaweb (all interactions across the entire spatial-temporal extent) (C), the mean
 species richness across each local network \bar{S} , the mean connectance of each local network \bar{C} , the mean
 β -diversity among overlapping species across all pairs of network species ($\bar{\beta}_{OS}$), and the mean β -diversity
 among all species in the metaweb ($\bar{\beta}_{WN}$). Both metrics are computed using KGL β -diversity (Koleff *et al.*
 2003)

Network	Type	N	S	C	\bar{S}	\bar{C}	$\bar{\beta}_{OS}$	$\bar{\beta}_{WN}$
Kopelke <i>et al.</i> (2017)	Food Web	100	98	0.037	7.87	0.142	1.383	1.972

Network	Type	N	S	C	\bar{S}	\bar{C}	$\bar{\beta}_{OS}$	$\bar{\beta}_{WN}$
Thompson & Townsend (2000)	Food Web	18	566	0.014	80.67	0.049	1.617	1.594
Havens (1992)	Food Web	50	188	0.065	33.58	0.099	1.468	1.881
Ponisio <i>et al.</i> (2017)	Pollinator	100	226	0.079	23.0	0.056	1.436	1.870
Hadfield <i>et al.</i> (2014)	Host-Parasite	51	327	0.085	32.71	0.337	1.477	1.952
Closs & Lake (1994)	Food Web	12	61	0.14	29.09	0.080	1.736	1.864
CaraDonna <i>et al.</i> (2017)	Pollinator	86	122	0.18	21.42	0.312	1.527	1.907

In each of these datasets, the joint probability of co-occurrence $P(AB)$ is decisively greater than our expectation if species co-occur in proportion to their relative abundance $P(A)P(B)$. This suggests that there may not be as many “neutrally forbidden links” (Canard *et al.* 2012) as we might think, and that the reason we do not have records of interactions between rare species is probably due to observation error. This has serious ramifications for the widely observed property of nestedness seen in bipartite networks (Bascompte & Jordano 2007)—perhaps the reason we have lots of observations between generalists is because they are more abundant, and this is particularly relevant as we have strong evidence that generalism drives abundance (Song *et al.* 2022), not vice-versa.

The impact of false-negatives on network properties and prediction

Here, we assess the effect of false negatives on our ability to make predictions about interactions, as well as their effect on network structure. The prevalence of false-negatives in our data is the catalyst for interaction prediction in the first place, and as a result methods have been proposed to counteract this bias (Poisot *et al.* (2022)). However, it is feasible that the FNR is so high that it could induce too much noise for an interaction prediction model to detect the signal of possible interaction between species.

To test this we use the dataset from Hadfield *et al.* (2014) that describes host-parasite interaction networks sampled across 51 sites, and the same method as Strydom *et al.* (2021) to extract latent features for each species in this dataset based on co-occurrence. We then predict a metaweb (equivalent to predicting true or false for an interaction for each species pair, effectively a binary classification problem) from these

species-level features using four candidate models for binary classification—three often used machine-learning (ML) methods (Boosted Regression Tree (BRT), Random Forest (RF), Decision Tree (DT)), and one naive model from classic statistics (Logistic Regression (LR)). Each of the ML models are bootstrap aggregated (or bagged) with 100 replicates each. We partition the data into 80-20 training-test split, and then seed the training data with false negatives at varying rates, but crucially do nothing to the test data. We fit all of these models using MLJ.jl, a high-level Julia framework for a wide-variety of ML models (Blaom *et al.* 2020). We evaluate the efficacy of these models using two common measures of binary classifier performance: the area under the receiver-operator curve (ROC-AUC) and the area under the precision-recall curve (PR-AUC), for more details see (Poisot 2022) Here, PR-AUC is slightly more relevant as it is a better indicator of prediction of false-negatives. The results of these simulations are shown in fig. 4(A) and (B).

[Figure 4 about here.]

One interesting result seen in fig. 4(A) and (B) is that the ROC-AUC value does not approach random in the same way the PR-AUC curve does as we increase the added FNR. The reason for this is that ROC-AUC is fundamentally not as useful a metric in assessing predictive capacity as PR-AUC. As we keep adding more false-negatives, the network eventually becomes a zeros matrix, and these models can still learn to predict “no-interaction” for all possible species pairs, which does far better than random guessing (ROC-AUC > 0.5) in terms of the true and false positive rates (the components of ROC-AUC). This highlights a more broad issue of label class imbalance, meaning there are far more non-interactions than interactions in data. A full treatment of the importance of class-balance is outside the scope of this paper, but is explored in-depth in (Poisot 2022).

Although these ML models are surprisingly performant at link prediction given their simplicity, there have been several major developments in the field applying deep-learning methods to many tasks in network inference and prediction—namely graph-representation learning (GRL, Khoshraftar & An (2022)) and graph convolutional networks (Zhang *et al.* 2019). At this time, these advances can not yet be applied to ecological networks because they require far more data than we currently have. We already have lots of features that could be used as inputs into these models (i.e. species level data about occurrence, genomes, abundance, etc.), but our network datasets barely get into the hundreds of local networks sampled across space and time tbl. 1. Once we start to get into the thousands, these models will

become more useful, but this can only be done with systematic monitoring of interactions. This again highlights the need to optimize our sampling effort to maximize the amount of information contained in our data given the expensive nature of sampling interactions.

We also consider how the FNR affects network properties. In fig. 4(C) we see the mean trophic level across networks simulated using the niche model (as above), across a spectrum of FNR values. In addition to the clear dependence on richness, we see that mean trophic level, despite varying widely between niche model simulations, tends to be relatively robust to false negatives and does not deviate widely from the true value until very large FNRs, i.e. $p_{fn} > 0.7$.

Discussion

Species interactions enable the persistence and functioning of ecosystems, but our understanding of interactions is limited due to the intrinsic difficulty of sampling. Here we have provided a null model for the expected number of false-negatives in an interaction dataset. We demonstrated that we expect many false-negatives in species interaction datasets purely due to the intrinsic variation of abundances within a community. We also, for the first time to our knowledge, measured the strength of association between co-occurrence and interactions (Cazelles *et al.* 2016) across many empirical systems for the first time, and found that these positive associations are both very common, and showed algebraically that they increase the realized FNR. We have also shown that false-negatives could further impact our ability to both predict interactions and infer properties of the networks, which highlights the need for further research into methods for correcting this bias in existing data.

A better understanding of how false-negatives impact our inference of network structure and dynamics is prediction of ecological networks by both using information about individual species interactions and the structure of metawebs on large scales is a practical necessity. False-negatives could pose a problem for many forms of inference in network ecology. For example, inferring the structural or dynamic stability of a network could be prone to error if the observed network is not sampled “enough”. What exactly “enough” means is then specific to the application, and should be assessed via methods like those here when designing samples. Further, predictions about network rewiring (Thompson & Gonzalez 2017) due to range shifts in response to climate change could be error-prone without accounting for interactions that have not been observed but that still may become climatically infeasible. As is evident from Figure 1(A),

we can never guarantee there are no false-negatives in data. In recent years, there has been interest toward explicitly accounting for false-negatives in models (Stock *et al.* 2017; Young *et al.* 2021), and a predictive approach to networks—rather than expecting our samples to fully capture all interactions (Strydom *et al.* 2021). As a result, better models for predicting interactions are needed for interaction networks. This includes explicitly accounting for observation error (Johnson & Larremore 2021)—certain classes of models 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 interactions in the future.

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. The same logic that we apply to false-negatives could easily be applied to false-positives, e.g. that we can be much more confident that an interaction is a true positive if we have observed it 50 times rather than only once, and we could similarly model this using the geometric distribution as in fig. 2(A). However, because ecological networks are so sparse, there are far more negatives than positives in the dataset, and therefore likely to be far more false-negatives than false-positives in absolute terms.

This work has several practical consequences for the design of interaction samples. Simulating the process of observation could be a powerful tool for estimating the sampling effort required by a study that takes relative abundance into account, and provides a null baseline for expected FNR. It is necessary to take the size of the species pool into account when deciding how many total samples is sufficient for an “acceptable” FNR (fig. 2(C & D)). Further the spatial and temporal turnover of interactions means any approach to sampling prioritization must be spatiotemporal. We demonstrated earlier that observed negatives outside of the range of both species aren’t informative, and therefore using species distribution models could aid in this spatial prioritization of sampling sites.

Our work highlights the need for a quantitatively robust approach to sampling design, both for interactions (Jordano 2016) and all other aspects of biodiversity (Carlson *et al.* 2020). As anthropogenic forces create rapid shifts in our planet’s climate and biosphere, this is an imperative to maximize the amount of ecological information we get in our finite samples, and make our inferences and decisions based on this data as robust as possible. Where we choose to sample, and how often we choose to sample there, has strong impacts on the inferences we make from data. Incorporating a better understanding of sampling effort and bias to the design of biodiversity monitoring systems, and the inference and predictive models we apply to this data, is imperative in understanding how biodiversity is changing, and making

294 actionable forecasts about the future of ecological interactions on our planet.

295 **References**

296 preBanville, F., Vissault, S. & Poisot, T. (2021). [Mangal.jl and EcologicalNetworks.jl: Two complementary](#)
297 [packages for analyzing ecological networks in Julia](#). *Journal of Open Source Software*, 6, 2721.

298 Bascompte, J. & Jordano, P. (2007). [Plant-Animal Mutualistic Networks: The Architecture of Biodiversity](#).
299 *Annual Review of Ecology, Evolution, and Systematics*, 38, 567–593.

300 Becker, D.J., Albery, G.F., Sjodin, A.R., Poisot, T., Bergner, L.M., Dallas, T.A., *et al.* (2021). [Optimizing](#)
301 [predictive models to prioritize viral discovery in zoonotic reservoirs](#).

302 Bezanson, J., Edelman, A., Karpinski, S. & Shah, V.B. (2015). [Julia: A Fresh Approach to Numerical](#)
303 [Computing](#).

304 Blanchet, F.G., Cazelles, K. & Gravel, D. (2020). [Co-occurrence is not evidence of ecological interactions](#).
305 *Ecology Letters*, 23, 1050–1063.

306 Blaom, A.D., Kiraly, F., Lienart, T., Simillides, Y., Arenas, D. & Vollmer, S.J. (2020). [MLJ: A Julia package](#)
307 [for composable machine learning](#). *Journal of Open Source Software*, 5, 2704.

308 Boakes, E.H., Rout, T.M. & Collen, B. (2015). [Inferring species extinction: The use of sighting records](#).
309 *Methods in Ecology and Evolution*, 6, 678–687.

310 Canard, E., Mouquet, N., Marescot, L., Gaston, K.J., Gravel, D. & Mouillot, D. (2012). [Emergence of](#)
311 [Structural Patterns in Neutral Trophic Networks](#). *PLOS ONE*, 7, e38295.

312 CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., *et al.* (2017).
313 [Interaction rewiring and the rapid turnover of plantpollinator networks](#). *Ecology Letters*, 20, 385–394.

314 Carlson, C.J., Dallas, T.A., Alexander, L.W., Phelan, A.L. & Phillips, A.J. (2020). [What would it take to](#)
315 [describe the global diversity of parasites?](#) *Proceedings of the Royal Society B: Biological Sciences*, 287,
316 20201841.

317 Cazelles, K., Araújo, M.B., Mouquet, N. & Gravel, D. (2016). [A theory for species co-occurrence in](#)
318 [interaction networks](#). *Theoretical Ecology*, 9, 39–48.

319 Closs, G.P. & Lake, P.S. (1994). [Spatial and Temporal Variation in the Structure of an Intermittent-Stream](#)
320 [Food Web](#). *Ecological Monographs*, 64, 1–21.

321 de Aguiar, M.A.M., Newman, E.A., Pires, M.M., Yeakel, J.D., Boettiger, C., Burkle, L.A., *et al.* (2019).
322 [Revealing biases in the sampling of ecological interaction networks](#). *PeerJ*, 7, e7566.

323 Gauzens, B., Legendre, S., Lazzaro, X. & Lacroix, G. (2013). Food-web aggregation, methodological and
324 functional issues. *Oikos*, 122, 1606–1615.

325 Giacomuzzo, E. & Jordán, F. (2021). [Food web aggregation: Effects on key positions](#). *Oikos*, 130,
326 2170–2181.

327 Griffiths, D. (1998). [Sampling effort, regression method, and the shape and slope of sizeabundance](#)
328 [relations](#). *Journal of Animal Ecology*, 67, 795–804.

329 Hadfield, J.D., Krasnov, B.R., Poulin, R. & Nakagawa, S. (2014). [A Tale of Two Phylogenies: Comparative](#)
330 [Analyses of Ecological Interactions](#). *The American Naturalist*, 183, 174–187.

331 Havens, K. (1992). [Scale and Structure in Natural Food Webs](#). *Science*, 257, 1107–1109.

332 Johnson, E.K. & Larremore, D.B. (2021). [Bayesian estimation of population size and overlap from random](#)
333 [subsamples](#).

334 Jordano, P. (2016). [Sampling networks of ecological interactions](#). *Functional Ecology*, 30, 1883–1893.

335 Joseph, M.B. (2020). [Neural hierarchical models of ecological populations](#). *Ecology Letters*, 23, 734–747.

336 Kenall, A., Harold, S. & Foote, C. (2014). [An open future for ecological and evolutionary data?](#) *BMC*
337 *Evolutionary Biology*, 14, 66.

338 Khoshraftar, S. & An, A. (2022). [A Survey on Graph Representation Learning Methods](#).

339 Koleff, P., Gaston, K.J. & Lennon, J.J. (2003). [Measuring beta diversity for presenceabsence data](#). *Journal*
340 *of Animal Ecology*, 72, 367–382.

341 Kopelke, J.-P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S. & Roslin, T. (2017). [Food-web structure of](#)
342 [willow-galling sawflies and their natural enemies across Europe](#). *Ecology*, 98, 1730–1730.

343 MacDonald, A.A.M., Banville, F. & Poisot, T. (2020). [Revisiting the Links-Species Scaling Relationship in](#)
344 [Food Webs](#). *Patterns*, 1.

345 Makiola, A., Compson, Z.G., Baird, D.J., Barnes, M.A., Boerlijst, S.P., Bouchez, A., *et al.* (2020). Key
 346 Questions for Next-Generation Biomonitoring. *Frontiers in Environmental Science*, 7.

347 Martinez, N.D., Hawkins, B.A., Dawah, H.A. & Feifarek, B.P. (1999). [Effects of Sampling Effort on](#)
 348 [Characterization of Food-Web Structure](#). *Ecology*, 80, 1044–1055.

349 McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., *et al.* (2021). [Sampling and](#)
 350 [asymptotic network properties of spatial multi-trophic networks](#). *Oikos*, 130, 2250–2259.

351 Moore, A.L. & McCarthy, M.A. (2016). [Optimizing ecological survey effort over space and time](#). *Methods*
 352 *in Ecology and Evolution*, 7, 891–899.

353 Niedballa, J., Wilting, A., Sollmann, R., Hofer, H. & Courtiol, A. (2019). [Assessing analytical methods for](#)
 354 [detecting spatiotemporal interactions between species from camera trapping data](#). *Remote Sensing in*
 355 *Ecology and Conservation*, 5, 272–285.

356 Paine, R.T. (1988). [Road Maps of Interactions or Grist for Theoretical Development?](#) *Ecology*, 69,
 357 1648–1654.

358 Poisot, T. (2022). [Guidelines for the prediction of species interactions through binary classification](#).

359 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., *et al.* (2021). [Global knowledge](#)
 360 [gaps in species interaction networks data](#). *Journal of Biogeography*, 48, 1552–1563.

361 Poisot, T., Ouellet, M.-A., Mollentze, N., Farrell, M.J., Becker, D.J., Brierly, L., *et al.* (2022). [Network](#)
 362 [embedding unveils the hidden interactions in the mammalian virome](#).

363 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). [Beyond species: Why ecological interaction networks vary](#)
 364 [through space and time](#). *Oikos*, 124, 243–251.

365 Ponisio, L.C., Gaiarsa, M.P. & Kremen, C. (2017). [Opportunistic attachment assembles plantpollinator](#)
 366 [networks](#). *Ecology Letters*, 20, 1261–1272.

367 Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004). [Effects of Body Size and](#)
 368 [Temperature on Population Growth](#). *The American Naturalist*, 163, 429–441.

369 Song, C., Simmons, B.I., Fortin, M.-J. & Gonzalez, A. (2022). [Generalism drives abundance: A](#)
 370 [computational causal discovery approach](#). *PLOS Computational Biology*, 18, e1010302.

371 Stephenson, P. (2020). [Technological advances in biodiversity monitoring: Applicability, opportunities](#)

372 [and challenges](#). *Current Opinion in Environmental Sustainability*, Open Issue 2020 Part A: Technology
373 Innovations and Environmental Sustainability in the Anthropocene, 45, 36–41.

374 Stock, M., Poisot, T., Waegeman, W. & De Baets, B. (2017). [Linear filtering reveals false negatives in](#)
375 [species interaction data](#). *Scientific Reports*, 7, 45908.

376 Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., *et al.* (2021). [A](#)
377 [roadmap towards predicting species interaction networks \(across space and time\)](#). *Philosophical*
378 *Transactions of the Royal Society B: Biological Sciences*, 376, 20210063.

379 Thompson, P.L. & Gonzalez, A. (2017). [Dispersal governs the reorganization of ecological networks under](#)
380 [environmental change](#). *Nature Ecology & Evolution*, 1, 1–8.

381 Thompson, R.M. & Townsend, C.R. (2000). [Is resolution the solution?: The effect of taxonomic resolution](#)
382 [on the calculated properties of three stream food webs](#). *Freshwater Biology*, 44, 413–422.

383 Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). [Neutral theory and relative species abundance](#)
384 [in ecology](#). *Nature*, 424, 1035–1037.

385 Walther, B.A., Cotgreave, P., Price, R.D., Gregory, R.D. & Clayton, D.H. (1995). [Sampling Effort and](#)
386 [Parasite Species Richness](#). *Parasitology Today*, 11, 306–310.

387 Williams, R.J. & Martinez, N.D. (2000). [Simple rules yield complex food webs](#). *Nature*, 404, 180–183.

388 Willott, S.j. (2001). [Species accumulation curves and the measure of sampling effort](#). *Journal of Applied*
389 *Ecology*, 38, 484–486.

390 Young, J.-G., Valdovinos, F.S. & Newman, M.E.J. (2021). [Reconstruction of plantpollinator networks from](#)
391 [observational data](#). *Nature Communications*, 12, 3911.

392 Zhang, S., Tong, H., Xu, J. & Maciejewski, R. (2019). [Graph convolutional networks: A comprehensive](#)
393 [review](#). *Computational Social Networks*, 6, 11.

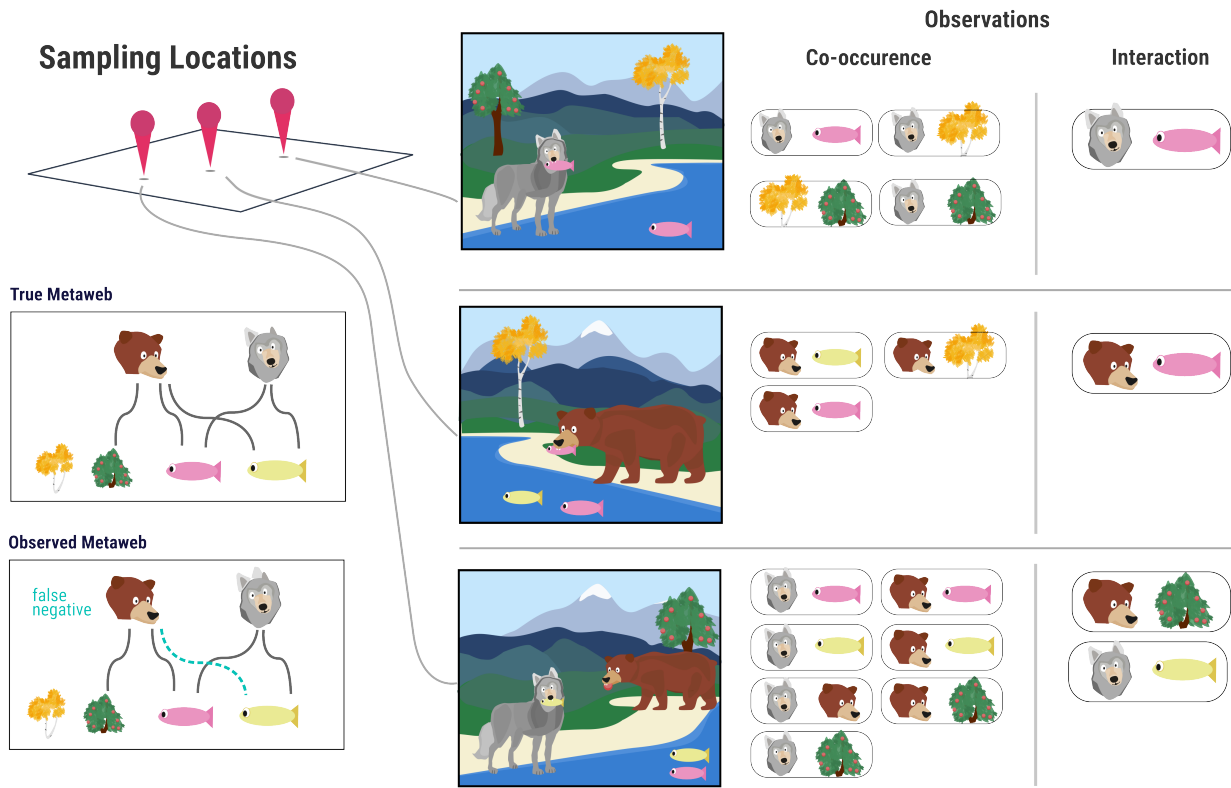


Figure 1: This conceptual example considers a sample of the trophic community of bears, wolves, salmon (pink fish), pike (yellow fish), berry trees, and aspen trees. The true metaweb (all realized interactions across the entire spatial extent) is shown on the left. In the center is what a hypothetical ecologist samples at each site. Notice that although bears are observed co-occurring with both salmon and pike, there was never a direct observation of bears eating pike, even though they actually do. Therefore, this interaction between bears and pike is a false negative.

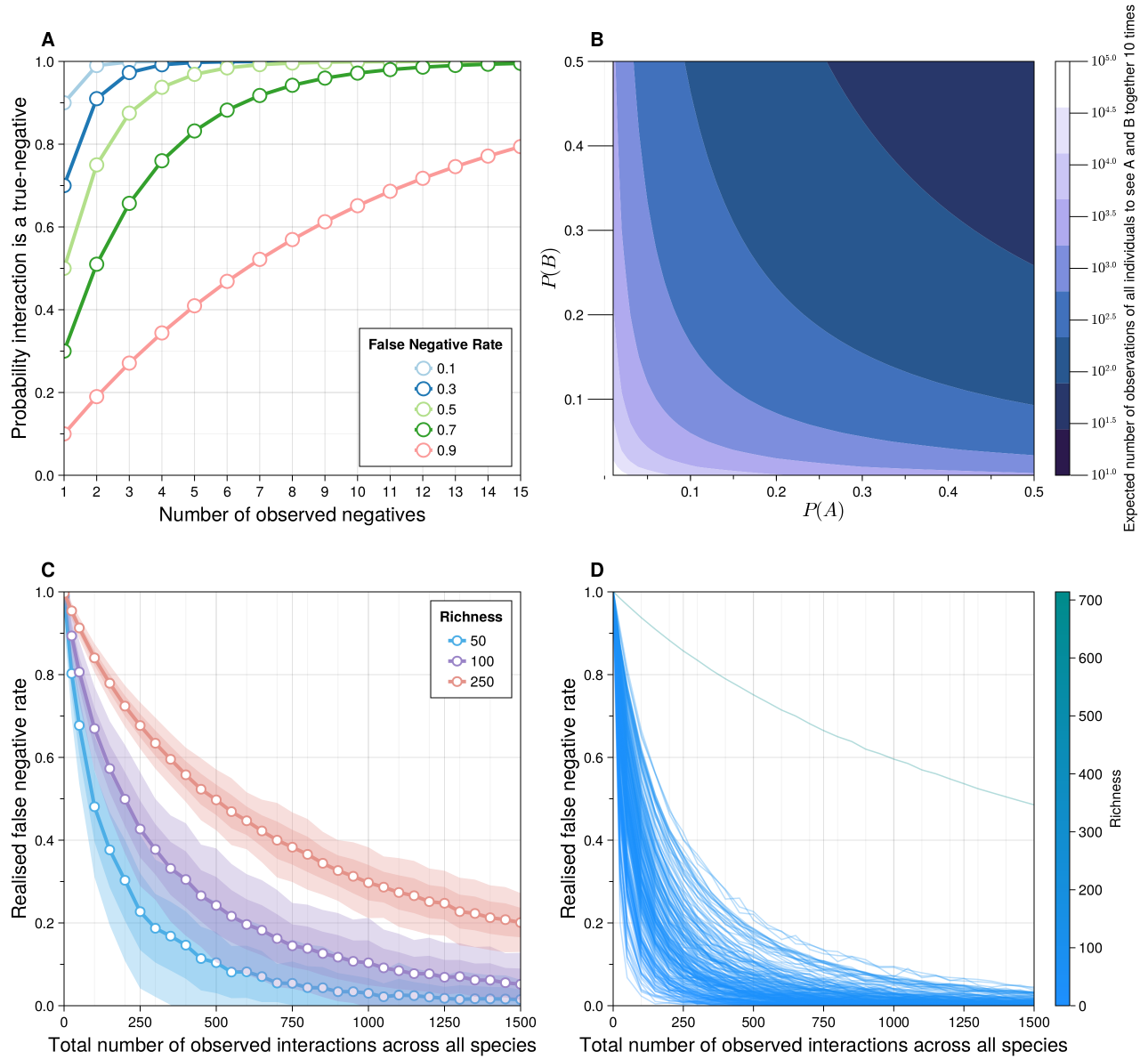


Figure 2: (A) The probability that an observed interaction is a true negative (y-axis) given how many times it has been sampled as a non-interaction (x-axis). Each color reflects a different value of p_{fn} , the false-negative rate (FNR)—this is effectively the cdf of the geometric distribution. (B): The expected needed observations of all individuals of all species (y-axis) required to obtain a goal number of observations (colors) of a particular species, and a function of the relative abundance of that focal species (x-axis). (C): False negative rate (y-axis) as a function of total sampling effort (x-axis) and network size, computed using the method described above. For 500 independent draws from the niche model (Williams & Martinez (2000)) at varying levels of species richness (colors) with connectance drawn according to the flexible-links model (MacDonald *et al.* (2020)) as described in the main text. 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 1 in the first shade and 2 in the second. (D): Same as (C), except using empirical food webs from Mangal database, where richness. The outlier on (D) is a 714 species food-web.

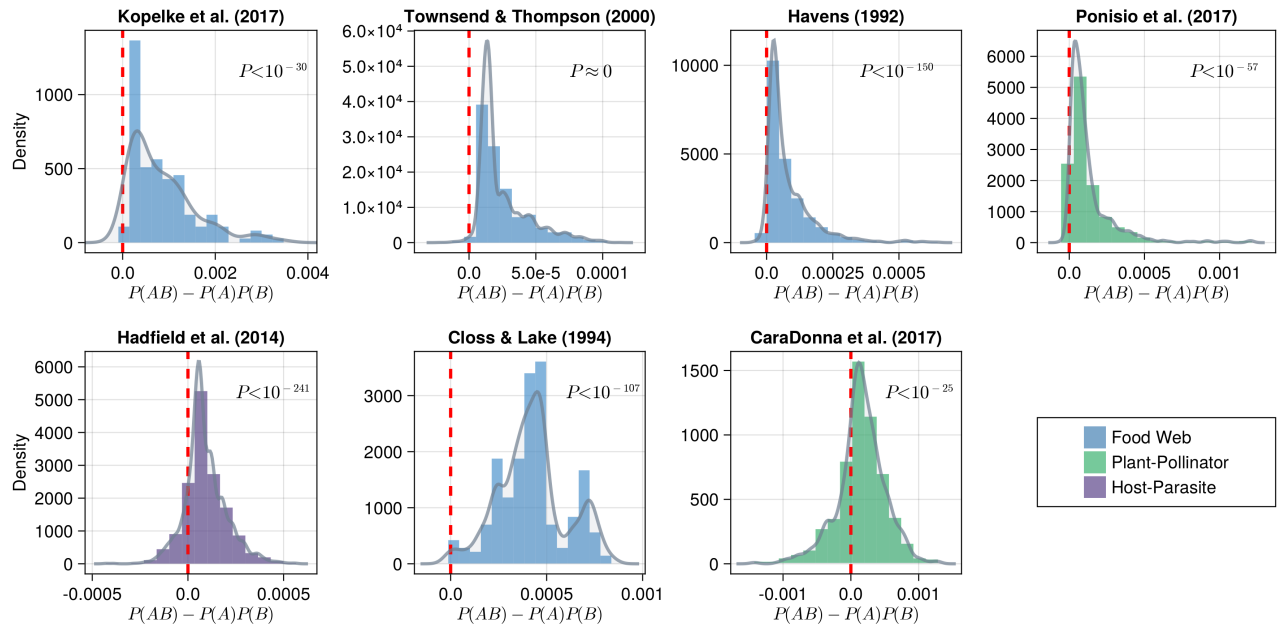


Figure 3: The difference between joint-probability of co-occurrence ($P(AB)$) and expected probability of co-occurrence under independence ($P(A)P(B)$) for interacting species for each dataset. The red-dashed line indicates 0. Each histogram represents a density, meaning the area of the entire curve sums to 1. The continuous density estimate (computed using local smoothing) is shown in grey. The p-value on each plot is the result of a one-sided t-test comparing the mean of each distribution to 0.

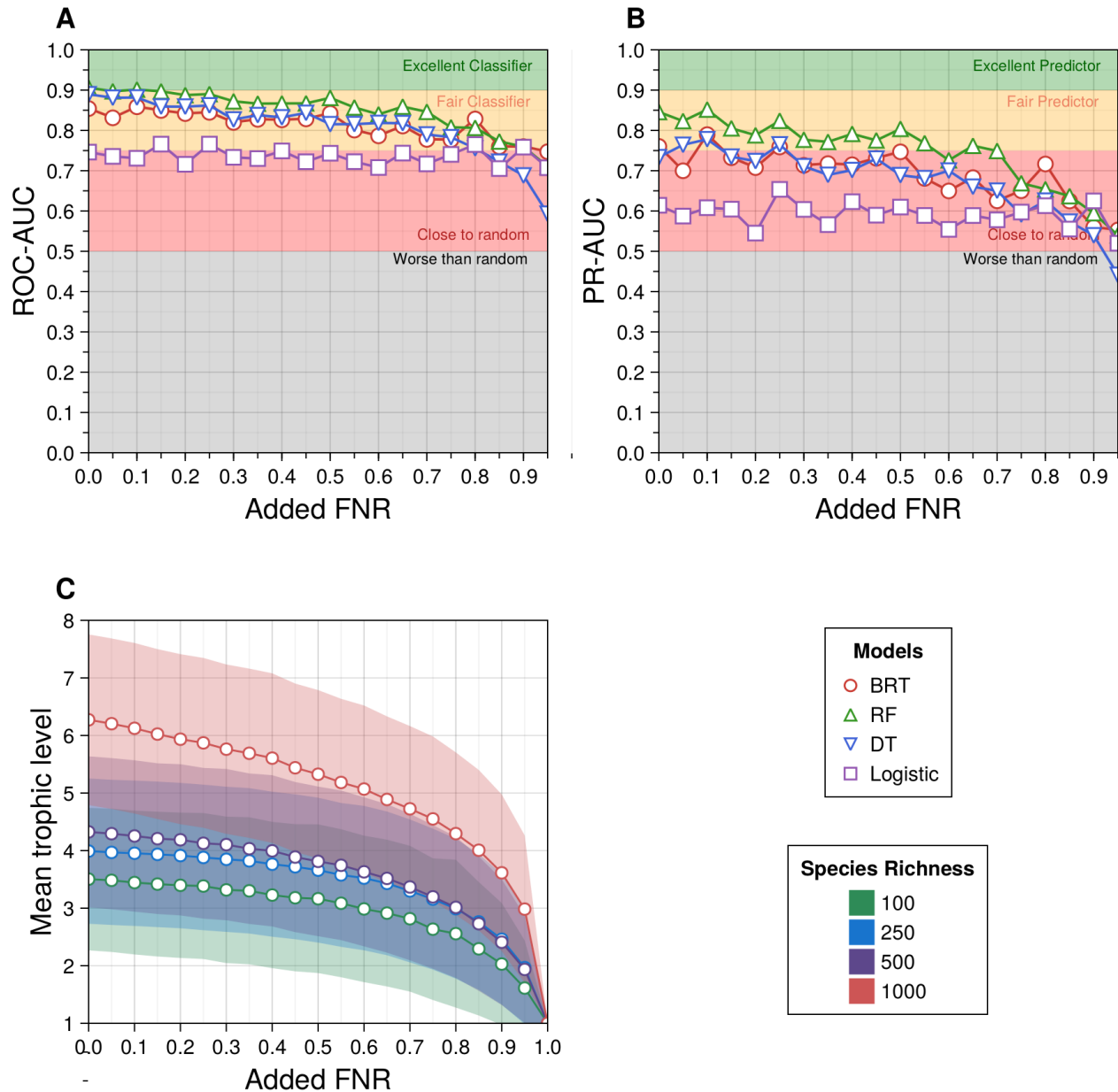


Figure 4: (A) The area-under the receiver-operator curve (ROC-AUC) and (B) The area-under the precision-recall curve (PR-AUC; right) for each different predictive model (colors/shapes) across a spectrum of the proportion of added false negatives (x-axis). (C) The mean trophic-level of all species in a network generated with the niche model across different species richnesses (colors). For each value of the FNR, the mean trophic level was computed across 50 replicates. The shaded region for each line is one standard-deviation across those replicates.