Received: 5 July 2024 | Revised: 8 November 2024 | Accepted: 26 November 2024

DOI: 10.1002/ecy.70014

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Combining observational and experimental data to estimate environmental and species drivers of fungal metacommunity dynamics

Hedvig Kristina Nenzén[1] | **Helen Moor**[2] | **Robert B. O'Hara**[3] | **Mari Jönsson**[1] | **Jenni Nordén**[4] | **Elisabet Ottosson**[1] | **Tord Snäll**[1]

[1]SLU Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

[2]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[3]Department of Mathematical Sciences, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

[4]Norwegian Institute for Nature Research (NINA), Oslo, Norway

Correspondence
Hedvig Kristina Nenzén
Email: hedvig.nenzen@slu.se

Handling Editor: Kathryn L. Cottingham

Abstract

Understanding the distribution and dynamics of species is central to ecology and important for managing biodiversity. The distributions of species in metacommunities are determined by many factors, including environmental conditions and interactions between species. Yet, it is difficult to quantify the effect of species interactions on metacommunity dynamics from observational data. We present an approach to estimate the importance of species interactions that combines data from two observational presence–absence inventories (providing colonization–extinction data) with data from species interaction experiments (providing informative prior distributions in the Bayesian framework). We further illustrate the approach on wood-decay fungi that interact within a downed log through competition for resources and space, and facilitate the succession of other species by decomposing the wood. Specifically, we estimated the relative importance of species interactions by examining how the presence of a species influenced the colonization and extinction probability of other species. Temporal data on fruit body occurrence of 12 species inventoried twice were jointly analyzed with experimental data from two laboratory experiments that aimed to estimate competitive interactions. Both environmental variables and species interactions affected colonization and extinction dynamics. Late-successional fungi had more colonization interactions with predecessor species than early-successional species. We identified several species interactions, and the presence of certain species changed the probability that later-successional species colonized by −81% to 512%. The presence of certain species increased the probability that other species went extinct from a log by 14%–61%. Including the informative priors from experimental data added two colonization interactions and one extinction interaction for which the observational field data was inconclusive. However, most species had no detectable interactions, either because they did not interact or because of low species occupancy, meaning data limitation. We show how temporal presence-absence data can be combined with experimental data to identify which species influence the colonization-extinction dynamics of others. Accounting for species interactions in metacommunity models, in addition to environmental drivers, is important because interactions can have cascading effects on other species.

KEYWORDS
colonization–extinction dynamics, dynamic occupancy model, metacommunity, metapopulation, species interactions, wood-decay fungi

INTRODUCTION

Understanding the distribution and dynamics of species is central to ecology, as it allows us to better understand population declines, predict past and future trends and thus manage biodiversity. Variables such as the environment and dispersal are known to affect species distributions, but interactions between species also affect whether they are able to coexist. However, species interactions are the least understood drivers of species distributions as interactions are often difficult to quantify (Case et al., 2005; Hortal et al., 2015).

Co-occurrence models have been used to study potential species interactions in distribution data for a long time. Co-occurrence models are based on analyzing which species are present together in one location at one time, applying different concepts or methods, including co-occurrence theory (Diamond, 1975; Gotelli et al., 2010), joint species distribution models (Ovaskainen et al., 2017; Pollock et al., 2014), and multi-species occupancy models (Rota et al., 2016; Tobler et al., 2019). However, it is still unclear how co-occurrence is shaped by species interactions (Hortal et al., 2015). To improve these models, various methods supplement the identification of interactions with additional information (Morales-Castilla et al., 2015). For example, body size or other traits can be assumed to reflect trophic interactions (Laigle et al., 2018). Controlled experiments can provide evidence for small subsets of species. However, it is a challenge for co-occurrence analyses to identify known interactions (Barner et al., 2018; Hastings, 1987). Static co-occurrence models have been found to be limited because it is ecologically unclear how co-occurrence measured at a single time relates to species interactions (Blanchet et al., 2020; Thurman et al., 2019).

In contrast to static distribution models, in dynamic metapopulation models, the species distributions result from colonization and extinction events (Levins, 1969), and these can be affected by the presence of other species (Fukami et al., 2010). Dynamics of multispecies communities (metacommunities) are impossible to infer from one snapshot dataset (Götzenberger et al., 2012; Zurell et al., 2018), but temporal metacommunity data can increase our understanding of species distributions and their temporal dynamics (Pagel & Schurr, 2012; Yackulic et al., 2015). Dynamic models are preferred when the species' current distribution is not at equilibrium with the environment, which is typically the case (García-Valdés et al., 2015). In practice, dynamic models have predicted changes through time better than static models (Briscoe et al., 2021) and are thus preferred for prediction and management (Cuddington et al., 2013).

Following which species colonize a location first (predecessors) and later (successors) can help to separate the environmental conditions and species interactions that affect the colonization and persistence of species (Fukami et al., 2010). Here, we use the presence of another predecessor species as an explanatory variable, in the same manner as environmental variables (MacKenzie et al., 2004). A temporal analysis can thus identify species interactions that generate the metacommunity distribution patterns, and the direction of the interaction (Kissling et al., 2012). Therefore, interactions estimated from temporal data can be interpreted as dynamic interactions driving the colonization–extinction processes (Kawatsu et al., 2021; Vázquez et al., 2009). The dynamic colonization and extinction interactions that we estimate can be mapped to well-known ecological interactions. We consider negative colonization interactions to represent competitive interactions where one species impedes the other from establishing. We consider positive colonization interactions to represent facilitation (Bertness & Callaway, 1994). For extinction interactions when both species are present, we consider positive extinction interactions to be competition, where the presence of a species increases the extinction probability of another species.

Despite the general advantages of models for temporal dynamics rather than static patterns of metacommunties, it is a challenge to estimate species interactions from only temporal metacommunity dynamics (Ives et al., 2003; Mutshinda et al., 2009). By leveraging prior knowledge about the system, via "informative prior distributions" of the Bayesian framework (Gelman & Hill, 2006), it is possible to identify additional interactions and reduce uncertainty around estimates. An informative prior distribution will nudge the estimation of the interaction in the direction of the additional data, which is useful when data are sparse. The Bayesian framework also helps in uniting data from different independent sources and scales (Talluto et al., 2016), which is especially valuable for data-hungry dynamic models with the aim to estimate pairwise interactions in both colonization and extinction with presence–absence information. There have been few attempts to supplement dynamic metacommunity models with independent data to infer interactions (see Kotta et al., 2019 for a static occupancy model including known interactions; Clark et al., 2020 for a population abundance model with informative priors).

We aim to present a general approach that utilizes additional independent experimental information to model colonization–extinction dynamics of species in the metacommunity. For example, the succession of wood-decay fungi on a downed log has been both observed in the field (Niemelä et al., 1995; Renvall, 1995) and shown experimentally (Holmer & Stenlid, 1997; Toljander et al., 2006). However, it is not understood to what extent this succession is influenced by log characteristics or interactions between fungal species (Fukami et al., 2010). In a downed log, there is competition for space and resources, and fungi interfere with or parasitize each others' mycelia or they facilitate other species by decomposing the log in a way that makes the environmental conditions suitable for another species (Boddy, 2000). The specific fungal species that occupy a log influences log decay rates (Fukami et al., 2010; Fukasawa & Matsukura, 2021). Therefore, understanding how fungal species interact is important to understand log decay rates and decomposition dynamics of forests, and to develop biological control agents of wood-decay fungi with pathogenic abilities, for example, the root-rot fungi (*Heterobasidion*, Boddy, 2000). Here, we develop a model for metacommunity dynamics of wood-decay fungi that includes estimating interaction strengths from observational temporal colonization–extinction data, supplemented with experimental data.

We test effects of both environmental variables and variables aimed to estimate species interactions, with an aim of distinguishing co-occurrences based on shared environmental preferences from actual species interactions. The successional pathways in wood-decay fungi may result from species having the same environmental preferences for logs of a certain size or decay stage (Jönsson et al., 2008; Moor et al., 2021). These shared environmental preferences might be interpreted as interactions, so what seems like a positive interaction between two species is because they co-occur when the environmental conditions are the same (Ovaskainen et al., 2010; Pollock et al., 2014). Our specific questions are as follows: (1) What is the relative importance of environmental conditions and species interactions in driving the metacommunity dynamics? We expect late-successional species to have both more positive (facilitation; increasing colonization) and more negative (competition; decreasing colonization, increasing extinction) colonization interactions than early-successional species, as they interact with species present in the log. (2) Can informative prior distributions based on experimental data increase the number of identified colonization–extinction interactions?

MATERIALS AND METHODS

Modeling rationale and overview

We developed metacommunity models where the response variable is log colonization or extinction of each individual species. To statistically explain each species' dynamics, explanatory variables were environmental variables and the presence of other species on the log. Thus, the occurrence of each other predecessor species already on the log became an explanatory variable for the modeled species, and the parameter is interpreted as the species interaction. First, we fit species-level models to experimental data, where competitive interactions were estimated by placing species together and observing their survival and growth (Holmer & Stenlid, 1997; Toljander et al., 2006). Next, we fit models to repeated field inventories where the presence–absence of the species on logs provide colonization–extinction data (Figure 1). Finally, we test if including the species interactions estimated from experimental data as informative priors improve the estimation of species interactions in the field data. Specifically, interactions determined from the experimental data were included as informative priors in the estimation of the interactions in the observational data.

Observational data

We pooled data from two studies that surveyed the presence or absence of wood-decay fruit bodies on a total of 1379 dead Norway spruce (*Picea abies*) logs. The logs were surveyed twice, 6 years apart. The study sites were composed of old-growth unmanaged forests where we studied naturally fallen logs. In Brattiken nature reserve (Sweden, 65°25″ N, 16°06′ E), 843 logs were inventoried in autumn of 1997 and 2003 (Edman & Jonsson, 2001; Jönsson et al., 2008). In Rörstrand nature reserve

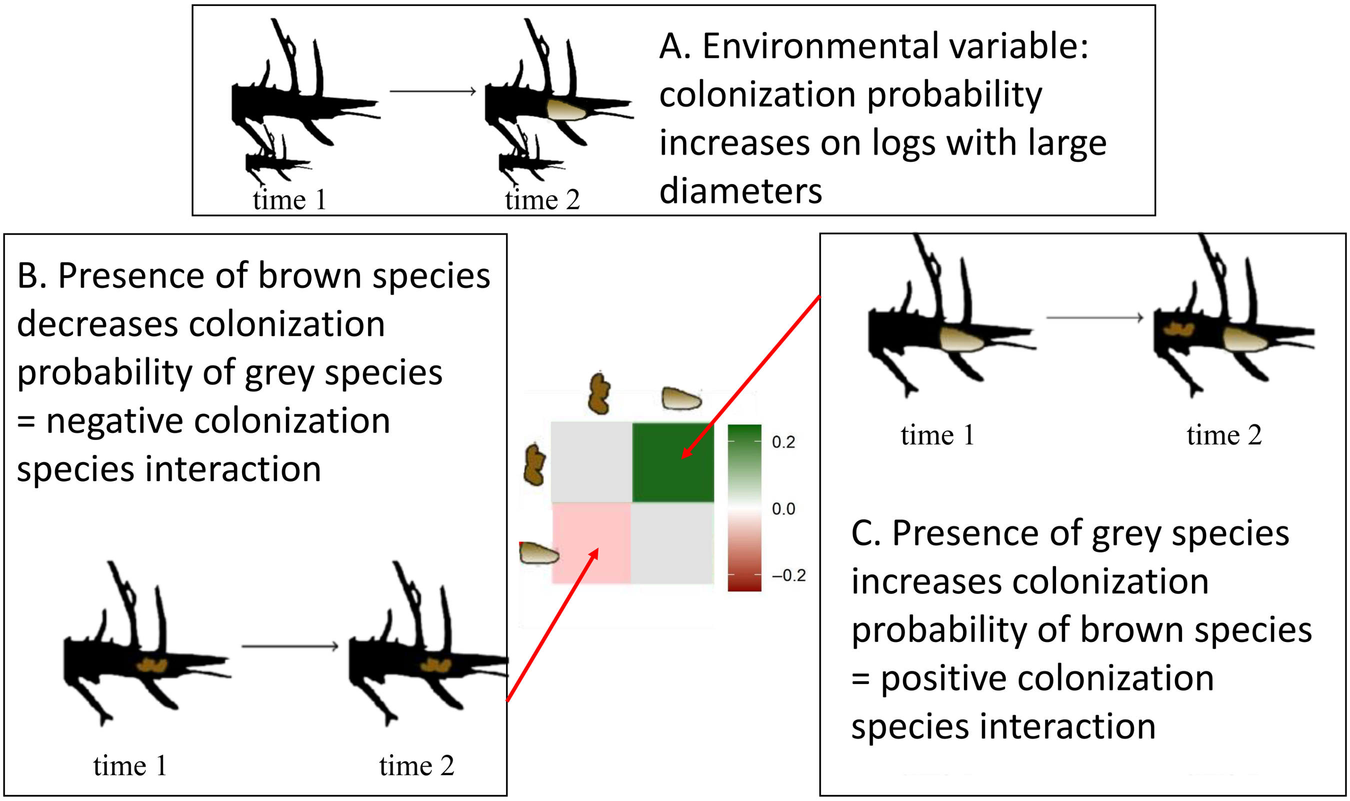

FIGURE 1 Model schema. (A) If the gray species has an increasing higher probability of colonizing logs with larger diameters more often than logs with smaller diameters, there is a positive effect of log diameter on colonization. (B) If the presence of the brown species in the first survey decreases the colonization probability of the gray species in the second survey, it has a negative colonization interaction on the gray species. (C) If the presence of the gray species in the first survey increases the colonization probability of the brown species in time 2, it has a positive colonization interaction on the brown species. The corresponding interaction strengths matrix is shown in the middle. Image credit: Hedvig Nenzén.

(Finland, 60°27″ N, 25°11′ E), 536 logs were inventoried in autumn of 2002 and 2008 (Ottosson et al., 2014; Ovaskainen et al., 2010). Among a total of 210 fungal species identified, only 24 were present in both sites. From those, we chose 12 species that were present on at least 30 logs and grow predominantly on already dead spruce logs (Table 1). Species are rare (average prevalence of 7%), so there were generally few species on each log. In the original data, 16.5% logs had three to eight species, and in the final data, only 6.8% of logs had three to six species. We used additional repeat visit data to account for imperfect detection (as Moor et al., 2021). Dead fruit bodies were excluded from the analysis (but see similar interaction results including dead fruit bodies in Appendix S1: Table S1, Figure S5). We included two log-level variables that are well-known to explain species occurrences: log decay stage (Appendix S1: Table S2) and log diameter (cm) (Appendix S1: Figure S3). All environmental variables were transformed to mean zero and unit standard deviation (subtracting the mean and dividing each value by the standard deviation). We also included the decay stage variable squared, as some species are most frequent (in terms of occupancy, i.e., number of presences divided by number of logs) in logs of intermediate decay.

Experimental data

To reduce uncertainty and improve estimates of species interactions, we leveraged prior information from experiments that estimated interactions. We identified two published studies that placed wood chips or discs inoculated with known species together, and recorded growth rates and survival. One experiment tested which species survived or went extinct when combining 1 to 16 wood-decay fungi (Toljander et al., 2006), and the other recorded how many sectors of wood substrate species were able to capture from each other (Holmer & Stenlid, 1997). We reasoned that these microcosm dynamics contained information on the dynamics of colonization and extinction observed in the field (See Appendix S1: Experimental data and

TABLE 1 Rows show species-specific colonization and extinction events and rates, mean occupancy in both surveys (number of presences/number of logs), mean decay stage (% dead wood of log), and mean diameter of logs (cm) where species are present in the both surveys, and the type of rot mechanism utilized by the species (brown or white rot).

Species	No. non-colonizations	No. colonizations	No. extinctions	No. non-extinctions	Probability of colonization	Probability of extinction	Prevalence (% presences on all logs)	Mean diameter (cm)	Mean decay stage	Decay type
Fomitopsis pinicola	1227	70	34	48	0.05	0.41	7.2	25.6	22.7	Brown
Heterobasidion parviporum	1307	36	18	18	0.03	0.50	3.3	24.9	33.4	White
Trichaptum abietinum	1068	98	144	69	0.08	0.68	13.8	25.3	20.4	White
Phlebia centrifuga	1351	13	13	2	0.01	0.87	1.1	35.3	25.8	White
Phellinidium ferrugineofuscum	1308	23	40	8	0.02	0.83	2.9	28.8	22.5	White
Fomitopsis rosea	1336	8	21	14	0.01	0.60	2.1	37.5	29.4	Brown
Postia caesia	1265	71	38	5	0.05	0.88	4.3	18.7	22.5	Brown
Neoantrodia serialis	1191	99	64	25	0.08	0.72	7.7	22.1	30.6	Brown
Fuscoporia viticola	1010	127	94	148	0.11	0.39	18.8	17.6	34.5	White
Gloeophyllum sepiarium	1320	10	39	10	0.01	0.80	2.5	27.3	47.0	Brown
Skeletocutis brevispora	1365	6	5	3	0.00	0.62	0.6	28.9	35.9	White
Phellopilus nigrolimitatus	1029	101	65	184	0.09	0.26	19.4	28.0	70.1	White

Note: The species are ordered in increasing successional stage in the same order throughout the manuscript.

informative prior estimation). Both experimental datasets together contained data on 20 of the total 132 possible pairwise (interspecific) interactions (Appendix S1: Figure S1).

Metacommunity dynamics modeling framework with environmental and species variables

For each successor species, we modeled colonization and extinction dynamics driven by environmental conditions and interactions with other predecessor species (Figure 1) (Kery & Royle, 2020). Each log is a resource unit "island" or independent patch in the meta-community perspective, and the scale at which fungi interact. This clear, well-defined scale helps avoid scale-dependency issues that may hide interactions (Münkemüller et al., 2020).

The colonization–extinction dynamics of all 12 species were modeled independently one after another, and log characteristics and presences of other predecessor species on the same log were included as explanatory variables. Specifically, the colonization probability (c) of species i on log n in time $t+1$ was modeled as being linear on the logit scale:

$$\mathrm{logit}(c_{i,n,t+1}) = \alpha_c + \sum_k \beta_{i,k} X_{k,n,t} + \sum_j \delta_{i,j} Z'_{j,n,t}, \tag{1}$$

where α_c was the intercept, $\beta_{i,k}$ was the effect of environmental variables, and $\delta_{i,j}$ was the effect of other species j presence on colonization probability of the species i. X was k environmental variables (decay stage, log diameter), and Z' was the presence or absence of other species j (binary 0 or 1) on each log n in time t (Z was occurrence of species i).

The extinction probability (e) of species i on log n in time t was modeled in a similar way:

$$\mathrm{logit}(e_{i,n,t+1}) = \alpha_e + \sum_k \gamma_{i,k} X_{k,n,t} + \sum_j \varepsilon_{i,j} Z'_{j,n,t}, \tag{2}$$

where α_e was the intercept, $\gamma_{i,k}$ was the effect of environmental variables on extinction probability of species i and $\varepsilon_{i,j}$ the effect of other species j presence on extinction probability of species *i*. For both processes, the intercepts are the baseline log-odds of colonization–extinction of a species in absence of other species and under average environmental (abiotic) conditions. Species occupancy ψ in the following year was.

$$\psi_{i,n,t+1} = (1 - Z_{i,n,t})c_{i,n,t+1} + Z_{i,n,t}(1 - e_{i,n,t+1}). \quad (3)$$

For all species, models included four environmental variables, both linear and quadratic log diameter and decay stage, and 11 species variables, resulting in 15 colonization variables and 15 extinction variables. The models were fitted using a Bayesian approach, with the prior distributions described below. The estimation was carried out using Markov chain Monte Carlo simulations with the R library jagsUI (Plummer, 2003; R Core Team, 2018). Three MCMC chains were run for each species, using 50,000 iterations of three chains, of which 10,000 were discarded as burn-in. Model evaluation was carried out through visually examining the posterior chains, and checking if the potential scale reduction statistic ($\hat{R}$) was below 1.1, which indicates chain mixing (Gelman & Hill, 2006).

Estimating posterior distributions of species interactions in experimental data

We estimated the posterior distributions of the colonization and extinction interaction parameters (δ_{ij} and $\varepsilon_{i,j}$, Equations 1 and 2) from experimental data, so that they could subsequently be used as informative prior distributions for these parameters in the modeling of the observational data. The Toljander et al. (2006) data contained species presences and absences; therefore, we used exactly the same Bayesian model with Bernoulli distributions that was used to estimate posteriors from the observational data (Equations 1 and 2). However, to reflect the fact that the response variable in Holmer and Stenlid (1997) was a count (number of wood disc sectors occupied by a species), we instead used a Poisson distribution. We used the means of the estimated posterior distributions (i.e., the species interactions) as informative priors when updating the modeling of the observational data. We did not use the variance of the estimated posterior distributions as the variance of the informative priors were set by the stochastic search variable selection (SSVS) procedure (see below).

Selection of environmental and species interaction variables

Given the large number of environmental and species variables, we used SSVS to select important variables for each species model (George & McCulloch, 1993; O'Hara & Sillanpää, 2009). SSVS was a robust way to combine variable selection and informative priors. As the experimental data and the observational data are collected differently, the posteriors from the experimental data could potentially be poor priors for the observational data if used directly as priors. We thus took a more cautious approach in which the experimental data changes the prior probability of an effect, which we can implement in SSVS. Instead of using an informative prior for a variable that may be irrelevant for the modeled process, SSVS uses an informative prior that may or may not be relevant. SSVS is also a suitable alternative because it has been shown to select among 60 potentially important covariates (George & McCulloch, 1993) and is a one-step selection approach because the irrelevant variables have no effect on results.

SSVS estimates the probability that individual variables should be included in a regression model. To do so, it uses two normally distributed prior distributions for each variable, but with different variances. More specifically, SSVS uses "spike and slab" prior distributions; the wide slab distribution (variance $\sigma^2 = 1.4$) (Northrup & Gerber, 2018) is selected for variables that should be in the model, and the spike distribution ($\sigma^2 = 0.01$) is selected for the irrelevant variables. If the inclusion of the variable is supported by the data, there will be higher probability for the wide slab prior than the spike prior, and vice versa. We set the prior probability of a wide prior, that is, a non-zero interspecific interaction, to 0.2 (as Mutshinda et al., 2009). The MCMC sampling then provides an estimate of the posterior odds of whether a variable should be in the model. Finally, we estimate the amount of evidence for including or not including a variable in the model, the Bayes factor (BF), which is the ratio of the posterior odds and prior odds. We compare the prior odds of a (environmental or species) variable being important (set to 0.2, see above) to the posterior odds estimated by the model. If the quadratic variable was selected by SSVS, we always included the corresponding original linear variable.

Combining informative priors and variable selection to simultaneously identify important interactions and select variables

We tested if informative prior distributions based on experimental data can increase the number of identified species interactions. To improve the estimation of species interactions, we utilized informative prior distributions obtained from combining interaction estimates from the experimental data with the SSVS variable selection method. The mean (μ) of an informative prior for each pairwise species interaction was taken from the experimental estimate (i.e., the posterior mean of $\delta_{ij} \vee \varepsilon_{i,j}$, Equations 1 and 2). If there was no experimental data for an interaction, the non-informative prior mean was zero. The two prior variances (σ^2) were set in the SSVS (wide or narrow priors), for both informative and non-informative priors. Thus, for example, say the posterior estimate of one species' effect on another was 0.5 in the experimental data. In that case, the slab prior was N(0.5, 1.4) and the spike prior was N(0.5, 0.01). If no experimental data were available for a species pair, the priors would be N(0, 1.4) and N(0, 0.01), respectively. We present results from fitted models combining informative priors for the 20 experimentally tested species interactions with non-informative priors for remaining species interactions, and for non-informative priors for all species.

Effects of the environment and species interactions on colonization and extinction probabilities

We present results on colonization and extinction probabilities for each species based on partial regression plots for continuous environmental variables (linear and squared terms were combined if both were used). A species interaction strength was quantified as the estimated value of the parameter associated with the species variable (i.e., the presence and absence of another species on a log). However, to obtain the species interaction on an interpretable scale, the interaction was defined as the partial effect of the interaction parameter of the species on the colonization and extinction dynamics on the modeled species average predictive difference, (Gelman & Hill, 2006). In other words, the interaction strength was calculated as the difference of a species' probability of colonizing a log without any species minus the probability of colonizing a log if the interacting species was present. When calculating the interaction strength, we set the environmental variables to their mean (zero as they were scaled). Species interactions δ (for colonization) and ε (for extinction) can be zero (no interaction), positive (presence of species increases the probability of colonization or extinction of another species), and negative (presence of species decreases the probability of colonization or extinction of another species). We present all interaction strengths in a S × S community matrix (Clark et al., 2020; Ives, 2003), and also as the percentage difference of how the presence of the predecessor species changes the colonization or extinction probability of the successor species. For example, if the probability of colonizing an empty log is 0.05, and with a certain predecessor species it is 0.1, the percentage increase is 50%.

We carried out variance partitioning to assess whether the selected environmental or species variables for each species contributed the most variance to the results. To do so, we multiplied the squared parameter estimate for each variable by the variable's variance, and divided by the summed variance of all variables. The variance was calculated separately for species and environmental variables, and for colonization and extinction models.

RESULTS

Drivers of metacommunity dynamics

The metacommunity dynamics of all species were mostly affected by environmental variables, but species interactions had a minor effect on later successional species (Figure 2). Environmental covariates explained all variance in colonization and extinction for the early successional species such as *Fomitopsis pinicola* and *Trichaptum abietinum*, while species variables explained around 10%–20% of the variance of later successional *Neoantrodia serialis* and *Phellopilus nigrolimitatus*. For most species, multiple environmental and species variables were important (Figure 2). However, for rare species with low occupancy no variables were selected as important, possibly due to sparse data.

Environmental effects

Five species showed an increasing probability of colonizing logs with larger diameters, including *P. nigrolimitatus*, while *Fuscoporia viticola* colonized smaller-diameter logs (Figure 3a, Appendix S1: Figures S8–S19). Eight of the 12 species had increasing probability of colonizing a less-decayed log, especially the early-successional *F. pinicola* and *T. abietinum* (Figure 3b). For extinction, there was weaker evidence for environmental variables influencing the dynamics. *Fomitopsis pinicola* and *P. nigrolimitatus* had an increasing probability of going extinct from smaller logs (Figure 3c). Several species had an increasing probability of going extinct from a highly decayed log (Figure 3d).

Species interactions

Species had both positive and negative colonization interactions with other species, whereas only two species had extinction interactions (Figures 4a and 5a).

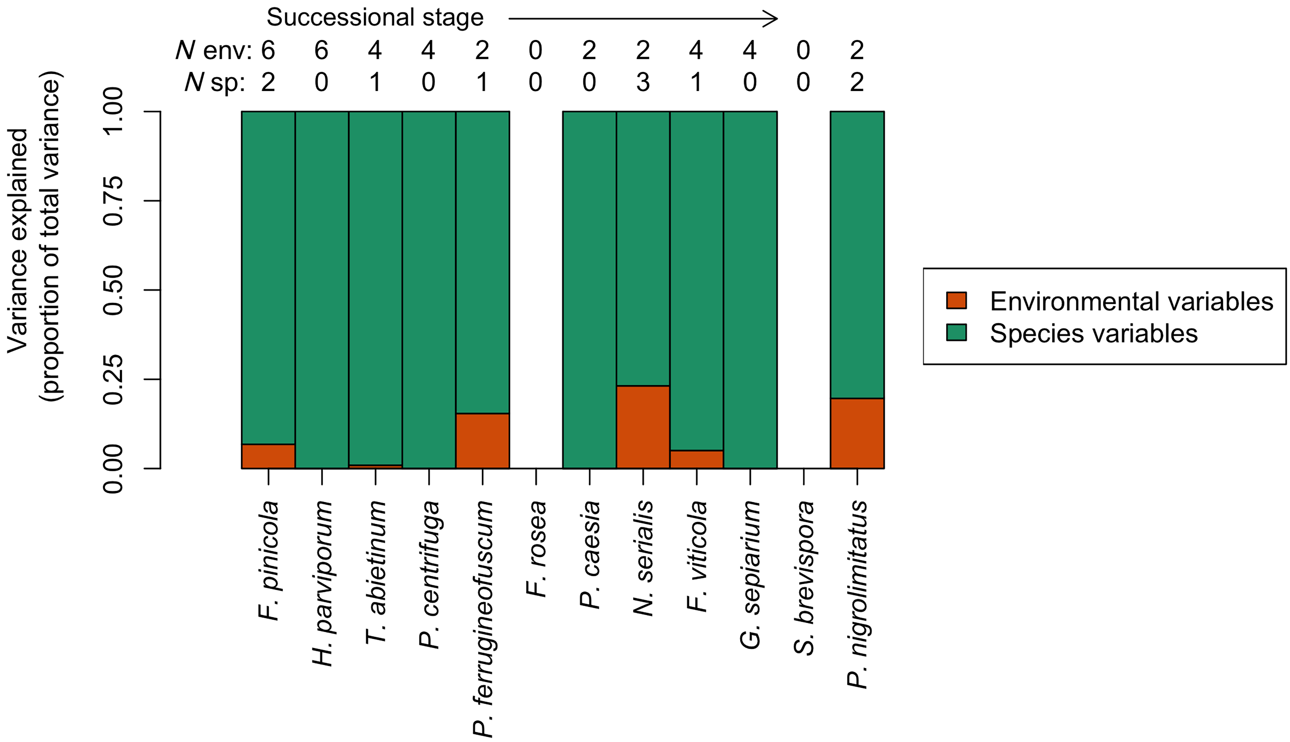

FIGURE 2 Variance partitioning for both colonization and extinction dynamics of the study species ordered from early (left) to late successional. The numbers above each species bar refer to the number of environmental (*N* env, including quadratic variables) and interacting species (*N* sp) variables that were important for explaining dynamics.

If *F. pinicola* and *F. viticola* occurred on a log 6 years earlier, this increased the probability of colonization of two other successor species (Figure 4a, with informative priors). For example, presence of *F. pinicola* increased colonization probability of *N. serialis* by 512% (Figure 4c). *Trichaptum abietinum* had a negative effect on the colonization probability of successor species, and its presence decreased the probability of colonization of *Phellinidium ferrugineofuscum*, *F. viticola*, and *P. nigrolimitatus* by 70% (Figure 4c). One or two predecessor species usually interacted with successor species, and later-successional species were possibly affected by more species than early successional species. Fewer interactions were identified for extinction dynamics, and presence of *F. viticola* increased the extinction probability of *F. pinicola* by 14%, and *P. nigrolimitatus* increased the extinction probability of *N. serialis* by 61% (Figure 5a,c).

Changed interactions when adding independent experimental information

Adding information from experiments in the form of informative prior distributions for the pairwise interactions influenced the final estimated interactions for three species pairs associated with colonization and extinction. With informative priors, two additional interactions were identified, one was dropped for colonization interactions (Figure 4c,d), and one additional interaction was identified for extinction interactions, compared with estimates from models with non-informative priors (Figure 5c,d). For example, the laboratory study (Holmer & Stenlid, 1997) found a strongly negative effect of *P. viticola* on the colonization probability of *F. pinicola* (Appendix S1: Figure S1). This informative prior increased the evidence that *P. viticola* had a negative effect on *F. pinicola* colonization, so that it was included in the final model (BF >3, Appendix S1: Figure S6). In contrast, the informative prior removed an interaction that was identified with non-informative priors. There was a positive interaction of *F. pinicola* on probability of *P. viticola* colonization in both the prior and the interaction estimated with non-informative priors (Appendix S1: Figure S7). However, the value of the prior (0.7, from experimental data) was lower than the interaction estimated with non-informative priors (1.5). Therefore, the informative prior pulled the estimate closer to zero and away from the observational data estimate, weakening the evidence and making the interaction unimportant as defined by BF <3. For extinctions, the informative priors

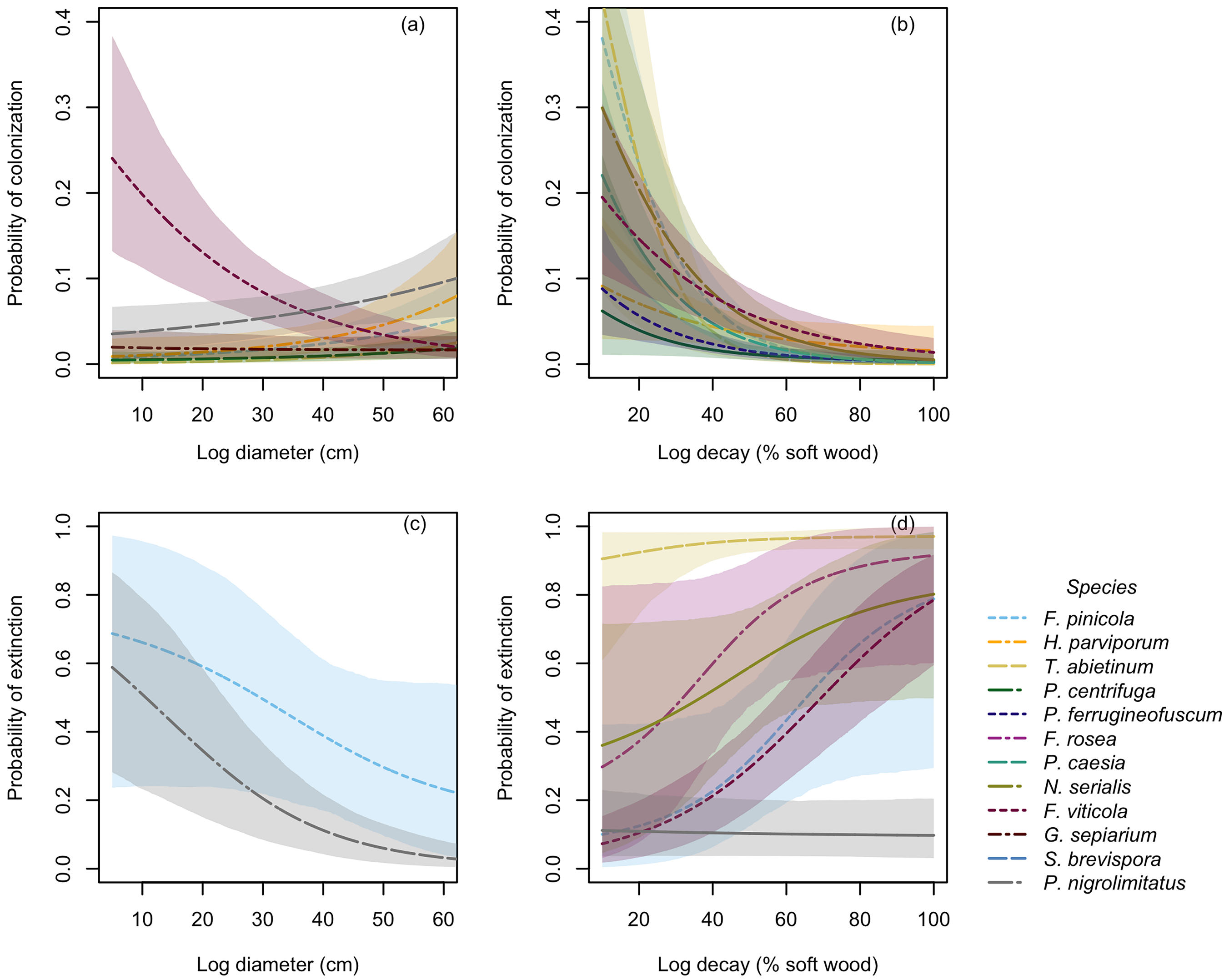

FIGURE 3 Partial probability of each species colonizing (a,b) and going extinct from (c,d) a log with log diameter (a, c) and decay (b,d). Lines only show species with important relationships as identified by SSVS model selection. Shown are also 95% Bayesian credible intervals.

identified one additional interaction compared with using only observational data (Figure 5c,d).

DISCUSSION

This study provides an approach to more accurately disentangle environmental and species interaction drivers of metacommunity dynamics by using independent experimental data. Previous approaches have been suitable to identify interactions between a limited number of other species (Dubart et al., 2019; Rota et al., 2016). Few studies have analyzed directional interactions between >10 species (Clark et al., 2020; Kawatsu et al., 2021; Ottosson et al., 2014), because the number of parameters increases strongly whereby the statistical inference becomes difficult. Other studies of large metacommunities have applied statistical approaches that examine residual correlation in species co-occurrences (Ovaskainen et al., 2010; Tobler et al., 2019). However, such approaches cannot easily combine observational and experimental data. Here, we show how to analyze a large number of potentially interacting species by combining informative prior distributions and variable selection in a Bayesian inference framework. SSVS was a rapid way to select between many variables, which allows estimating directional interactions in even larger communities.

The informative priors are a tool to include additional knowledge identified in experiments. However, to extrapolate from experiments to observational data, one must assume that the same mechanisms occur in nature as in the experiment. We assume this to be the case in our system because fungi interact with specific species chemically through hyphal interference (Boddy, 2000), and that

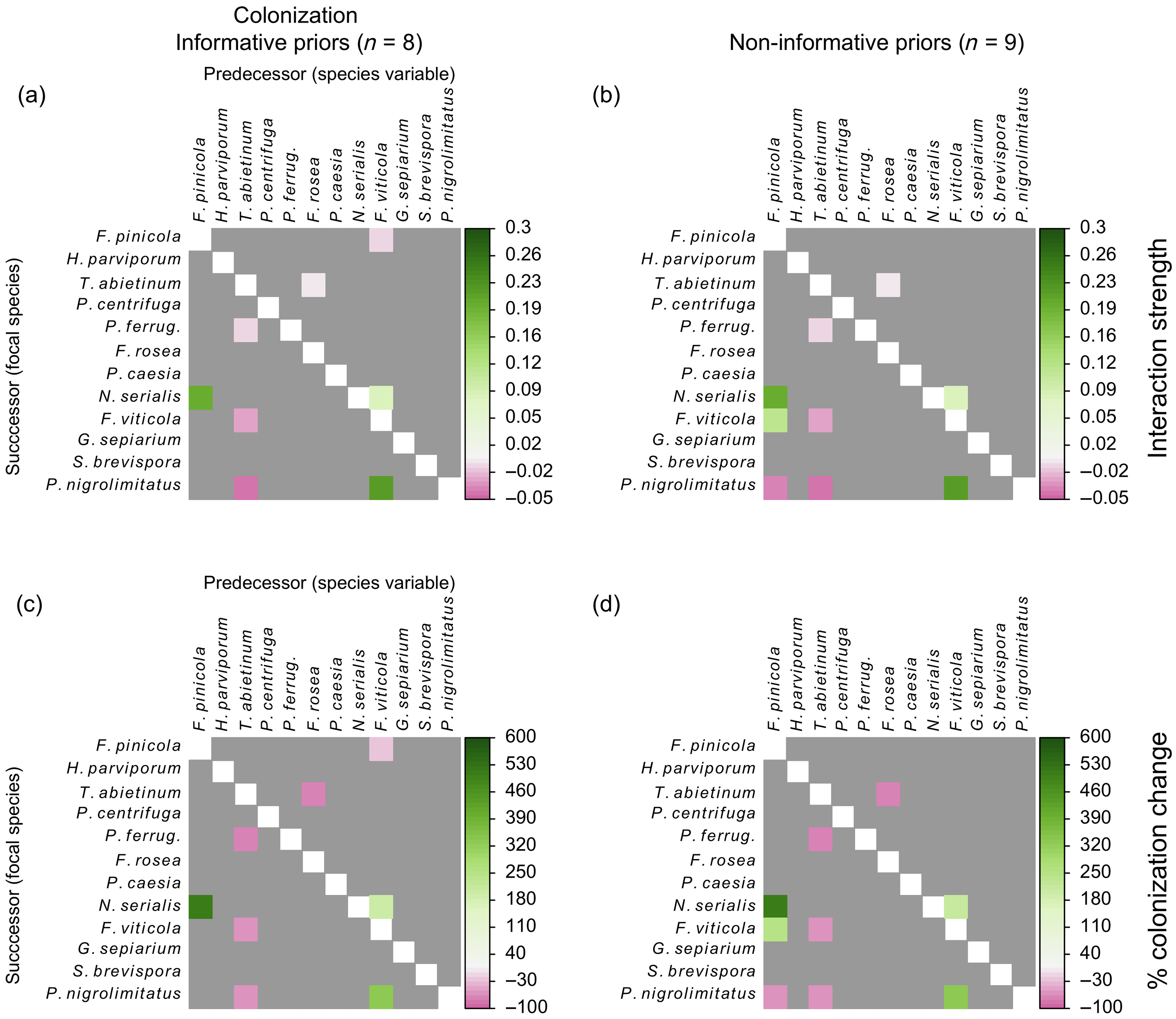

FIGURE 4 Colonization interaction strengths estimated with (a, c) informative and (b, d) non-informative priors. Rows indicate how the colonization probability (color shading) of each successor species *i* is affected by the presence of predecessor (variable) species *j* (columns). The gray boxes indicate that there was no evidence for that interaction (BF < 3). *n* indicates the number of important interactions identified by SSVS model selection. The interaction strengths (a, b) are calculated as the species *i* predicted probability of colonizing an empty log minus the predicted probability of colonizing a log occupied by species *j*. The percentage colonization changes (b, d) are calculated as the difference in probability of colonizing a log with and without the predecessor species.

the identity of the interacting species in these chemical interactions would be the same in nature and experiments. This assumption is supported because the experimental species interactions were largely in the same direction as estimated observational interactions (Appendix S1: Figure S2). As the interactions are chemical, there is no introduced bias that the smaller-scale experiments would only represent interactions in smaller logs. Therefore we argue that in this system it is reasonable to extrapolate from interaction experiments, and we also show results without informative priors. However, for other species groups simple experiments may not be informative of more complex systems with indirect and higher-order interactions in the field (Barner et al., 2018).

One limitation of our study is that inferences from informative priors need to be interpreted carefully when there is little observational data. In the Bayesian framework, abundant observational data usually overwhelms informative priors; thus, the observational data determines the estimated interaction. In the case of sparse observational data as here, informative priors added three interactions that could not be identified with

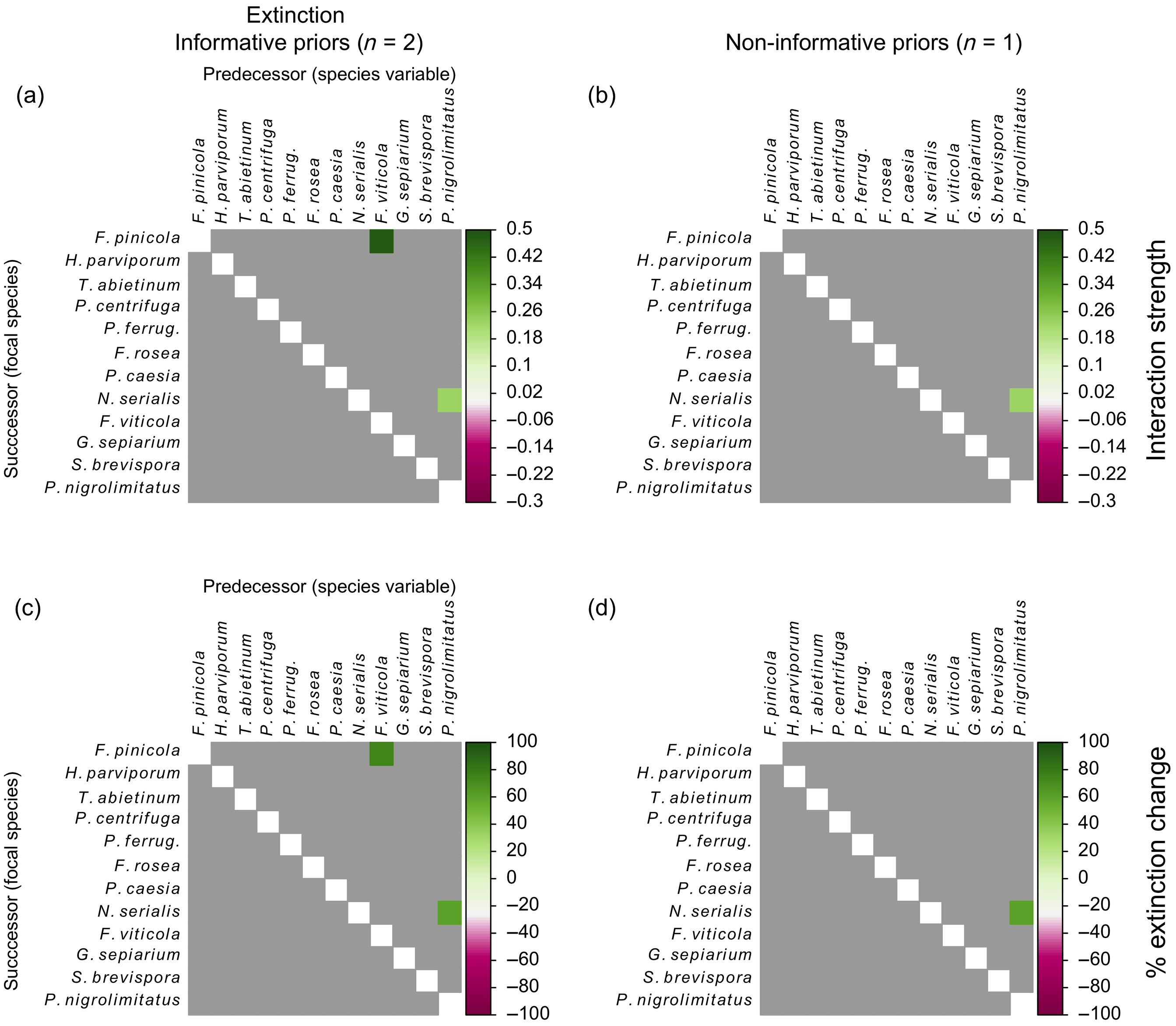

FIGURE 5 Extinction interaction strengths estimated with (a, c) informative and (b, d) non-informative priors. Rows indicate how the extinction probability of each successor species *i* is affected by the presence of predecessor (variable) species *j* (columns). The interaction strengths (a, b) are calculated as the species *i* predicted probability of going extinct from an empty log minus the predicted probability of going extinct from a log occupied by species *j*. The percentage changes (b, d) are calculated as the difference in probability of going extinct from a log with and without the predecessor species.

observational data alone. However, for one interaction, the informative prior overwhelmed the posterior based on the observational data, making the posterior estimate non-significant (based on BF <3). In cases where there is enough information in the observational data about the interaction, there may be little gained from using informative priors, so non-informative priors are probably preferred.

One of the goals in ecology is understanding the relative strength of interspecific interactions and environmental conditions in shaping metacommunity dynamics. The metacommunity approach allows us to separate colonization and extinction dynamics, and we provide evidence that both biotic species interactions and abiotic environmental variables affect the colonization dynamics, while extinctions are mostly explained by environmental conditions. The colonization dynamics of most species were mostly explained by environmental variables (as Norberg et al., 2019). Even though they were few, some identified species interactions were strong, for example, if *F. pinicola* was present on a log, the chance of observing *N. serialis* increased by 500%.

As hypothesized, late-successional fungi had more colonization interactions with predecessor species than early-successional species. This is probably because late-successional fungi are forced to invest more in competition compared with early-successional communities that colonize a fresh resource (Fukasawa & Matsukura, 2021).

We found interactions between 6% of species pairs (8 of 132 possible interactions). Some species had multiple positive or negative interactions with others that could yield a successional pathway. *Fomitopsis pinicola* had a positive effect on the colonization of two other species, including *F. viticola*, which in turn had a positive effect on two other species. *F. pinicola* occurrence is known to be positively correlated with the presence of other species (Ylisirniö et al., 2009) and thus overall log biodiversity (Pouska et al., 2013). In an analysis of metacommunity dynamics similar to this one but with DNA-based inventories (Norberg et al., 2019), primary colonizer *F. pinicola* had a positive effect on *N. serialis*, just as we found (but see Kubartová et al., 2015). *Fomtopsis viticola* increased the probability that two other species colonized the log and decreased the probability that one other species went extinct from the log, however this might be a statistical artifact as it often occupies smaller, crown parts of the log (Renvall, 1995) and hence may coexist by spatial separation. At the other extreme, *T. abietinum* had a negative effect on the colonization of three species. Other studies have also found that logs with *T. abietinum* were less likely to host *P. nigrolimitatus* and *F. viticola* (Ovaskainen et al., 2010; Ylisirniö et al., 2009). Overall, there were fewer species interactions for extinction than colonization.

Our results support the idea that a dynamic metacommunity model can better disentangle a random co-occurrence from a species interaction that results in a colonization or extinction. Compared with a snapshot analysis of the same data (Ottosson et al., 2014), our method identified five additional interactions. Previous studies have found a positive (Ottosson et al., 2014; Ovaskainen et al., 2010) or negative (Weslien et al., 2011) association between *F. pinicola* and *T. abietinum*. Our dynamic analysis shows that they do not interact despite often co-occurring on the same log (Appendix S1: Figure S4), but instead that they co-occur because they have similar environmental preferences (large-diameter logs) and occupy different parts of the log. They may also be able to coexist because they have different decay mechanism, as *F. pinicola* is a brown-rot species and *T. abietinum* is a white-rot species (Ovaskainen et al., 2010). The same could be true for interactions between *F. rosea* and *P. nigrolimitatus* and *N. serialis* identified in Ottosson et al. (2014), which in our case was explained by shared environmental effect (positive effect of log decay stage on extinction). Our results suggest that data on distribution dynamics is more indicative of species interactions than static distribution data (Briscoe et al., 2021).

There are some limitations to this work. Species interactions were difficult to identify because both observational and experimental data were limited. The few species interactions identified may be because too few logs were inventoried leading to few presences for these rare species (low occupancy, Table 1). This generated a small amount of data, which limits our statistical power to estimate effects (Rajala et al., 2019). Even though it is known that interactions among wood-decay fungi take place within the log, Ovaskainen et al. (2016) found fewer interactions at the log scale than at larger scales, and attribute this to lower statistical power at the smaller scale with fewer co-occurrences. There is also more stochasticity at the smaller log scale than at larger scales (Norberg et al., 2019). The 6-year inventory gap might be too long, giving colonizers time to go extinct so they are never observed. Another limitation is that our model only considers pairwise interactions. Indirect and higher-order interactions could be important drivers of metacommunity dynamics (Clark et al., 2020), but studying species interactions between all species would raise the number of interactions exponentially. We focus on pairwise interactions as only 6% of logs have more than two species.

The few interspecific interactions identified may also be explained by the use of fruit body data, which results in the detection of fewer species per log compared with using DNA-based surveys (Kubartová et al., 2012; Saine et al., 2020). Our limited number of species presences may therefore have led to a lower statistical power to infer interactions, as compared with species present only as DNA (representing presumably mostly living or dead mycelium) (Saine et al., 2020). DNA data has been shown to yield consistent interactions, but also greater number of species-to-species associations compared with fruit body data (Saine et al., 2020). Therefore, including many species detected as DNA traces in logs may lead to more spurious interactions between species that are actually not interacting (Saine et al., 2020). Interactions inferred with fruit body data are less spurious because species typically form fruit bodies only after occupying sufficient space and resources within dead wood (Ovaskainen et al., 2013), and during this growth they are also more likely to interact with other species (Kubartová et al., 2012).

In summary, we provide an analytic approach that combines temporal presence–absence data with experimental data, to understand how both environmental conditions and species interactions shape metacommunity dynamics. Accounting for species interactions is important because interactions change species distributions and can have cascading effects on other species. Knowing which and how species interact is important for managing biodiversity (Harvey et al., 2017; Niemelä et al., 1995). Herein, *F. pinicola* and *F. viticola* had positive effects on colonization probabilities of other successor species. *Fomitopsis pinicola* is an important species for the old-forest forest indicator species *Pycnoporellus fulgens* (Nitare, 2019) and parasitized by the critically endangered *Antrodiella citrinella* (SLU Artdatabanken, 2020; Wieners et al., 2023). Combining observational and experimental data in a Bayesian framework to identify species interactions, as done here, can improve ecological understanding in other communities.

AUTHOR CONTRIBUTIONS

Hedvig Kristina Nenzén, Robert B O'Hara, and Tord Snäll conceived the ideas. Hedvig Kristina Nenzén, Robert B O'Hara, Helen Moor and Tord Snäll designed methodology; Jenni Nordén, Mari Jönsson, and Elisabet Ottosson designed the data collection; Hedvig Kristina Nenzén analyzed the data; Hedvig Kristina Nenzén led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

This study was funded by grant 2019-00353 from Formas and grant 2019-03795 from the Swedish Research Council to Tord Snäll. Jenni Nordén was funded by the Norwegian Institute for Nature Research (NINA). The computations were enabled by resources provided by the Swedish National Infrastructure for Computing (SNIC) at UPPMAX partially funded by the Swedish Research Council through grant agreement no. 2018-05973, and we especially thank Douglas Scofield for his assistance with software. Thanks to Matt Low for statistical support. We thank three anonymous reviewers for improving the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Nenzen, 2025) are available in Zenodo at https://doi.org/10.5281/zenodo.14718612.

ORCID

Hedvig Kristina Nenzén https://orcid.org/0000-0002-0189-4283

Jenni Nordén https://orcid.org/0000-0001-8894-5815

REFERENCES

Barner, A. K., K. E. Coblentz, S. D. Hacker, and B. A. Menge. 2018. "Fundamental Contradictions among Observational and Experimental Estimates of Non-trophic Species Interactions." *Ecology* 99: 557–566.

Bertness, M. D., and R. Callaway. 1994. "Positive Interactions in Communities." *Trends in Ecology & Evolution* 9: 191–93.

Blanchet, F. G., K. Cazelles, and D. Gravel. 2020. "Co-Occurrence Is Not Evidence of Ecological Interactions." *Ecology Letters* 23: 1050–63.

Boddy, L. 2000. "Interspecific Combative Interactions between Wood-Decaying Basidiomycetes." *FEMS Microbiology Ecology* 31: 185–194.

Briscoe, N. J., D. Zurell, J. Elith, C. König, G. Fandos, A. K. Malchow, M. Kéry, H. Schmid, and G. Guillera-Arroita. 2021. "Can Dynamic Occupancy Models Improve Predictions of species' Range Dynamics? A Test Using Swiss Birds." *Global Change Biology* 27: 4269–82.

Case, T. J., R. D. Holt, M. A. McPeek, and T. H. Keitt. 2005. "The Community Context of species' Borders: Ecological and Evolutionary Perspectives." *Oikos* 108: 28–46.

Clark, J. S., C. Lane Scher, and M. Swift. 2020. "The Emergent Interactions that Govern Biodiversity Change." *Proceedings of the National Academy of Sciences* 117: 17074–83.

Cuddington, K. M., M.-J. Fortin, L. R. Gerber, A. Hastings, A. M. Liebhold, M. O'Connor, and C. Ray. 2013. "Process-Based Models Are Required to Manage Ecological Systems in a Changing World." *Ecosphere* 4: 1–12.

Diamond, J. 1975. "Assembly of Species Communities." In *Ecology and Evolution of Communities*, edited by M. L. Cody and J. M. Diamond, 342–44. Boston: Harvard University Press.

Dubart, M., J. H. Pantel, J. P. Pointier, P. Jarne, and P. David. 2019. "Modeling Competition, Niche, and Coexistence between an Invasive and a Native Species in a Two-Species Metapopulation." *Ecology* 100: 1–15.

Edman, M., and B. G. Jonsson. 2001. "Spatial Pattern of Downed Logs and Wood-Decaying Fungi in an Old-Growth Picea Abies Forest." *Journal of Vegetation Science* 12: 609–620.

Fukami, T., I. A. Dickie, J. Paula Wilkie, B. C. Paulus, D. Park, A. Roberts, P. K. Buchanan, and R. B. Allen. 2010. "Assembly History Dictates Ecosystem Functioning: Evidence from Wood Decomposer Communities." *Ecology Letters* 13: 675–684.

Fukasawa, Y., and K. Matsukura. 2021. "Decay Stages of Wood and Associated Fungal Communities Characterise Diversity-Decomposition Relationships." *Scientific Reports* 11: 8972.

García-Valdés, R., N. J. Gotelli, M. A. Zavala, D. W. Purves, and M. B. Araújo. 2015. "Effects of Climate, Species Interactions, and Dispersal on Decadal Colonization and Extinction Rates of Iberian Tree Species." *Ecological Modelling* 309: 118–127.

Gelman, A., and J. Hill. 2006. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge: Cambridge University Press.

George, E. I., and R. E. McCulloch. 1993. "Variable Selection Via Gibbs Sampling." *Journal of the American Statistical Association* 88: 881–89.

Gotelli, N. J., G. R. Graves, and C. Rahbek. 2010. "Macroecological Signals of Species Interactions in the Danish Avifauna." *Proceedings of the National Academy of Sciences* 107: 5030–35.

Götzenberger, L., F. de Bello, K. A. Bråthen, J. Davison, A. Dubuis, A. Guisan, J. Lepš, et al. 2012. "Ecological Assembly Rules in Plant Communities-Approaches, Patterns and Prospects."

Biological Reviews of the Cambridge Philosophical Society 87: 111–127.

Harvey, E., I. Gounand, C. L. Ward, and F. Altermatt. 2017. “Bridging Ecology and Conservation: From Ecological Networks to Ecosystem Function.” *Journal of Applied Ecology* 54: 371–79.

Hastings, A. 1987. “Can Competition Be Detected Using Species Co-Occurrence Data?” *Ecology* 68: 117–123.

Holmer, L., and J. Stenlid. 1997. “Competitive Hierarchies of Wood Decomposing Basidiomycetes in Artificial Systems Based on Variable Inoculum Sizes.” *Oikos* 79: 77–84.

Hortal, J., F. de Bello, J. A. F. Diniz-Filho, T. M. Lewinsohn, J. M. Lobo, and R. J. Ladle. 2015. “Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity.” *Annual Review of Ecology, Evolution, and Systematics* 46: 523–549.

Ives, A. R., B. Dennis, K. L. Cottingham, and S. R. Carpenter. 2003. “Estimating Community Stability and Ecological Interactions from Time-Series Data.” *Ecological Monographs* 73: 301–330.

Jönsson, M., M. Edman, and B. G. Jonsson. 2008. “Colonization and Extinction Patterns of Wood-Decaying Fungi in a Boreal Old-Growth Picea Abies Forest.” *Journal of Ecology* 96: 1065–75.

Kawatsu, K., M. Ushio, F. J. F. van Veen, and M. Kondoh. 2021. “Are Networks of Trophic Interactions Sufficient for Understanding the Dynamics of Multi-Trophic Communities? Analysis of a Tri-Trophic Insect Food-Web Time-Series.” *Ecology Letters* 24: 543–552.

Kery, M., and J. A. Royle. 2020. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS Volume 2: Dynamic and Advanced Models*. London: Academic Press.

Kissling, W. D., C. F. Dormann, J. Groeneveld, T. Hickler, I. Kühn, G. J. Mcinerny, J. M. Montoya, et al. 2012. “Towards Novel Approaches to Modelling Biotic Interactions in Multispecies Assemblages at Large Spatial Extents.” *Journal of Biogeography* 39: 2163–78.

Kotta, J., J. Vanhatalo, H. Jänes, H. Orav-Kotta, L. Rugiu, V. Jormalainen, I. Bobsien, et al. 2019. “Integrating Experimental and Distribution Data to Predict Future Species Patterns.” *Scientific Reports* 9: 1821.

Kubartová, A., E. Ottosson, A. Dahlberg, and J. Stenlid. 2012. “Patterns of Fungal Communities among and within Decaying Logs, Revealed by 454 Sequencing.” *Molecular Ecology* 21: 4514–32.

Kubartová, A., E. Ottosson, and J. Stenlid. 2015. “Linking Fungal Communities to Wood Density Loss after 12 Years of Log Decay.” *FEMS Microbiology Ecology* 91: 1–11.

Laigle, I., I. Aubin, C. Digel, U. Brose, I. Boulangeat, and D. Gravel. 2018. “Species Traits as Drivers of Food Web Structure.” *Oikos* 127: 316–326.

Levins, R. 1969. “Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control.” *Bulletin of the Ecological Society of America* 15: 237–240.

MacKenzie, D. I., L. L. Bailey, and J. D. Nichols. 2004. “Investigating Species co-Occurrence Patterns when Species Are Detected Imperfectly.” *Journal of Animal Ecology* 73: 546–555.

Moor, H., J. Nordén, R. Penttilä, J. Siitonen, and T. Snäll. 2021. “Long-Term Effects of Colonization–Extinction Dynamics of Generalist Versus Specialist Wood-Decaying Fungi.” *Journal of Ecology* 109: 491–503.

Morales-Castilla, I., M. G. Matias, D. Gravel, and M. S. Araújo. 2015. “Inferring Biotic Interactions from Proxies.” *Trends in Ecology & Evolution* 30: 347–356.

Münkemüller, T., L. Gallien, L. J. Pollock, C. Barros, M. Carboni, L. Chalmandrier, F. Mazel, et al. 2020. “Dos and Don’ts when Inferring Assembly Rules from Diversity Patterns.” *Global Ecology and Biogeography* 29: 1212–29.

Mutshinda, C. M., R. B. O’Hara, and I. P. Woiwod. 2009. “What Drives Community Dynamics?” *Proceedings of the Royal Society B: Biological Sciences* 276: 2923–29.

Nenzen, H. 2025. “Combining observational and experimental data to estimate environmental and species drivers of fungal metacommunity dynamics.” [Dataset]. Zenodo. https://doi.org/10.5281/zenodo.14718612

Niemelä, T., P. Renvall, and R. Penttila. 1995. “Interactions of Fungi at Late Stages of Wood Decomposition.” *Annales Botanici Fennici* 32: 141–152.

Nitare, J. 2019. Skyddsvärd skog - Naturvårdsarter och andra kriterier för naturvärdesbedömning, Skogsstyrelsen

Norberg, A., P. Halme, J. S. Kotiaho, T. Toivanen, and O. Ovaskainen. 2019. “Experimentally Induced Community Assembly of Polypores Reveals the Importance of both Environmental Filtering and Assembly History.” *Fungal Ecology* 41: 137–146.

Northrup, J. M., and B. D. Gerber. 2018. “A Comment on Priors for Bayesian Occupancy Models.” *PLoS One* 13: 1–13.

O’Hara, R. B., and M. J. Sillanpää. 2009. “A Review of Bayesian Variable Selection Methods: What, how and which.” *Bayesian Analysis* 4: 85–118.

Ottosson, E., J. Nordén, A. Dahlberg, M. Edman, M. Jönsson, K. H. Larsson, J. Olsson, R. Penttilä, J. Stenlid, and O. Ovaskainen. 2014. “Species Associations during the Succession of Wood-Inhabiting Fungal Communities.” *Fungal Ecology* 11: 17–28.

Ovaskainen, O., N. Abrego, P. Halme, and D. Dunson. 2016. “Using Latent Variable Models to Identify Large Networks of Species-to-Species Associations at Different Spatial Scales.” *Methods in Ecology and Evolution* 7: 549–555.

Ovaskainen, O., J. Hottola, and J. Shtonen. 2010. “Modeling Species co-Occurrence by Multivariate Logistic Regression Generates New Hypotheses on Fungal Interactions.” *Ecology* 91: 2514–21.

Ovaskainen, O., D. Schigel, H. Ali-Kovero, P. Auvinen, L. Paulin, B. Nordén, and J. Nordén. 2013. “Combining High-Throughput Sequencing with Fruit Body Surveys Reveals Contrasting Life-History Strategies in Fungi.” *ISME Journal* 7: 1696–1709.

Ovaskainen, O., G. Tikhonov, D. Dunson, V. Grøtan, S. Engen, B. E. Sæther, and N. Abrego. 2017. “How Are Species Interactions Structured in Species-Rich Communities? A New Method for Analysing Time-Series Data.” *Proceedings of the Royal Society B: Biological Sciences* 284: 20170768.

Pagel, J., and F. M. Schurr. 2012. “Forecasting Species Ranges by Statistical Estimation of Ecological Niches and Spatial Population Dynamics.” *Global Ecology and Biogeography* 21: 293–304.

Plummer, M. 2003. “JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling.” In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, edited by K. Hornik, F. Leisch, and A. Zeileis. Vienna.

Pollock, L. J., R. Tingley, W. K. Morris, N. Golding, R. B. O'Hara, K. M. Parris, P. A. Vesk, and M. A. Mccarthy. 2014. "Understanding co-Occurrence by Modelling Species Simultaneously with a Joint Species Distribution Model (JSDM)." *Methods in Ecology and Evolution* 5: 397–406.

Pouska, V., M. Svoboda, and J. Lepš. 2013. "Co-Occurrence Patterns of Wood-Decaying Fungi on Picea Abies Logs: Does Fomitopsis Pinicola Influence the Other Species?" *Polish Journal of Ecology* 61: 119–133.

R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/

Rajala, T., S. C. Olhede, and D. J. Murrell. 2019. "When Do we Have the Power to Detect Biological Interactions in Spatial Point Patterns?" *Journal of Ecology* 107: 711–721.

Renvall, P. 1995. "Community Structure and Dynamics of Wood-Rotting Basidiomycetes on Decomposing Conifer Trunks in Northern Finland." *Karstenia* 35: 1–51.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. "A Multispecies Occupancy Model for Two or More Interacting Species." *Methods in Ecology and Evolution* 7: 1164–73.

Saine, S., O. Ovaskainen, P. Somervuo, and N. Abrego. 2020. "Data Collected by Fruit Body- and DNA-Based Survey Methods Yield Consistent Species-to-Species Association Networks in Wood-Inhabiting Fungal Communities." *Oikos* 129: 1833–43.

SLU Artdatabanken. 2020. *Rödlista 2020 – övergripande delar*. Uppsala: SLU.

Talluto, M. V., I. Boulangeat, A. Ameztegui, I. Aubin, D. Berteaux, A. Butler, F. Doyon, et al. 2016. "Cross-Scale Integration of Knowledge for Predicting Species Ranges: A Metamodelling Framework." *Global Ecology and Biogeography* 25: 238–249.

Thurman, L. L., A. K. Barner, T. S. Garcia, and T. Chestnut. 2019. "Testing the Link between Species Interactions and Species co-Occurrence in a Trophic Network." *Ecography* 42: 1658–70.

Tobler, M. W., M. Kéry, F. K. C. Hui, G. Guillera-Arroita, P. Knaus, and T. Sattler. 2019. "Joint Species Distribution Models with Species Correlations and Imperfect Detection." *Ecology* 100: 1–14.

Toljander, Y. K., B. D. Lindahl, L. Holmer, and N. O. S. Högberg. 2006. "Environmental Fluctuations Facilitate Species co-Existence and Increase Decomposition in Communities of Wood Decay Fungi." *Oecologia* 148: 625–631.

Vázquez, D. P., N. Blüthgen, L. Cagnolo, and N. P. Chacoff. 2009. "Uniting Pattern and Process in Plant-Animal Mutualistic Networks: A Review." *Annals of Botany* 103: 1445–57.

Weslien, J., L. B. Djupström, M. Schroeder, and O. Widenfalk. 2011. "Long-Term Priority Effects among Insects and Fungi Colonizing Decaying Wood." *Journal of Animal Ecology* 80: 1155–62.

Wieners, M., C. Bässler, and M. Scholler. 2023. "Mycoparasitism of *Fomitopsis pinicola* (Sw.) P. Karst. By *Antrodiella citrinella* Niemelä & Ryvarden." *Mycological Progress* 22: 55.

Yackulic, C. B., J. D. Nichols, J. Reid, and R. Der. 2015. "To Predict the Niche, Model Colonization and Extinction." *Ecology* 96: 16–23.

Ylisirniö, A. L., H. Berglund, T. Aakala, T. Kuuluvainen, A. M. Kuparinen, Y. Norokorpi, V. Hallikainen, K. Mikkola, and E. Huhta. 2009. "Spatial Distribution of Dead Wood and the Occurrence of Five Saproxylic Fungi in Old-Growth Timberline Spruce Forests in Northern Finland." *Scandinavian Journal of Forest Research* 24: 527–540.

Zurell, D., L. J. Pollock, and W. Thuiller. 2018. "Do Joint Species Distribution Models Reliably Detect Interspecific Interactions from co-Occurrence Data in Homogenous Environments?" *Ecography* 41: 1812–19.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Nenzén, Hedvig Kristina, Helen Moor, Robert B. O'Hara, Mari Jönsson, Jenni Nordén, Elisabet Ottosson, and Tord Snäll. 2025. "Combining Observational and Experimental Data to Estimate Environmental and Species Drivers of Fungal Metacommunity Dynamics." *Ecology* 106(2): e70014. https://doi.org/10.1002/ecy.70014