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Observed Ecological Communities Are Formed by Species Combinations That Are among the Most Likely to Persist under Changing Environments

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ABSTRACT: Despite the rich biodiversity found in nature, it is unclear to what extent some combinations of interacting species, while conceivable in a given place and time, may never be realized. Yet solving this problem is important for understanding the role of randomness and predictability in the assembly of ecological communities. Here we show that the specific combinations of interacting species that emerge from the ecological dynamics within regional species pools are not all equally likely to be seen; rather, they are among the most likely to persist under changing environments. First, we use niche-based competition matrices and Lotka-Volterra models to demonstrate that realized combinations of interacting species are more likely to persist under random parameter perturbations than the majority of potential combinations with the same number of species that could have been formed from the regional pool. We then corroborate our theoretical results using a 10-year observational study, recording 88 plant-herbivore communities across three different forest successional stages. By inferring and validating plant-mediated communities of competing herbivore species, we find that observed combinations of herbivores have an expected probability of species persistence higher than half of all potential combinations. Our findings open up the opportunity to establish a formal probabilistic and predictive understanding of the composition of ecological communities.

Keywords: community composition, environmental change, niche framework, persistence, probability, species pool, structural stability.

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Introduction

The Earth contains millions of species that can form ecological communities, but only a small fraction of all possible combinations of species are observed in nature (Diamond 1975). Understanding and anticipating which combinations of interacting species from a regional pool should be observed at a given locality is a long-standing problem in ecology (Fukami 2015; Vellend 2016). Numerous studies have revealed that the specific combination of species observed in a given place and time is the result of a complex interplay between many ecological and evolutionary processes, including species interactions (Chase and Leibold 2003), environmental conditions (Kraft et al. 2015), dispersal (Moore et al. 2008), priority effects (Fukami 2015), phylogenetic relationships (Maherali and Klironomos 2007; Song et al. 2018a), and stochasticity (Rosindell et al. 2011). Although each of these processes can have important effects at different stages of community assembly, we still lack a simple framework that would allow us to anticipate which specific combinations of interacting species are more likely to be observed in nature.

Typically, the composition of a local community results from an assembly (or disassembly) process that starts from a regional pool and gives rise to a subset of coexisting species (Odum 1969; Holyoak et al. 2005). Essentially, this subset emerges from the compatibility of each species with local environmental conditions (which we define as abiotic filters) and with each other (i.e., biotic interactions; Chase and Leibold 2003; Kraft et al. 2015). However, abiotic and biotic factors are in constant change, and their relative importance in shaping communities is also

expected to change over time (Odum 1969; Fukami 2015). Therefore, there is a great degree of uncertainty about how environmental filtering, species arrival order, population dynamics, and other factors will impact the final composition of a community (Chase 2010; Fukami 2015; Cadotte and Tucker 2017). This accumulated uncertainty from measuring multiple ecological factors indicates that to understand which combinations of species should emerge from a regional pool, we need to work under a probabilistic framework (Cazelles et al. 2016; Serván et al. 2018; Song et al. 2020).

In this line, previous work has already established the question of what the probability is that a species can invade a feasible community with a given structure (typically characterized by an interaction matrix; Case 1990). In the case of unstructured communities (e.g., random matrices built from a probability distribution centered around zero), it has been shown that this probability is about 0.5 (Rossberg and Barabás 2019). Instead, when one considers structured communities, the probability can be different from an unbiased coin toss (Case 1990). Similarly, one can treat the invasion problem as the equilibrium between extinct residents and new colonizers, leading to the problem of the expected fraction of persistent species from a regional pool. It has also been shown that the fraction of persistent species follows a distribution with central tendency, and the expected fraction can be either half the pool or different from half depending on the community structure (Goh and Jennings 1977; Serván et al. 2018). Nevertheless, while the expected fraction of persistent species from a regional pool may be possible to anticipate, knowing which of the potentially many combinations with the same fraction of species should be realized is still an open challenge in community ecology (Fukami 2015; Friedman et al. 2017; Song et al. 2018a; Maynard et al. 2020). Yet answering this question could aid in the development of strategies for maintaining biodiversity in the face of environmental change (Walther 2010; Dirzo et al. 2014).

Across many areas of biology, the structuralist view has provided a systematic and probabilistic platform of understanding the diversity (or lack of diversity) that we observe in nature (Alberch 1989; Solé and Valverde 2004; Valverde et al. 2017). In particular, in community ecology, the structural approach posits that communities with a wider range of environmental conditions compatible with their persistence should have a higher probability of being observed under changing environments (Cenci et al. 2018b). While traditional approaches to community dynamics typically analyze environmental filtering and ecological dynamics separately (Kraft et al. 2015; Cadotte and Tucker 2017), the structural approach phenomenologically integrates external perturbations (e.g., changes in abiotic factors) and internal constraints (e.g., species interactions) to estimate

the probability of persistence of a given community (Song et al. 2018b, 2020). In particular, the structural approach uses tractable population dynamics models, such as the Lotka-Volterra model, to establish the internal rules of design of a community. Then, under these models, the structural approach investigates the range of parameter values compatible with the persistence of a community to determine the set of external perturbations under which a community may be observed (Solé and Valls 1992; Bastolla et al. 2005; Rohr et al. 2014; Saavedra et al. 2014, 2017b). In this sense, the structural approach in community ecology allows us to hypothesize which communities we are more likely to observe given the often unobserved abiotic variations at a given locality (Song et al. 2017).

Here we follow a structural approach based on feasibility and stability conditions to investigate whether combinations of species that result from Lotka-Volterra competition dynamics within a structured regional pool have a less, equal, or greater chance to persist under changing environmental conditions than potential combinations that could have been formed from the regional pool (fig. 1). More specifically, we test the hypothesis that while the fraction of persistent species from a regional pool can be the result of an unbiased die (i.e., a distribution with central tendency), the observed combination of species is the result of a biased die regardless of the fraction of persistent species (i.e., many of the combinations are almost never observed because of the constraints imposed by biotic interactions). This structural hypothesis is based on the notion that under changing environments (i.e., under abiotic variation), observed combinations of species should be among the most probable to persist, where this expected probability is given by their community structure outside of the regional pool (fig. 1). We first illustrate our hypothesis using competition communities generated with a niche framework and performing simulations of Lotka-Volterra dynamics. Then, we test our hypothesis using a 10-year observational study, recording a total of 88 annual plant-herbivore communities that comprise three different forest successional stages.

Methods

Expected Probability of Species Persistence under Changing Environments

Following recent work (Saavedra et al. 2017b; Cenci and Saavedra 2018; Song et al. 2020), we use a structural approach to study the expected probability of species persistence in a given community under changing environmental conditions. In what follows, we describe our framework, which relies on the following motivation and assumptions:

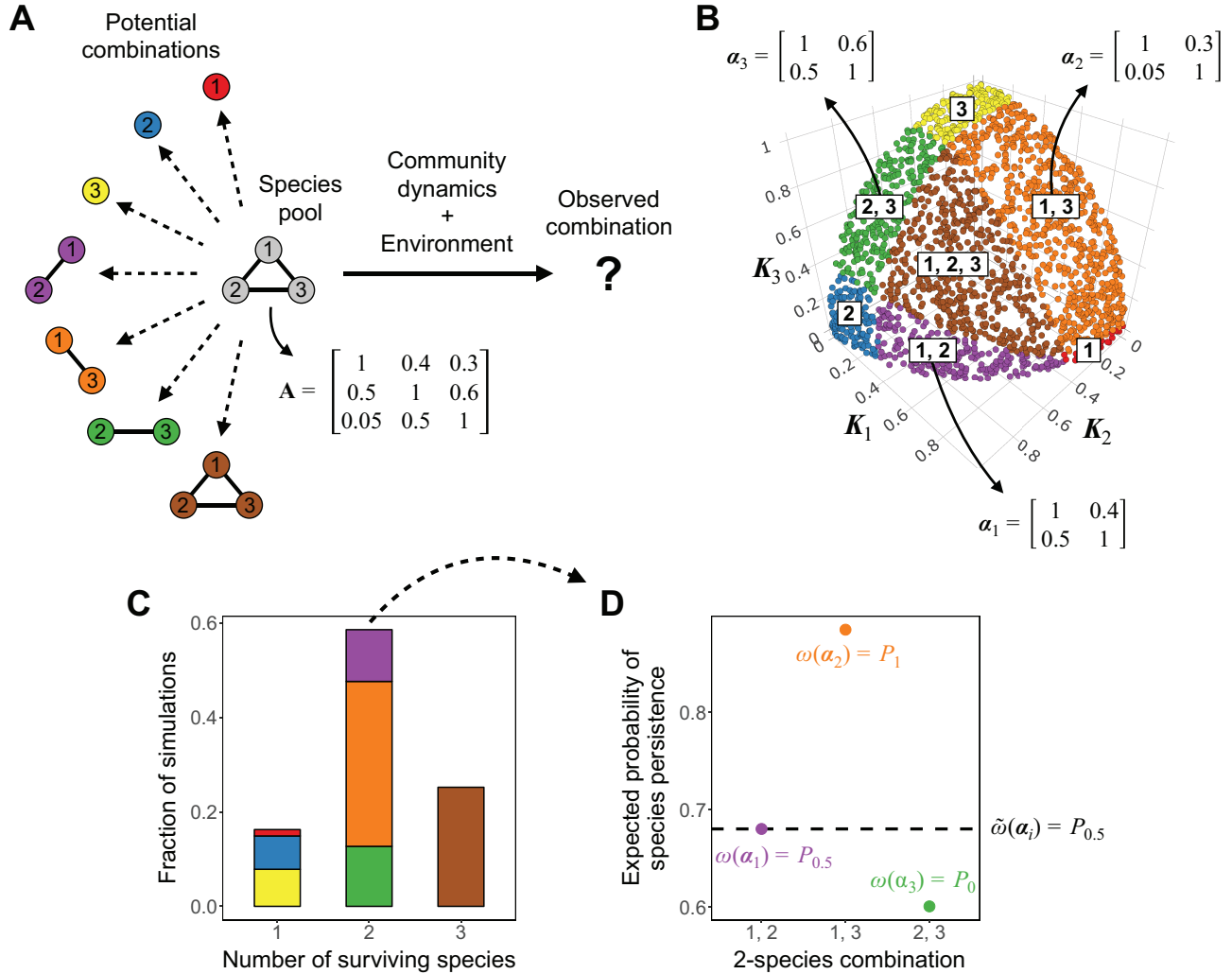


Figure 1: Illustration of our structural hypothesis stating that observed combinations of interacting species should have a higher expected probability of species persistence than potential combinations that could be formed from a regional species pool. *A*, Illustration of a regional pool of three species (*center*) from which seven combinations of interacting species can be formed (*left*). Links represent the direct effects between species, and the matrix A contains the interaction coefficients of the Lotka-Volterra dynamics (eq. [1]). After community dynamics proceed in a given environment, which combination of competing species is more likely to be observed (*right*)? *B*, Resulting species combinations after 2,000 simulations of the Lotka-Volterra dynamics (each with a different direction of the carrying capacity vector \mathbf{K} , where $\|\mathbf{K}\| = 1$ and $K_i > 0 \forall i$) starting from the regional pool shown in *A*. Species combinations are represented using the same colors as in *A*, and the three interaction submatrices (α_1 , α_2 , and α_3) with two species are shown. *C*, Fraction of simulations in which one, two, or three species persisted. Each bar is partitioned into the fraction of simulations that resulted in each species combination (colors as in *A*). Note that the number of persistent species follows a distribution with central tendency. *D*, Illustration of our structural hypothesis, showing that from the expected number of persistent species, the two-species combination that is most likely to be observed under changing environments is the one with the expected probability of species persistence ($\omega(\alpha)$) higher than the median across all potential two-species combinations ($\tilde{\omega}(\alpha_i) = P_{0.5}$), which is shown as a dashed line. The r th percentile is represented as P_r .

(i) we consider Lotka-Volterra competition models to leverage on their mathematical tractability; (ii) we assume constant and direct pairwise interactions based on the time-invariant assumption of direct interactions under Lotka-Volterra dynamics; (iii) we focus on niche-based species interactions, which produce ecologically motivated and globally stable interaction matrices; and (iv) we use no prior

information on how environmental perturbations will impact ecological dynamics and therefore assume that all directions of environment-related parameters are equally likely.

We assume that community dynamics can be described by any competition model topologically equivalent to the classic Lotka-Volterra model (Vandermeer 1975):

$$\frac{dN_i}{dt} = N_i \frac{r_i}{K_i} \left(K_i - \sum_{j=1}^S a_{ij} N_j \right), \quad (1)$$

where N_i represents the abundance (or biomass) of species i , $r_i > 0$ represents the intrinsic growth rate of species i , $K_i > 0$ represents the carrying capacity of species i , and S denotes the number of species, whereas $a_{ij} > 0$ and $a_{ii} = 1$ are elements in the unitless interaction matrix \mathbf{A} , representing the per capita effect of species j on species i relative to its own self-regulation (Case 2000). The classic Lotka-Volterra model in equation (1) is a phenomenological competition model written in a K -formalism, implying that carrying capacities (K_i) represent the summary effect between mortality rate and resource intake on the growth rate of species i and thus are linked to environmental conditions (Case 2000). We opted to write the classic Lotka-Volterra model in the K -formalism to conform with our assumption of niche-based community structures (MacArthur and Levins 1967). Note that under the niche framework, interaction matrices \mathbf{A} are by construction unitless and Volterra dissipative, which guarantees global stability of the feasible fixed point (Goh 1977; app. sec. A1; the appendix is available online). Also note that a population dynamics model is considered to be topologically equivalent to the classic Lotka-Volterra model if the phase portrait of the candidate model can be mapped into the phase portrait of equation (1) (Cenci and Saavedra 2018; for details, see app. sec. A5).

To investigate the expected probability of species persistence under changing environments in a community defined by a niche-based interaction matrix \mathbf{A} and governed by Lotka-Volterra competition dynamics, we focus on the necessary (i.e., feasible solution) and sufficient (i.e., global stability) conditions for species persistence (Strobeck 1973). Because niche-based matrices are globally stable by construction (MacArthur and Levins 1967), it is necessary only to satisfy the feasibility condition to guarantee persistence. Note that a feasible solution represents the necessary condition for persistence and permanence (Hofbauer and Sigmund 1998). The feasible equilibrium of equation (1) is given by $\mathbf{N}^* = \mathbf{A}^{-1}\mathbf{K}$, where $\mathbf{N}^* = [N_1^*, \dots, N_S^*]^T$ ($N_i^* > 0$) is the vector of abundances at equilibrium, $\mathbf{K} = [K_1, \dots, K_S]^T$ is the vector of carrying capacities, \mathbf{A}^{-1} is the inverse of the interaction matrix, and the superscript T is the transpose operator. Importantly, for a given interaction matrix \mathbf{A} , feasibility in equation (1) will be satisfied as long as \mathbf{K} falls inside the feasibility domain $D_F(\mathbf{A}) = \{\mathbf{K} | \mathbf{K} = N_1^* \mathbf{v}_1 + \dots + N_S^* \mathbf{v}_S, \text{ with } N_1^*, \dots, N_S^* > 0\}$, where \mathbf{v}_i is the i th column vector of the interaction matrix \mathbf{A} (Song et al. 2018b). Note that if \mathbf{K} falls inside the feasibility domain, any vector $c\mathbf{K}$ ($c > 0$) has the same direction as \mathbf{K} and therefore also leads to a feasible solution.

Following Song et al. (2020), we calculate the expected probability of species persistence under changing environmental conditions within a community \mathbf{A} with S competing species as

$$\omega(\mathbf{A}) = \left(\frac{2^S \text{vol}(D_F(\mathbf{A}) \cap \mathbb{B}^S)}{\text{vol}(\mathbb{B}^S)} \right)^{1/S}, \quad (2)$$

where $\text{vol}(\mathbb{B}^S)$ represents the volume of the S -dimensional unit ball, 2^S normalizes the unit ball to the positive orthant, and $\text{vol}(D_F(\mathbf{A}) \cap \mathbb{B}^S)$ corresponds to the volume of the intersection of the feasibility domain with the unit ball (Song et al. 2018b). Given that the intersection of the feasibility domain with the unit ball is effectively a solid angle spanned by the column vectors of \mathbf{A} , $\omega(\mathbf{A})$ is a measure of this solid angle normalized by the unit ball. Because we are interested only in the direction of positive \mathbf{K} -vectors, we can consider only vectors \mathbf{K} for which $\|\mathbf{K}\| \leq 1$ and normalize the size of the feasibility domain using the positive orthant of the unit ball (i.e., $\mathbb{B}^S \cap \mathbb{R}_{\geq 0}^S$). That is, the volume of the unit ball must be scaled by 2^{-S} . Note that we are fixing the magnitude of the \mathbf{K} -vectors to one under the Euclidean norm (i.e., $\|\mathbf{K}\| = 1$); however, the analysis can be done using any norm without altering the conclusions (Rohr et al. 2016).

Thus, $\omega(\mathbf{A}) \in [0, 1]$ is a probabilistic measure and can be efficiently computed for even relatively large communities (app. sec. A1; Song et al. 2018b). Ecologically, $\omega(\mathbf{A})$ can be interpreted as either the probability of persistence of a randomly chosen species or the expected fraction of persistent species within community \mathbf{A} under changing environmental conditions (Song et al. 2018b)—that is, the expected probability of species persistence under changing conditions. Note that Song et al. (2020) have used $\omega(\mathbf{A})$ to study the expected switches of interaction classes within a feasible community. Here we use this methodology to study the properties of realized combinations of interacting species formed from a regional pool under changing environments. Recall that by changing the direction of the \mathbf{K} -vector, we can phenomenologically represent changes in resource availability associated with the abiotic environment.

Theoretical Analysis

To investigate our structural hypothesis theoretically, we follow a niche framework to generate ecologically motivated interaction matrices (MacArthur and Levins 1967; Rohr et al. 2016; app. sec. A2). Specifically, we randomly generate $S \times S$ -dimensional matrices \mathbf{A} (regional species pools), whose elements are constructed as

$$a_{ij} = \exp\left(-\frac{\|\mu_i - \mu_j\|}{4\sigma^2}\right), \quad (3)$$

where μ_i (drawn randomly from a uniform distribution in $[0, 1]$) gives the position of species i in a one-dimensional niche space and σ corresponds to the niche width (Svirezhev and Logofet 1983). We assume the same σ for all species. However, confirming previous work (Rohr et al. 2016), relaxing this constraint does not affect our conclusions (app. sec. A2). To obtain a desired mean competition strength $\rho(\mathbf{A})$ in the regional pool, we tune σ so that

$$\frac{\sum_{i \neq j} a_{ij}}{(S-1)S} = \rho(\mathbf{A})$$

on average. Note that as long as $\rho(\mathbf{A})$ is small enough such that matrices remain diagonally dominant (i.e., the sum of its off-diagonal elements must be less than its diagonal element for each row, $\sum_{j \neq i} a_{ij} < a_{ii} \forall i$), interaction matrices generated via this niche framework are Volterra dissipative and guaranteed to be globally stable (Goh 1977; Lu 1998). Additionally, we explore other niche-based methodologies to generate structured interaction matrices and obtain the same qualitative results (app. sec. A2).

We start our simulations by generating 500 globally stable matrices \mathbf{A} (as described above), representing regional pools of size $S = 20$ for three different values of mean competition strength ($\rho(\mathbf{A}) \in \{0.025, 0.05, 0.1\}$; total = 1,500 matrices; fig. 2A). Then we compute $\omega(\mathbf{A})$ for each of the regional pools \mathbf{A} to get an estimate of the expected fraction of species that would be present (i.e., persist) in the realized combinations after running Lotka-Volterra competition dynamics (eq. [1]). Recall that $\omega(\mathbf{A})$ can be interpreted as the expected fraction of persistent species within community \mathbf{A} under changing environmental conditions. Then, for 30 matrices (10 for each value of $\rho(\mathbf{A})$), we randomly sample 100 directions of \mathbf{K} -vectors uniformly on the positive orthant of the S -dimensional unit ball. Therefore, we ran 1,000 simulations per $\rho(\mathbf{A})$ value. Initial species abundances ($\mathbf{N} = [N_1, \dots, N_S]^T$) and intrinsic growth rates ($\mathbf{r} = [r_1, \dots, r_S]^T$) were chosen to be 1 for every species (i.e., $N_i = 1$ and $r_i = 1 \forall i$) and do not affect our results because of the global stability condition (Takeuchi 1996).

Next, for each level of competition strength $\rho(\mathbf{A})$ and regional pool \mathbf{A} , we reach the global equilibrium point \mathbf{N}^* after numerical integration of equation (1). We record the realized combination formed by the subset of $s \leq S$ persistent species (i.e., the subset $\mathbf{N}^* = [N_1^*, \dots, N_s^*]^T$, with $N_i^* > 0 \forall i$). For each realized combination, we define its interaction matrix α as the submatrix of \mathbf{A} , where indexes of rows and columns belong to the s persistent species. This generated 100 submatrices α of different sizes s (i.e., one matrix for each sampled direction of the \mathbf{K} -vector) from each regional pool \mathbf{A} . Therefore, we generated 1,000 submatrices per $\rho(\mathbf{A})$ value. Note that global stabil-

ity is also guaranteed for every α that is a principal submatrix of a globally stable matrix \mathbf{A} (Cross 1978; Takeuchi 1996). Thus, for each realized combination defined by submatrix α , we compute its expected probability of species persistence under changing conditions $\omega(\alpha)$ following equation (2). Finally, we define the set of all potential combinations with the same number of species as α as $\Psi = \{\alpha_1, \dots, \alpha_k\}$, where $|\Psi| = k = \binom{S}{s}$ denotes the total number of such combinations and $\alpha_1, \dots, \alpha_k$ denotes all the possible $s \times s$ -dimensional submatrices that can be formed from the regional pool \mathbf{A} . For each realized combination α , we sampled 500 potential combinations α_i from Ψ and computed $\omega(\alpha_i)$ for each of the potential combinations. Note that our random sampling from the species pool allows the same potential combination to be sampled twice; however, this resampling effect can be considered negligible with $S = 20$ and 500 potential combinations. Next, using the empirical cumulative distribution function of $\omega(\alpha_i)$, we computed the percentage of $\omega(\alpha_i)$ values below $\omega(\alpha)$. That is, we computed the percentile rank r ($0 \leq r \leq 1$) of the r th percentile $P_r = \omega(\alpha)$ of the distribution of $\omega(\alpha_i)$.

Following a structuralist view, we hypothesize that while the number of species forming the realized combinations has a distribution with central tendency linked to $\omega(\mathbf{A})$, the expected probability of species persistence within the realized combination $\omega(\alpha)$ should be biased toward top percentile rank values regardless of the size of the realized combination. Specifically, we computed the percentage of all percentile rank values (1,000 values per $\rho(\mathbf{A})$ value) that were above 0.5, which corresponds to the median $P_{0.5} = \tilde{\omega}(\alpha_i)$ of $\omega(\alpha_i)$. We use a one-sided binomial test (unbiased binomial trial with probability of success = 0.5) to test whether the percentile rank of $\omega(\alpha)$ is above 0.5 (i.e., the percentile rank of the median $\tilde{\omega}(\alpha_i)$) for the majority of realized combinations. Note that our simulation settings were chosen simply for illustration purposes, and preliminary analyses showed that changing the number of species pools (\mathbf{A}) built, the number of carrying capacity vectors (\mathbf{K}) sampled, or the number of potential combinations (α_i) sampled does not affect our conclusions.

Empirical Analysis

To test our structural hypothesis, we use a data set of 88 annual local communities formed by 22 herbivore species and 15 plant species on average from a total of 521 herbivore species feeding on 138 plant species. The study site is located in the tropical dry forest at the Chamela-Cuixmala Biosphere Reserve ($19^\circ 22' - 19^\circ 39' \text{N}$, $104^\circ 56' - 105^\circ 10' \text{W}$) in Jalisco, Mexico (Boege et al. 2019). Specifically, the data comprise monthly records during the rainy seasons (from

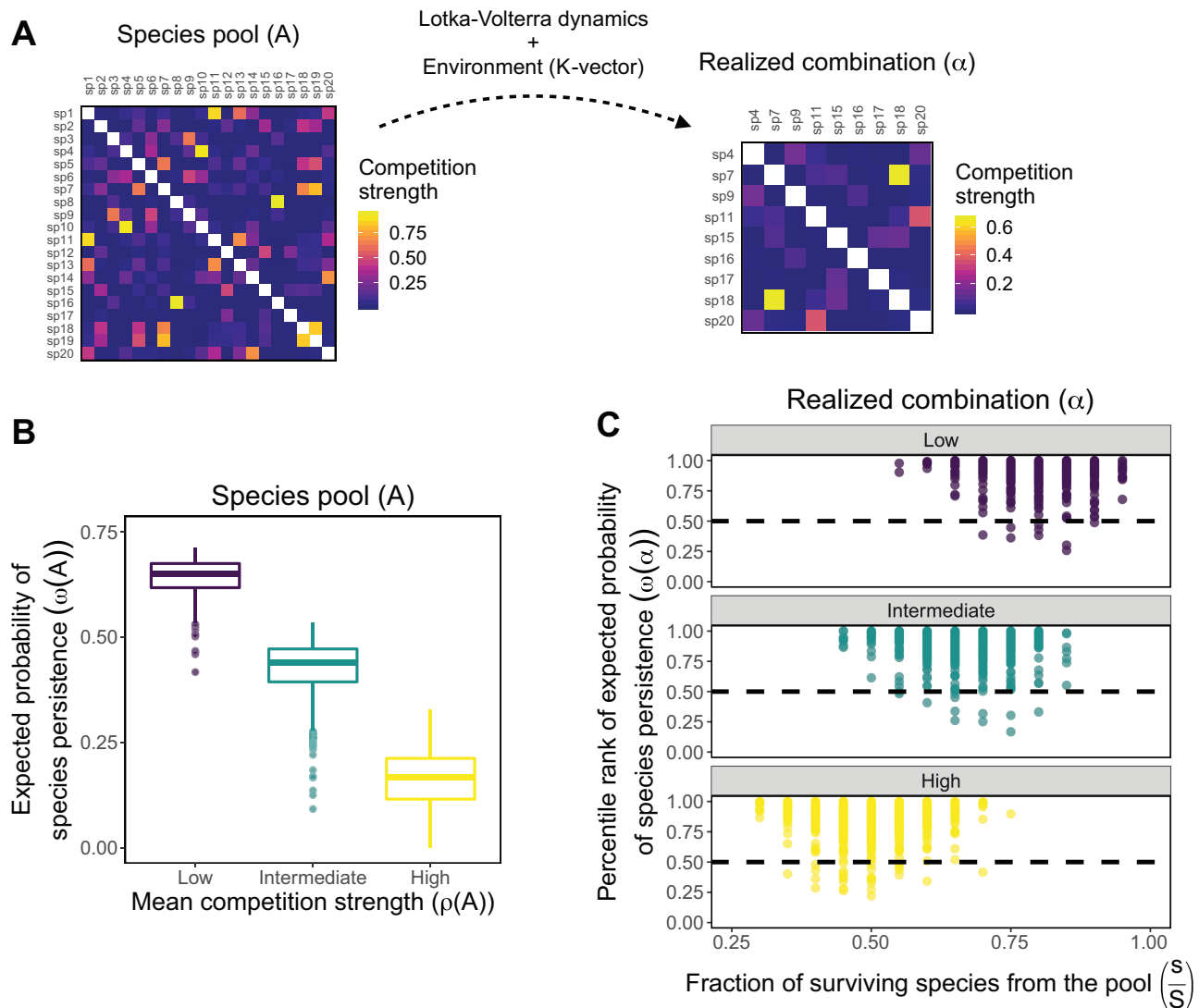


Figure 2: Theoretical results of our structural hypothesis using competition communities generated with a niche framework and performing simulations of Lotka-Volterra dynamics. *A, left*, illustrative example of a regional species pool (matrix A) with $S = 20$ competing species generated following a niche framework with a high mean competition strength ($\rho(A) = 0.1$). *Right*, illustrative example of a realized combination (submatrix α) formed by $s = 9$ competing species obtained by simulating Lotka-Volterra dynamics on the regional pool with a given direction of the K -vector. Colors represent the level of competition strength α_{ij} . Diagonal elements (α_{ii}) are all set to one (see “Methods”) and are not colored to improve visualization. *B*, Expected probability of species persistence under changing environments of 500 model-generated regional pools ($\omega(A)$) for each value of mean competition strength (low: $\rho(A) = 0.025$; intermediate: $\rho(A) = 0.05$; high: $\rho(A) = 0.1$). Boxplots denote the median and interquartile range. *C*, Percentile rank values (r) of the expected probability of species persistence of realized combinations ($\omega(\alpha)$) as a function of the fraction of persistent species (s/S) and level of mean competition strength. Note that each percentile rank is computed by comparing a given realized combination within the population formed by 500 sampled potential combinations with the same number of species. Each point corresponds to one of 1,000 different simulations (i.e., different directions of K -vectors) per level of mean competition strength. Within each level of mean competition strength, more than 95% of the points are above the percentile rank of the median (dashed line). Furthermore, the fraction of persistent species decreases as mean competition strength increases, as anticipated by the expected probability of species persistence within the regional pool ($\omega(A)$) reported in *B*. In *B* and *C*, colors indicate different levels of mean competition strength: the lighter the color, the higher the level.

July to October) from 2007 to 2017. The data collection was carried out for three stages of secondary succession: initial stage (approximately 6 years after being excluded and protected from cattle ranching use), middle stage (approximately 20 years after being excluded and protected), and late stage (more than 50 years without anthropogenic perturbations). We had three independent sampling plots of 20 m × 50 m for each successional stage (nine plots in total per year), with a minimum distance of 3 km between them. For each plot, monthly records were aggregated to build annual communities. The sites were not sampled in 2015 because of extreme bad weather conditions caused by Hurricane Patricia, and there was no access to one site in 2016 and 2017, providing a total of 88 annual plant-herbivore communities (for further details, see table A1, available online).

It is known that herbivores can negatively affect each other through a variety of mechanisms, such as induction of plant defenses or attraction of parasitoids and predators (Pallini et al. 1998; Denno et al. 2000; Redman and Scriber 2000; Ohgushi 2005). Therefore, our data set allows us to test the hypothesis that observed combinations of plant-mediated communities of competing herbivores are among the most likely to persist under the within- and across-year climatic changes that occurred across the 10-year period, including the impact of two hurricanes. Furthermore, negative effects among herbivores are expected to increase along forest succession because of an increase in host plant phylogenetic diversity and hence greater opportunities for niche differentiation, particularly for specialist herbivore species that are constrained to feed on particular plant taxa (Saavedra et al. 2017a). Thus, we leverage on these expected biotic changes across ecological succession and investigate our hypothesis separately for each forest successional stage.

For each of the 88 observed combinations (local communities) of herbivore species, we inferred their corresponding regional pool \mathbf{A} . For this purpose, we first reconstructed a binary regional pool matrix \mathbf{B} ($b_{ij} = 1$ if plant species i is consumed by herbivore species j , and $b_{ij} = 0$ otherwise) by merging all herbivore species from the same year and successional stage that fed on plant species present at a given plot. For example, to reconstruct the regional pool for plot 5 in 2011 in the middle successional stage, we merged all herbivore species from plots 4, 5, and 6 (i.e., the other plots from 2011 and the middle successional) that fed on plants from plot 5. The rationale behind this approach is that the regional pool for a given plot must contain all herbivores that could potentially feed on the plant species present at this plot. Thus, each regional pool contained only plant-herbivore interactions observed in our data set, and therefore we do not assume that herbivores could feed on any arbitrary plant species. Note that

herbivore species, plant species, and their interactions changed across years and successional stages. We also performed our analyses using different methods to reconstruct the regional pools (merging herbivores only by year or only by stage) and obtained the same qualitative results (app. sec. A3).

Next, because we have no information about the level of interaction strength among herbivore species, we follow a niche framework to infer the herbivore competition matrix \mathbf{A} by computing the normalized monopartite projection of the binary bipartite matrix \mathbf{B} (Cenci et al. 2018a). Specifically, we project the binary matrix on the herbivore layer as $\mathbf{A} = \mathbf{B}^T\mathbf{B}$, and then we normalize the columns of matrix \mathbf{A} to sum one and set its diagonal elements to one afterward. By doing so, we eliminate tuning parameters that could be used to infer interaction coefficients (Saavedra et al. 2014). Thus, the matrix element a_{ij} after normalization can be interpreted as an approximation to the negative indirect effect of herbivore j on herbivore i and is proportional to the number of shared plant species between j and i while taking into account the total number of plant species consumed by j . Note that the effect of species j on i is not necessarily the same as the effect of species i on j . This niche-based methodology generates diagonally dominant and consequently globally stable regional pool matrices \mathbf{A} (app. sec. A4).

To estimate the expected fraction of species that could be observed from these inferred pools after ecological dynamics, we compute $\omega(\mathbf{A})$ for each of the 88 regional pool matrices \mathbf{A} . We also perform prediction analyses to show that the Lotka-Volterra dynamics together with the inferred interaction coefficients can be used to perform accurate out-of-sample predictions of temporal changes in species composition and therefore support our inference methodology as a reasonable approximation of interaction matrices (app. sec. A4). In addition, we obtain the same qualitative results by performing our analyses using different niche-based methods to infer interaction coefficients (app. sec. A4).

Finally, we infer the observed interaction matrices α for each of the 88 observed plant-mediated communities of competing herbivores. We parameterize these matrices following the niche-based methodology mentioned above by computing the normalized monopartite projection of its binary bipartite matrix β , in which $\beta_{ij} = 1$ if plant species i is consumed by herbivore species j and $\beta_{ij} = 0$ otherwise. We then use these inferred matrices α to calculate the expected probability of species persistence of observed combinations under changing environments ($\omega(\alpha)$). Then, to deal with the trade-off between computational constraints and statistical support, we sample a population Ψ of 1,000 potential combinations α_i with the same size as α from the regional pool \mathbf{A} . We normalize each of these potential combinations as we did for observed

combinations. Then, similarly to our theoretical analyses, we compute the percentile rank r of the r th percentile $P_r = \omega(\alpha)$ of the distribution of $\omega(\alpha_i)$. For each successional stage, we perform a one-sided binomial test (unbiased binomial trial with probability of success = 0.5) to test whether the percentile rank of $\omega(\alpha)$ is above 0.5 (i.e., the percentile rank of the median $\tilde{\omega}(\alpha_i)$) for the majority of observed combinations.

Results

Theoretical Results

We first illustrate our structural hypothesis by performing Lotka-Volterra simulations with a toy three-species competition community. Figure 1A shows this three-species regional species pool (matrix \mathbf{A} ; *center*) and all potential combinations of interacting species (*left*) that could result from community dynamics under a given environment (i.e., a given direction of the \mathbf{K} -vector). Figure 1B shows the realized community composition after simulating Lotka-Volterra dynamics (eq. [1]) under many different environments. Each point on the positive orthant of the unit ball represents one of 2,000 random directions of \mathbf{K} -vectors (i.e., environmental conditions) used to simulate the dynamics. The figure shows that the feasibility domain $D_F(\mathbf{A})$ (i.e., the direction of \mathbf{K} -vectors for which the three species have positive abundances at equilibrium) is much smaller than the domain of infeasibility. In particular, different species combinations (i.e., different colors in fig. 1B) have different probabilities of being observed under random environmental conditions. Figure 1C confirms that the fraction of persistent species follows a distribution with central tendency. In this case, the expected number of persistent species is two, with three possible combinations (i.e., {1, 2}, {1, 3}, {2, 3}). The question we are addressing in this study is which of these combinations we are more likely to observe in nature. Figure 1D shows the expected probability of species persistence under changing environments ($\omega(\alpha)$) for each of these two-species combinations. Our hypothesis is that the two-species combination α_2 containing species 1 and 3 is more likely to be observed, as it has an expected probability of species persistence higher than half of all possible combinations.

To show the generality of our hypothesis, we present our results for niche-based regional pools \mathbf{A} with $S = 20$ competing species under three different levels of mean competition strength (see “Methods”; fig. 2A). We found that Lotka-Volterra dynamics together with changing environmental conditions (phenomenologically represented by equally probable directions of \mathbf{K} -vectors) lead to realized combinations of interacting species that are among the most probable to persist. In particular, figure 2B shows

that the expected probability of species persistence within the regional pools ($\omega(\mathbf{A})$) was higher for communities with a lower mean competition strength (low: 0.641 ± 0.045 ; intermediate: 0.422 ± 0.069 ; high: 0.162 ± 0.065 ; mean \pm SD). As a consequence, figure 2C shows that the expected fraction of persistent species (s/S) was also higher for communities with a lower mean competition strength (low: 0.784 ± 0.068 ; intermediate: 0.655 ± 0.073 ; high: 0.488 ± 0.075). These results confirm that the expected fraction of persistent species (forming realized combinations of competing species) follows a distribution with central tendency linked to $\omega(\mathbf{A})$.

Importantly, figure 2C shows that the expected probability of species persistence of realized combinations ($\omega(\alpha)$) exhibits a bias toward the top percentile rank values of the distribution of potential combinations ($\omega(\alpha_i)$). Specifically, for the vast majority of realized combinations, $\omega(\alpha)$ was above the median $\tilde{\omega}(\alpha_i)$ of potential combinations within all three levels of mean competition strength (percentage of values above the median: low, 99.1%; intermediate, 98.8%; high, 97.3%; $P < .0001$ for all levels of competition strength for one-sided unbiased binomial tests). We confirmed these results by building regional pools according to different frameworks (figs. A1–A4; figs. A1–A10 are available online) and by performing simulations with modified Lotka-Volterra models (figs. A9, A10).

Empirical Results

We corroborated our structural hypothesis using an empirical data set of 88 plant-herbivore communities (table A1). These communities were sampled across a 10-year observational period, allowing us to test our hypothesis across three different successional stages encompassing different abiotic and biotic conditions (i.e., environmental conditions as well as herbivore and plant species change over time). As mentioned in “Methods,” we first reconstructed regional pools by merging herbivore species from the same year and successional stage. Then, we inferred herbivore interaction matrices following a niche framework with no tuning parameters by computing normalized monopartite projections for the regional pools \mathbf{A} , observed combinations α , and potential combinations α_i (fig. 3A). In line with our theoretical results, we found that regardless of the number of observed interacting species, the majority of observed species combinations have an expected probability of species persistence higher than half of all the potential combinations that could have been formed with the same number of species from the reconstructed regional pools.

Figure 3B shows that the expected probability of species persistence of reconstructed regional pools ($\omega(\mathbf{A})$) is

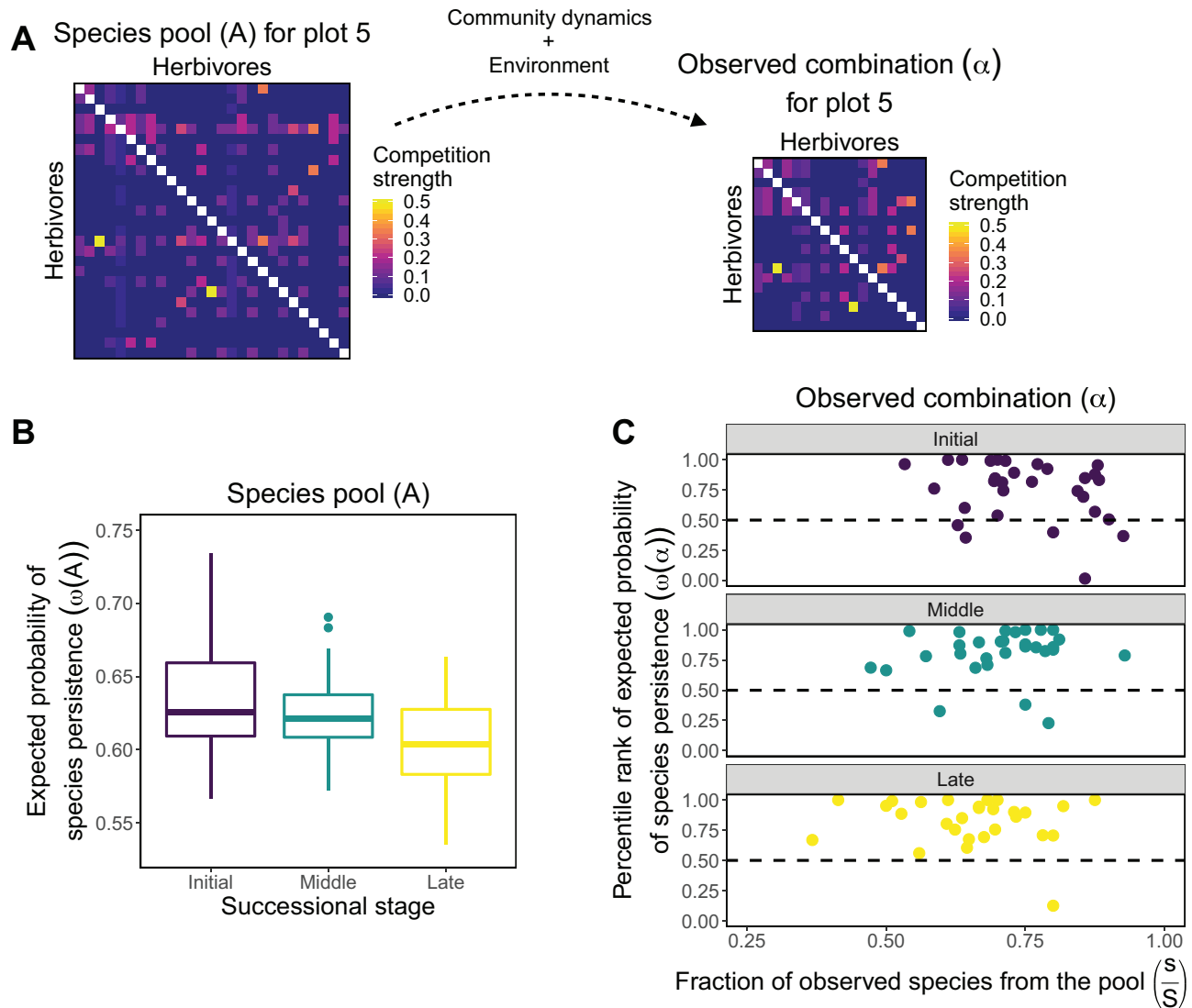


Figure 3: Empirical test of our structural hypothesis using a 10-year data set recording 88 plant-herbivore communities across three different forest successional stages. *A, left*, illustrative example of a reconstructed regional species pool (matrix A) with $S = 27$ competing herbivores mediated by plant resources from plot 5 (2011, middle successional stage). *Right*, observed combination (submatrix α) with the $s = 18$ competing herbivores from plot 5. Colors represent the interaction strength α_{ij} , which is proportional to the number of shared plant species. Diagonal elements (α_{ii}) are all set to one (see “Methods”) and are not colored to improve visualization. *B*, Expected probability of species persistence under changing environments of the 88 reconstructed regional pools ($\omega(A)$) separated by successional stage. Boxplots denote the median and interquartile range. We removed one outlier point from the late stage to improve visualization. *C*, Percentile rank values (r) of the expected probability of species persistence of observed combinations ($\omega(\alpha)$) as a function of the fraction of observed species (s/S) and successional stage. Note that each percentile rank is computed by comparing a given observed combination within the population formed by 1,000 sampled potential combinations with the same number of species. Each point corresponds to one of 88 different empirical communities. Within each successional stage, more than 80% of the points are above the percentile rank of the median (dashed line). Furthermore, the fraction of observed species decreases along forest succession, as suggested by the expected probability of species persistence within the regional pool ($\omega(A)$) reported in *B*. In *B* and *C*, colors indicate different successional stages: the lighter the color, the later the stage.

slightly higher in initial successional stages (initial: 0.637 ± 0.045 ; middle: 0.625 ± 0.030 ; late: 0.615 ± 0.051), although the difference between stages is not statistically significant (one-way ANOVA: $F(2, 85) = 1.917$, $P = .153$). Figure 3C shows that the expected fraction of ob-

served species (i.e., the number of observed species s divided by the number of species in the regional pool S) is higher in initial successional stages (initial: 0.750 ± 0.107 ; middle: 0.704 ± 0.101 ; late: 0.653 ± 0.120 ; one-way ANOVA: $F(2, 85) = 5.722$, $P = .005$). This result

suggests a link between $\omega(\mathbf{A})$ and the expected number of species forming observed combinations for our empirical data.

Furthermore, figure 3C shows that observed combinations exhibit a bias toward top percentile rank values of the expected probability of species persistence ($\omega(\alpha)$). Specifically, for the majority of observed combinations, $\omega(\alpha)$ was above the median $\tilde{\omega}(\alpha_i)$ of potential combinations within all three successional stages (initial: 83.3%; middle: 90.0%; late: 96.4%; $P < .001$ for all successional stages for one-sided unbiased binomial tests). These results hold for different methods of reconstructing the regional pool (figs. A5–A7).

Discussion

Several studies have elucidated key mechanisms that are likely to drive the assembly of ecological communities (Odum 1969; Maherali and Klironomos 2007; Fukami 2015; Kraft et al. 2015). For example, it has been shown how mechanisms such as environmental filtering (Kraft et al. 2015), phylogenetic constraints (Maherali and Klironomos 2007; Song et al. 2018a), population dynamics (Serván et al. 2018), and ecological succession (Odum 1969; Fukami 2015) can structure the composition of such communities. Nevertheless, we still lack a framework to understand and anticipate the actual combination of species that should be expected to be observed in nature. Yet answering this question requires obtaining extensive amounts of data, knowing the governing community dynamics, and understanding how environmental conditions change and affect biological populations within each community. Such complexity reveals that this answer may be addressed only under a probabilistic framework (Cazelles et al. 2016; Serván et al. 2018; Song et al. 2020).

In this line, here we have adopted a structuralist and probabilistic approach to enhance our understanding about what is likely to be seen in nature and what is not. Indeed, a fundamental question about biological systems in general is whether the forms and structures that we observe in nature represent the whole spectrum of all possible systems or only a small proportion of all potential diversity (Diamond 1975; Alberch 1989; Solé and Valverde 2004). Following this reasoning, we have combined a theoretical framework with a comprehensive data set to investigate whether the combinations of interacting species that we observe (or ought to observe) in a given place and time represent the full spectrum of possibilities or only a small fraction of them. We have postulated a testable hypothesis grounded on the feasibility and stability of population dynamics models (Saavedra et al. 2017b; Song et al. 2020). Specifically, we tested whether observed com-

binations of interacting species forming ecological communities are among the ones more likely to persist under changing environmental conditions within all the possible combinations that could have been formed with the same number of species from a regional pool of species.

Corroborating our hypothesis, we have found that the observed species combinations are not all equally likely or unlikely to be seen; rather, they are among the most likely to persist under changing environments. Specifically, we have found that half of all potential combinations of interacting species (i.e., those with expected probabilities of species persistence below the median) were rarely observed theoretically and empirically. This result suggests that the interplay between internal rules of design (i.e., community dynamics) and external forces (e.g., environmental perturbations) constrains the set of combinations of interacting species that can be realized in nature (Alberch 1989; Solé and Valverde 2004; Song et al. 2017). We have first demonstrated the validity of our hypothesis using model-generated communities and simulations of Lotka-Volterra competition dynamics. Because a model is only an approximation of the real world, we have corroborated our hypothesis using an extensive longitudinal data set comprising 88 different combinations of interacting herbivore species mediated by plant resources subject to within- and across-year variation of abiotic factors.

It is worth mentioning that our methodology is phenomenological by construction, meaning that no causative knowledge should be directly derived. Moreover, our proposed methodology is built on four important assumptions. First, community dynamics are governed by population dynamics models topologically equivalent to the classic Lotka-Volterra model (eq. [1]). Therefore, extensions of density feedback, such as Lotka-Volterra models with type II functional response, can be integrated into our framework. We show a confirmation of this in appendix section A5. Models with higher-order interactions are not integrated into our framework. However, it has been shown that these higher-order polynomial models can produce mathematical artifacts, limiting our capacity to understand ecological dynamics (AlAdwani and Saavedra 2019). Second, species interactions are defined as constant direct pairwise interactions. That is, regardless of whether two species interact within a regional pool or within a subset of such a pool, their interactions remain the same. Furthermore, we also assume that species interactions are not affected by evolutionary processes in the short timescales that we are studying, but our framework can be used to explore adaptive processes (Saavedra et al. 2017a; Cenci et al. 2018a).

Third, we assume that communities are structured following a niche framework. While this is ecologically motivated and minimizes the choice of free-tuning parameters,

this framework imposes the property of global stability for persistence that may not be necessarily met in nature. While persistence may also be attained in the absence of a stable equilibrium through stochastic processes or switching dynamics (Hofbauer and Sigmund 1998; Schreiber et al. 2019), a careful analysis of these nonequilibrium processes is outside of the scope of our work. Nevertheless, previous work (Cenci and Saavedra 2018) has shown that the structural and probabilistic approach presented here can be used for Lotka-Volterra models with demographic stochasticity, as these models are topologically equivalent to the classic Lotka-Volterra model (eq. [1]). We show a confirmation of this in appendix section A5. Fourth, we assume that all environmental conditions are equally probable. While this imposes a uniform distribution as a prior, this allows us to separate the role of interactions from the environment in shaping the realized combinations of interacting species given that any combination from the regional pool is initially possible. That being said, previous work (Cenci et al. 2018*b*; Song et al. 2020) has shown how this assumption can be modified if researchers have clear information about the directionality of environmental changes.

Finally, we stress that our results should be taken only as a first-order approximation of the probabilities of a randomly chosen species. Similarly, the matrices inferred from our empirical data should be taken only as an approximation of species interactions mediated by plant resources and natural enemies present at each plot. Nevertheless, the structural and probabilistic thinking that we have established here can serve as a basis for future theoretical and experimental work aiming to answer more specific questions in different ecological systems under changing environments. For example, our results have shown that while the realized combinations of interacting species appear to be the result of a biased die (i.e., many potential combinations are very unlikely to be observed), these realized combinations are not necessarily the ones maximizing the expected probability of species persistence under changing environments. Indeed, previous work has shown that community structures may be responding to environmental pressures (Song et al. 2017). Thus, the expected probability of species persistence can be higher in places where environmental variability is greater (Cenci and Saavedra 2019). This implies that it is essential to understand and anticipate how directional and nondirectional environmental stressors can change the bias of the dice again in ecological communities.

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Statement of Authorship

L.P.M. and S.S. designed the study; K.B. and E.d.-V. designed and carried out the fieldwork to obtain empirical data; A.Z.-R. carried out the molecular analysis for species identification; L.P.M. performed the analyses; S.S. supervised the study; L.P.M. and S.S. wrote a first version of the manuscript; and all authors contributed with substantial revisions.

Data and Code Availability

The R code and data supporting the results are archived on GitHub (https://github.com/MITEcology/AmNat_Medeiros_etal_2020) and Zenodo (<https://doi.org/10.5281/zenodo.4026319>).

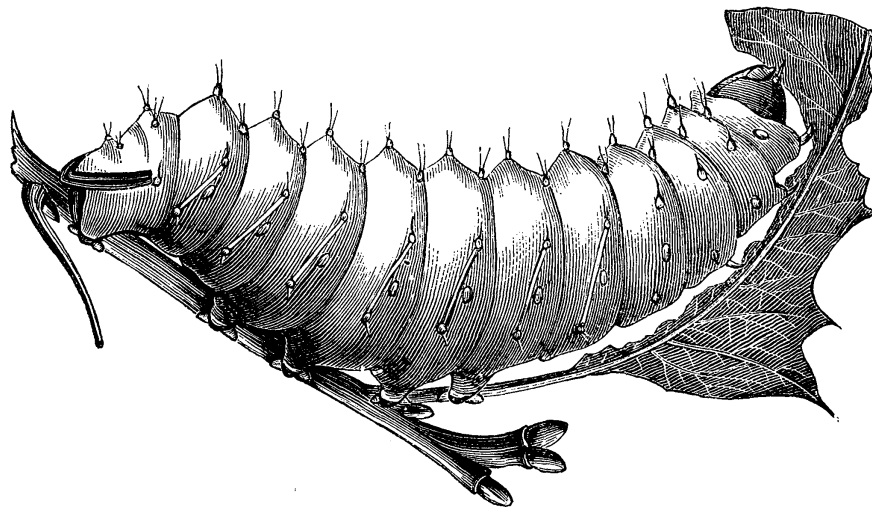
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“The cocoons of *Platysamia Cecropia* may be rendered of some commercial value, as the silk can be carded, but the chief objection as stated above, is the difficulty of raising the larva. The *Polyphemus* worm spins a strong, dense, oval cocoon, which is closed at each end, while the silk has a very strong and glossy fibre.” From “The American Silk Worm” by L. Trouvelot (*The American Naturalist*, 1867, 1:30–38).