

Reorganization of interaction networks modulates the persistence of species in late successional stages

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Abstract

1. Ecological interaction networks constantly reorganize as interspecific interactions change across successional stages and environmental gradients. This reorganization can also be associated with the extent to which species change their preference for types of niches available in their local sites. Despite the pervasiveness of these interaction changes, previous studies have revealed that network reorganizations have a minimal or insignificant effect on global descriptors of network architecture, such as connectance, modularity and nestedness. However, little is known about whether these reorganizations may have an effect on community dynamics and composition.
2. To answer the question above, we study the multi-year dynamics and reorganization of plant–herbivore interaction networks across secondary successional stages of a tropical dry forest. We develop new quantitative tools based on a structural stability approach to estimate the potential impact of network reorganization on species persistence. Then, we investigate whether this impact can explain the likelihood of persistence of herbivore species in the observed communities.
3. We find that resident (early-arriving) herbivore species increase their likelihood of persistence across time and successional stages. Importantly, we demonstrate that, in late successional stages, the reorganization of interactions among resident species has a strong inhibitory effect on the likelihood of persistence of colonizing (late-arriving) herbivores.
4. These findings support earlier predictions suggesting that, in mature communities, changes of species interactions can act as community-control mechanisms (also known as priority effects). Furthermore, our results illustrate that the dynamics and composition of ecological communities cannot be fully understood without attention to their reorganization processes, despite the invariability of global network properties.

KEYWORDS

community control, network reorganization, plant–herbivore interactions, species coexistence, structural stability, succession dynamics

1 | INTRODUCTION

Ecological communities continuously reorganize in response to the multiple disturbances coming in abundance from the environment (CaraDonna et al., 2017; Levins, 1968; Lu et al., 2016; Ramos-Jiliberto, Valdovinos, Moisset de Espans, & Flores, 2012; Saavedra, Rohr, Fortuna, Selva, & Bascompte, 2016; Trøjelsgaard & Olesen, 2016). This reorganization can be associated with the extent to which species change their preference for types of niches available in their local sites (Chase, 2003; Tilman, 2004). That is, as environmental conditions change or as species alter their environment, different interspecific interactions can emerge as species deplete and consume new resources (Fukami, 2015). Interestingly, the majority of studies have concluded that the reorganization of species interactions across successional stages and environmental gradients has a minimal or insignificant effect on the global descriptors of the architecture of interaction networks, such as connectance, modularity and nestedness (Carstensen, Sabatino, Patricia, & Morellato, 2016; Morris, Gripenberg, Lewis, & Roslin, 2013; Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008; Trøjelsgaard & Olesen, 2016; Villa-Galaviz, Boege, & del Val, 2012). Therefore, one may rashly conclude that network reorganization has no effect on the dynamics and future composition of ecological communities.

However, earlier studies have suggested that active changes of species interactions can act as community-control mechanisms, especially in well-structured communities of late successional stages (Margalef, 1968; Odum, 1969). These community-control mechanisms are also known as priority effects (Chase, 2003; Fukami, 2015; Viana, Cid, Figuerola, & Santamaría, 2016), where resident (early-arriving) species can limit and modify the resources available in their local sites, generating facilitative or inhibitory effects on new colonizing (late-arriving) species. Despite the ecological relevance of the potential association between network reorganization and community-control mechanisms, this association has not been validated for almost half a century due to the lack of data or mathematical tools. Yet, validating these predictions can improve our understanding about the ecological mechanisms governing community-assembly processes (Drake, 1990; Fukami, 2015).

To shed new light onto these predictions, we test the hypothesis that the reorganization of plant–herbivore interaction networks modulates the likelihood of persistence of herbivore species in late successional stages, despite the invariability of global network properties. We focus on plant–herbivore interaction networks because the reorganization of these interactions has been well documented (Bryant & Chapin, 1986; Bryant et al., 1991; Denno et al., 2000; Villa-Galaviz et al., 2012). While it has been shown that the persistence of herbivore species depends on many factors, such as resource availability, the presence of host species, natural enemies and environmental variations, among others; it is still unclear the extent to which the reorganization of plant–herbivore interaction networks can also provide information about the likelihood of herbivore persistence across successional stages (Gripenberg, Morrien, Cudmore, Salminen, & Roslin, 2007; Tack, Ovaskainen, Harrison, & Roslin, 2009; Villa-Galaviz et al., 2012).

Importantly, as plants continuously induce defences against herbivore attacks (through the production of secondary metabolites and physical defences), they can alter the browsing patterns and interaction networks within mammal and insect communities (Bryant et al., 1991; Erb, Robert, Hibbard, & Turlings, 2011; Poelman, Broekgaarden, Loon, & Dicke, 2008; Villa-Galaviz et al., 2012; Viswanathan, Lifchts, & Thaler, 2007). For instance, new antagonistic interactions can arise among herbivore species through the modification of plant quality after initial herbivore damage (Anderson, Inouye, & Underwood, 2009; Denno et al., 2000). Similarly, new synergistic interactions can occur across successional stages, as is the case of ecosystem engineering species, which structurally modify the environment or host plants and may facilitate the establishment of new herbivore species (Lill & Marquis, 2003). Thus, the reorganization of plant–herbivore interaction networks may provide valuable information about the potentially changing plant-mediated effects acting on the persistence of herbivore species (Ali & Agrawal, 2014; Redman & Scriber, 2000).

In this paper, we describe and analyse the multi-year dynamics and reorganization of plant–herbivore interaction networks across secondary successional stages of a tropical dry forest. In particular, we focus on herbivore communities characterized by plant-mediated (indirect) negative effects. As a proxy for these negative effects, we use the number of plants shared between herbivores following a niche-overlap framework (MacArthur & Levins, 1967; Rohr et al., 2016; Saavedra, Rohr, Gilarranz, & Bascompte, 2014). To estimate the potential impact of network reorganization on the persistence of herbivore species, we develop new quantitative tools following a structural stability approach applied on a population dynamics model (Rohr, Saavedra, & Bascompte, 2014; Saavedra, Rohr et al., 2017). Then, we perform a statistical analysis to investigate the association between the observed herbivore persistence and the estimated impact of network reorganization across successional stages.

2 | MATERIALS AND METHODS

2.1 | Empirical data

We studied on a yearly basis over 4 years (during the rainy season of each year in the period 2007–2010) the dynamics and reorganization of nine plant–herbivore interaction networks. In total, we observed 140 tree (plant) species and 471 Lepidopteran (herbivore) species. These networks were located in a Mexican tropical dry forest under different stages of secondary succession (19°22′–19°39′N, 104°56′–105°10′W). Tropical dry forests represent one of the most threatened ecosystems in the world due to anthropogenic land-use change (Trejo & Dirzo, 2000), where the reorganization of species interactions is a highly active process (Villa-Galaviz et al., 2012). Secondary succession in these forests typically corresponds to the recovery process after being transformed and abandoned by human activities (mainly agriculture and livestock production; Odum, 1969; Villa-Galaviz et al., 2012). Three of these networks were at an early successional stage (6–8 years of abandonment from cattle ranching activities), three at a middle stage (14–16 years of abandonment), and the last three were

at a late stage of succession (more than 20 years of abandonment; Avila-Cabadilla, Stoner, Henry, & Alvarez-Añorve, 2009; Villa-Galaviz et al., 2012).

Each of our nine plant–herbivore interaction networks were located in 20×50 m plots, with four transects of 2×20 m established every 10 m within each plot. Plots were separated from each other by at least 3 km. In each transect, we marked all woody plants ≥ 1 cm in diameter and ≥ 50 cm trees, excluding lianas. These plants were sampled looking for lepidopteran larvae in leaves and stems four–five times each year during the rainy season (19 samples in total). Larvae were reared in the laboratory to confirm the trophic interaction with host plants and to produce adults for taxonomic identification. Trees were taxonomically identified in the laboratory. Lepidopterans were identified using traditional taxonomy complemented with molecular identification of operational taxonomic units. With this purpose, DNA bar coding was performed following the techniques previously specified in Hebert, Stoeckle, Zemplak and Francis (2004). Sequences were edited with Sequencher version 4.0.5 (Gene Codes) and aligned manually based on their translated amino acids. All the COI and 28S sequences obtained were deposited in <http://www.boldsystems.org/> (Saavedra, Cenci, del Val, Boege, & Rohr, 2017). All plant–herbivore interaction networks are available in Dryad (Saavedra, Cenci, et al., 2017).

Figure 1 illustrates the dynamics present in each of these nine plant–herbivore interaction networks. For each of the 4 years t under investigation (2007–2010), each of the observed networks were characterized by a subset of interacting plant and herbivore species that were present in the previous year $t - 1$ —what we call resident species, and a remaining set of new interacting species—what we call colonizing

species. We observed on average 30% and 85% of turnover between years for resident and colonizing species respectively. Note that tropical dry forests are typically characterized by a high beta diversity (Trejo & Dirzo, 2000). Despite this significant species turnover, the global architectural properties of these networks (number of species, connectance, nestedness and modularity) did not differ much from year to year (see Villa-Galaviz et al., 2012 for information about these statistics). In fact, this observed global architectural invariability appears to be a general feature among temporally or spatially similar ecological networks (Carstensen et al., 2016; Morris et al., 2013; Petanidou et al., 2008; Trøjelsgaard & Olesen, 2016; Villa-Galaviz et al., 2012).

Importantly, along with the species turnover reported above, we also observed a substantial reorganization of plant–herbivore interactions among resident species—approximately 60% of interactions were replaced from year $t - 1$ to year t among the species that were present in both years (see Figure 1 for a graphical example). This allowed us to investigate whether the reorganization of plant–herbivore interactions among resident species can modulate the likelihood of persistence of herbivore species across successional stages, despite the invariability of the global network architecture.

2.2 | Quantitative analysis

We carried out the quantitative analysis of our hypothesis in three steps. First, because plant–herbivore interactions can better represent the direct and indirect dependency of herbivores on plants rather than the other direction (Bryant et al., 1991; Erb et al., 2011; Gripenberg et al., 2007; Poelman et al., 2008; Tack et al., 2009) and because which insect eats which plant is the only information we

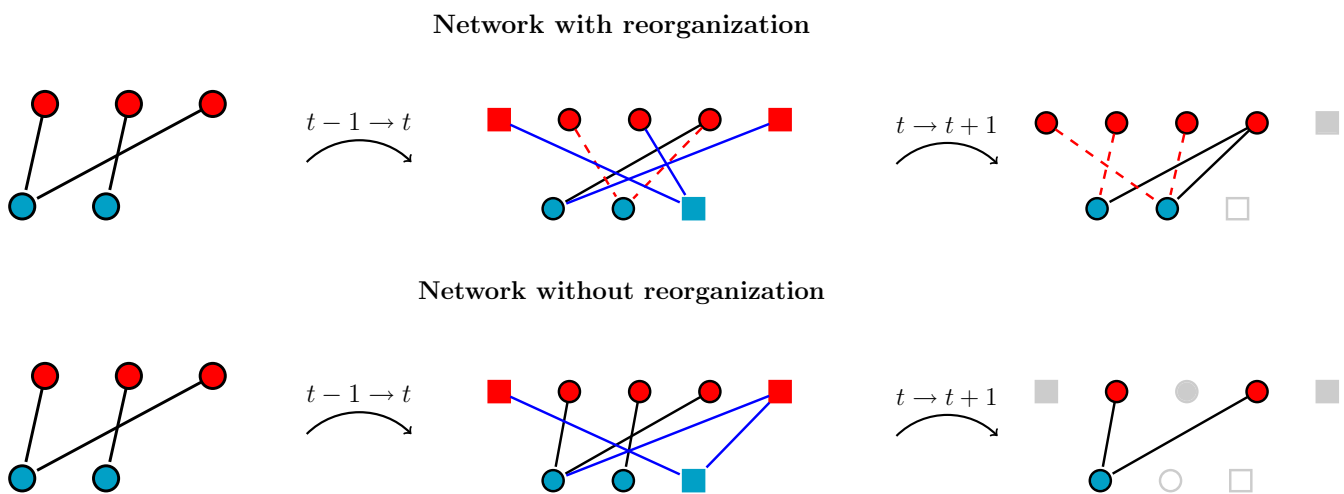


FIGURE 1 Dynamics and reorganization of plant–herbivore interaction networks. The top and bottom panels correspond to a fictitious example of species turnover with and without network reorganization. Symbols and links correspond to species interactions respectively. Both panels start at year $t - 1$ with a community of interacting resident species that persist to year t . Different colours represent different sets of species, such as plants and herbivores. At year t , new colonizing species arrive (squares) establishing interactions with resident and other colonizing species (blue links). The top panel shows a scenario where interactions among residents species change (network reorganization) from year $t - 1$ to year t (dashed red links), whereas the bottom panel shows a scenario where all interactions among resident species remain the same (no reorganization). As the new formed community in year t moves forward to year $t + 1$, some species are not able to persist (gray symbols). Following Margalef (1968) and Odum (1969), we test the hypothesis that changes of species interactions (network reorganization) can act as a community-control mechanism, especially in late successional stages [Colour figure can be viewed at wileyonlinelibrary.com]

have about our communities, we focused on herbivore communities characterized by plant-mediated (indirect) negative effects. These negative effects are derived from the number of shared plants between herbivores following a niche-overlap framework (MacArthur & Levins, 1967; Rohr et al., 2016; Saavedra et al., 2014). Second, we calculated the impact of network reorganization on the likelihood of herbivore persistence following a theoretical approach based on the mathematical notion of structural stability applied to a competition dynamics model (Rohr et al., 2014; Saavedra, Rohr, Fortuna, et al., 2016; Saavedra, Rohr, Olesen, & Bascompte, 2016; Saavedra, Rohr, et al., 2017). Third, we studied the effect of this theoretical impact on the observed persistence of resident and colonizing herbivore species from a given year (when both types of species co-occur) to the next one (when only some of these species persist) across sites and successional stages. We discuss these points below.

2.3 | Linking species persistence and network reorganization

To investigate species persistence in plant-mediated herbivore communities, we used a general Lotka–Volterra competition model of the form (MacArthur & Levins, 1967; Rohr et al., 2016; Saavedra et al., 2014; Saavedra, Rohr, et al., 2017):

$$\frac{dN_i}{dt} = N_i(r_i - \sum_{j=1}^n \alpha_{ij}N_j),$$

where the variable N_i denotes the abundance of herbivore i , and the parameter $r_i > 0$ is the intrinsic growth rate of herbivore i . The indirect effects (α_{ij}) are derived from the plant–herbivore interaction networks using a niche overlap framework (MacArthur & Levins, 1967; Rohr et al., 2016; Saavedra et al., 2014). The level of intraspecific effect (α_{ii}) for each herbivore species i is defined by the number of host plants of species i , and the indirect effect (α_{ij}) of herbivore j on herbivore i is defined by the number of common plants between herbivore species i and j scaled by a factor μ . This factor μ controls the overall level of interspecific effect relative to the intraspecific effect (Saavedra et al., 2014).

This parameterization should only be taken as an approximation to the potential plant-mediated indirect effects between two herbivore species. Because the actual effect of plant–herbivore interactions on herbivore persistence continues to be debatable (Ali & Agrawal, 2014; Gripenberg et al., 2007; Redman & Scriber, 2000; Tack et al., 2009), the rationale of our parameterization is to test the extent to which plant–herbivore interactions and their changes provide any information about the different factors affecting herbivore persistence through shared plants. We also chose this model and parameterization given the possibility to track analytically the multidimensional properties of large ecological communities (Logofet, 1993; Svirezhev & Logofet, 1983), and the simple biologically sounded interpretation of interspecific interactions as the extent of niche overlap (Case, 2000; MacArthur & Levins, 1967).

Mathematically, under the studied competition Lotka–Volterra model all species persist when two conditions are satisfied: global stability and feasibility (Hofbauer & Sigmund, 1998; Rohr et al., 2014).

The former condition implies that the trajectories of the dynamical system eventually converge to a stable point attractor (i.e. an equilibrium point N_i^* of the Lotka–Volterra model). The latter condition implies that the equilibrium point at which the trajectories converge is feasible from an ecological perspective, i.e. that all species have positive biomass ($N_i^* > 0$). Note that feasibility is the mathematical necessary condition for species persistence, while the global stability of a feasible equilibrium point provides the sufficient condition for persistence (Hofbauer & Sigmund, 1998). However, stability does not necessarily imply that the system is located at the equilibrium point. It only represents a property of the dynamical space in which the system evolves (Lewontin, 1969). That is, the system most likely moves around the feasible equilibrium point, as stochasticity will almost surely induce fluctuations around the attractor (Levins, 1968).

In our parameterization and model, the stability condition can be computed from the eigenvalues of the interaction matrix α (Logofet, 1993; Saavedra et al., 2014; Svirezhev & Logofet, 1983). Because our interaction matrix is symmetric by construction, as long as the eigenvalues are all positive, the trajectories converge to one and only one globally stable equilibrium point N_i^* (Logofet, 1993; Saavedra et al., 2014; Svirezhev & Logofet, 1983). As soon as one eigenvalue is negative, any feasible equilibrium point becomes unstable; as a consequence, the system may depart from any feasible equilibrium point even under infinitesimal perturbations to species abundances. This implies that the parameter μ (controlling the overall level of interspecific effects) needs to be constrained between zero and a critical level μ_{\max} ($0 < \mu < \mu_{\max}$), such that all eigenvalues are positive (Saavedra et al., 2014).

The feasibility condition involves both the interaction matrix α and the vector of species intrinsic growth rates r . As mentioned before, feasibility corresponds to the existence of an equilibrium point at which all species have positive abundances ($N_i^* > 0$). Such an equilibrium point is necessarily the solution of the linear equation $r = \alpha N$. Importantly, not all possible vectors of intrinsic growth rates lead to feasibility. To satisfy the feasibility condition, a vector of intrinsic growth rates needs to counterbalance the negative interspecific effects and their imbalance (Rohr et al., 2016; Saavedra et al., 2014; Saavedra, Rohr, et al., 2017). Consequently, only a specific set of vectors of intrinsic growth rates leads to feasibility. This set is generally called the feasibility domain (Rohr et al., 2014; Saavedra et al., 2014; Saavedra, Rohr, et al., 2017).

Thus, the feasibility domain is by definition the set of intrinsic growth rates leading to a positive equilibrium point ($N_i^* > 0$), which is equivalent to a positive solution of the linear equation $r = \alpha N$. Following a structural stability approach (Rohr et al., 2014 2016; Saavedra et al., 2014; Saavedra, Rohr, et al., 2017; Saavedra, Rohr, Fortuna, et al., 2016; Saavedra, Rohr, Olesen, et al., 2016), the feasibility domain of intrinsic growth rates in this competition model can be computed based on the interaction matrix α . That matrix can be written on the format of columns vectors

$$\alpha = \begin{bmatrix} \alpha_{11} & \cdots & \alpha_{1n} \\ \vdots & \ddots & \vdots \\ \alpha_{n1} & \cdots & \alpha_{nn} \end{bmatrix} = \begin{bmatrix} \vdots & \vdots & \vdots \\ \mathbf{v}_1 & \mathbf{v}_2 & \cdots & \mathbf{v}_n \\ \vdots & \vdots & \vdots & \vdots \end{bmatrix} \quad (1)$$

from which we can derive the feasibility domain

$$D_f(\alpha) = \{r = N_1^* v_1 + \dots + N_n^* v_n, \text{ with } N_1^* > 0, \dots, N_n^* > 0\} \quad (2)$$

Geometrically, the feasibility domain is represented by the conical hull made by the positive combinations of the vectors v_1, \dots, v_n forming the columns of the interaction matrix α . This domain is called an algebraic cone (Logofet, 1993; Saavedra, Rohr, Fortuna, et al., 2016; Saavedra, Rohr, Olesen, et al., 2016; Svirezhev & Logofet, 1983). Any vector of intrinsic growth rates inside this cone forms part of the feasibility domain and is compatible with species persistence (see Figure 2 for a graphical example).

Following the rationale above, we calculated the potential impact of network reorganization on species persistence by computing the displacement in the feasibility domain of an interaction matrix before α_1 and after reorganization α_2 . Recall that interaction matrices are derived from the plant–herbivore interaction network. For each year t of observation, the plant–herbivore interaction network used to derive the interaction matrix after reorganization was exactly

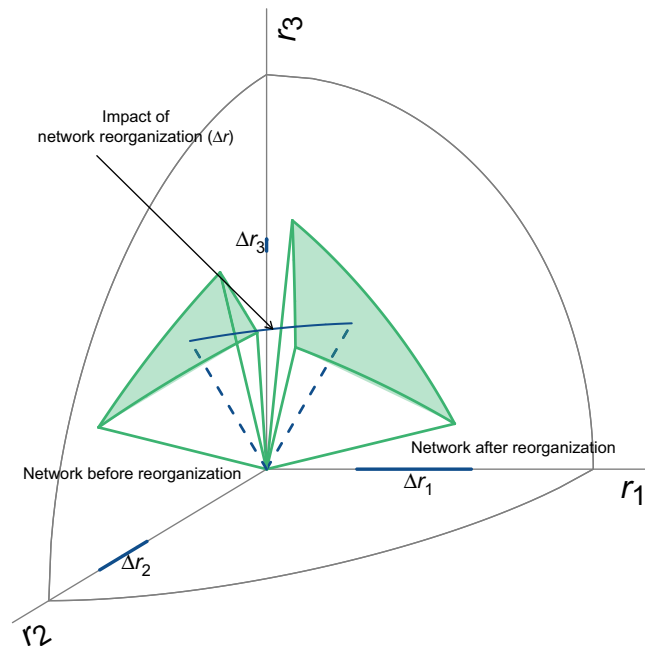


FIGURE 2 Graphical example of the theoretical impact of network reorganization on species persistence. For a fictitious network of three species, the green cones represent the feasibility domains (volume of intrinsic growth rates compatible with the persistence of the three species) generated by the interaction matrices before (without) and after (with) reorganization. Note that each axis corresponds to the intrinsic growth rate values of a species. The displacement between feasibility domains is measured by the difference in the geometric centroids (dashed blue lines) between the two domains. We call this displacement the change in structural growth rates. The thicker blue lines on each of the axes correspond to the projection of the displacement in structural growth rate for each of the species. This projection corresponds to the impact of network reorganization on each species (Δr_i). Note that this impact does not necessarily has to be the same for all species [Colour figure can be viewed at wileyonlinelibrary.com]

that as observed at time t . To derive the interaction matrix before reorganization, we also used the plant–herbivore interaction network observed at time t , but all the interactions between resident species were replaced by the ones that were previously observed at time $t - 1$. This mimics the hypothetical scenario of a plant–herbivore interaction network without reorganization from year $t - 1$ to t , but corrected for each species presence or absence (for an illustration, see Figure 1).

In particular, we measured the potential impact of network reorganization on species persistence by computing (as a first order of approximation) the displacement of the geometric centroid of the feasibility domains before and after reorganization. The geometric centroid of the feasibility domain is quantified by the so called structural vector of intrinsic growth rates (see Figure 2 for a graphical example; Rohr et al., 2014 2016; Saavedra et al., 2014; Saavedra, Rohr, et al., 2017). For a given interaction matrix α , this vector is computed by

$$r_s(\alpha) = \frac{\frac{v_1}{\|v_1\|} + \dots + \frac{v_n}{\|v_n\|}}{\left\| \frac{v_1}{\|v_1\|} + \dots + \frac{v_n}{\|v_n\|} \right\|}$$

The displacement of structural vectors before and after reorganization, given by the corresponding interaction matrices α_1 and α_2 , is computed by

$$\Delta r = |r_s(\alpha_1) - r_s(\alpha_2)|$$

This displacement corresponds to the potential impact on the intrinsic growth rate that herbivore species would have to absorb due to network reorganization in order to continue counterbalancing the plant-mediated negative effects that could lead to exclusion. At the individual level, the higher the displacement in the element i of the structural vector in a community, the higher the theoretical impact of network reorganization on herbivore species i . See Figure 2 for a graphical example. The code to compute the impact of network reorganization is archived in Dryad (Saavedra, Cenci, et al., 2017).

2.4 | Linking theory and data

To investigate the association between the theoretical impact of network reorganization and the observed persistence of herbivore species according to our data, we used a generalized linear mixed effect model (Zar, 2010) for resident and colonizing herbivore species separately. In our model, for each plant-mediated herbivore community at year t of observation, the response variable (e_{ijk}) is a binary variable representing whether herbivore i (at site j and successional stage k) has persisted from year t to year $t + 1$. That is, $e_{ijk} = 1$ if herbivore species i is observed at time t and at time $t + 1$ in our data, $e_{ijk} = 0$ otherwise. To eliminate biases due to absence of colonizing species at a certain observation period, each time t in our statistical analysis needs to have both resident and colonizing herbivore species. That is, from the 4 years of observation in each site, we could only use the second and third as time t in order to have information about plant–herbivore interactions at time $t - 1$, and presence or absence of herbivore species at time $t + 1$.

The co-variables in the model for each plant-mediated herbivore community at time t are given by the theoretical impact of network reorganization on herbivore species i (Δr_{ijk}), the number of herbivore species n_{jk} , the year of observation y_{jk} and as random factor the site s_j . Note that for each community we have nine sites, three successional stages and 2 years t of observations. Years are independent of successional stage as all observations are initialized in 2007. The random factor for each site accounts for individual details of previous management, soil characteristics, distance to conserved forest or other potential environmental filters (Avila-Cabadilla et al., 2009; Tilman, 2004).

Importantly, the number of species, year of observation and site are not independent variables. That is, a simple linear model explains about 85% of the variation in number of herbivore species, using year of observation and site as co-variables. This means that we cannot use these three variables together in a model due to collinearity issues (Legendre & Legendre, 2012). Therefore, to assess the effect of the theoretical impact of network reorganization on the observed likelihood of herbivore persistence, and how this effect is modulated by the successional stage, we used a model averaging technique (Claeskens & Hjort, 2008). Specifically, we assumed that the response variable (e_{ijk}) follows a binomial distribution and the logit of its probability of being one (i.e. persistence) is given by:

$$\begin{aligned} \text{Prob}(e_{ijk} = 1) &= p_{ijk} \text{ with } \text{logit}(p_{ijk}) = \alpha_k + \beta_k \Delta r_{ijk} + \gamma_1 y_{jk} + s_j \\ \text{Prob}(e_{ijk} = 1) &= p_{ijk} \text{ with } \text{logit}(p_{ijk}) = \alpha_k + \beta_k \Delta r_{ijk} + \gamma_2 n_{jk} + s_j \end{aligned} \quad (3)$$

The parameters of the two models above correspond to the intercepts α_k as a function of the stage k , the slopes β_k of the effect of network reorganization as a function of the stage k , the slope γ_1 of the effect of the year of observation, the slope γ_2 of the effect of the number of herbivore species and the random effect due to the site j is given by $s_j \sim \mathcal{N}(0, \sigma_s^2)$. Both parameters α_k and β_k were averaged between the two models. Note that α_k represents the basal effect of the successional stage k on the observed likelihood of persistence, while β_k represents the effect of the theoretical impact of network reorganization on the observed likelihood of herbivore persistence.

Additionally, given that it is virtually impossible to know the level of interaction strength in each plant-mediated herbivore community, and how this varies across communities and successional stages, we studied as exhaustively as possible values in the range $0 < \mu < \mu_{\max}$. Thus, for each community, we repeated the statistical analysis 200 times by drawing at random a different level of μ . Note that every time we compared the feasibility domain between interaction matrices before and after reorganization, we used the same value of μ for each matrix in the pair. Because of our randomization procedure, reporting p -values would be misleading as they can be decreased simply by increasing the number of randomizations. That is, the standard error is proportional to the inverse of the square root of the number of data points (randomizations; Zar, 2010). Therefore, we focused on comparing the boxplot (i.e. the variation) of the scaled effect in our model parameters (α_k , β_k , γ_1 , and γ_2 drawn from 200 randomizations of the interspecific strength μ). All the statistical analyses were done with R

(R Core Team, 2017) and the models were fitted using the library lme4 (Bates, Mächler, Bolker, & Walker, 2015).

Finally, to test the extent to which the observed variation of scaled effects is not an artefact of either our theoretical methodology or our sampling procedure, we performed two different null models. In the first null model, we generated random sequences for each site, where the observed plant-herbivore interactions are randomly shuffled. This null model preserves the number of species and interactions, but modifies the observed plant-herbivore interaction networks. This has the purpose of testing whether our theoretical methodology is driving the variation of scaled effects, regardless of the observed network reorganization. In the second null model, the random sequences for each site were generated by drawing both the identity and the interactions from a metaweb according to the successional stage of the community (Saavedra, Rohr, Fortuna, et al., 2016). This metaweb is the aggregation of all species and interactions observed in a given successional stage. This second null model preserves the number of species, observed interactions and species turnover, but modifies the identity of species. This has the aim of testing whether a different sampling procedure could have generated the same variation of scaled effects as the observed networks. For each null model, we generated 200 random sequences (with 200 changes each of the strength factor μ) and analysed the variations in scaled effects following our statistical model above. Note again that no statistical significance can be calculated from these null models (given that the number of randomizations conditions the p -values), only the variations.

3 | RESULTS

Across all plant-mediated herbivore communities and successional stages, we found that 75% of all herbivore species display a non-zero theoretical impact (displacement) on the structural growth rate as a consequence of network reorganization. Figure 3 shows the variability (density plot) of this theoretical impact on a log scale. In general, we found that the theoretical impact of network reorganization is characterized by a bimodal distribution, revealing that one group of herbivore species can be more affected than other. Moreover, resident herbivore species (right panel in figure) and colonizing herbivore species (left panel in figure) display different distributions across successional stages (illustrated by different colours in figure). Specifically, resident herbivore species change from a unimodal to a bimodal distribution across successional stages, with smaller impacts in the late stages. In contrast, colonizing herbivore species always present a bimodal distribution across successional stages, with higher impacts in the late stages. Thus, these patterns raise the question of whether this theoretical impact of network reorganization can explain the observed persistence of herbivore species, especially in late successional stages.

Following our statistical methods above, we estimated the scaled effect of the number of species, year of observation, and theoretical impact of network reorganization on the observed persistence of herbivore species across successional stages. Figure 4 shows that the number of species and year of observation have opposite effects.

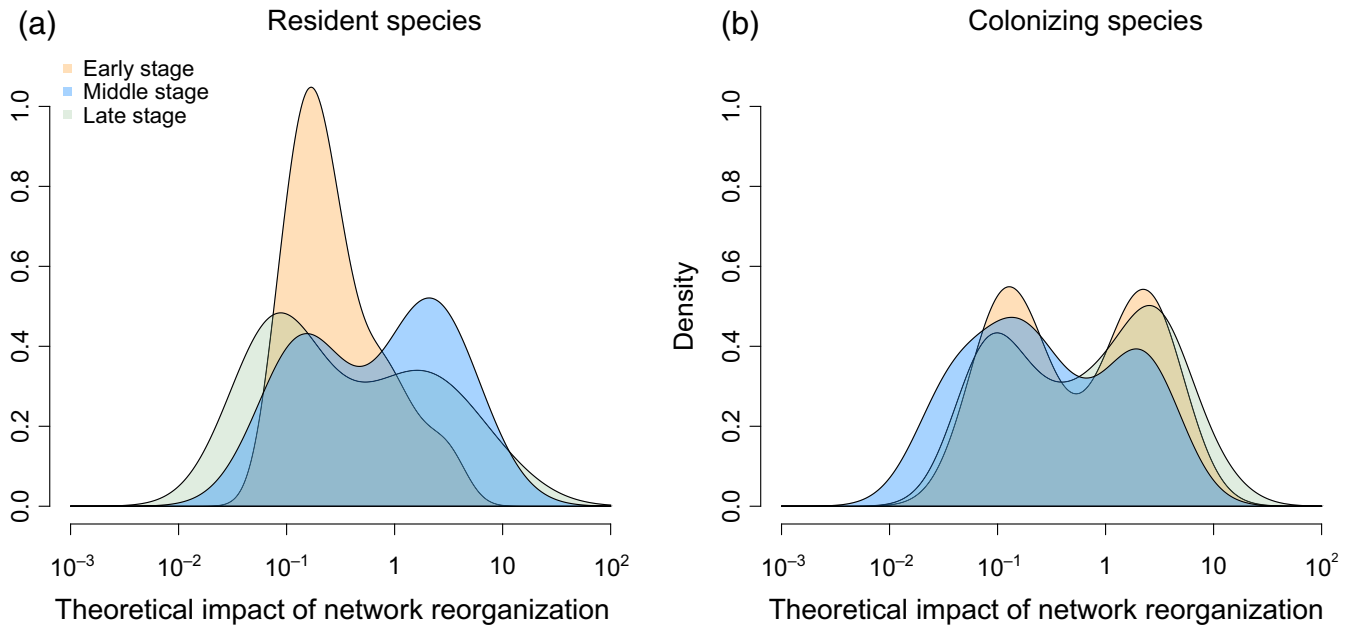


FIGURE 3 Distribution of the theoretical impact of network reorganization on species persistence across successional stages. The left and right panels represent the density plots of the impact (Δ_r on a log scale) on resident and colonizing herbivore species respectively. Each panel is divided into the three successional stages analysed (illustrated by different colours). This shows that network reorganization does not have the same impact on all species and successional stages [Colour figure can be viewed at wileyonlinelibrary.com]

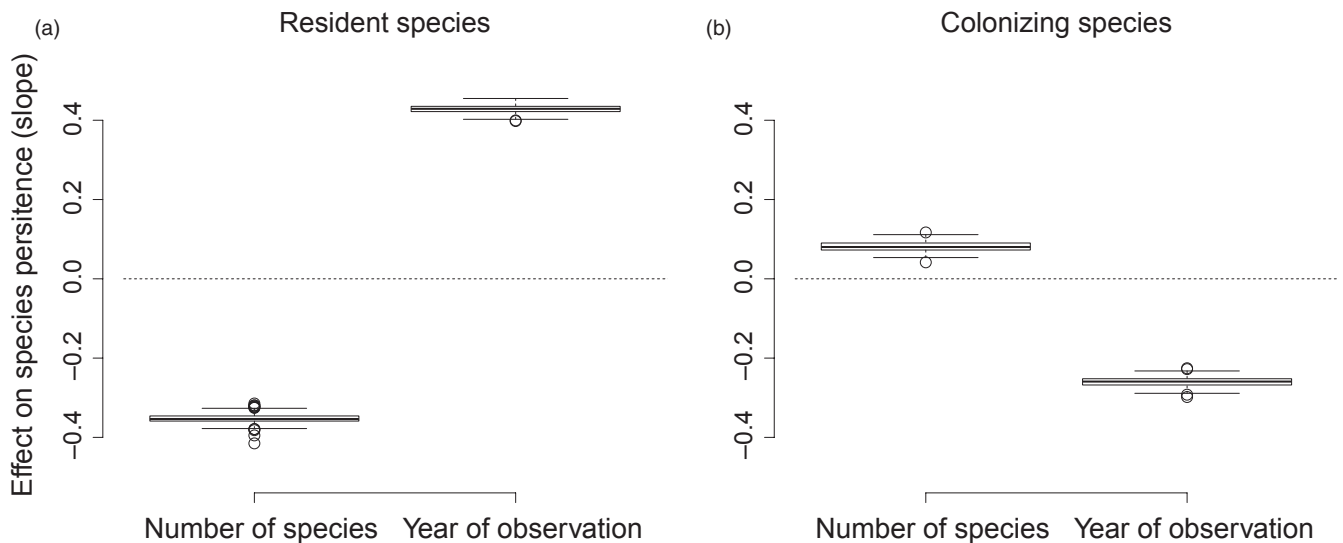
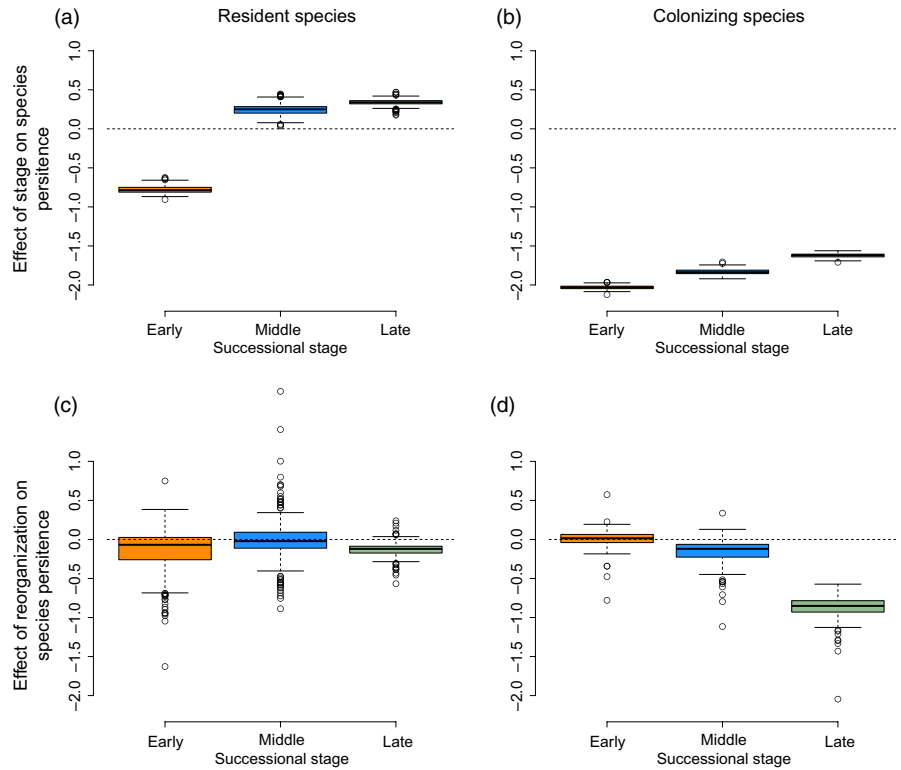


FIGURE 4 Scaled effect of the number of species and year of observation on the observed likelihood of species persistence. (a, b) It shows the variation (standard boxplots) of scaled effects of the parameters number of herbivore species and year of observation for resident and colonizing herbivore species respectively. Scaled effects are extracted from our statistical analysis (see Materials and methods). Note that the number of species and year of observation have opposite effects on resident and colonizing herbivore species. The dashed horizontal lines correspond to the scaled effect of zero

Specifically, the number of species has a negative effect on residents but a positive effect on colonizing herbivore species. In contrast, the more recent the year of observation in a site, the larger and smaller the likelihood of persistence for resident and colonizing herbivore species respectively. This suggests that in older communities, resident herbivore species may have larger chances of persistence than colonizing herbivore species.

Figure 5 (top panels) confirms the assumptions above. We found that late successional stages have a positive effect on the likelihood of persistence of resident herbivore species. In contrast, this effect is always negative for colonizing species. This further reveals that not only colonizing herbivore species have lower chances to persist in a mature community but resident herbivore species can also increase their likelihood of persistence across successional stages.

FIGURE 5 Network reorganization as an emergent community-control mechanism in late successional stages. The top panels show the basal scaled effect (intercepts from the statistical model) of the successional stage on the likelihood of herbivore persistence. The bottom panels show the scaled effect (slopes from the statistical model) of network reorganization on the likelihood of herbivore persistence. In each panel, boxplots correspond to the variation in the scaled effects for the early, middle and late successional stages, from left to right. The left and right panels show the scaled effects for resident and colonizing herbivore species respectively. The dashed horizontal lines correspond to the scaled effect of zero [Colour figure can be viewed at wileyonlinelibrary.com]



Finally, Figure 5 (bottom panels) shows that the reorganization of interactions among resident species has a strong inhibitory effect on the persistence of colonizing herbivore species in the late successional stage of the communities. Note that per construction of our statistical model, the effect of network reorganization is additional to the effects of year of observation and successional stage. Additionally, in both of our null models (see Materials and methods), the effect of network reorganization is zero across all successional stages (see Figures S1 and S2). This confirms that the observed negative effect of network reorganization on colonizing herbivore species in the late successional stage is not an artefact of our theoretical methodology nor our sampling procedure. Overall, these findings support earlier predictions that changes in species interactions can act as community-control mechanisms in mature communities (Margalef, 1968; Odum, 1969).

4 | DISCUSSION

By assessing changes in plant–herbivore interaction networks across forest succession, we have derived changing indirect negative effects between herbivores mediated by their shared host plants. We have used the extent to which two herbivores share their host plants as a proxy for how they can directly and indirectly affect each other. As new colonizing herbivore species arrive, plants respond to their attacks and can affect other herbivores' browsing patterns. Hence, changes in plant communities across forest succession generates the opportunity for the reorganization of plant–herbivore interaction networks and has the potential to change the strength of interspecific effects between herbivores (Villa-Galaviz et al., 2012). These changes can be promoted

as direct resource competition (Kaplan & Denno, 2007; McGeoch & Chown, 1997; Tack et al., 2009), or plant mediated indirect effects among herbivores (Ali & Agrawal, 2014). For example, evidence has shown indirect effects mediated by plants (Ali & Agrawal, 2014; Cunan, Powell, & Weis, 2015; Lynch, Kaplan, Dively, & Denno, 2006; Pan et al., 2016; Poelman et al., 2008), pathogens (Redman & Scriber, 2000) and predators (Karban, Hougén-Eitzmann, & English-Loeb, 1994; Pallini, Janssen, & Sabelis, 1998), and have demonstrated their impacts on herbivore performance (Ali & Agrawal, 2014; Lynch et al., 2006) and population dynamics (Karban et al., 1994; but see Gripenberg et al., 2007; Tack et al., 2009). However, rather of focusing on a single mechanism, our framework allows the inclusion of all factors promoting indirect negative effects from the host overlap between herbivores (Gomes, Merckx, & Saavedra, 2017; Rohr et al., 2016; Saavedra et al., 2014). Yet, future work should disentangle the role of these different ecological processes in both network reorganization and species persistence.

Our work cannot establish direct causal links between the estimated impact of network reorganization and species persistence (Saavedra, Rohr, Dakos, & Bascompte, 2013). That is, our approach uses a population dynamics model that summarizes all the factors defining species persistence by two parameters: the intrinsic growth rates of species and their interspecific effects (Rohr et al., 2016; Saavedra et al., 2014; Saavedra, Rohr, et al., 2017). This means that we are not taking into account stochastic environmental processes, species abundances as modulators, the exact timing of arrivals, spatial scales, species traits nor the phylogenetic structure, all of which can be important for species persistence (Bennett & Pärtel, 2017; Carboni et al., 2016; Domènech & Vilà, 2006; Li et al., 2016; Olito & Fukami, 2009; Tilman, 2004; Viana et al., 2016). Yet, as we have shown, with the introduction

of appropriate null models, our framework can be used to estimate the contribution of the reorganization of plant–herbivore interaction networks to species persistence, and may be used to study the transition between successional stages. Equivalently, changes in the vector of intrinsic growth rates or changes in the overall interspecific effect may be used to study the impact of the direction and strength of environmental fluctuations (Rohr et al., 2016; Saavedra et al., 2014).

In line with current successional studies and theory (Dini-Andreote, Stegen, van Elsas, & Salles, 2015; Fukami, 2015; Li et al., 2016), our analysis of plant-mediated herbivore communities has revealed that during early successional stages, the likelihood of persistence is low for both resident and colonizing herbivore species. This shows that during initial successional stages, many of the persistence factors appear to follow a random process. That is, stochasticity through environmental filtering and the timing of arrival seems to be the key determinant of early community assembly (Chase, 2003; Domènech & Vilà, 2006; Olito & Fukami, 2009; Tilman, 2004). But our study has also revealed that as some species get established and the community matures into subsequent successional stages, resident herbivore species increase their likelihood of persistence across time and successional stage. This is also in line with the concept of priority effects (Chase, 2003; Fukami, 2015; Viana et al., 2016), where early-arriving species can prevent colonization of late-arriving species by niche preemption and modification (Fukami, 2015; Viana et al., 2016). Importantly, these processes involve biotic filtering or resistance (Tilman, 2004), which is a central theme in community ecology (Fukami, 2015; Viana et al., 2016). In fact, our study has shown that the number of species has an opposite effect on resident and colonizing herbivore species. Moreover, our analysis has revealed that in late successional stages, the reorganization of species interactions among resident species can have a strong inhibitory effect on the likelihood of persistence of colonizing herbivore species. Network reorganization may prove to be an important community-control mechanism operating in many ecological communities (CaraDonna et al., 2017; Saavedra, Rohr, Fortuna, et al., 2016).

Indeed, nearly half a century ago, pioneer work on ecosystem ecology predicted that not only changes of environmental conditions should modulate community composition but also changes of species interactions, especially in late successional stages (Margalef, 1968; Odum, 1969). By combining new advancements on theoretical tools and empirical data, our results have given support to these long-standing predictions. Our findings also suggest that depending on the level of maturity of a community, network reorganization can be used to anticipate changes in the composition of ecological communities. For instance, because network reorganization appears to act as a community-control mechanism against late-arriving species, we anticipate that external perturbations to species interactions in late successional stages can have detrimental effects for early-arriving species. This may have important consequences for conservation strategies (Dirzo et al., 2014).

An open question is how network reorganization affects community dynamics and persistence (CaraDonna et al., 2017; Lu et al., 2016; Ramos-Jiliberto et al., 2012; Saavedra, Rohr, Fortuna, et al., 2016; Trøjelsgaard & Olesen, 2016). While many studies have shown that network reorganizations have a minimal or insignificant effect on the global architecture of species interaction networks

(Carstensen et al., 2016; Morris et al., 2013; Petanidou et al., 2008; Trøjelsgaard & Olesen, 2016; Villa-Galaviz et al., 2012), our work has illustrated that network reorganization does play an important role modulating community composition, despite the invariability of global network properties. This suggests that the dynamics and biodiversity patterns characterizing ecological communities cannot be fully understood without attention to their network reorganization processes. We believe that increasing our understanding of the mechanisms inhibiting or facilitating the reorganization of interaction networks can take us to improve our ability to anticipate how and when communities will change or be invaded (Levin, 2005; Yamada & Bork, 2009).

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AUTHORS' CONTRIBUTIONS

S.S. and R.P.R. designed the study; S.S., S.C., R.P.R. performed analysis; E.d.-V. and K.B. designed field work; and S.S. wrote a first version of the manuscript. All authors contributed with significant revisions to the manuscript.

DATA ACCESSIBILITY

The data and computational code are archived in Dryad Digital Repository <https://doi.org/10.5061/dryad.5h187> (Saavedra, Cenci et al., 2017).

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SUPPORTING INFORMATION

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Figure S2: (Supporting Online Figure) Statistical results from null model 2. Equivalent to our Figure 5 in the main text but using null model 2. Recall that null model 2 generates random sequences of network by randomly drawing species and interactions from a metaweb of each successional stage (see Methods in main text). Here, the variation of the scaled effect of network reorganization on the persistence of colonizing herbivore species is around zero. Note that because we are preserving the observed species turnover across successional stages, the scaled effects of stage on persistence are similar to Figure 5.