ARTICLE

Changes in species composition and community structure during plant–pollinator community assembly

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Abstract

The assembly of plant–pollinator communities has traditionally been explored from the perspective of species composition, often overlooking how interaction structure and the roles species play in their communities can change even when species composition remains constant. Here, we use 10 years of data to investigate the assembly of plant–pollinator networks in an intensively managed agricultural landscape. We compare the characteristics of assembling communities to those of mature and unrestored communities to explore if and how changes are reflected in species composition, network structure, and species' roles therein. Unexpectedly, we found that although species' composition of mature communities became increasingly dissimilar over time, the overall community structure and individual species' roles in assembling communities remained unchanged. Yet, the network structure of assembling communities gradually converged toward that of mature communities. Our results suggest that even when traditional diversity measures remain relatively invariant, network structure can uncover the dynamic nature of ecological communities, rendering interaction networks an important component of community assembly studies. Our findings advance the understanding of essential ecological processes underlying community assembly and provide insights into the mechanisms shaping species' roles within ecological networks.

KEYWORDS
ecological networks, mutualism, network alignment, network structure, restoration, species roles

INTRODUCTION

Ecological communities are composed of species that affect each other in different ways, forming networks of interactions. The patterns behind community assembly and the processes that underlie them have been the focus of ecologists since the earliest formal ecological studies (Chase, 2003; Clements, 1916; Fukami, 2015; Gleason, 1917), and this work has primarily been shaped by two contrasting viewpoints. On the one hand, the Clementsian climax-community hypothesis states that ecological communities will steadily progress toward a local climax state (Chase, 2003; Clements, 1916). As such, different communities in the same geographic area and successional stage are expected to be similar due to niche-based processes determining species composition (Pontin, 1982; Tokeshi, 1993). Although the strict determinism of the Clementsian paradigm is no longer generally accepted (e.g., Hubbell, 2011), the concept of succession to climax community is widely applied (e.g., Poorter et al., 2023). In contrast, the Gleasonian hypothesis proposes that community assembly is shaped, at least partially, by stochastic species immigration and a fluctuating environment (Gleason, 1917), an idea that underlies later theories of biogeography (Wilson & MacArthur, 1967) and neutral theory (Hubbell, 2011). In a Gleasonian scenario, early-immigrating species create priority effects that may facilitate or hinder colonization by additional species (Chase, 2003; Fukami, 2015; Stuble & Souza, 2016; Weidlich et al., 2021). Thus, communities from the same geographic area and assembly stage would differ in their species composition and exhibit different structural patterns (Chase, 2003). While the relative importance of these processes has been an area of vigorous debate and much research, relatively few studies have tested their importance in shaping species interactions and in the structure of these interaction networks (Bascompte & Stouffer, 2009; Poisot et al., 2012).

Different ecological measures can be used to track community assembly in interaction networks. From traditional measures of species diversity and compositional dissimilarity (e.g., beta-diversity) to the organization of interactions between species (e.g., metrics of community structure) and the roles individual species play in the community (Bramon Mora et al., 2020; Cirtwill et al., 2018; Gaiarsa et al., 2021; Ponisio, 2020). In interaction networks, species play different roles based on their interactions with other species. A species' network role can be characterized by its position in the network (e.g., centrality and trophic position), the number of interactions it engages in (e.g., degree distribution), and the extent to which it interacts with other species (e.g., whether it is a specialist or a generalist) (Cirtwill et al., 2018). Building upon the Clementsian perspective of assembly, in addition to species' composition, both the structure of interaction network and roles species play would progress toward a climax state over time (Clements, 1916). Communities of similar age or stage would thus have similar network structures, and a species' network role should be more similar among communities at the same successional stage than those at different stages. In contrast, if the assembly process is more stochastic (i.e., Gleasonian viewpoint; Chase, 2003; Fukami, 2015; Hubbell, 2011; Stuble & Souza, 2016), there would be no definitive community assembly climax. As a result, rapid fluctuations in community organization would lead to indiscernible patterns in network structure and species roles when comparing communities at similar stages of assembly (Bascompte & Stouffer, 2009).

Various studies have documented the dynamics of mutualistic interactions across different temporal scales (Alarcón et al., 2008; CaraDonna et al., 2021; Olesen et al., 2008, 2011; Petanidou et al., 2008; Ponisio, 2020; Zoller et al., 2023) and have shown that the roles played by different species in their network can undergo significant changes, both within (Bramon Mora et al., 2020) and across seasons (Cirtwill et al., 2018; Gaiarsa et al., 2021; Petanidou et al., 2008; Ponisio et al., 2017), reflecting the considerable amount of variation encountered in interaction patterns through time (Peralta et al., 2020; Petanidou et al., 2008; Tylianakis & Morris, 2017). However, most studies typically focus on one or a few flowering seasons. In contrast, changes in network structure and species' network roles during longer-term community assembly remain under-explored (Bascompte & Stouffer, 2009; CaraDonna et al., 2021). Understanding the mechanisms underlying the assembly of mutualistic networks can provide insights into the level of determinism in ecological communities and help generate more precise predictions for restoration efforts. For example, within a Clementsian framework, the ultimate goal might be to achieve a specific network structure representing a climax community, whereas in a Gleasonian framework, there is a low probability that multiple communities will assemble into a specific interaction structure.

Here, we use a 10-year dataset of plant–pollinator interactions that tracked communities from weedy to restored communities within an intensively managed agricultural landscape in California's Central Valley. Our goal is to understand the long-term changes in species composition, network structure, and individual species' roles within plant–pollinator communities as they change following restoration. Specifically, across

multiple years, we compare communities at three different restoration stages—assembling communities (i.e., communities restored 1 year before the study), mature communities (i.e., communities restored >10 years prior), and unrestored communities (Figure 1a). We test how similarity in (1) species composition, (2) network structure, and (3) species' network roles, changes through time both within and between community types (assembling, mature, and unrestored). If communities progress toward a common local optimum or climax, we hypothesize that (H1) dissimilarity in species composition and network structure within assembling communities would decrease through time as communities mature. In contrast, we would expect no change in dissimilarity within mature and unrestored communities (Figure 1b). Additionally, we further expect that (H2) dissimilarity between assembling and mature communities will decrease over time as assembling communities progress toward a climax state. In contrast, the dissimilarity between assembling and unrestored communities would increase through time (Figure 1c). Likewise, if species roles are determined by their intrinsic characteristics and niche-based processes, such as body size and dietary breadth, rather than neutral foraging processes like abundance, we expected that (H3) species' roles would be conserved within and between sites regardless of the presence of other species. Alternatively, if species exhibit spatiotemporal variation in their network role, processes other than species identity may be determining their network roles.

METHODS

Study sites and data collection

The study sites ($N = 32$) were located in the Central Valley of California in Yolo, Colusa, and Solano Counties and sampled across 10 years. This is an agricultural landscape composed primarily of conventionally managed monoculture crop fields (~30 ha) (Appendix S1: Figure S1). Sampling sites belong to three different experimental treatments: (1) assembling communities (hedgerows where native plants were installed at the beginning of the study, in 2006; $N = 7$), (2) mature communities (hedgerows where native plants had been installed >10 years prior; $N = 13$), and (3) unrestored communities (no restoration intervention; $N = 12$). Restoration was performed by planting the same set of native perennial shrubs and trees on the field borders, and unrestored sites comprise field margins geographically matched to assembling communities that were sampled over the same time period (see Kremen & M'Gonigle, 2015, and Appendix S1 for further details on site characteristics). The assembly of the pollinator community and plant–pollinator network at the assembling sites was monitored for up to 10 years post-restoration (from 2006 to 2015, Appendix S1: Table S1; mean =6 years of sampling per site). Mature sites were monitored over the same period as assembling and unrestored sites, but at lower frequencies (Appendix S1: Table S1, mean = 3 years of sampling per site). The study sites were selected to be adjacent to crops that were not attractive to pollinators (i.e., wheat and almond [blooms in February before surveys]).
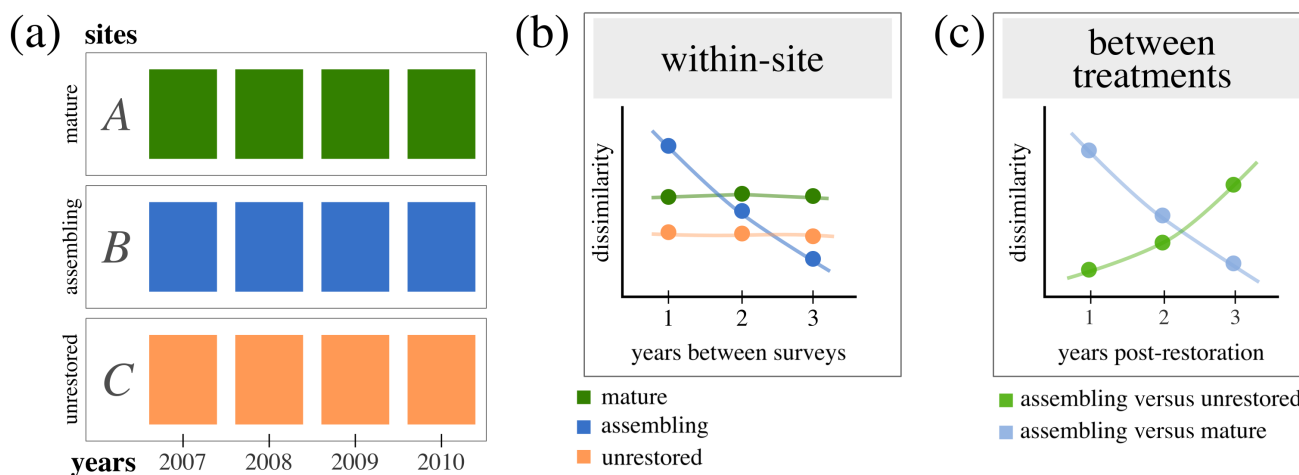

FIGURE 1 Schematic diagram illustrating our approach to evaluate long-term changes in plant–pollinator communities following restoration. (a) Each rectangular box represents one sampling site (A, B, C) across years (2007–2010). Colors represent different restoration treatments: (A) mature (dark green), (B) assembling (dark blue), and (C) unrestored (light orange). (b) Based on the Clements climax model, as time since restoration increases, the compositional and structural dissimilarity of assembling sites will decrease, whereas in mature (climax) and unrestored sites, no discernible pattern will emerge. (c) We hypothesized that compositional and structural dissimilarity between assembling and mature sites would decrease through time (light blue), whereas dissimilarity would increase between assembling and unrestored communities (light green).

On average, sites were 15 km apart, and the minimum distance among sites sampled in the same year was 1 km. The entire survey area spanned almost 300 km^2 (Appendix S1: Figure S1). We sampled sites between April and August up to five times per year (Appendix S1: Table S1; mean 3.4 surveys per site, per year), in a randomized fashion, and only when wind speed was below 2.5 m/s and temperatures greater than 21°C. In each sampling site, hedgerows were between 3 and 6 m wide and approximately 350 m long. We sampled each transect for 1 h, pausing the timer while handling specimens. We collected flower visitors that touched floral reproductive parts and recorded the plant species in which specimens were collected. We focused on wild bees only because they are the most abundant and effective flower visitors in this system (Brittain et al., 2013; Kremen et al., 2002; Morandin et al., 2016). Honeybees (*Apis mellifera*) were not sampled because their ubiquitous presence as managed pollinators meant they were widespread and uniformly abundant across sites. As such, their impact is likely uniform across the entire landscape. Expert taxonomists identified bee specimens either to species level or morpho-species for specimens in the *Lasioglossum*, *Nomada*, and *Sphecodes* genera. Plants were identified at the species level.

We constructed interaction networks for each combination of site and year, totaling 129 networks across all three experimental treatments, comprised of 9971 specimens from 130 different bee species, 119 different plant species, and 863 unique plant–pollinator interactions. We sampled the 32 sites included in the dataset (12 unrestored, 13 mature, and 7 assembling; Appendix S1: Figure S1, Table S1) in at least two different years and the networks composed of at least five plants and five pollinators (cf. Simmons et al., 2019), given that our goal is to explore how community structure and composition changed through time. Because the number of sampling rounds per site varied across years (Appendix S1: Table S1), we used the mean number of flower visits between each species pair (plant–pollinator) at each site to represent the interaction frequency in a year (Appendix S1: Table S1). Although we focus on pollinator assembly, given that plant species were installed in the studied sites for restoration, plants are inherently part of mutualistic networks and, therefore, are indirectly incorporated into our analyses.

Community-level dissimilarity

Using the aforementioned 129 networks, we computed dissimilarity within and between sites to compare communities in the early steps of restoration (assembling communities) to unrestored communities and their late-stage counterparts (mature communities; Figure 1). We first compared years between surveys to explore how within-site dissimilarity changes through time. If there is an optimal state, dissimilarity within assembling sites would decrease through time as communities mature and progress toward the global optima (H1; Figure 1b). Thus, within-site dissimilarity measures how dissimilarity changes through time (years of assembly) within each site and looks for consistent patterns across sites and treatments.

Next, we also explored between-treatments dissimilarity by comparing sites at different restoration stages in the same sampling year, to explore if assembling communities become increasingly similar to climax communities through time as assembly progresses (Figure 1c). If this is the case, we expect that dissimilarity between assembling and mature communities would decrease through time (years post-restoration) and that dissimilarity between assembling and unrestored communities would increase through time (H2; Figure 1c).

We calculated within-sites and between-treatments dissimilarity in three different ways: (1) focusing on the species composition of the communities (within-site community dissimilarity and between-treatments community dissimilarity), (2) focusing on the network structure of the communities (within-site structural dissimilarity and between-treatments structural dissimilarity), and (3) at the species level focusing on the network roles of different species (within-site role dissimilarity and between-treatments role dissimilarity). Below, we describe each metric in more detail.

Dissimilarity in species composition

We calculated dissimilarity in species composition as the Chao estimator that incorporates species abundances and accounts for unobserved species (Chao et al., 2005), implemented in the vegdist function in the vegan package (Oksanen et al. 2020). For within-site dissimilarity, we created a pollinator-by-year matrix for each site in which each element was the number of flower visits observed for each pollinator species in each year. We computed within-site dissimilarity from this species-year matrix. For between-treatments dissimilarity, we created a pollinator-by-site matrix for each year of sampling in which each element was the mean number of flower visits observed for each pollinator at each site in a year. We then computed dissimilarity between sites of different restoration treatments from this species-site matrix.

Dissimilarity in network structure

We used network alignment methods (Bramon Mora, Gravel, et al., 2018) to characterize the dissimilarity in network structure within sites and between treatments. Alignment enables different networks to be mapped onto each other by pairing species in those networks that interact in similar ways (Kuchaiev et al., 2010). We first characterized species' roles in each network (see below for details) and then calculated the alignment of network pairs based on the similarity of their constituent species' roles (Bramon Mora, Cirtwill, et al., 2018; Bramon Mora, Gravel, et al., 2018). In this method, two species from different networks are perfectly aligned if both their roles and the roles of their interaction partners are the same in the two networks (Appendix S1: Figure S2; Bramon Mora, Gravel, et al., 2018). From this species-level alignment—a measure of structural dissimilarity between network pairs—we use the optimal alignment cost between them (Bramon Mora, Gravel, et al., 2018): the greater the similarity between species, the smaller the alignment cost between them. In particular, given the best alignment among networks, we calculate the optimal alignment cost as the average pairwise role dissimilarity across pairs of aligned species. That is, we calculated the dissimilarity between pairs of species as one minus Pearson's correlation between their roles and averaged these across aligned pairs (eq. 4 in Bramon Mora, Gravel, et al., 2018). As with dissimilarity in species composition, we computed network structural dissimilarity in this way both within sites from the same treatment across time (Figure 1b) and between treatments (Figure 1c).

Species-level dissimilarity

In addition to exploring network dissimilarity at the community level, we focused on the species level to explore if and how species roles change as communities assemble, both within communities over time and between treatments across sites. We defined pollinator species' roles in their networks using network motifs (Cirtwill et al., 2018; Stouffer et al., 2012). Motifs represent the set of unique patterns of species interactions and provide a consistent way to describe network substructure (Milo et al., 2002; Stouffer et al., 2012). As such, motifs highlight specific configurations of the interactions among species that occur more frequently than would be expected by chance alone and provide a measure of how unique the position of each species is within a network, and how that varies through space and time (Bramon Mora et al., 2020). Thus, the strength of the motif approach lies in its ability to offer detailed insights into specific interaction patterns

at the species level. Because interaction strength, that is, number of links or interactions, is an important component of network structure, we computed species' roles using motif profiles that incorporate information on interaction strengths (see Bramon Mora, Cirtwill, et al., 2018). We normalized each motif profile based on network size to make species' roles comparable between networks of different sizes. Then, to examine how species' roles shift through time, we focused on the 15 pollinator species that appeared in multiple networks across treatments and calculated two dissimilarity metrics, following a similar approach as described above. Within-site role dissimilarity measures how species' role dissimilarity changes between years at each site (Figure 1b), and we calculated it for every unique interaction each species appeared in. To measure how a species' role changes between restoration treatments through time (years post-restoration), we calculated between-treatments role dissimilarity in a given year by comparing assembling communities to both unrestored and mature communities. We used the Chao index in the `vegan` package (Oksanen et al., 2020), which accounts for unseen species pairs when calculating dissimilarity (Chao et al., 2005).

Statistical analysis

We used Bayesian generalized linear mixed models to analyze how dissimilarity changed within sites (i.e., assembling, mature, and unrestored; Figure 1b) and between treatments (i.e., assembling–mature and assembling–unrestored; Figure 1c). Because each of the six aforementioned metrics (within-site compositional, structural, and role dissimilarity; between-treatments compositional, structural, and role dissimilarity), fall within the open interval (0,1), we fit beta-distributed generalized linear models (please refer to Appendix S1 for a complete description of the statistical models used for each analysis described below). We fit our models using STAN via the package `brms` (Bürkner, 2017, 2018). We used uninformative priors (see Appendix S1) and ran four chains for 3000 iterations with 1000 warm-up iterations. We then determined convergence using R-hat values, bulk, and tail effective sample size (Bulk ESS) and examined the chains.

For the within-site models, we included site status (assembling, mature, and unrestored), distance between years, and their interaction as explanatory variables. We modeled site and species identity as being drawn from a common distribution (i.e., referred to as random effects in a frequentist framework).

For the between-treatments models, we included treatment comparison (assembling–mature and assembling–unrestored), year of assembly, and their interaction as

explanatory variables, as well as site and species identity as a random effect. Finally, to understand the within-site and between-treatments relationships for each species, we included a random slope per species and treatment to the models described above. We restricted our analyses to species for which we had at least two data points—that is, were seen at least twice.

To determine support for our hypotheses, we evaluated whether or not the credible interval of the different models included zero (refer to Appendix S1 for model estimates, SE, lower credible intervals, upper credible intervals, Rhat, and Bulk ESS). We performed all analyses in R 4.0.2 (R Core Team, 2018).

RESULTS

For the dissimilarity in species composition, we found mixed support for our hypotheses (Figure 1b,c). Contrary to the Clementsian prediction (H1), for within-site dissimilarity, we found that dissimilarity increased over time only in mature communities (estimate = 0.36, SE = 0.18; Figure 2a, Appendix S1: Table S2). However, for community dissimilarity between treatments, we only found support for decreasing dissimilarity when comparing assembling to mature communities (estimate = −0.21, SE = 0.10; Figure 2b, Appendix S1: Table S3).

For the dissimilarity in network structure, we found no association for within-site community structural dissimilarity (Figure 2c, Appendix S1: Table S4). However, in line with the Clementsian prediction (Figure 1c), we found that structural dissimilarity between assembling and mature communities decreased through time (estimate = −0.17, SE = 0.08; Figure 2d, Appendix S1: Table S5), but no effect of for the structural dissimilarity between assembling and unrestored communities (Figure 2d, Appendix S1: Table S5).

Lastly, we found no support for an effect of species role dissimilarity either within sites (Appendix S1: Figure S3a, Table S7) or between treatments (Appendix S1: Figure S3b, Table S8). When examining species that were seen at least twice, we also failed to find a consistent pattern both within sites (Figure 3, Appendix S1: Table S6) and between treatments (Appendix S1: Figure S4, Table S9).

DISCUSSION

We examined the changes in species composition, community structure, and species' roles in plant–pollinator networks over 10 years as assembly progressed. Specifically, we compared the dynamics of assembling versus mature and unrestored habitats in an intensively managed agricultural landscape. Our results are threefold. First, considering dissimilarity within sites, we found no evidence for an effect of dissimilarity in assembling communities for either species composition or network structure (H1; Figure 2a,c). However, for dissimilarity between treatments, we found that both species composition and network structure of assembling communities became increasingly similar to those of mature communities as restoration progresses (Figure 2b,d), which partially supports our expectation (H2; Figure 1c). Thus, although mature communities are changing through time, as indicated by the positive effect of within-site community dissimilarity, the decreasing dissimilarity between assembling and mature communities over time suggests that mature communities potentially serve as the moving target for assembling communities. Finally, we found no effect of role dissimilarity within and between communities, suggesting that species' roles across networks in mature and assembling communities are unpredictable and highly variable, both within sites and between treatments. In this sense, species identity may not be a good predictor of their roles, suggesting that mechanisms other than species identities per se may be at play when communities are assembling. Below, we discuss each of these findings in more detail.

An increasing number of studies have used a network approach beyond the temporal variability of mutualistic networks (CaraDonna et al., 2021; Gaiarsa et al., 2021; Petanidou et al., 2008) to study the effects of restoration interventions (Gaiarsa & Bascompte, 2022; Kaiser-Bunbury et al., 2017). Studies have found a high turnover of species and interactions (Ponisio et al., 2017), with restored sites usually exhibiting greater functional diversity (Ponisio et al., 2016) and higher species richness than unrestored sites (Devoto et al., 2012; Kaiser-Bunbury et al., 2017; Noreika et al., 2019). In this work, we take it a step further to explore whether dissimilarity in species composition within assembling communities and between assembling and mature communities would decrease as assembling communities developed and became more established (Figure 1b), as restoration progressed. However, contrary to our expectations, we only found support for a positive effect on within-site dissimilarity in mature communities (Figure 2a). In intensively managed agricultural landscapes such as our study site, environmental filtering may limit species' arrival to these habitat patches (Ponisio et al., 2016; Tylianakis & Morris, 2017). Thus, if an inhospitable landscape matrix limits the species pool, it is reasonable to expect a slower colonization process, leading to the more homogeneous species composition we observe in unrestored and assembling communities.

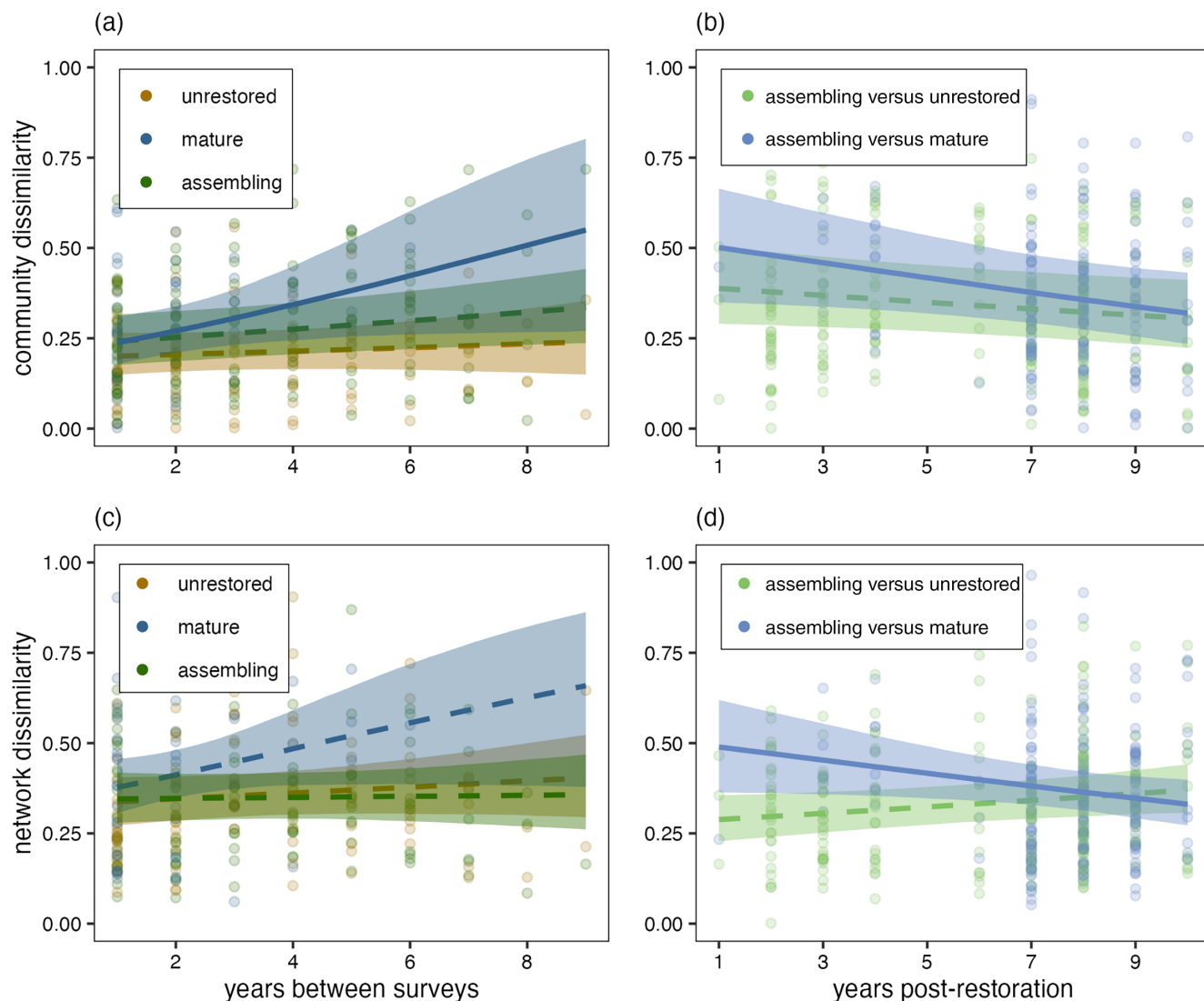Alternatively, mature sites may have had longer to differentiate from one another through species loss and

FIGURE 2 Community and structural dissimilarity within sites of the same treatment (unrestored, mature, assembling) (a, c) and between treatments (assembling vs. unrestored and mature communities) (c, d). Within-site community dissimilarity increased with years between surveys in mature communities (a; solid line), whereas between treatments, dissimilarity decreased with years post-restoration between assembling and mature communities (b). We found no association for within-site structural dissimilarity (c; dashed line), whereas between-treatments community dissimilarity decreased with years post-restoration between assembling and mature communities (d). Solid and dashed lines represent the means, and shaded areas represent the 95% credible interval, with solid lines representing slopes where the posterior distribution was consistently above or below zero. Refer to Appendix S1: Tables S2a, S3b, S4c, and S5d for the model's estimates and credible interval values.

species gain processes, which could result in higher dissimilarity in mature communities. Previous studies in this system have shown that hedgerows promote the occurrence of specialized floral visitors (M'Gonigle et al., 2015)—which are usually rare species (Vázquez et al., 2007)—and that 5 years post-restoration was when the majority of consistent increase in species richness and diversity was recorded (Kremen et al., 2018). Alongside the evidence that rare species are more vulnerable to extinction and usually lost first after habitat destruction (Aizen et al., 2012; Zoller et al., 2023), the

combined increase in richness and specialized pollinator species may explain the increase in within-site dissimilarity we observed in the mature communities. These results highlight the importance of maintaining long-term restoration patches to increase species diversity.

When we compared assembling and mature communities between treatments, we found that both species composition and community structure became increasingly similar as restoration progressed (Figure 2b,d). This pattern suggests that as plant–pollinator networks assemble, their structure is slightly progressing toward a
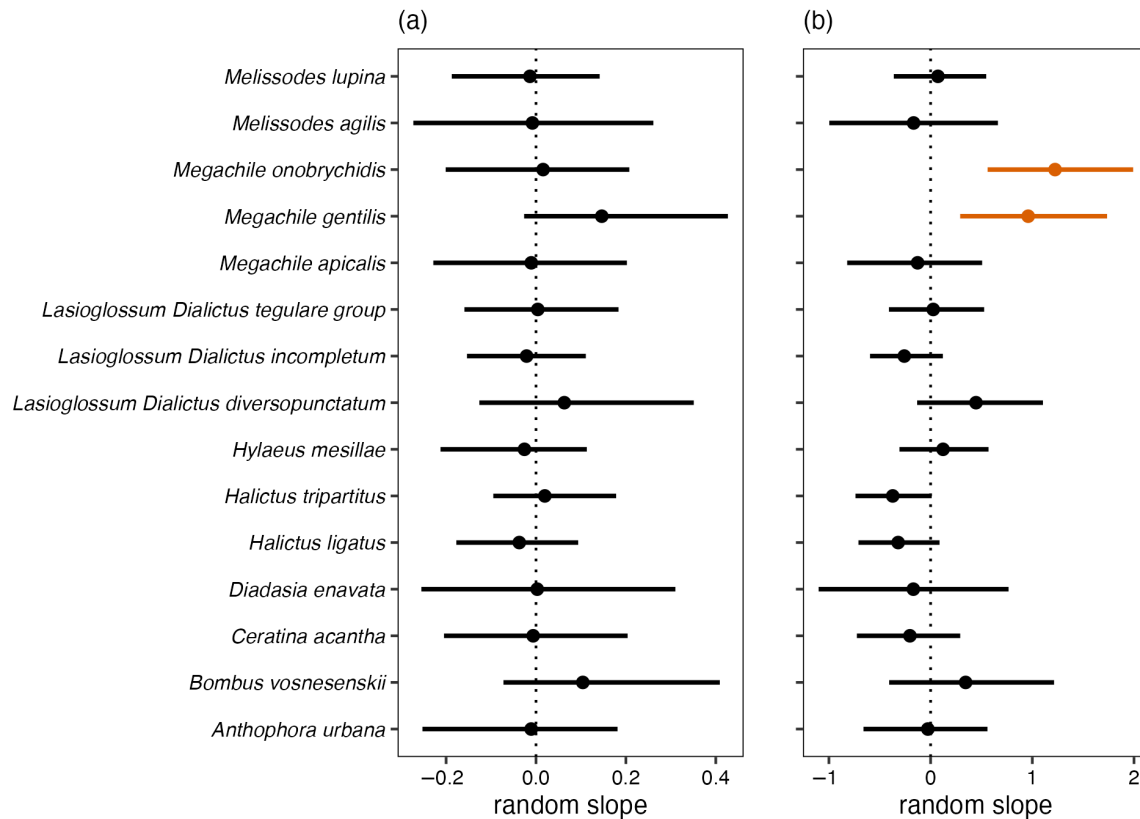
FIGURE 3 Within-site species role dissimilarity in assembling (a) and mature (b) communities for the 15 species that appeared in multiple sites and years across treatments. Positive values indicate a positive relation between role dissimilarity and years of assembly, suggesting that role dissimilarity increases as assembly progresses. The opposite is true for a negative value. We highlight species that have credible intervals that do not overlap with zero. Lines represent credible intervals (refer to Appendix S1: Table S6 for estimates and credible interval values).

specific structure exhibited by the mature communities. In contrast, our within-site analyses show no major differences for assembling communities, indicating that the structure of each individual community does not progress toward a specific general structure. The absence of an ideal global optimum toward which species and communities are progressing in the dynamic context in which these communities are embedded suggests the existence of different optimal states (Chase, 2003; Fukami & Nakajima, 2011). These alternative transient states (Fukami & Nakajima, 2011) may be shaped by a combination of stochastic species immigration and a fluctuating environment, resulting in different communities (Beisner et al., 2003; Ponisio et al., 2016). In this sense, there may be a fluctuating optimum according to the ever-changing biotic and abiotic conditions of the different habitat patches, which are situated in a landscape that is intensively managed for agriculture and frequently affected by severe droughts.

After exploring the dissimilarity in species composition and community structure, we focused on individual species and their roles in their networks as communities change and restoration progresses. We found no effect of within-site and between-treatments on role dissimilarity, which suggests that species' structural roles change in unpredictable and indiscernible ways as plant–pollinator communities assemble. These findings further emphasize the high variability in interaction patterns exhibited by pollinators in this (Gaiarsa et al., 2021; Ponisio et al., 2017) and other landscapes (CaraDonna et al., 2021; Petanidou et al., 2008). This variability may be even stronger in mature communities, where we see a small increase in role dissimilarity over time, although insignificant (Appendix S1: Figure S3a). However, if we assume that mature communities exhibit less variability over time due to the established plant community, this could lead to greater resource availability. Consequently, an increase in role dissimilarity could be interpreted as significant changes in the overall role profile in a site between years, which could explain the higher dissimilarity observed in mature communities. In a previous study conducted in this same system (Gaiarsa et al., 2021), we found that species that were more flexible in their interaction patterns—and thus able to occupy more different

network roles (motifs positions)—had higher colonization and occupancy rates when compared to less flexible species. Taking these results together, we could hypothesize that species with higher occupancy rates are the primary drivers of the observed changes in the mature communities.

Notably, the most abundant pollinator species in the landscape (such as *Halictus ligatus*, *Halictus tripartitus*, and *Lasioglossum* spp.) showed no clear trend in role dissimilarity in either assembling or mature communities (values centered around zero; Figure 3). The ability of these species to occupy different network roles (Gaiarsa et al., 2021) could be driving the lack of a discernible pattern in our results. Our analyses specifically targeted species observed over multiple years and at different sites, which are typically those with higher abundance. Describing species' roles based on their motif profiles has become an increasingly common approach to studying community dynamics (Bramon Mora et al., 2020; Cirtwill et al., 2018; Simmons et al., 2019), and it is an important determinant of species ability to colonize and persist in the landscape (Gaiarsa et al., 2021). Our findings expand this discussion by suggesting that roles might be not only species-specific but also context-dependent—while the role of some species does not change through time regardless of restoration status (e.g., *Lassioglossum* spp.), other species exhibit role changes in mature but not in assembling communities (e.g., *Megachile onobrychidis*; Figure 3).

Habitat modification is one of the main drivers of pollinator decline (Potts et al., 2010; Tylianakis & Morris, 2017). A decrease in floral resources may be a critical consequence of habitat modification, and in an increasingly changing world, ecosystem restoration is an important way to maintain ecological function. Many studies highlight ecological networks as a powerful tool to measure restoration effectiveness. For example, the abundance and richness of pollinators increase when restoration targets plants that are more central in their networks (Maia et al., 2019), and both network structure and species centrality are related to an increase in pollinator persistence (Gaiarsa & Bascompte, 2022). In a seed-dispersal network study in the highly invaded Oahu island in Hawaii, Vizentin-Bugoni et al. (2021) showed that invasive species often played important roles in their networks and that interactions were driven primarily through plants' seed size rather than through plant abundance, indicating the importance of niche-based processes in addition to neutral-based processes ruled by abundance. Our work expands the increasing discussion on the development of predictive theories on communities' responses to global change (Noreika et al., 2019; Poisot et al., 2012) and helps unravel the mechanisms behind how communities and interaction networks assemble to strengthen ecosystem restoration and the creation of robust, stable communities.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data is available in Zenodo in Magaiarsa (2021) at https://doi.org/10.5281/zenodo.4485996 and code is available in Bramon Mora (2025) at https://doi.org/10.5281/zenodo.14650710.

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SUPPORTING INFORMATION

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