

# Intraspecific variation in species interactions promotes the feasibility of mutualistic assemblages

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## Abstract

Patterns of resource use observed at the species level emerge from the way individuals exploit the range of available resources. Hence, accounting for interindividual differences in resource use, such as pollinator use by plants, is essential to advance our understanding of community assembly and persistence. By using finely resolved data on plant–pollinator interactions, we evaluated how interindividual plant variation in pollinator use scales up to affect community structure and dynamics. All co-occurring plant species comprised specialists interacting with proper subsets of pollinators that visited generalists, and differences in interaction patterns were driven by among-individual trait variation. Furthermore, the nested structure and feasibility of plant–pollinator communities were maximised at higher levels of interindividual plant variation in traits and pollinator use. Our study sheds light on how pervasive properties of community structure arise from individual-level processes and contributes to elucidate the importance of preserving intraspecific variation in traits and resource use within populations.

## KEY WORDS

community persistence, individual specialisation, interindividual variation, mutualism, network stability, plant–pollinator interactions, pollination, population niche

## INTRODUCTION

The niche concept has been pivotal to mainstream ecological research since its origins (Grinnell, 1917) and has permeated most theories aiming to explain biodiversity patterns. Traditionally, ecological niches have been described at the population level, treating conspecific individuals as functionally equivalent (Bolnick et al., 2011; Soulé & Stewart, 1970). However, niche variation within populations is a widespread phenomenon in such a way that many apparently generalised populations can be composed of individuals that greatly differ in the way they exploit the range of available resources (Van Valen, 1965; Violle et al., 2012). This among-individual variation might be a result of trait differences and environmental variation in resource availability across

space and time. Although largely neglected, interindividual differences in resource use may have important consequences for population dynamics, species interactions, community structure and long-term coexistence (Barabás & D'Andrea, 2016; Bolnick et al., 2011; Costa-Pereira et al., 2019). Dismissing this level of analysis among individuals limits our understanding of the build-up processes that underpin complex ecological interaction networks.

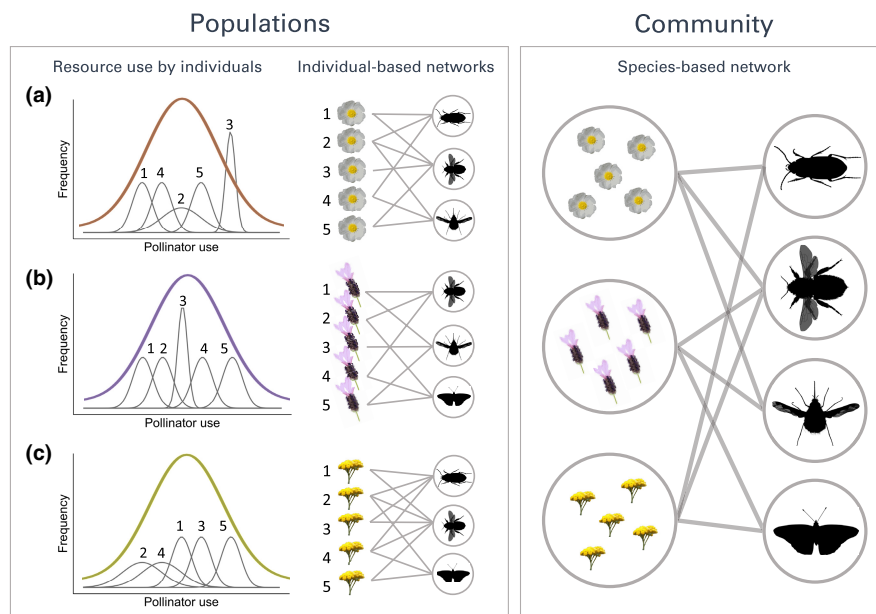
The generalised interaction patterns we frequently document at the species level are often the outcome of nonrandom mixtures of specialists (i.e., individuals using small subsets of the population niche) and generalists (i.e., those using a large proportion of the entire population niche; Bolnick et al., 2003). Describing these complex patterns of resource use by multiple individuals

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can be achieved using individual-based bipartite networks, where at least one of the two sets of nodes represent individuals and the links connecting them depict the interactions they establish (Guimarães, 2020; Olesen et al., 2010). The heuristic value of this individual-based approach has already revealed new insights into the ecological and evolutionary dynamics of species interactions (e.g., Dáttilo et al., 2014; Rodríguez-Rodríguez et al., 2017). For instance, among-individual variation in interaction patterns with pollinators is associated with plant individual's attractiveness, determined by plant phenotypic traits and neighbourhood composition (e.g., Arroyo-Correa et al., 2021; Dupont et al., 2014; Gómez & Perfectti, 2012). Unfortunately, empirical studies considering interindividual variation in interaction patterns usually focus on single species, giving little guidance as to how variance is distributed across multiple species and how it scales up to affect the community-level network structure and dynamics. Over the last decades, community ecology has classically used network theory to summarise and analyse ecological interactions at the species level (e.g., between plant and pollinator species; Ings et al., 2009; e.g., Bastolla et al., 2009; Vázquez et al., 2009). This approach often treats interindividual variation as noise, or as a black box, rather than as an important feature of ecological interactions. Moreover, we do not yet know how the properties of species-level interaction networks are affected by different patterns of among-individual variation in resource use (Figure 1, Clark et al., 2011).

Community-level mutualistic networks (i.e., species-based) usually exhibit nested patterns, wherein specialist species interact with a subset of those species with which generalist species also interact (Bascompte et al., 2003). More nested structures are predicted to have larger feasibility domains (i.e., to persist longer in time; Roberts, 1974; Goh, 1979; Saavedra et al., 2016). Feasibility domains describe the range of tolerated combinations of species demographic features, such as intrinsic growth rates, under which all species can have positive abundances (Rohr et al., 2014; Song et al., 2018). In the presence of an environmental perturbation, such as climate change or habitat loss, it is less likely that any of the species in a very feasible community will decline to extinction, as there is a wide range of conditions in which all species coexist stably. However, there is no evidence to date on how among-individual variation within mutualistic assemblages may affect communities' structure and persistence capacity. For instance, in a plant–pollinator community, an increase in the variability of pollinator use among plant individuals would be reflected in a higher number of pollinator species with which each plant species interacts (i.e., larger niche breadth), affecting the overlap in pollinator use among plant species, the overall structure of the interaction network and the predicted dynamics. Bridging the gap between community structure and dynamics becomes crucial under global change, as many populations are drastically decreasing in size and becoming more homogenous in traits (Sala et al., 2000; Tylianakis et al., 2008).



**FIGURE 1** Upscaling from individual plant variation in pollinator use to the network of interactions among plant and pollinator species within communities. Within the populations of different plant species (a–c), individuals differ in how they use pollinator resources, leading to different levels of specificity in interaction patterns among plant individuals, which can be represented and analysed using individual-based networks. Because ecological interactions among species actually occur between individuals, these individual-based networks provide the building blocks for community-level networks (i.e., species-based networks). For the analysis at the community level, all these individuals' interactions within each plant species are usually aggregated (i.e., summed) in order to incorporate plant species-level interaction assemblages into the species-based network.

By integrating principles of niche theory and network approaches, we aimed to elucidate how community-level pervasive properties emerge as a result of interactions established by individuals and their consequences for community persistence. To that end, we used highly resolved data on plant–pollinator interactions collected at the plant individual level in Mediterranean shrublands. First, we evaluated how interindividual plant variation in interaction patterns is distributed across co-occurring species. The interaction patterns of each plant individual were estimated as the number of pollinator morphotypes used and the overlap in pollinator use with conspecific plants. Second, we assessed the drivers of this interindividual plant variation by analysing the contribution of plant attributes (i.e., phenotypic traits and neighbourhood characteristics). Third, we evaluated how interindividual variation in a key plant attribute, flower production, influences the structure (i.e., nestedness) and dynamics (i.e., feasibility) of community-level plant–pollinator networks. To disentangle the underlying mechanisms, we analysed the impact of interindividual variation in this plant attribute on the number of pollinator morphotypes used by plant species and the overlap in pollinator use among plant species, which in turn may affect the structure and dynamics of communities.

## MATERIALS AND METHODS

### Study site and sampling

The study was performed in Doñana National Park (37°0'29.736" N -6°30'24.919" W, 25 m a.s.l.), on the Atlantic coast of southwestern Spain. Our study area was located on the slopes of stabilised sand dunes, where the vegetation is composed mainly of Mediterranean sclerophyllous shrublands. We selected six 1200 m<sup>2</sup> plots, which were 300 m distance apart, that included 11 insect-pollinated shrub species (Figure S1). We used these six plots to capture locally variable environmental conditions and compositional variation in plant communities, as they differed in the relative abundance and density of shrub species and the depth of the water table.

We conducted surveys to record pollinator visitations in the study plots during the peak flowering period of the plant community (Figure S2, 164 days between early February and mid-July 2021). For each plant species, a variable number of plant individuals were selected (stratified random sampling, Figure S3) depending on local abundance within each plot, totalling 700 plant individuals (see Table S1 for sampling completeness). We performed weekly surveys on each flowering plant individual using video cameras (GoPro HERO7; GoPro Inc., Germany) together with visual censuses along random transects (Appendix S1.1). Pollinators were considered as all those insects landing on the flower and touching its reproductive structures and were identified at the species

level when possible (27.27%, Tables S2 and S3). We defined pollinator morphotypes as groups of pollinator specimens with very similar or identical morphology. We excluded two plant species from our analyses due to the extremely low abundance and the very early flowering period. Data obtained with video recordings were merged with those obtained with random transects by standardising all interaction data as the frequency of visits per minute to create an overall interaction dataset combining both methods (Appendix S1.2). An individual-based network for each plant species was built by creating an adjacency matrix  $A$ , where elements  $a_{ij}$  represent the frequency of interactions per time between the pollinator morphotype  $i$  and the plant individual  $j$ . Therefore, this network is only partially individual-based because we aimed to characterise the resource use (i.e., pollinator resources) by plant individuals within each species. To that end, we aggregated pollinator individuals at the morphotype level by summing all interactions established by pollinator individuals from the same morphotype. The individual-based network for each plant species was constructed by pooling data from all plots to include the complete range of environmental variation.

### Plant attributes and topological roles

We estimated a series of intrinsic and extrinsic attributes for each individual plant. The intrinsic attributes included the plant height, total number of flowers produced along the season and flowering phenology, while the extrinsic attributes comprised the cover of conspecific and heterospecific neighbours expressed in terms of their relative abundance within a 1.5 m radius. This radius was identified as a good proxy for pollinator-mediated interactions (e.g., competition or facilitation; Ghazoul, 2006; Hegland, 2014). The neighbourhood composition was obtained with the help of drone flights (Appendix S1.3). We also calculated the flowering synchrony of a plant individual compared with conspecific and heterospecific neighbours within the plot following (Marquis, 1988; Appendix S1.4), which ranges from 1 (complete flowering overlap with neighbours) to 0 (no flowering overlap with neighbours). As we found strong evidence that plant height was correlated with the number of flowers produced (Pearson's  $r = 0.57$ ,  $p < 0.001$ ), we excluded plant height from analyses.

For each plant individual within the individual-based network of the plant species it belongs to, we calculated two topological metrics that reflect how interactions with pollinator morphotypes are assembled: degree and niche overlap ('bipartite' R package, Dormann et al., 2008). The degree is the total number of pollinator morphotypes used by a given plant individual and therefore represents the level of interaction specificity of this plant on pollinator use. The niche overlap represents the similarity between a given plant individual and all the other

conspecific plants in the use of pollinator morphotypes, and is estimated by calculating the average Bray–Curtis similarity (e.g., Gómez et al., 2010) in pollinator assemblage (i.e., the set of interacting pollinator partners) between this plant individual and every other plant in the population. It ranges between 0 and 1 and represents how quantitatively similar a given plant individual is in pollinator use (i.e., both in composition and abundance), compared with conspecifics (Appendix SI.5).

## Statistical analyses

### Interindividual plant variation in pollinator assemblage and topological roles

To explore variation among plant individuals and species in interaction patterns with pollinator morphotypes, we created an overall adjacency matrix by combining all plant individuals from all species, so each cell represents the frequency of interactions per time between a pollinator morphotype and a plant individual. We estimated the pairwise beta diversity of pollinator composition among plant individuals from all species as a Bray–Curtis distance in order to obtain a distance matrix among pairs of plant individuals (Anderson et al., 2011). Using this distance matrix, we tested whether plant species were similar in pollinator use (both in composition and abundance) using a permutational analysis of variance (PERMANOVA) and whether homogeneity of variances in pollinator composition differed among plant species using the PERMDISP2 procedure. To visualise differences and spread in beta-diversity measures among plant species, we used a nonparametric multidimensional scaling (NMDS). These analyses were done with the ‘vegan’ R package (Oksanen et al., 2022).

We further analysed the level of interindividual variation in pollinator use by assessing the range (coefficient of variation, CV) and distribution shape (skewness,  $S$  and kurtosis,  $K$ ) of individuals' degree and overlap within each plant species (Appendix SI.7; Figure S5). Skewness quantifies the asymmetry of a given distribution (e.g., a skewed distribution indicates the dominance of extreme values in degree or overlap). Kurtosis quantifies the relative peakedness of a distribution and the relative density of its tails (e.g., a lower kurtosis reflects a more even distribution of values of degree or overlap). We analysed the deviation of the observed skewness and kurtosis values from those expected in a normal distribution (‘moments’ R package, Komsta & Novomestky, 2015). We also evaluated whether generalists contributed to enlarge the pollinator assemblage within a plant population composed of a mixture of specialist (lower degree) and generalist (higher degree) individuals. To do that, we estimated the nestedness (NODF, Almeida-Neto et al., 2008) of the individual-based network within each plant species (Appendix SI.8).

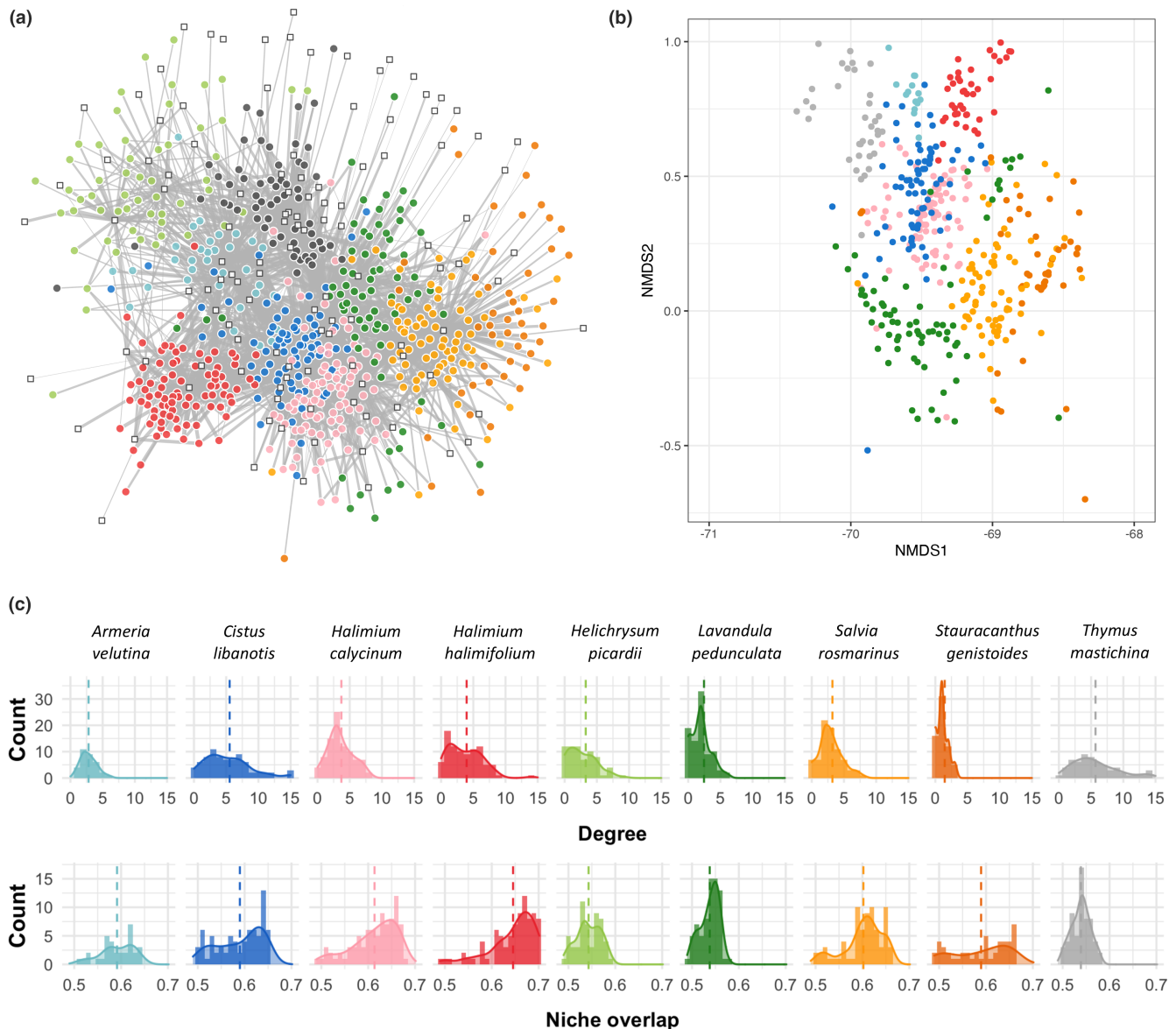
### Correlates of interindividual plant variation in topological roles

We assessed the drivers of the interindividual variation in degree and overlap, for each plant species using linear models with degree and overlap as response variables and plant attributes as predictor variables. Individual-level metrics were log-transformed, and all predictor variables were scaled (ranging from 0 to 1) to allow meaningful comparisons. These models were fitted using the ‘lme4’ R package (Bates et al., 2015), and assumptions were tested with the ‘Dharma’ R package (Hartig, 2022). We assessed the relative contribution of each plant attribute in explaining interindividual variation in degree and overlap (‘relaimpo’ R package, Grömping, 2007).

### Effects of interindividual variation on community-level network structure and dynamics

To analyse how interindividual plant variation is translated into community-level effects, we started by constructing an overall, individual-based network within the plant community by including all plant individuals from all species (Figure 2a). Then, we created a series of new resampled networks differing in interindividual variation in a key plant attribute, flower production, which generates networks differing in interindividual variation in interaction patterns with pollinators. Overall, the aim of our resampling procedure was to generate networks with high interindividual variation in flower production and networks with low interindividual variation in flower production. Networks with high interindividual variation were obtained by resampling plant individuals regardless of their flower production, capturing subsets of plant individuals that were heterogeneous in flower production. Meanwhile, networks with lower interindividual variation were obtained by resampling plant individuals only with low, medium and high flower production, capturing more internally homogeneous subsets of plant individuals.

To obtain resampled networks with high interindividual variation in flower production, we generated  $N = 100$  networks by randomly sampling  $m = 100$  plant individuals from the overall individual-based network, distributed among plant species proportional to their relative abundance. By doing so, we obtained a set of 100 resampled networks (i.e., ‘random’ set) that captures the observed interindividual variability in our community. Resampled networks with lower interindividual variability compared with the ‘random’ set were obtained by partitioning our individual-based interaction network into three equal networks, each containing one-third of the plant individuals. To define these terciles, plant individuals were arranged in order from lowest to highest flower production. We obtained three individual-based



**FIGURE 2** (a) Weighted bipartite network depicting interactions between plant individuals (circled nodes) and pollinator morphotypes (squared nodes) at the community. The links between nodes indicate flower visitation interactions while the width of the links refers to the strength of the interaction (i.e., number of interactions recorded). The layout of the network representation was created using an energy-minimisation algorithm. Different colours represent different plant species. (b) NMDS visualising beta diversity of pollinator composition among plant individuals. The spread of points describes differences in beta diversity of plant individuals of different plant species (colours). (c) Frequency distributions of degree (i.e., number of pollinator morphotypes used) and niche overlap (i.e., overlap in pollinator use with conspecifics) of plant individuals from different plant species (columns) in their individual-based networks. Dashed lines represent mean values. Shaded overlays are the density values (smoothed) for the distributions.

networks differing in flower production per plant individual: the ‘lower tercile’ (lowest flower production), the ‘middle tercile’ (medium flower production) and the ‘upper tercile’ (highest flower production) networks. As for the ‘random’ set, for each of these three individual-based networks, representing different levels of flower production, we generated  $N = 100$  resampled networks by randomly sampling  $m = 100$  plant individuals, distributing  $m$  among plant species proportional to their relative abundance. Hence, all this resampling procedure generates a set of networks with higher interindividual

variation in flower production (‘random’ set, capturing heterogeneous subsets of plant individuals) and lower interindividual variation (‘lowest tercile’, ‘middle tercile’ and ‘upper tercile’ sets, capturing more homogeneous subsets of plant individuals with low, medium and high flower production, respectively; [Figure S7](#)).

We transformed each of these resampled individual-based networks into a species-based binary network by summing the interactions established by plant individuals at the species level. Each species-based network is therefore represented as an adjacency matrix  $A$ , where

elements  $a_{ij}$  indicates the presence of an interaction (1 when an interaction occurs and 0 otherwise) between the pollinator morphotype  $i$  and the plant species  $j$ . As the theoretical background on the feasibility of mutualistic networks and its relationship with topology has currently only been developed for binary networks, we used the binary version of our species-based networks to estimate feasibility and nestedness. For each species-based network, we first calculated a nestedness measure (NODF; Almeida-Neto et al., 2008). Because NODF values can be influenced by the number of pollinator morphotypes included in the resampled networks, we illustrated these effects in Figure S8. Second, we calculated the feasibility conditions of each species-based network using a generalised Lotka–Volterra model to describe its population dynamics (Appendix SI.9). The range of feasible conditions (i.e., those leading to positive abundances for all co-occurring species) for a given community is known as the feasibility domain (Logofet, 1993). The larger the size of the feasibility domain, the larger the range of environmental conditions leading to a feasible community and the higher the tolerance of a community to random environmental variations (Rohr et al., 2014).

For each species-based network, we also estimated the average degree of plant species (i.e., number of pollinator morphotypes used) and the average overlap in pollinator use among plant species using the qualitative version of the Bray–Curtis similarity index (i.e., qualitative overlap of pollinator morphotypes among plant species, Appendix SI.6). The overlap among plant species was calculated as qualitative because our nestedness and feasibility estimations were based on binary networks. To test the effects of community size  $m$  on network properties, we repeated all the above procedures with different community sizes (Figure S9). Network- and species-level metrics were estimated using the ‘bipartite’ R package (Dormann et al., 2008). We tested the effects of the incorporation of interindividual variation on species-level interaction patterns and community properties using linear models. We set the degree of plant species and overlap among plant species in pollinator use, community-level nestedness (NODF) and feasibility as response variables, and the level of interindividual variation as the predictor variable. We considered two levels of interindividual variation in flower production, high variation for the ‘random’ set and low variation for the ‘lower tercile’, ‘middle tercile’ and ‘upper tercile’ sets.

To assess the hypothesis that interindividual variation in flower production ultimately determines community-level network structure and dynamics, we used a structural equation model (SEM), which allows us to quantify direct and indirect effects by linking multiple variables into a single causal framework (Lefcheck, 2016). We proposed a model in which the mean and variance of the number of flowers produced per individual may simultaneously affect plant species-level degree and overlap in pollinator use among plant species. Because the structure

and dynamics of species-based plant–pollinator networks depend on how interactions among mutualistic partners are assembled, we included the plant species-level degree and the overlap in pollinator use among plant species as potential drivers of nestedness and feasibility. The model proposed was performed with a ratio of 36 data points per parameter to be estimated. We performed these analyses using the ‘piecewiseSEM’ R package (Lefcheck, 2016) and tested the overall fit based on Fisher's C statistics (Shipley, 2009).

## RESULTS

Across the flowering season, we obtained 694.74 h of video recordings ( $1.48 \pm 0.78$  per plant individual, [mean  $\pm$  SD]) and performed approximately 1,000 h of visual censuses along random transects. We recorded a total of 34,775 interactions between 583 plant individuals (nine species) and 121 pollinator morphotypes (Figure 2a).

### Interindividual plant variation in pollinator assemblage and topological roles

Beta-diversity of pollinator assemblages within plant species (i.e., dissimilarity in composition and abundance of pollinator morphotypes among conspecific plant individuals) ranged between 0.57 and 0.85 across plant species ( $0.72 \pm 0.09$  [mean  $\pm$  SD across plant species]). We found moderate evidence that pollinator composition of plant individuals differed between plant species (PERMANOVA,  $F = 40.65$ ,  $R^2 = 0.36$ ,  $p = 0.01$ ; Figure 2b) indicating that individuals were more similar to other individuals of the same species than to individuals of other species. The variance of beta diversity among plant individuals was very different between plant species (PERMDISP2,  $F = 12.78$ ,  $p < 0.001$ ).

We found variation among plant individuals in the role they played in the individual-based plant–pollinator network within the species they belong to. Across plant species, the coefficient of variation ranged between 44.64 and 63.68% for degree and 3.63 and 9.89% for overlap in pollinator use with conspecifics (Figure S4). We found strong evidence of kurtosis and skewness in the distributions of individual values of degree and overlap (Figure 2c; Figure S4). Specifically, we found a positive skewness in degree (i.e., number of pollinator morphotypes used) and a negative skewness in overlap for most plant species. Therefore, most plant species comprised a few plant individuals that were generalists (i.e., higher degree) and that interacted with a distinct pollinator assemblage compared with its population (i.e., lower overlap). Several plant species exhibited a low kurtosis in overlap and therefore comprised many individuals differing in overlap with conspecifics (Figure S4). We found evidence that specialist plant individuals (lower degree)

interacted with subsets of the pollinators visiting generalist plant individuals (higher degree; [Table S4](#)).

## Correlates of interindividual plant variation in topological roles

Plant individuals' attributes affected their degree (i.e. number of pollinator morphotypes used) and overlap with conspecifics, but the direction and effect size highly depended on the plant species they belong to (see [Tables S5](#) and [S6](#) for the degree of evidence of effects). We found that the number of flowers produced positively affected the individual degree and overlap in most plant species. Therefore, those plant individuals that produced more flowers interacted with more pollinator morphotypes (higher degree) and shared more pollinators with conspecifics (higher overlap). For several plant species, the plant individuals' degree and overlap with conspecifics were also positively and negatively affected by conspecific and heterospecific flowering synchrony, respectively (see [Figure S6](#) for effect sizes). Overall, variation in degree was mostly explained by flower production, while overlap in pollinator use with conspecifics was more explained by conspecific flowering synchrony ([Table 1](#)).

## Effects of interindividual variation on community-level network structure and dynamics

In communities with higher interindividual variation (i.e., 'random set', capturing subsets of individuals heterogeneous in flower production), plant species overlapped less in pollinator use ( $t = -26.81$ ,  $p < 0.001$ ) despite interacting with the same number of pollinator

morphotypes ( $t = -1.13$ ,  $p = 0.26$ ) compared with communities with low interindividual variation in flower production (i.e., 'lower tercile', 'middle tercile' and 'upper tercile sets', capturing more homogeneous subsets of individuals with low, medium and high flower production, respectively; [Figure 3c](#)). Besides, plant–pollinator communities with higher interindividual variation in flower production showed higher nestedness ( $t = 3.51$ ,  $p < 0.001$ ), ([Figure 3b](#)) and persistence capacity (i.e., feasibility,  $t = 5.30$ ,  $p < 0.001$ , [Figure 3a](#)).

The structural equation model revealed that the mean number of flowers produced per plant individual and the interindividual variation in this plant attribute within a population influenced the feasibility of plant–pollinator communities through their effects on species-level interaction patterns. This model adequately represented the data and supported the hierarchical structure proposed (Fisher's  $C = 12.93$ ,  $p = 0.11$ ). We found strong evidence that the higher the flower production per plant individual, the higher the plant species-level degree and the overlap among plant species in pollinator use. Both plant species-level degree and among-species overlap decreased with interindividual variation in flower production. We also found evidence that nestedness increased with plant species-level degree and decreased with among-species overlap. The feasibility of plant–pollinator communities increased directly with plant species-level degree and decreased with among-species overlap in pollinator use, and was positively associated with nestedness (see [Figure 4](#) for effect sizes). While the mean flower production per individual accounted for 69.89% of the total effects of individual flower production on the feasibility of communities, 30.11% were due to interindividual variation in this plant attribute (i.e., variance).

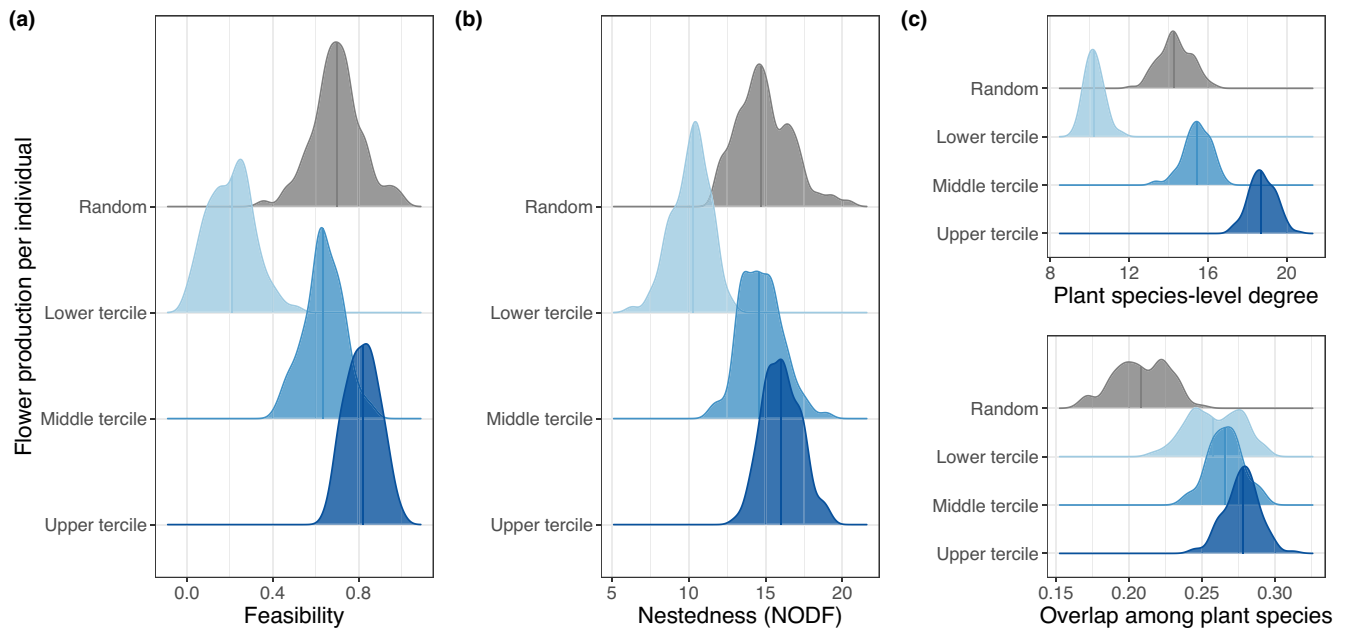
## DISCUSSION

Ecological interactions established by individuals constitute the building blocks for the assembly of networks of interacting species. While in the last decades the importance of interindividual variability in natural populations has been widely recognised (Bolnick et al., 2003), little is known about how interacting assemblages of species within communities are influenced by this kind of variation. Using plant–pollinator communities as a study system, we showed that the underlying variation in plant attributes mediating the establishment of interactions with pollinators (e.g., flower production) translated into variation in interaction properties among plant individuals. Our results provide novel insights into how this variation can scale up to influence the emerging structure and the persistence capacity of species interaction networks and the mechanisms underlying these effects.

Plant populations of single species have been shown to exhibit high levels of partitioning in pollinator use by individuals (e.g., Arroyo-Correa et al., 2021; Dupont

**TABLE 1** Relative contribution of different plant attributes on the explained variance of plant individuals' degree (i.e., number of pollinator morphotypes used) and niche overlap (i.e., overlap in pollinator use with conspecifics). A mean  $\pm$  *SD* percentage contribution was calculated for each plant attribute across plant species. These values were obtained as the average relative contribution of each predictor to the  $R^2$  of the overall model over orderings of predictors

Plant attribute	Degree	Niche overlap
Number of flowers	45.98 $\pm$ 25.87	24.97 $\pm$ 21.55
Conspecific flowering synchrony	20.10 $\pm$ 18.46	36.03 $\pm$ 20.27
Heterospecific flowering synchrony	16.15 $\pm$ 11.85	21.03 $\pm$ 16.72
Conspecific neighbourhood cover	6.04 $\pm$ 6.72	6.49 $\pm$ 7.12
Heterospecific neighbourhood cover	11.74 $\pm$ 15.91	11.19 $\pm$ 21.47



**FIGURE 3** Frequency distribution of community feasibility (a), nestedness (b), plant species-level degree (i.e., number of pollinator morphotypes used) and among-species overlap (i.e., overlap in pollinator used among plant species) (c) of species-based plant–pollinator networks. The ‘random’ set represents networks with high interindividual variation in flower production, capturing heterogeneous subsets of plant individuals. The ‘lower tertile’, ‘middle tertile’ and ‘upper tertile’ sets represent networks with lower interindividual variation in flower production, capturing more homogeneous subsets of plant individuals within the lower, middle and upper tertile of flower production, respectively. Within each set, we generated 100 species-based plant–pollinator networks by randomly selecting 100 plant individuals distributed among plant species proportionally to their relative abundance and summing the interactions established by these plant individuals at the species level. The vertical solid line within each distribution represents the mean value.

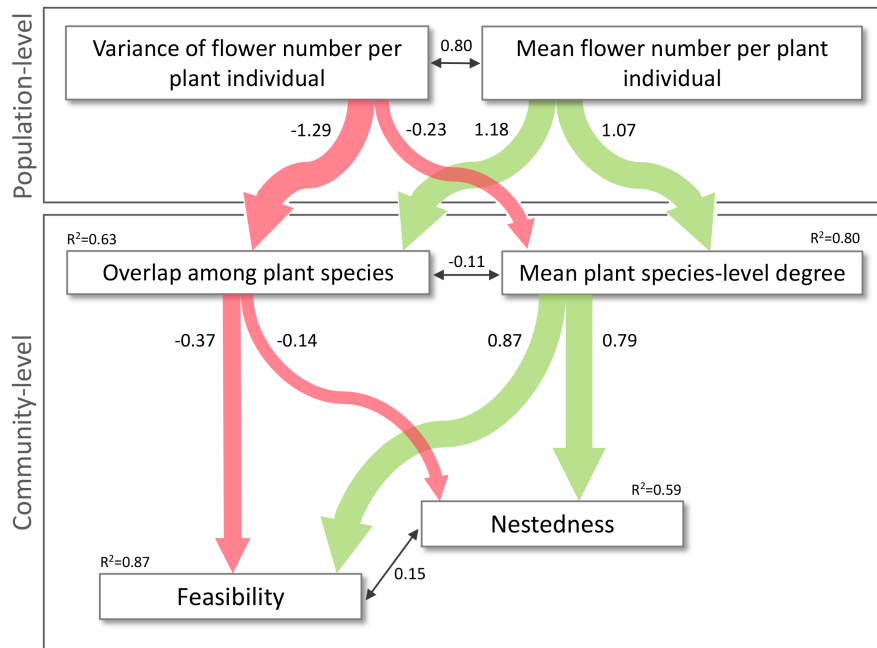
et al., 2014; Rodríguez-Rodríguez et al., 2017). Here, we extend this knowledge by exploring this interindividual partitioning simultaneously across multiple species. All plant species were composed of individuals that differed in pollinator use, and generalist plant individuals contributed to its population's pollinator assemblage by adding pollinator morphotypes that do not visit specialist plant individuals. These findings are in accordance with substantial evidence across different taxonomic groups that species of ecological generalists are in fact heterogeneous collections of relative generalist and specialist individuals (Bolnick et al., 2007; Van Valen, 1965).

To date, variation within species has been mostly assessed by estimating the variance or coefficient of variation across individuals (Benedetti-Cecchi, 2003; Start, 2019; Violle et al., 2011). We found that the coefficient of variation was higher for plant individuals' degree (i.e., number of pollinator morphotypes used) than for the overlap in pollinator use with conspecifics. Despite a large variation in degree, plant individuals within each species slightly differed in pollinator overlap, probably because they interacted with a common set of most abundant pollinator partners. Moreover, the skewness and kurtosis of individual roles' distribution within species can also reveal novel information about interindividual variation. The skewness and kurtosis of species functional traits' distributions explain a larger proportion of ecosystem functionality compared with the mean and

variance of these distributions (Gross et al., 2017; Gross et al., 2021). Across plant species, we showed the predominance of individuals interacting with larger numbers of pollinator morphotypes and overlapping less in pollinator use with conspecifics compared with all other individuals. As disassortative mutualistic interactions may affect population dynamics through highly skewed reproductive outcomes (Gómez & Perfectti, 2012), the observed patterns suggest that plant individuals may contribute differently to population persistence. This individual information is crucial to shift from a phenomenological to a mechanistic understanding of population dynamics, in which the system is predicted from the properties of its components (Plard et al., 2019).

Because sampling effort per plant individual was independent of the number of flowers produced, the effects of individual flower production on degree were produced by the distinctiveness in attraction between plant individuals differing in flower production. Besides, more synchronous plant individuals, both with conspecifics and heterospecifics, tended to show larger overlap in pollinator use with conspecifics and higher degree. Therefore, the patterns of interactions of a focal plant were not a function only of that plant's attributes but also of neighbouring plants' attributes. These results are in line with previous studies highlighting the importance of context-dependency of ecological interactions for single species (e.g., Arroyo-Correa et al., 2021; Dupont





**FIGURE 4** Structural equation model showing the effects of potential drivers of the structure (i.e., nestedness) and dynamics (i.e., feasibility) in plant–pollinator communities, starting from the mean flower production per plant individual and its variance within populations (i.e., interindividual variation). The mean plant species-level degree represents the mean number of pollinator morphotypes used by plant species and the overlap among plant species indicates the overlap in pollinator use among plant species. Standardised coefficients are presented as numbers next to arrows. Arrow widths are scaled to standardised coefficients. Green and red solid arrows indicate strong evidence ( $P < 0.001$ ) of positive and negative effects, respectively. Double black arrows indicate covariance.  $R^2$  values show the proportion of explained variance in the response variables.

et al., 2014). In our multispecific approach, the contribution of the variation of different plant attributes on plant–pollinator interaction patterns was highly variable between plant species, suggesting that context dependency of interactions across species varies at small spatial scales. For example, while for some plant species, pollinator attraction was particularly affected by the number of flowers produced by plant individuals; for other co-occurring plant species, the flowering synchrony between individuals influenced more how they interacted with pollinators. Future research explicitly addressing the spatial processes generating patterns of interactions among individuals in a community context is needed (see Dupont et al., 2014; Pasquaretta et al., 2017 for single species).

It has been long acknowledged that interspecific variation influences community assembly, stability and ecosystem services (Cardinale et al., 2002; Tilman et al., 1998), but much less attention has been paid to the ecological importance of intraspecific variation. Trait variation within species can be as large as the trait variation across species (Albert et al., 2010), and consequently, intraspecific variation may influence ecosystem structure and function as much as variation among species (Des Roches et al., 2018). The incorporation of interindividual variation in an important plant attribute, flower production, within plant communities greatly reduced the overlap in pollinator use among plant species.

Interindividual variation in flower production was partially influenced by variation in plant size, although it was also probably affected by water availability or genetic predisposition, among other factors. Regardless of the causes of interindividual variation in flower production, this result provides evidence on how intraspecific variation can shift a population's position along the niche continuum, shaping the patterns of species overlap in resource use, and potentially resulting in facilitative or competitive relationships among these species (Start, 2019). By controlling the relative importance of niche and neutral processes, which greatly depends on the among-species overlap in resource use, intraspecific variation might influence community dynamics (Gravel et al., 2006).

Through its effects on plant species-level degree (i.e., number of pollinator morphotypes used by plant species) and among-species overlap, interindividual variation scaled up to influence nested patterns and persistence capacity of plant–pollinator communities. One of the mechanisms underlying the effect of interindividual variation in flower production on community-level nestedness was related to the effects on plant species-level degree. The higher the interindividual variation in flower production, the higher the number of pollinator morphotypes used by plant species, and the higher the nestedness of plant–pollinator communities (Figure S8). It has been previously demonstrated

that there is a positive association between the structure and dynamics of communities in mutualistic assemblages (Saavedra et al., 2016). Our results provide insights into how this association between network topology and feasibility emerges. We found that community feasibility was maximised with high plant species-level degree and low overlap among species. Whereas the number of flowers produced per individual largely increased community feasibility by increasing plant species-level degree, we also found that interindividual variation had an important role in promoting feasibility by lessening the overlap in pollinator use among plant species. Lower among-species niche overlap meant a broader range of conditions leading to coexistence, consistent with earlier results (Barabás et al., 2014). Communities composed of variable populations were on average 28% more feasible than communities comprising similar individuals, especially when those had low flower production. Hence, these results support the idea that any process homogenising traits (e.g., disturbances or management actions such as fires or clear-cuts) throughout populations may strongly affect community persistence. Although we are not yet able to incorporate theoretically the effect of individual-level variation in community dynamics, future work should explicitly address how nonrandom mixtures of generalist and specialist individuals composing populations may affect the predicted dynamics of communities. Besides, considering that interaction strengths could influence community persistence outcomes, we would need prospective research that seeks to develop a theoretical basis for incorporating quantitative interaction data into the estimation of mutualistic communities' feasibility (Grilli et al., 2017).

Intraspecific variation is both the product and the foundation of evolutionary and ecological processes. Our study provides an in-depth understanding of the interplay between individual trait variation, individual interaction variation, the emerging species' interaction patterns and their subsequent effects on community structure and dynamics. By taking into account the direct effects of interindividual trait variation on community feasibility, we highlight the importance of preserving within-population intraspecific variation in ecological interactions. Current conservation efforts, which are usually focused on species, overlook intraspecific variation and its corresponding ecological effects (Angelini et al., 2011; Power et al., 1996). However, variation within species is particularly subject to human impacts through declines in population genetic diversity and local extirpation (Miraldo et al., 2016; Moran et al., 2016; Palkovacs et al., 2012). In fact, current extinction rates of populations are orders of magnitude greater than extinction rates of species (Ceballos et al., 2015; Leclère et al., 2020). Thus, a deep comprehension of the ecological consequences of intraspecific variation is essential for predicting how rapid and widespread changes

in diversity within species will impact communities and ecosystems.

## AUTHOR CONTRIBUTIONS

BA-C contributed to the conceptualisation, methodology, fieldwork, data curation, analysis, writing—original draft preparation, writing—reviewing and editing, visualisation and project administration. IB contributed to the conceptualisation, methodology, supervision, project administration, funding acquisition, visualisation, writing—original draft preparation, and writing—reviewing and editing. PJ contributed to the conceptualisation, methodology, supervision, project administration, funding acquisition, Visualisation, writing—original draft preparation, and writing—reviewing and editing.

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## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data and R code generated for this study are available at Zenodo Digital Repository (<https://doi.org/10.5281/zenodo.7326843>, Arroyo-Correa et al., 2022) and the GitHub repository (<https://github.com/BlancaAC>).

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## SUPPORTING INFORMATION

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