Integrating intraspecific variation into population dynamics reveals how interacting species persist in mutualistic communities

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ABSTRACT

Mutualistic interactions among organisms are fundamental to the origin and maintenance of biodiversity. Yet the study of community dynamics often relies on values averaged at the species level, ignoring how intraspecific variation can affect those dynamics. We propose a theoretical framework for evaluating the extent to which various forms of variation within populations can influence species' persistence in mutualistic systems. Next, drawing from detailed empirical data on plant–pollinator interactions and plant fitness, we quantify intraspecific variation in the mutualistic benefits received by plants and incorporate this variation into estimations of the community's structural stability, a robust theoretical measure of species' likelihood of persistence. Through explicit consideration of intraspecific variation, we are able to demonstrate that having different combinations of specialized and generalized individuals within plant populations promotes the persistence of pollinator communities. Further, we find that these heterogeneous mixtures of plant individuals reduce the probability of exclusion of focal plant species by promoting indirect effects across the broader plant–pollinator community. By providing a framework that explicitly accounts for individual-level variation, we open the door to a better understanding of the mechanisms promoting biodiversity in mutualistic communities and beyond.

INTRODUCTION

Ecological interactions, such as those involving pollination, seed dispersal or herbivory, have been shown to play a key role in shaping community assembly and ecosystem functioning (Bascompte & Jordano, 2007; Elton, 1927). Even though these interactions are usually summarized at the species level (Vázquez *et al.*, 2009), natural populations often display intraspecific differences in traits among individuals and thus exhibit differences in the interactions those individuals can potentially establish (Siefert *et al.*, 2015; Van Valen, 1965; Van Valen & Grant, 1970). Most populations are in fact composed of heterogeneous collections of specialized individuals, which interact only with a small portion of the available partners, and generalized individuals, which interact with a larger portion of these partners (Araújo *et al.*, 2008; Arroyo-Correa *et al.*, 2023; Bolnick *et al.*, 2003; Violle *et al.*, 2012).

Despite the fact that intraspecific variation is both well documented (Bolnick *et al.*, 2003; Violle *et al.*, 2012) and expected to influence species coexistence (Hart *et al.*, 2016; Stump *et al.*, 2022), its effects on species persistence remain unclear. This is likely due to both the difficulty of obtaining the necessary fine-scale data, but also because of the current limitations of theoretical approaches. In competitive contexts, several conceptual works have suggested different mechanisms by which intraspecific variation can influence community dynamics (Barabás & D'Andrea, 2016; Bolnick *et al.*, 2011; Hart *et al.*, 2016). For example, within species differences in competitive ability can 'blur' between species differences in competitive ability, and therefore individual variation is expected to break down competitive hierarchies, promoting coexistence (Clark *et al.*, 2010; Fridley *et al.*, 2007; Hubbell, 2005). In contrast, classical niche theory posits that intraspecific niche variation might lead to an increase in species-level niche overlap, diminishing the probability of species coexistence (Doebeli, 1996; Roughgarden, 1972; Slatkin, 1980).

Unlike competitive communities, we know substantially less about how intraspecific variation affects the persistence of mutualistic assemblages, despite their standing as the cornerstone of many ecological systems (Bastolla *et al.*, 2009; García *et al.*, 2018; Winfree, 2013). In mutualistic plant–animal communities, combinations of specialized and generalized individuals (in terms of resource use, e.g., pollinators used by plants, fruits used by seed dispersers) are expected to strongly impact dynamics through effects on fitness and niche differences between species. For instance, in plant–pollinator assemblages, if different individuals of the same plant species vary in their attractiveness to different pollinators, these plant individuals may also differ in the fitness benefits received from the pollinators with which they interact (Arroyo-Correa *et al.*, 2021). Generalized plant individuals are likely

to interact with more beneficial pollinators merely by attracting a wider range of pollinator species, leading to more successful fitness outcomes on the whole (Arroyo-Correa *et al.*, 2021; Gómez *et al.*, 2007). Therefore, the extent to which co-occurring plant species are composed of more generalized or more specialized individuals is likely to determine differences between co-occurring plant species in fitness. Plant individuals' specialization/generalization in pollinator use can also shape the patterns of pollinator sharing among plant species, thereby creating indirect plant–plant interactions, which are also predicted to affect the scope for coexistence within communities (Bastolla *et al.*, 2009). Through these effects, we expect intraspecific differences in plant generalization to impact the persistence of mutualistic systems and hence, the ability of species to sustain themselves within the community. Therefore, acknowledging a connection between intraspecific variation in mutualistic assemblages, either within one guild (e.g., plants) or across multiple guilds (e.g., plants and pollinators), and community dynamics may advance our understanding of the mechanisms fostering diversity.

A necessary condition for all species to persist in a community is that those species can maintain positive abundances. Using population-dynamics models, we can quantify the range of parameters that can fulfill that condition (Grilli *et al.*, 2017; Saavedra *et al.*, 2016; Song *et al.*, 2018). This range is called the feasibility domain, and can be thought of as the set of environmental conditions under which all co-occurring and interacting species in a given site and time can exhibit positive abundances (Cervantes-Loreto *et al.*, 2023; Rohr *et al.*, 2014; Song & Saavedra, 2018). In a nutshell, this "structural stability approach" posits that the larger the feasibility domain, the greater the opportunities to coexist under different environmental pressures. Despite its proven power to predict species persistence (Domínguez-García *et al.*, 2024), this approach has yet to be employed to explore how observable variation among individuals may influence the dynamics of ecological assemblages.

Here, we demonstrate how to expand the structural stability framework to incorporate intraspecific (i.e., within-population) variation in ecological interactions to the population dynamics of plant–animal mutualistic communities. Our proposed framework serves as a tool for evaluating the extent to which various forms of within-population variation could influence the emergent dynamics of mutualistic communities, and the range of conditions under which species can be sustained. After presenting the underlying theory, we work through an empirical case study to illustrate how observed intraspecific plant variation in pollinator use influences species' persistence in plant–pollinator communities. First, we empirically estimate the mutualistic benefits received by plant individuals from different pollinator species. We used this information to parameterize plant intraspecific variation in

the proposed theoretical framework describing the dynamics of mutualistic communities. Second, we assess how this intraspecific plant variation within a single plant species influences the feasibility of its mutualistic assemblage, and thus, affects the persistence ability of the pollinator community visiting that plant species. Finally, we investigate whether this intraspecific variation in a single plant species can reduce the likelihood of its exclusion by promoting indirect effects across the broader plant–pollinator community.

THEORETICAL FRAMEWORK

Population dynamics in mutualistic communities

The dynamics of plant and animal populations in a community composed of multiple plant species that interact mutualistically with multiple animal species can be approximated using a generalized Lotka–Volterra system of the form:

$$\begin{cases} \dfrac{dP_i}{dt} = P_i \left(r_{P_i} - \displaystyle\sum_{j \in \text{plants}} \alpha_{P_i P_j} P_j + \sum_{j \in \text{animals}} \gamma_{P_i A_j} A_j \right) \\ \dfrac{dA_i}{dt} = A_i \left(r_{A_i} - \displaystyle\sum_{j \in \text{animals}} \alpha_{A_i A_j} A_j + \sum_{j \in \text{plants}} \gamma_{A_i P_j} P_j \right) \end{cases} \tag{1}$$

where P_i and A_i denote the abundance of plant species i and animal species i, respectively. The parameters of this mutualistic model correspond to the populations' intrinsic per capita growth rates (r_{P_i} and r_{A_i}, which represent how plant species P_i and animal species A_i grow in isolation), within-guild interactions ($\alpha_{P_i P_j}$ and $\alpha_{A_i A_j}$), and between-guild interactions ($\gamma_{P_i A_j}$, $\gamma_{A_i P_j}$). These within-guild or between-guild interactions represent per-capita biotic effects of species P_j or A_j on the per-capita growth rates of species P_i or A_i. Hereafter, we will use the term 'species' to refer to all individuals that belong to the same single-species population. In a community comprising two plant species and two animal species, the collective population dynamics can be expressed in matrix form as follows:

$$\begin{bmatrix} \frac{dP_i}{dt} \\ \frac{dP_j}{dt} \\ \frac{dA_i}{dt} \\ \frac{dA_j}{dt} \end{bmatrix} = diag\left(\begin{bmatrix} P_i \\ P_j \\ A_i \\ A_j \end{bmatrix}\right)\left(\begin{bmatrix} r_{P_i} \\ r_{P_j} \\ r_{A_i} \\ r_{A_j} \end{bmatrix} - \begin{bmatrix} \alpha_{P_iP_i} & \alpha_{P_iP_j} & -\gamma_{P_iA_i} & -\gamma_{P_iA_j} \\ \alpha_{P_jP_i} & \alpha_{P_jP_j} & -\gamma_{P_jA_i} & -\gamma_{P_jA_j} \\ -\gamma_{A_iP_i} & -\gamma_{A_iP_j} & \alpha_{A_iA_i} & \alpha_{A_iA_j} \\ -\gamma_{A_jP_i} & -\gamma_{A_jP_j} & \alpha_{A_jA_i} & \alpha_{A_jA_j} \end{bmatrix}\begin{bmatrix} P_i \\ P_j \\ A_i \\ A_j \end{bmatrix}\right) \tag{2}$$

where $diag(\mathbf{x})$ creates a diagonal matrix with values from the vector $\mathbf{x}$ on the diagonal and zeros everywhere else.

Incorporating within-population variation

Any given species might be potentially composed of individuals or groups of individuals that differ in ecologically meaningful ways. Here we assume that individuals act as representative subsets of the larger population ('individual types' hereafter), similar to 'phenotypes' in eco-evolutionary contexts (Maynard *et al.*, 2019). For the sake of simplicity, we will start by considering how to specify the population dynamics of a community solely consisting of two different individual types, s and t, within a single plant species i which interact with two different individual types, s and t, within a single animal species i. If the relative proportions of the individual types making up the total populations of the corresponding species are known, then we can transform a vector of the total abundances of the two species (P_i and A_i) into a vector of abundances of the individual types with matrix algebra using:

$$\begin{bmatrix} P_{is} \\ P_{it} \\ A_{is} \\ A_{it} \end{bmatrix} = \overbrace{\begin{bmatrix} \pi_{P_{is}} & 0 \\ 1 - \pi_{P_{is}} & 0 \\ 0 & \pi_{A_{is}} \\ 0 & 1 - \pi_{A_{is}} \end{bmatrix}}^{\Pi}\begin{bmatrix} P_i \\ A_i \end{bmatrix} \tag{3}$$

where P_{is} denotes the total abundance of individual type s of plant species i, A_{is} denotes the total abundance of individual type s of animal species i, $\pi_{P_{is}}$ represents the relative proportion of individual type s of plant species i in the total plant population, and $\pi_{A_{is}}$ represents the relative proportion of individual type s of the animal species i in the total animal population. The matrix Π, therefore, captures the partitioning of total species abundances into individual types' population abundances. Note that regardless of the number of individual types in a given species, the values in

the corresponding column of the matrix Π must sum to one.

We are particularly interested in understanding the implications of different individual types engaging in different interactions and consequently making different net contributions to the maintenance of their populations as a whole. However, as members of the same overarching population, different individual types should have equal intrinsic growth rates (i.e., growth in the absence of any ecological interactions). The population dynamics of such a community can thus be described as:

$$\begin{bmatrix} \frac{dP_{is}}{dt} \\ \frac{dP_{it}}{dt} \\ \frac{dA_{is}}{dt} \\ \frac{dA_{it}}{dt} \end{bmatrix} = diag\left(\Pi \begin{bmatrix} P_i \\ A_i \end{bmatrix}\right) \left(\overbrace{\begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix}}^{\rho} \begin{bmatrix} r_{P_i} \\ r_{A_i} \end{bmatrix} - \overbrace{\begin{bmatrix} \alpha_{P_{is}P_{is}} & \alpha_{P_{is}P_{it}} & -\gamma_{P_{is}A_{is}} & -\gamma_{P_{is}A_{it}} \\ \alpha_{P_{it}P_{is}} & \alpha_{P_{it}P_{it}} & -\gamma_{P_{it}A_{is}} & -\gamma_{P_{it}A_{it}} \\ -\gamma_{A_{is}P_{is}} & -\gamma_{A_{is}P_{it}} & \alpha_{A_{is}A_{is}} & \alpha_{A_{is}A_{it}} \\ -\gamma_{A_{it}P_{is}} & -\gamma_{A_{it}P_{it}} & \alpha_{A_{it}A_{is}} & \alpha_{A_{it}A_{it}} \end{bmatrix}}^{M} \Pi \begin{bmatrix} P_i \\ A_i \end{bmatrix} \right) \tag{4}$$

where within-population variation is enabled by the fact that the within-type, between-type, and across-type interaction coefficients may all take distinct values (e.g., $\gamma_{P_{is}A_{is}}$ may differ from $\gamma_{P_{it}A_{is}}$, and so on). The matrix ρ imposes the constraint that individual types of the same species have identical growth rates.

If we call the vector of individual types' growth rates $\dot{\mathbf{N}}$, the vector of intrinsic growth rates $\mathbf{r}$, the vector of total population abundances $\mathbf{N}$, and the type-by-type interaction matrix M, we can more compactly write the population-dynamics equations as:

$$\dot{\mathbf{N}} = diag\left(\Pi\,\mathbf{N}\right)\left(\rho\,\mathbf{r} - M\,\Pi\,\mathbf{N}\right) \tag{5}$$

Feasible conditions

Given complete information about the interaction strengths in M, the mapping of individual types to populations encoded in ρ, and the individual types' proportions within populations quantified in Π, the "unknowns" in the equilibrium condition for this model are $\mathbf{r}$ and $\mathbf{N}^*$.

The core idea underpinning the feasibility domain is therefore to explore whether M, ρ, and Π,

impose strong or weak constraints on species' abilities to sustain positive equilibrium abundances (Rohr *et al.*, 2014; Saavedra *et al.*, 2013; Song *et al.*, 2018). By restricting ourselves to any and all feasible equilibria (i.e., vectors $\mathbf{N}^*$ containing only positive values), we shift $\mathbf{N}^*$ into the "knowns" category. Consequently, one can mathematically define the feasibility domain as the set of vectors $\mathbf{r}$ for which all equilibrium abundances in $\mathbf{N}^* = (\rho^+ M\Pi)^{-1}\,\mathbf{r}$ are positive, where ρ^+ is the generalized inverse of the rectangular matrix ρ.

The domain of intrinsic growth rate vectors ($\mathbf{r}$) leading to positive species abundances ($\mathbf{N}^*$) is geometrically described by an algebraic cone, where the borders are established by the column vectors of the corresponding interaction matrix $\rho^+ M\Pi$. The normalized solid angle of the cone generated by this matrix can be interpreted as the probability of sampling randomly a vector of intrinsic growth rates that fall inside that cone. Analytically, the size of the feasibility domain can be calculated by the cumulative function of a multivariate Gaussian distribution (Song *et al.*, 2018). The higher this volume in a given community, the higher its potential to accommodate variations in species growth rates while maintaining feasibility.

Importantly, all the ecological variation in interaction coefficients across plant individual types ($\alpha_{P_{is}P_{it}}$, $\gamma_{P_{is}A_{is}}$) and across animal individual types ($\alpha_{A_{is}A_{it}}$, $\gamma_{A_{is}P_{is}}$) incorporated in matrix M will be aggregated into single values ($\alpha_{P_iP_i}$, $\gamma_{P_iA_i}$, and $\alpha_{A_iA_i}$, $\gamma_{A_iP_i}$, respectively) in the species–species interaction matrix that results from the matrix product $\rho^+ M\Pi$. Indeed, the matrix product $\rho^+ M\Pi$ for our specific two-species example as defined by Eq. (4) produces a 2×2 interaction matrix of the form $\begin{bmatrix} \alpha_{P_iP_i} & -\gamma_{P_iA_i} \\ -\gamma_{A_iP_i} & \alpha_{A_iA_i} \end{bmatrix}$.

Though interactions can—and likely do—vary within, across, and between individual types, feasibility of the vector $\mathbf{N}^*$ is therefore still measured at the species level (i.e., at the level of the two overarching populations, belonging to species P_i and A_i).

EMPIRICAL CASE STUDY

The theoretical framework proposed above explicitly incorporates variation within populations when describing the dynamics of mutualistic communities. To illustrate how empirically observable intraspecific variation in ecological interactions modulates the dynamics of a real mutualistic community, we used finely resolved data of pollinator visitation to plant individuals and plant fitness proxies measured on these same individuals. First, we empirically estimated the mutualistic benefits given

by different pollinator species to each plant individual by integrating multiple sources of intraspecific variation across plants (pollinator assemblage, visitation rates and flower production) and fitness data (fruit and seed production). Second, we used these estimates to characterize variation among plant individuals in the mutualistic benefits they received, and therefore, in how they are expected to contribute to the dynamics of their plant populations. With the parameterized model, we explored how this intraspecific variation within each focal plant species can influence the size of the feasibility domain of their populations' mutualistic assemblages in the absence of heterospecific plant competitors (i.e., the ability of these species to sustain themselves as well as their pollinators). We then evaluated whether the observed intraspecific variation in mutualistic benefits received by plant individuals has cascading effects across the broader plant–pollinator community, thereby affecting the persistence probability of co-occurring plant species, which is influenced by the shape of the feasibility domain of the *whole* community (Fig. 1).

Study system

Here we focus on three representative plant species sampled in Mediterranean shrublands of Doñana National Park, located in the Atlantic coast of southwestern Spain (37°00'29.736"-N –6°30'24.919"-W, 25 m a.s.l.). These focal species belong to the Cistaceae family and flower consecutively throughout the flowering period of the plant community (starting with *Halimium calycinum*, followed by *Cistus libanotis* and ending with *Halimium halimifolium*), overlapping each other's to some extent. Plant individuals of these focal species were sampled in six different study plots within an area of one square kilometre to capture environmental heterogeneity. We recorded pollinator visits to these plant individuals during the 2021 peak flowering season, between early February and mid July. For each of the three focal shrub species and each plot, we selected 15 plant individuals following a stratified random sampling scheme to capture within-plot heterogeneity, totalling 90 individuals per plant species. Pollinators were considered as all insects touching flowers' reproductive structures, and were identified as morphospecies ('species' hereafter). On average, interaction sampling completeness was above 85% for all plant individuals sampled (Arroyo-Correa *et al.*, 2023). For each plant individual, we used these records to estimate the frequency of interactions per minute established by each pollinator species along the entire flowering season (Arroyo-Correa *et al.*, 2023), and measured two proxies of female plant fitness at the flower level: fruit set (i.e., proportion of flowers setting final-sized fruits) and seed set (i.e., number of seeds per flower). All plant species produced multiple inflorescences and multiple flowers per inflorescence. We randomly selected five inflorescences per plant individual and estimated whether flowers produced at the beginning of the season in these inflorescences resulted

in any fruit production at the end of the season. To estimate seed production in each plant, we randomly sampled 10 fully developed fruits from different randomly selected inflorescences to obtain the number of seeds per fruit. Each week along the flowering season, we also counted the number of individual flowers in each plant individual and summed the weekly number of flowers as an estimate of the total number of flowers produced by a plant individual.

All these plant species were composed of a mixture of plant individuals ranging from more specialized (i.e., interacting with a small proportion of the available pollinator species) to more generalized (i.e., interacting with a large proportion of the available pollinator species) (Arroyo-Correa *et al.*, 2023). We considered that the plant individuals sampled in the field are representative types of individuals within their populations (i.e., proper subsets spanning the whole range of individual variation), and therefore we used each of these individuals to characterize a separate 'individual type' in our theoretical framework. Here we focus on how intraspecific plant variation in the generalization level of pollinator use impacts the dynamics of mutualistic plant–pollinator communities. We regarded intraspecific variation within a plant population as comprising variable mixtures of both specialized and generalized plant individuals versus being consistently composed of a higher proportion of specialized individuals.

Theoretical framework adapted to the empirical case

By leveraging the proposed theoretical framework, we can describe the population dynamics of these plant species composed of different plant individuals, which act as representative individual types that differ in the interactions they establish with pollinator species. For reasons we will expand on below, we focus here on understanding how different plant individual types, engaging in different interactions, make different contributions to the maintenance of their plant populations and the interacting pollinator community *as a whole*. If, for example, we consider a single plant species whose population comprises two different types of individuals, the vector of total abundances of the focal plant population and their interacting pollinator community can be transformed as follows:

$$\begin{bmatrix} P_{is} \\ P_{it} \\ A_i \\ A_j \end{bmatrix} = \overbrace{\begin{bmatrix} \pi_{P_{is}} & 0 \\ 1 - \pi_{P_{is}} & 0 \\ 0 & \pi_{A_i} \\ 0 & 1 - \pi_{A_i} \end{bmatrix}}^{\Pi} \begin{bmatrix} P_i \\ A \end{bmatrix} \tag{6}$$

where P_{is} denotes the total abundance of individual type s of plant species i, A_i denotes the total abundance of animal species i, $\pi_{P_{is}}$ represents the relative proportion of individual type s of plant species i in the total plant population P_i, and π_{A_i} represents the relative abundance of pollinator species i in the total pollinator community A. In slight contrast to Eq. 3, this adapted matrix Π therefore captures the partitioning of the total plant population abundance into plant individual types' abundances and the total pollinator community abundance into pollinator species' abundances. In this case, $\pi_{P_{is}}$ may indicate the proportion of the total population biomass, or the amount of floral resources, represented by individual type s in its population, which is expected to be proportional to the effects of this individual type on other individual types within its population. In the context of our specific case study, we assumed each plant individual type represents the same relative proportion (i.e., $\pi_{P_{is}} = 1/n$, where n is the number of different types of individuals) of their population. We used the relative visitation rates of pollinator species as a proxy for their relative abundances, assuming that pollinators' visitation rates are proportional to abundance (i.e., $\pi_{A_i} = \frac{\sum_{P_{is}} m_{P_{is}A_i}}{\sum_{P_{is},A_i} m_{P_{is}A_i}}$, where $m_{P_{is}A_i}$ is the number of visits per minute by pollinator species i to plant individual s of plant species i). As in the general case discussed above, the values in the corresponding column of the matrix Π must sum to one, both for plant individual types composing the plant population and for pollinator species composing the pollinator community. The dynamics in this community can be described as:

$$\begin{bmatrix} \frac{dP_{is}}{dt} \\ \frac{dP_{it}}{dt} \\ \frac{dA_i}{dt} \\ \frac{dA_j}{dt} \end{bmatrix} = diag\left(\Pi \begin{bmatrix} P_i \\ A \end{bmatrix}\right) \left(\overbrace{\begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix}}^{\rho} \begin{bmatrix} r_{P_i} \\ r_A \end{bmatrix} - \overbrace{\begin{bmatrix} \alpha_{P_{is}P_{is}} & \alpha_{P_{is}P_{it}} & -\gamma_{P_{is}A_i} & -\gamma_{P_{is}A_j} \\ \alpha_{P_{it}P_{is}} & \alpha_{P_{it}P_{it}} & -\gamma_{P_{it}A_i} & -\gamma_{P_{it}A_j} \\ -\gamma_{A_iP_{is}} & -\gamma_{A_iP_{it}} & \alpha_{A_iA_i} & \alpha_{A_iA_j} \\ -\gamma_{A_jP_{is}} & -\gamma_{A_jP_{it}} & \alpha_{A_jA_i} & \alpha_{A_jA_j} \end{bmatrix}}^{M} \Pi \begin{bmatrix} P_i \\ A \end{bmatrix} \right) \quad (7)$$

In this specific case, intraspecific plant variation (i.e., within-population variation) can be represented as variation in coefficients $\alpha_{P_{is}P_{it}}$ and $\gamma_{P_{is}A_i}$ across different types of plant individuals belonging to the same species. Furthermore, the matrix ρ imposes different constraints on the plant and pollinator components within this community. On the plant side, types of individuals belonging to the same species are expected to exhibit identical intrinsic growth rates (r_{P_i}). On the pollinator side, different species within the pollinator community are assumed to have equal intrinsic growth rates (r_A). We include this constraint for biological and mathematical reasons. First, by including pollinator

species' observed relative abundances, we are *conditioning* subsequent calculations of the feasibility domain on the actual pollinator community that the plant populations had available to them in the field. Therefore, this allows us to focus solely on the growth rate vectors ($\mathbf{r}$) whose corresponding feasible equilibria are consistent with this additional biotic constraint (Cervantes-Loreto *et al.*, 2023; Song *et al.*, 2018). Second, to make this constraint work mathematically we can only have as many unknown intrinsic growth rates (r_{P_i} and r_A) as "known" equilibrium abundances (P_i and A). Although the model describes the combined dynamics of the entire pollinator community, note that each pollinator species can still contribute differently to those dynamics through variation in α and γ coefficients. With this adapted framework, we focused on evaluating how the observed intraspecific variation in the mutualistic benefits received by plant individual types influences the ability of species to persist (Fig. 1).

Parameterization of interaction coefficients

We empirically parameterized the mutualistic benefits provided by each pollinator species to each plant individual type, denoted as $\gamma_{P_{is}A_i}$ in the adapted mathematical framework (Eq. 7). This parameterization was based on our empirical data on plant fitness proxies (i.e., proportion of flowers setting fruit and number of seeds produced per fruit), visitation rates and flower production (Box 1).

To maintain our focus on the effects of the observed intraspecific plant variation in the mutualistic benefits received, all other coefficients in the interaction matrix M ($\alpha_{P_{is}P_{is}}$, $\alpha_{A_iA_i}$ and $\gamma_{A_iP_{is}}$) were parameterized following a mean-field approximation (Appendix C), as previously done (García-Callejas *et al.*, 2023; Rohr *et al.*, 2014; Song *et al.*, 2018).

Intraspecific plant variation in mutualistic benefits

To visualize how different plant fitness components ultimately combine together to determine the number of seeds that a given plant individual contributes to the plant population's seed bank, we performed a principal component analysis (PCA) for each of our three focal plant species. In addition to the three components influencing plant fitness that are included in Eq. 10, the total mutualistic benefits received by plant individuals may also be influenced by the degree of these plant individuals (i.e., the richness of pollinator species with which they interact). The degree of plant individuals may increase the overall contribution of pollinators to a given plant individual's fitness (i.e., the sum of the contributions $\beta_{P_{is}A_i}$ of all pollinator species to a given plant). This procedure resulted in an ordination of plant individuals in relation to the multivariate space defined by these multiple components influencing plant individuals' fitness. This ordination allowed us to evaluate how the combination

of these components modulates fitness variation among plant individuals within a population, and therefore intraspecific variation in the mutualistic benefits received by plant individuals.

Effects of intraspecific plant variation on plant population's mutualistic assemblage

We evaluated how the inferred intraspecific plant variation in mutualistic benefits received ($\gamma_{P_{is}A_i}$) affected the feasibility of a system composed of individual types from a single plant species and their interacting pollinator community. Specifically, we focused on how mixtures of specialized and generalized plant individuals, which differ in the mutualistic benefits received, in a given plant species increased or decreased the feasibility of the collective system. This allows us to assess how these heterogeneous collections of plant individuals belonging to the same plant species can affect the persistence of its pollinator community, together with the persistence of the plant species itself. To address this question, we rely on the definition of specialized and generalized plant individuals based on their richness of pollinator visitors (i.e., degree), such that individuals range between more specialized (lower degree) to more generalized (higher degree) on pollinator use.

We estimated the feasibility of the system composed of a single plant population and its pollinator species over an increasing number of plant individual types (i.e., plant population size). In the first scenario, plant population size was increased by progressively including plant individuals selected at random (N=100 iterations), regardless of their degree. In the second scenario, we increased plant population size by including progressively plant individuals with increasing degree (i.e., from the most specialized to the most generalized individual types). To break ties, plant individual types with the exact same degree were incorporated based on decreasing specificity (i.e., decreasing coefficient of variation of interactions using visitation rates, Poisot *et al.*, 2012). For each plant population size and both scenarios, we estimated the volume of the feasibility domain of the mutualistic assemblage composed of the plant population and its pollinator species. Therefore, for a given plant population size, a difference in the feasibility domain volume between the first and second scenarios represents the consequence of the focal plant population being composed of specialized and generalized individuals compared to a population composed of a higher proportion of specialized individuals. Both plant individuals' degree and specificity were estimated using the `bipartite` R package (Dormann *et al.*, 2008).

Cascading effects of intraspecific plant variation across the plant community

After exploring how intraspecific variation in a single plant species affects its performance and the persistence capacity of its interaction assemblage, we upscaled to the plant community level to

disentangle the cascading effects that variation within a focal plant species has on other plant species in the community. We estimated these effects as changes in the probability of exclusion of plant species within its community. The probability of exclusion of a given species in the community ranges between 0 and 1, and quantifies the average probability of that species to be the first one excluded if a destabilizing perturbation took place in a feasible community under generalized Lotka–Volterra dynamics (Allen-Perkins *et al.*, 2023). The calculation of exclusion probabilities does not require an initial vector of growth rates, and probability values strongly depend on the shape of the feasibility domain. Within a community where all species show exactly the same interaction patterns (i.e., a symmetric community), all species are equally likely to be the first species excluded. We used the same scenarios as mentioned above but focused on a fixed number of individual types. In the first scenario, the plant community was composed of N=40 randomly selected plant individuals (100 replicates) of the focal plant species and all 90 plant individuals belonging to the other two plant species. In the second scenario, the plant community was composed of the N=40 most specialized plant individuals of the focal plant species and all 90 plant individuals belonging to the other two species. We calculated the exclusion probabilities of all three plant species in both scenarios. Therefore, the differences in species' exclusion probabilities between both scenarios indicate the effects of mixtures of specialized and generalized plant individuals within the focal species on any other plant species in the community.

In our specific case, the mutualistic benefits received by plant species (γ_{P_iA}) in the matrix product $\rho^+ M\Pi$ represent the per-capita seed production per visit by a pollinator. Therefore, to estimate the size of the feasibility domain for the whole community (i.e., considering all co-occurring plant species) we needed to account for differences between plant species on the visitation rates by the pollinator community. For each community replicate mentioned above, which differed in the composition of individuals of each plant species, we first calculated the number of visits received by all plant individuals belonging to the same plant species. Next, we scaled and centered the total number of visits to each plant species in each replicate so that the mean value across species becomes equal to 1. Then, in each replicate, we weighted γ_{P_iA} by the scaled number of visits received by plant species i in that replicate. All analyses were performed in `R` v4.3.1 (R Core Team, 2023).

RESULTS

Intraspecific plant variation in mutualistic benefits

Differences among plant individuals in pollinator use translated into variation in plant fitness merely due to differences among pollinator species in their fitness contribution to plants (Fig. 2A, Appendix

D). Moreover, the level of this intraspecific fitness variation driven purely by differences in plant individuals' pollinator assemblages changed when also incorporating intraspecific variation in flower production and visitation rates (Fig. 2B-C). A principal component analysis (PCA) for each of our three focal plant species revealed that these different sources of intraspecific variation explained most of the variance in realized plant individual fitness, expressed as the total number of seeds produced per plant individual (Fig. 2D). The first principal component (PC1) explained 48.11 ± 5.94% [mean ± SD across plant species] of intraspecific variation in fitness resulting from mutualistic interactions. Meanwhile, the second principal component (PC2) explained 26.79 ± 3.44% across plant species.

Effects of intraspecific plant variation on plant population's mutualistic assemblage

Considering each plant population separately, we found that the observed mixture of specialized and generalized individuals within these populations increased the feasibility of the population's mutualistic assemblage compared to a scenario composed of a higher proportion of specialized plant individuals (Fig. 3). We did not find a saturating response of the feasibility domain's size when increasing plant population size while increasing the generalization level of the constituent plant individuals. Therefore, just having a large number of generalized plant individuals (high degree) within the population was not sufficient to reach the feasibility levels promoted by having a mixture of specialized and generalized plant individuals. The effects of these mixtures of specialized and generalized plant individuals were maintained even when considering the study plots separately, indicating that even the reduced level of intraspecific plant variation found within study plots is sufficient to produce these effects (Appendix E).

Cascading effects of intraspecific plant variation across the plant community

Beyond its effects at the population level, the presence of both specialized and generalized individuals within specific plant species had implications at the community level by reshaping the probability of exclusion of these focal plant species as well as other species in the community. In two of the focal plant species, having a mixture of specialized and generalized individuals decreased the probability of those species being excluded from the larger community while increasing the probability of exclusion of any of the other plant species, compared to scenarios with a higher proportion of specialized individuals in those focal species (Fig. 4). For the remaining focal plant species, the presence of both specialized and generalized individuals did not affect its persistence ability or that of co-occurring species. This is likely due to specific features of the focal species, such as the low levels of mutualistic benefits received (see Figure S7) or the limited flowering overlap with other plant species, which may

prevent any cascading effect within the community.

DISCUSSION

Variation within populations has been identified as important as variation across species in ecological communities (Albert *et al.*, 2010; Siefert *et al.*, 2015), and thus, may potentially impact the functioning and stability of ecological systems (Bolnick *et al.*, 2011; Violle *et al.*, 2012). While widely recognized, the effects of intraspecific variation in shaping the dynamics of communities, especially those involving mutualistic partners, are virtually unknown. Downscaling to the level of individuals to understand ecological processes at this scale poses logistical and tractability challenges for empiricists and theoreticians. However, new sampling techniques now enable the collection of individual-level data with unprecedented accuracy (e.g., Besson *et al.*, 2022; Corcoran *et al.*, 2021; Droissart *et al.*, 2021; Lines *et al.*, 2022; Nathan *et al.*, 2022; Steen, 2017), and recent developments have expanded the analytical toolbox to deal with these data (e.g., Coblentz *et al.*, 2017; McCaslin *et al.*, 2021; Sibly *et al.*, 2013). The theoretical framework we propose here offers a pathway for further exploration of how intraspecific variation in interaction patterns shapes fitness variation, population dynamics, and the ability of species to persist within communities.

Through explicitly accounting for variation among individuals within populations in mutualistic assemblages, we were able to disentangle the lasting effects of this source of variation within communities, which ultimately determines species persistence in these local communities. In our study system, the positive effects of plant populations comprising heterogeneous collections of individuals differing in pollinator use specialization were observed at both the population and community levels. Plant populations with specialized and generalized individuals promoted the feasibility of their mutualistic assemblages, indicating that these observed levels of variability support more persistent pollinator communities. Furthermore, plant populations consisting of individuals with heterogeneous specialization levels in pollinator use increased the ability of these plant species to persist in communities. As expected, focal plant species differed in the magnitude of the effects they exerted across their community, which was likely due to differences in the mutualistic benefits they received. Overall, our results suggest that the presence of heterogeneous plant populations, whose individuals vary in the level of specialization in resource use, may promote biodiversity in mutualistic communities because such individual variation changes the overall patterns of direct and indirect pairwise interactions between species (see Fig. 1). Our findings are particularly critical in the context of global change scenarios, as populations are expected to experience significant declines in size, become more

homogeneous in traits, and exhibit a reduced level of generalization in resource use (Sala *et al.*, 2000; Tylianakis *et al.*, 2008).

Intraspecific variation in traits and ecological interactions is a significant driver of fitness variation within mutualistic communities (Arroyo-Correa *et al.*, 2021; Gómez & Perfectti, 2012). Our approach incorporates the variation in traits, mutualistic partners, and visitation rates across plant individuals, all of which determine the fitness benefits received. In contrast, an alternative approach that relies on a species-level value for each of these features, averaged across individuals, to estimate mutualistic benefits could result in inaccurate feasibility estimations at both population and community levels. In other words, a species-level value to parameterize mutualistic benefits calculated from averaged interaction strengths and traits exhibited by individuals is unlikely to represent the mutualistic benefits received by any particular individual within a given population. Consequently, using interaction and trait data averaged across individuals to calculate the fitness benefits received by a given species from its mutualistic partners may lead to biased predictions of species persistence. Moreover, our findings challenge conventional assumptions about the distribution of mutualistic benefits based solely on the number of mutualistic partners per species (e.g., Rohr *et al.*, 2014; Saavedra *et al.*, 2013, 2016). As we have shown, the benefits received by mutualistic partners cannot be accurately summarised by only considering the number of mutualistic partners at the species level, as they are ultimately defined by multiple factors that come into play at the level of individuals. We anticipate that species-level, aggregated analyses (e.g., based on average estimates of generalization/specialization in resource use) may underestimate the potential of species to persist in real communities. Therefore, our results suggest a more nuanced interaction outcome that warrants further exploration in order to effectively represent fitness variation in natural populations and capture this kind of variation in mutualistic communities' dynamic models.

By considering various forms of variation within populations, we are able to identify thresholds of minimum amount of variation that would need to be preserved to guarantee the conservation of stable and biodiverse local communities (Anderegg *et al.*, 2013; Brose *et al.*, 2012; Clark, 2010). For instance, if disturbance effects simplify populations by size-dependent mortality events (Gora & Esquivel-Muelbert, 2021), one can assess how this kind of perturbation may impact among-individual variance and its effects on the feasibility of the entire communities in which these populations are embedded. Moreover, our framework enables the identification of key species within mutualistic communities that have disproportionate impacts on community dynamics through intraspecific variation. Understanding the contributions of these key species (Cagua *et al.*, 2019; Jordán, 2009; Mello *et al.*,

2015; Timóteo *et al.*, 2023) allows us to better predict the resilience of mutualistic communities to environmental perturbations and human-induced disturbances. Only by downscaling from species to the most basic interacting elements (i.e., individuals) when assessing the dynamics of natural systems can we uncover the fine-scale mechanisms that foster species persistence, which would otherwise remain obscured (Cantwell-Jones *et al.*, 2024). Therefore, an individual-based approach may improve our predictive power regarding the structure and functioning of ecological systems under the effects of global change. This improved understanding would enable the development of conservation strategies that support the persistence of functional co-occurring populations within natural communities, such as planting trees of varying age classes or preserving size diversity and/or size hierarchies within populations (Des Roches *et al.*, 2017; Hughes *et al.*, 1997).

FUTURE DIRECTIONS

Given the critical role of intraspecific variation in shaping mutualistic communities, future research should prioritize unveiling the full impact of this variation within species across different ecological contexts and spatial scales. One promising direction involves extending the current framework to study the effects of intraspecific variation in a broader range of species and ecosystems, particularly under different environmental conditions. Upcoming research applying this framework to assess how intraspecific variation promotes the persistence of communities in disturbed ecosystems, such as those especially affected by climate change, would provide valuable insights into the mechanisms that support biodiversity.

In our empirical case study, we focused on assessing intraspecific variation in mutualistic benefits from a phytocentric perspective. In doing so, we ignored the effects of co-variation that could arise when also considering the fact that animal populations can be potentially composed of individuals differing in traits and ecological interactions (Bascompte & Jordano, 2007). One main limitation of considering both partners variability lies in the logistical challenges associated with gathering empirical data on the mutualistic benefits received by animal partners (Vázquez *et al.*, 2012), particularly when they are invertebrates such as insect pollinators. Future research efforts that transcend these sampling difficulties could gain from incorporating perspectives that focus on both plants and animals to comprehensively explore the overall picture of the influence of intraspecific variation on mutualistic communities. If these fine-scale data can be collected in the field, our dynamic model accounting for intraspecific variation is ready to be parameterized to gain even deeper insights into the ecological processes that shape mutualistic communities.

Our theoretical framework also has broader applications beyond testing the effects of intraspecific variation in mutualistic interactions, as it could be also be extended to other types of species interactions or organizational levels within ecological systems for which Lotka–Volterra models are useful to describe dynamics (Boucher, 1985; Pascual-García & Bastolla, 2017). Mutualism rarely occurs in isolation, but in combination with other types of interactions (e.g., antagonistic) so expanding this framework to multiple interaction types can be useful to test the extent to which within-species variation in various types of interactions can shape communities. We also offer a versatile tool for exploring dynamics at various scales, from genotypes within populations to communities within metacommunities and beyond. Thus, the flexibility of this tool allows us to explore various timely questions in ecology involving any kind of subsetting structure across multiple scales (Chase *et al.*, 2018). For instance, our framework facilitates delving into the temporal stability of genetically-structured populations, shedding light on the resilience and persistence of such populations over time (Booy *et al.*, 2000). Furthermore, at larger spatial scales, it enables us to evaluate how habitat fragmentation influences ecosystem functioning and stability (Mitchell *et al.*, 2015). In particular, this framework could be used to unveil how specific features of a set of habitat fragments, comprising connected populations of focal species within a landscape, can buffer against or exacerbate the impacts of global change on the persistence of those species. Therefore, the development of more sophisticated models that integrate intraspecific variation with other sources of ecological complexity, such as multi-trophic interactions, temporal dynamics, and spatial heterogeneity, represents an exciting avenue for future work.

Advancing methodological techniques to collect and capture fine-scale individual-level data across a broader range of species, particularly those that are difficult to study due to their intrinsic characteristics, will be essential. Leveraging new technologies, such as remote sensing, DNA barcoding, and automated tracking systems, can enhance our ability to collect high-resolution data on individual interactions and traits in natural settings (Besson *et al.*, 2022; Corcoran *et al.*, 2021; Kellner *et al.*, 2019; Koger *et al.*, 2023; Kress *et al.*, 2015; Lines *et al.*, 2022). These data could then be used to refine and parameterize models, improving the accuracy of predictions related to community dynamics and species persistence. By combining detailed empirical data with theory and mathematical models, we open the door to deeply understanding ecological processes underpinning diversity patterns.

In summary, future research directions should aim to broaden the scope of intraspecific variation studies across ecological contexts, refine theoretical models, enhance empirical data collection, and adopt interdisciplinary approaches to better understand the complex interplay between individual

variation and the maintenance of diversity. These efforts will enhance our predictive capabilities, which are crucial for addressing challenges posed by global change and mitigating its impacts on biodiversity and ecosystem services.

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Box 1. Empirical estimation of mutualistic benefits.

To parameterize the mutualistic benefits provided by each pollinator species, the first step is to specifically estimate the contribution of each pollinator species to a plant individual's fitness of a given plant species as the number of seeds produced per flower as a result of a single visit by each pollinator species. First, as the three focal plant species (*Cistus libanotis*, *Halimium calycinum*, *Halimium halimifolium*) produce fruits without a fixed maximum number of seeds, the number of seeds produced per fruit recorded in each plant individual can be modeled as a Poisson outcome with:

$$\begin{aligned} S_{P_{is}} &\sim \text{Poisson}(\lambda_{P_{is}}) \\ \lambda_{P_{is}} &= \mu_{P_{is}} + \left(\sum_{A_i} \beta_{P_i A_i} \, v_{P_{is} A_i} \right) \end{aligned} \tag{8}$$

where $S_{P_{is}}$ is the observed number of seeds produced in an individual fruit of plant individual s belonging to plant species i, $\lambda_{P_{is}}$ is the mean expected intensity, $\mu_{P_{is}}$ represents the intercept for plant individual s belonging to plant species i, $\beta_{P_i A_i}$ the coefficient of pollinator species i on plant species i, and $v_{P_{is} A_i}$ the frequency of interactions per flower between pollinator species i and plant individual s of plant species i along the entire flowering season (estimated using the visitation data we recorded in the field; Appendix A).

Second, since a flower can only produce seeds if it has previously set fruit, we also need to estimate the contribution of each pollinator species to the probability of a flower setting fruit. The fruit production per individual flower in each plant individual was recorded as either the presence or absence of fruit, and therefore can be treated as a Bernoulli outcome:

$$\begin{aligned} Y_{P_{is}} &\sim \text{Bernoulli}(p_{P_{is}}) \\ \log\left(-\log\left(1 - p_{P_{is}}\right)\right) &= \mu_{P_{is}} + \left(\sum_{A_i} \beta_{P_i A_i} \, v_{P_{is} A_i} \right) \end{aligned} \tag{9}$$

where $Y_{P_{is}}$ is the response variable denoting the presence or absence of a fruit on an individual flower of plant individual s belonging to plant species i, $p_{P_{is}}$ is the probability of the presence of a fruit, and all other parameters are defined above.

We integrated both fitness proxies—the probability of a flower setting fruit and the expected number of seeds per fruit—into a single model using a joint likelihood (Appendix B). The joint likelihood method simultaneously fits a likelihood to both data sources (fruit and seed production) while accounting for different data types but using equivalent parameter values for both (Ahmad Suhaimi *et al.*, 2021; Simmonds *et al.*, 2020). This is the reason why we used a cloglog link in the Bernoulli model (Eq. 9) to connect $p_{P_{is}}$ to the log intensity ($\lambda_{P_{is}}$) of the Poisson model (Eq. 8), so that $p_{P_{is}} \equiv 1 - e^{-\lambda_{P_{is}}}$ (Royle *et al.*, 2009). As a result, the parameters $\beta_{P_iA_i}$ are directly shared between both models, and we can simultaneously estimate the contribution of pollinator species i to both the probability of a flower setting fruit and the number of seeds produced per fruit in plant species i (Appendix B). Note that this equation implies that the probability of a flower not producing a fruit is equal to the probability of a fruit from that flower not producing any seeds.

With this statistical procedure, we estimated the contribution of each pollinator species to seed production per flower in a given plant species ($\beta_{P_iA_i}$). These pollinator species' contributions were then used to determine the specific mutualistic benefits received by plant individuals from each pollinator species, expressed as $\gamma_{P_{is}A_i}$ in matrix M of the mathematical framework for our specific case (Eq. 7). We estimated the mutualistic benefit of pollinator species i (A_i) to plant individual type s belonging to plant species i (P_{is}) as:

$$\gamma_{P_{is}A_i} \;=\; \beta_{P_iA_i} f_{P_{is}} \frac{v_{P_{is}A_i}}{\sum_t \; v_{P_{it}A_i}} \tag{10}$$

where $f_{P_{is}}$ is the total number of flowers produced by plant individual type s belonging to plant species i, and $v_{P_{is}A_i}$ is the frequency of visits per flower received by plant individual type s of plant species i from pollinator species i across the entire flowering season, which is normalized across all individuals of plant species i. Therefore, intraspecific variation in mutualistic benefits received by plant individuals from pollinator species (i.e., $\gamma_{P_{is}A_i}$) within a plant population is modulated by three components: pollinator assemblage and their associated contribution to fitness ($\beta_{P_iA_i}$), visitation rates ($v_{P_{is}A_i}$) and flower production across the flowering season ($f_{P_{is}}$). Note that $\gamma_{P_{is}A_i} = 0$ in the case that pollinator species A_i did not establish interactions with plant individual type P_{is} ($v_{P_{is}A_i} = 0$).

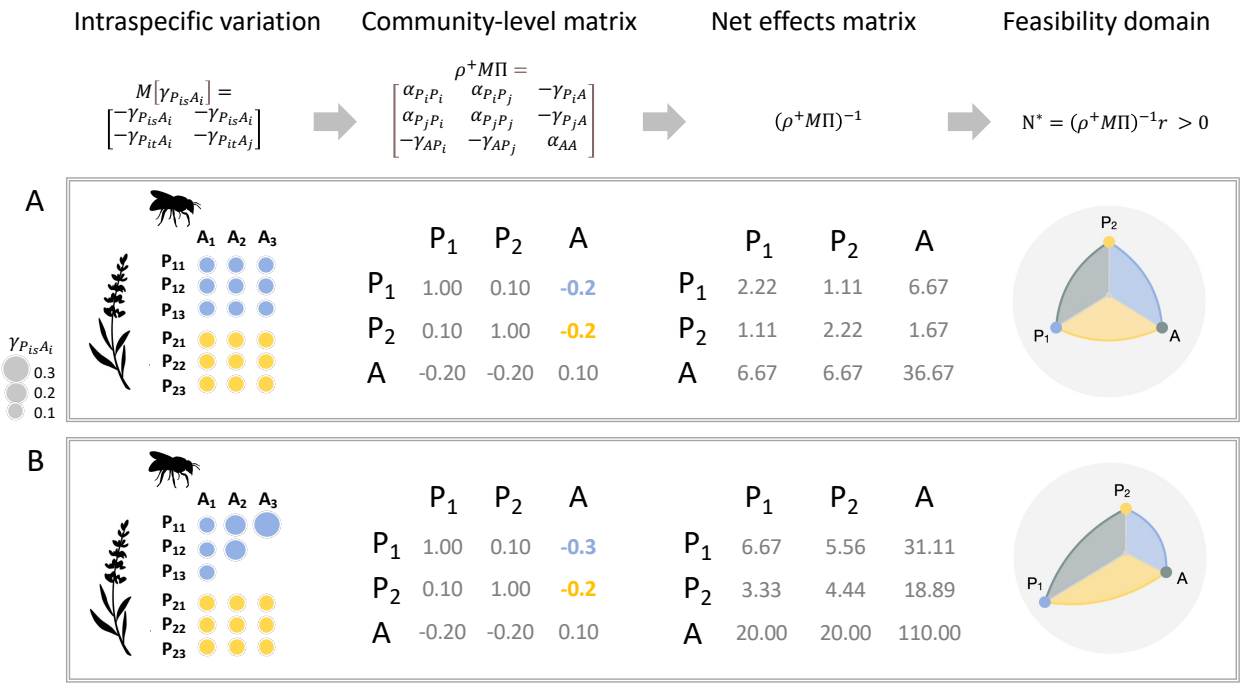

Figure 1: Conceptual overview of how intraspecific plant variation can impact species persistence in a plant–pollinator assemblage. The effects of intraspecific plant variation in the mutualistic benefits received from pollinators is illustrated with a simplified community composed of three individual types belonging to two plant species, which interact with three pollinator species. Intraspecific plant variation (i.e., within-population variation) is incorporated in the submatrix of the interaction matrix M containing the mutualistic benefits received by plant individuals from the pollinator species ($\gamma_{P_{is}A_i}$) with which they interact. The matrix product $\rho^+ M\Pi$ captures the interaction coefficients at the level of plant species and the pollinator community. The net effects matrix represents the per-capita effects of one species on the per-capita growth rate of another, including both direct and indirect effects. The feasibility domain represents the set of values of intrinsic growth rates that allows all plant species and the pollinator community to maintain positive abundances given the constraints imposed by the interaction coefficients contained in $\rho^+ M\Pi$. (A) In this hypothetical community, all types of plant individuals interact in the same way with all three pollinator species and receive exactly the same mutualistic benefits from them. (B) In this hypothetical community, there is intraspecific variation in the overall mutualistic benefits received by plant individual types belonging to plant species P_1 due to among-individual differences in pollinator assemblages and differences among pollinator species in their fitness contribution (i.e., variation in $\gamma_{P_{is}A_i}$). Based on empirical data, we represented plant–pollinator interaction patterns with a nested structure, in which pollinator species with lower degree have higher contribution to plant fitness. In the presence of intraspecific plant variation in plant species P_1 (i.e., mixture of generalized and specialized plant individuals), the patterns of direct and indirect effects in the community (i.e., net effects matrix) change when compared to the scenario without intraspecific plant variation. As a consequence, the size and the shape of the feasibility domain, and therefore the persistence probability of species (see Fig. 4) also change in the presence of intraspecific variation.

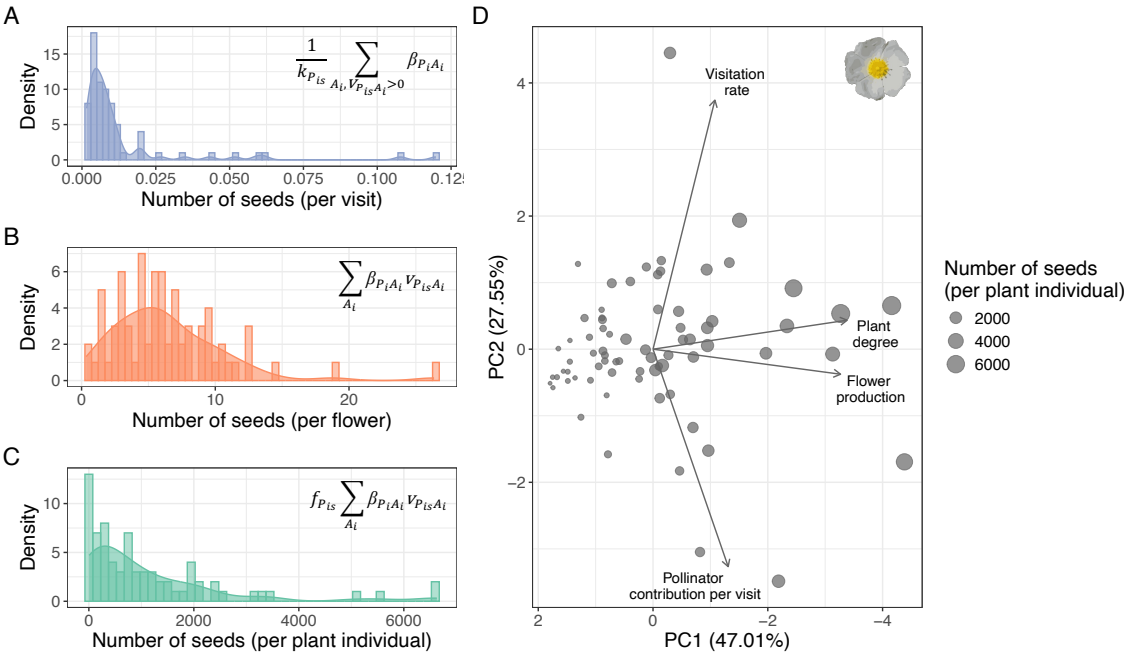

Figure 2: Sources of intraspecific variation influencing plant fitness. Intraspecific plant fitness variation within one of the study species (*Cistus libanotis*) when incorporating different components influencing plant fitness. (A) Histogram of the average number of seeds produced per visit across plant individuals, where intraspecific variation is promoted by differences in pollinator assemblages and their associated contribution to fitness. (B) Histogram of the number of seeds produced per flower across plant individuals, where intraspecific variation is promoted by differences in visitation rates in addition to differences in pollinator assemblages. (C) Histogram of the total number of seeds contributed to the population seed bank across plant individuals, where intraspecific variation is produced by differences in pollinator assemblages, visitation rates and flower production. (D) Principal Component Analysis (PCA) of plant individuals (dots) based on different sources of intraspecific variation influencing plant fitness. Dot size is proportional to the number of seeds produced and contributed to the seed bank of the population. Estimates of the number of seeds per visit (A), per flower (B) and per individual plant (C) were calculated following the equations shown in each panel, in which $k_{P_{is}}$ denotes the degree of plant individual P_{is}, $\beta_{P_iA_i}$ denotes the number of seeds per flower produced in plant species P_i per visit of pollinator species A_i, $v_{P_{is}A_i}$ is the visitation rate per flower of pollinator species A_i to plant individual P_{is}, and $f_{P_{is}}$ represents the number of flowers produced by plant individual P_{is}. We found similar patterns for other focal plant species (Appendix D).

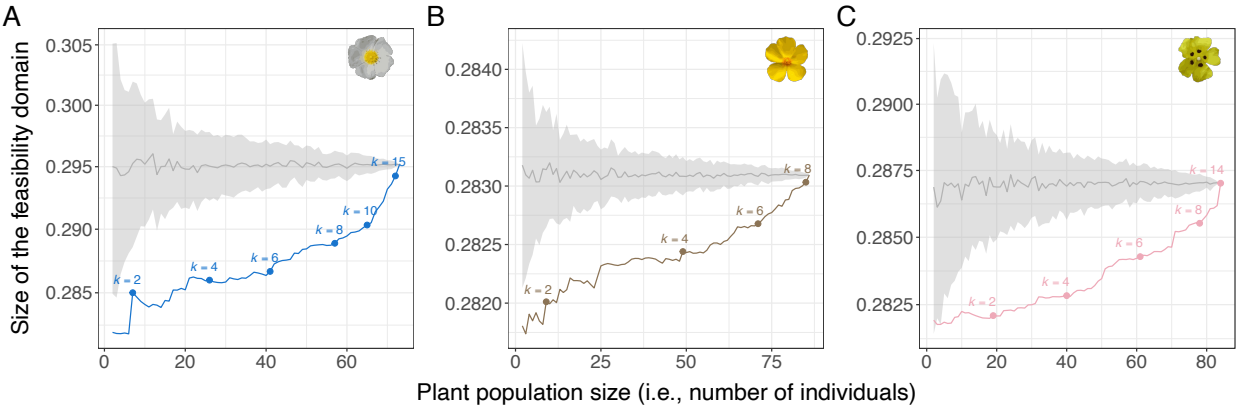

Figure 3: Effects of mixtures of specialized and generalized plant individuals in pollinator use on the feasibility of plant populations' mutualistic assemblages. For the three focal plant species (A, *Cistus libanotis*; B, *Halimium calycinum*; C, *Halimium halimifolium*), gray lines represent the size of the feasibility domain of the interaction assemblage of a given plant population over an increasing population size by including plant individuals regardless of their degree. Colored lines represent the size of the feasibility domain of this interaction assemblage over an increasing plant population size by incorporating plant individuals from lower to a higher degree (i.e., from more specialized to more generalized individuals). Plant individuals with the same degree were included in order of decreasing specificity (i.e., decreasing coefficient of variation of interactions). Colored dots represent the degree (k) of plant individuals being included to increase population size. Differences in the feasibility domain between the colored and gray lines for a given population size correspond to the effects of having a mixture of specialized and generalized individuals within the population compared to having a higher proportion of specialized individuals. Note that the lines corresponding to a higher proportion of specialized individuals (blue, brown, and pink) are located below the confidence interval of the random mixtures of specialized and generalized (grey) across all population sizes.

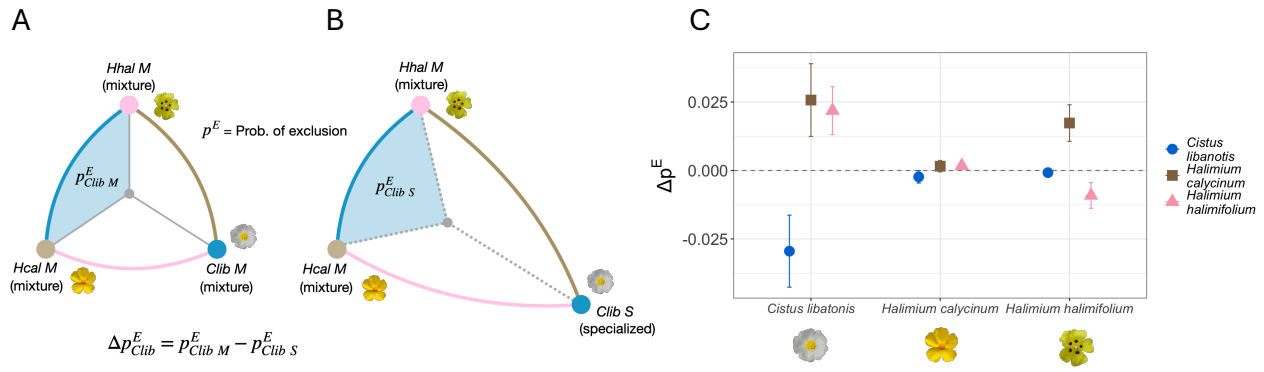

Figure 4: Effects of mixtures of specialized and generalized plant individuals in pollinator use on the persistence of co-occurring plant species. Conceptual representation of how we measure the effects of (A) random mixtures of generalized and specialized individuals within a focal species (*Cistus libanotis*) on the exclusion probability (p^E) of co-occurring species, compared to (B) a scenario with a higher proportion of specialized individuals in this focal species. Note that here we focus on the persistence ability of the plant side of the plant–pollinator community. (C) Differences in the probability of exclusion of three plant species in the mutualistic community when considering focal populations composed of a mixture of specialized and generalized individuals *versus* focal populations comprising a higher proportion of specialized individuals. A positive or negative difference indicates that a mixture of specialized and generalized individuals of the plant species denoted on the x-axis increases or decreases, respectively, the probability of exclusion of co-occurring plant species, represented with different colors and symbols. Error bars around dots represent variation between plant populations composed of random mixtures of N=40 individuals (i.e., including individuals with high and low degree within the population). In each focal species, a higher proportion of specialized plant individuals was created using populations composed of the N=40 most specialized (lowest degree) individuals. The probability of exclusion (p^E) of a given species in a community quantifies the average probability that this species is the first one to be excluded if a destabilizing perturbation took place in a feasible community under Lotka–Volterra dynamics.

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