Article

Interaction network structure explains species' temporal persistence in empirical plant–pollinator communities

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Despite clear evidence that some pollinator populations are declining, our ability to predict pollinator communities prone to collapse or species at risk of local extinction is remarkably poor. Here, we develop a model grounded in the structuralist approach that allows us to draw sound predictions regarding the temporal persistence of species in mutualistic networks. Using high-resolution data from a six-year study following 12 independent plant–pollinator communities, we confirm that pollinator species with more persistent populations in the field are theoretically predicted to tolerate a larger range of environmental changes. Persistent communities are not necessarily more diverse, but are generally located in larger habitat patches, and present a distinctive combination of generalist and specialist species resulting in a more nested structure, as predicted by previous theoretical work. Hence, pollinator interactions directly inform about their ability to persist, opening the door to use theoretically informed models to predict species' fate within the ongoing global change.

Pollinators are key components of ecological systems that provide a wide variety of ecosystem functions and services critical for human well-being, such as plant reproduction[1] and food security[2]. However, the maintenance of these functions is at risk due to the ongoing negative effects of global change drivers on pollinator abundance and diversity[3–5]. There have been several calls to face the global crisis of pollinator decline by providing tools that accurately predict their population dynamics, and therefore their probability of extinction[6]; however, our ability to achieve a predictive ecology is still limited[7]. The need to predict, and hence to understand, how ecological communities respond to ongoing environmental changes has historically fuelled intense research on ecological stability[8–10]. Yet, this research has been hampered by both a profound divide between the theoretical and the empirical studies[10–12], and an unclear definition of the concept of ecological stability itself[10,13]. This ongoing debate has not given a clear link between the structure of ecological communities, their stability and the persistence of the species constituting these communities[14]. As a

potential solution, the structuralist approach[15] and its recent application to ecology has been shown to provide a parsimonious theoretical benchmark to understand and predict the persistence of empirical ecological communities in changing environments[14,16].

The main prediction of the structuralist approach is that the network of biotic interactions among species composing an ecological community determines their opportunities to coexist[17]. Communities with larger coexistence opportunities, which in natural plant–pollinator communities correspond to more cohesive structures of biotic interactions (that is, nested)[14], are probably more persistent because they can tolerate a larger difference in intrinsic growth rates (that is, performance) among species. Importantly, species' performances are expected to be driven by the environment where they live, providing a phenomenological link with the current environmental conditions[18]. The degree of structural stability of an ecological community can be rigorously assessed by coupling mathematical theory to population models that describe the dynamics of the species based on these two

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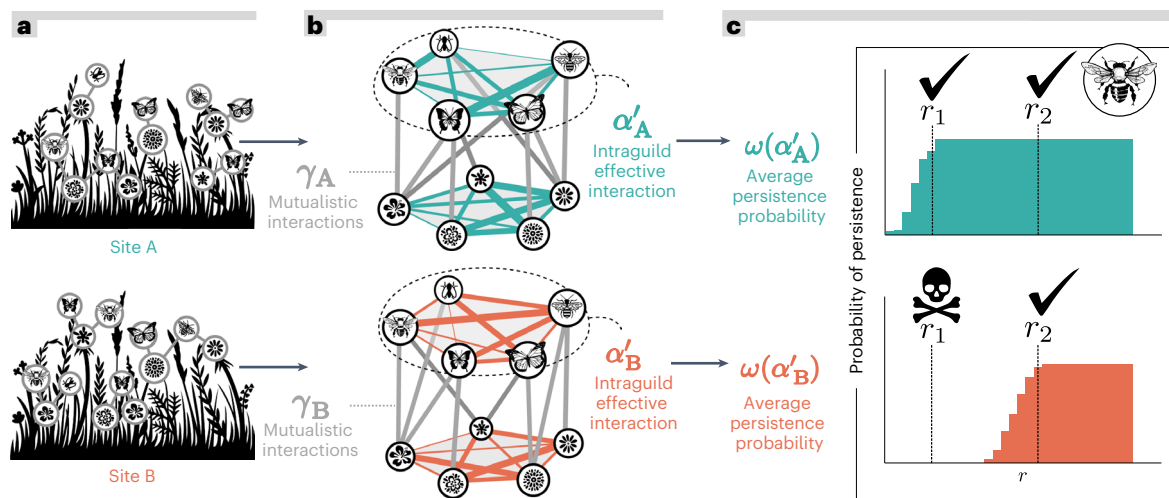
Fig. 1 | **Species' persistence probability in model communities. a**, Empirical observations determine the mutualistic plant–pollinator interactions (γ) of our dynamical model. **b**, From γ we obtain a matrix describing the intraguild effects among pollinators (α'), called the 'effective interaction matrix' (Methods). **c**, α' is then used to quantify the structural stability (Methods), which gives the average probability that any species in the community persists ($\omega(\alpha')$). At the species level, the different distribution of growth rates compatible with a given species' persistence (*Anthophora bimaculata* in this example) in sites A and B (colour coded) will determine the likelihood of that species' persistence when reproductive rates are sampled randomly (r_1, r_2). Note that fewer values of r are compatible with species persistence in site B (that is, it has a lower expected persistence probability, ω_i).

ingredients: species' performance and their interactions. However, for many communities such as pollinators, information on such performance is not available. In that case, the structuralist approach is still valid because it allows taking a probabilistic view to ask which communities are more likely to be observed, given the fact that environmental conditions can produce changes in species' performance in multiple directions, that is, increasing performance for some species but simultaneously decreasing it for others[14,16,19,20]. Hence, it is expected that the larger the range of species' performance compatible with its persistence, the larger the environmental fluctuations that the community can withstand, and the more probable its persistence.

Despite this theoretical framework providing a set of clear predictions and associated tools to assess the persistence of ecological communities, direct empirical tests are limited to micro-[21] or mesocosm experiments[22] and real-world tests are still lacking (but see refs. 16,23 for an approximation). These tests are of fundamental importance to ensure that the transfer of basic ecological knowledge to conservation planning is relevant in the real world. Part of this lack of progress comes from the difficulty of following plant–pollinator communities over long periods of time[24–27], which means that most of the empirical plant–pollinator networks studied are just a snapshot of a particular state of the community.

Here, we use a well-resolved dataset on abundances and interactions between plants and pollinators in a long-term study carried out on 12 independent sites exposed to changing environmental conditions over six years (adding up to 179 pollinator species and 1,470 plant–pollinator interactions; Methods). Following the structuralist approach, we investigated whether empirical observation of species persistence (that is, the average number of years across sites a species is observed in the community) is explained by the structural stability of the plant–pollinator communities emerging from the species interaction networks. In its probabilistic interpretation, structural stability represents the average probability that a randomly chosen species of the community persists despite varying its performance[18] (Fig. 1). Therefore, we predict that larger values of structural stability promote higher persistence of a pollinator community. To test our main prediction across levels of biological organization (both community and species level) we recorded the following across the 12 independent communities: (1) the abundances of pollinator species over time, with which we quantified empirical persistence; and (2) the mutualistic network of plant–pollinator interactions, with which we quantified the structural stability (that is, the expected average persistence probability of a species in a given community, ω). To quantify ω, we need to parameterize a model that describes reasonably well the population dynamics of plants and pollinators in terms of their biotic interactions. For this, we used a standard mutualistic dynamic model[14,18,28,29] where the mutualistic interactions are parameterized with the observed plant–pollinator networks (Methods and Fig. 1). From the plant–pollinator mutualistic interactions, we inferred the matrices describing the effective biotic interactions among pollinators (α'_A) and among plants (α'_P), following previous methodologies (Methods and Supplementary Information section H). Taken together, these matrices of species' interactions determine the range of species' growth rate values (r) compatible with its persistence[14]. In what follows, we centre our results on pollinators, but we advance that the framework also works to describe and predict which are the more persistent plant species (Supplementary Figs. 1 and 2).

Results and discussion

Although our analyses indicate a moderate change in ω across all 12 independent sites (ranging from 0.45 to 0.55), we find that this variation was sensitive enough to capture differences in empirical persistence between pollinator communities. Note that we studied natural communities within a single habitat type and for which the main drivers of environmental change are related to its fragmentation degree over space and weather variability over time. Hence, we do not expect large changes in species' persistence, in contrast to comparisons across habitats, or in situations where most of the focal habitat has been destroyed[4].

According to our main hypothesis, we observe that those pollinator communities with higher opportunities for species to coexist (that is, with higher values of ω) strongly correspond with higher mean pollinator persistence observed in the field (Spearman correlation coefficient, ρ, of 0.85), as shown in Fig. 2a. This result indicates that the structure of species' interactions in the studied communities contains information on how species, on average, can persist under changing environments (a result that holds when excluding species observed only once; Supplementary Fig. 3). Interestingly, our results additionally suggest that landscape fragmentation matters for determining
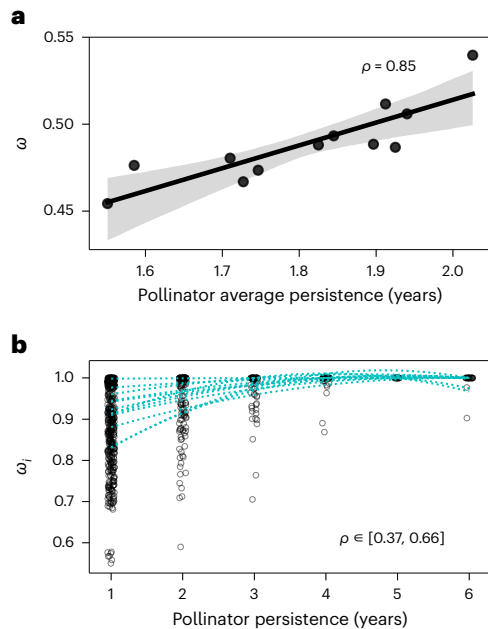
Fig. 2 | Theoretical expectation versus empirical values. a, Expected average persistence probability of pollinators (ω) versus mean persistence observed in the field for the 12 sites in the study. The shaded area represents the 95% confidence interval of the regression estimate. **b**, Expected pollinator persistence probability (ω_i) versus the number of years this pollinator is present in the field. Each point represents one pollinator species in one site, and all 12 sites are plotted together but analysed independently. The dotted blue lines represent the 50th quantile regression for each of the 12 sites, Spearman's rank correlation coefficient (ρ) is shown for **a**, and its range depending on the site in **b**. Note the differences in the *x* axis between **a** and **b**: while **a** indicates an average persistence in the field between 1.5 and 2 years across species, **b** represents the number of years each pollinator species was observed in the field (1–6 years).

the observed variation in the expected persistence probability with communities in larger habitat patches tending to exhibit higher persistence (correlation $\rho \approx 0.6$) and a more nested structure ($\rho \approx 0.7$) than those in smaller patches (Supplementary Fig. 4b), but not necessarily more diverse in species (Supplementary Fig. 4c). Note, however, that most of this trend in nestedness seems to be due to an increase in the degree of heterogeneity with patch size (Fig. 4d). Hence, landscape fragmentation, one of the consequences of more intensive agricultural practices, can have a negative impact on the ability of the species to withstand other changes, such as climate change.

While these results can give us information on the whole community, from a conservation point of view it is often important to also study the persistence of the individual species, especially those that are rare, endemic or threatened. For that, we quantified the expected probability of persistence for each species (*i*) in the 12 studied communities (ω_i)[16,20], and compared such probabilities with the number of years each species is present in the field (Fig. 2b and Supplementary Fig. 5). In agreement with our main prediction, we also find a positive relationship between the expected pollinator persistence probability in the model (ω_i) and the number of years that a pollinator is found in the field (ρ ranges from 0.37 to 0.65 depending on the site, and is always statistically significant), meaning that species that are more frequently expected to be locally extinct in the theoretical models also tend to have lower observed persistence in real communities. Some of the species more frequently predicted to be extinct are comparatively rare species (Supplementary Fig. 6a). Previous work suggests that the link between rare species and their lower probability to persist occurs when species are under a process of extinction debt[30], or, in open systems like our empirical communities, they

represent transient species just 'passing through', subject to source and sink dynamics[31,32].

In line with the theoretical developments, our analysis uses information on who interacts with whom (that is, unweighted mutualistic interaction networks) and a presence–absence metric of persistence. However, species' abundances can still be a confounding factor if they drive both the structure of species interaction networks and the probability of species' persistence. Using null models that generate randomized species interaction networks only from the species' abundance distributions[33], we show that although we are able to recover a general nested structure in the networks from the null model (Supplementary Fig. 12), we do not recover information on who interacts with whom (see also ref. 34 for similar results). Interestingly, the structural stability of these randomized interaction networks does not explain the observed pollinator persistence (Supplementary Fig. 13), indicating that besides the general correlation between the interaction network structure and expected persistence[14], who interacts with whom is the key factor for predicting species' persistence. In fact, further analyses involving null models show that the particular degree sequence of the empirical networks is one major driver of their structural stability (Supplementary Fig. 17). A detailed analysis of the effect of species' abundance as a confounding factor can be found in Supplementary Information sections I and J, and a detailed comparative with all the null models explored in Supplementary Information section K.

Our results therefore highlight that the structuralist approach is a useful theoretical framework to progress our mechanistic understating of two interrelated problems in ecology: the identification of dynamically stable species that persist despite environmental fluctuations[35], and how such stability permeates from species to communities[10].

Species might persist despite presenting strong temporal fluctuations in their abundances[36]. Thus, a natural next question to ask is whether this framework can not only identify persisting species, but also species with stable temporal fluctuations in abundance. Overall, we found no correlation between our theoretical measure of persistence (ω) and the observed temporal stability of the aggregated pollinator population (*S*; $\rho = 0.24$, not statistically significant), suggesting that structural stability is not a good predictor of temporal stability at the community level. If the structuralist approach is not a strong predictor of temporal stability, it opens the field to investigate which are instead its predictors. To shed light on this point, we performed a linear regression accounting for the three main variables known to drive temporal stability in plant and pollinator communities: species richness[37], temporal stability of species' populations[38] and population asynchrony[39] (Methods). Among these predictors, both pollinator richness (Fig. 3a) and temporal stability of pollinators' populations (Fig. 3b) were weakly and non-significantly correlated with the temporal stability of the community. Instead, more temporally stable communities are composed of pollinators with strong asynchronous responses (Fig. 3c), a result that we recover also with plants (Supplementary Fig. 2). This negative relationship, which is a common phenomenon observed in empirical studies including pollinators[40], is known as the biodiversity insurance or portfolio effect[41], and it indicates that the persistence dynamics that capture the structuralist approach are independent of those captured by the temporal stability of the community. While structural stability informs of the average persistence of communities and species, temporal stability informs of the asynchronous temporal fluctuation. At the species level, however, we found a weak but significant positive correlation between structural and temporal stability, caused by a subset of abundant species that sustain stable populations with a high expected probability of persistence (Supplementary Fig. 7).

Ecology is entering an exciting phase where models based on solid theory are being used to simultaneously understand ecological processes and predict the fate of ecological communities under global change[7]. Under these circumstances, the resurgence of monitoring programmes, including ambitious pollinator ones[42,43], holds great
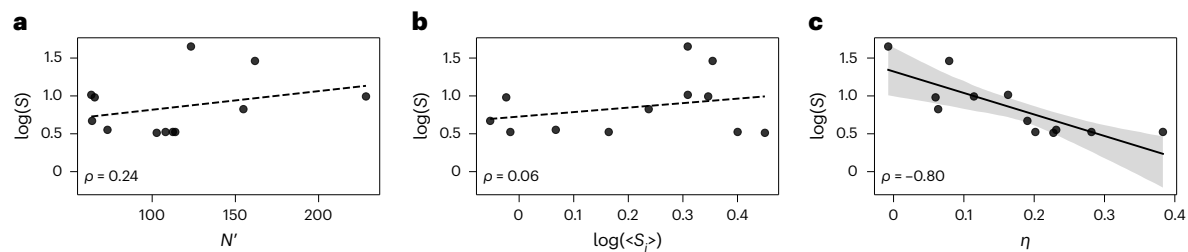
Fig. 3 | Predictors of temporal stability. a–c, Dependence of temporal stability of the aggregated pollinator population (log(S)) on pollinator estimated richness (N'; **a**), average pollinator population stability (log($<s_i>$)); **b**) and synchrony of pollinator populations (η; **c**). The shaded area represents the 95% confidence interval of the regression estimate. Each point represents one study site, and each figure includes Spearman's rank correlation coefficient (ρ) and the regression line (dashed when not statistically significant).

potential to seek the perfect empirical and theoretical marriage to rigorously describe and predict temporal changes in pollinator populations, which can directly inform to allow better conservation and management decisions. Here we build on previous work that highlights the importance of applying the structuralist approach to the network of biotic interactions to understand the species' demographic consequences[14,16,23]. By studying multiple independent sites, we empirically confirm that the interaction network structure of plant–pollinator communities can explain their temporal dynamics across levels of biological organization, a long-lasting open question in ecology[44]. That is, we can distinguish which communities and which particular species are more likely to persist or will die out in the face of ever-present environmental variation, thus providing promising tools for management that might allow designing actions to combat pollinator loss. Taken together, our results show the power to couple detailed empirical data with mathematical theory and associated modelling tools to understand pollination declines, opening new avenues of study and at the same time reinforcing previous theoretical results.

Methods
Empirical data
Data on species' population and interaction strength have been gathered during empirical observations through six consecutive years (2015–2020) along the spring season (from February to June). Each year we sampled twice a month for at least seven rounds during the full flowering season across 12 different sites situated in a landscape fragmentation gradient in the southwest of the Iberian Peninsula (Huelva and Seville), gathering data on plant–pollinator interaction frequency and flower abundance. Sites were at least 3 km apart (mean 7.17 ± 0.97 km; Supplementary Fig. 9), which is larger than the foraging distances of most pollinators[45] and hence can be viewed as independent. In each site, and during each round, we walked a 100 m straight line for 30 minutes in which we wrote down every plant–pollinator interaction seen, differentiating between the number of pollinator individuals and the number of visits per individual. This resulted in a total of more than 250 hours of field observations. In addition, we measured the abundance of plants by recording the number of flowers of each plant species in ten 1 m² subplots placed along the transect. Bees and plants that we were unable to identify in situ were collected for later identification. The time spent collecting specimens was discounted from the standardized sampling time. Bees were caught by hand-netting and preserved in a freezer at −20 °C until they could be pinned and labelled in the lab, and plants were preserved using plant presses. Later, they were identified using a binocular loupe and determination keys. Those specimens for which identification was unclear were sent to taxonomic experts. Although non-collected pollinators might be double-counted in transects, we believe this is unlikely given the behaviour of solitary bees, and in any case, this will not affect our main analysis based on unweighted metrics. This intensive fieldwork resulted in a dataset containing more than 179 pollinators and 1,470 plant–pollinator interactions (Supplementary Table 1).

Empirical measures of persistence and temporal stability
We obtained the yearly floral abundance of plant species in each site by aggregating the abundance of all rounds in the year. We measured pollinators' yearly abundance by aggregating through each year the number of times each pollinator species had interacted with any plant. Note that we recorded both the number of individuals and the number of visits per individual, and abundance metrics were always derived from individual counts, not visitation frequencies, to avoid confounding pollinator activity with its frequency. In both cases, we normalized the abundances with the sampling effort of that year (that is, the number of rounds).

To quantify the persistence of each species in each site, we measured the number of years the species was present in the field, and then obtained the mean persistence of plants and pollinators in each site as the average persistence of the species present in the site.

We quantified the temporal stability of plant and pollinator populations at two scales. At the community scale, we first obtained the total abundance of pollinators and flowers for each year by aggregating the abundance of all the species in the site, and then we measured the inverse of the coefficient of variation (σ/μ)[37] of such aggregated abundances, where μ represents the mean population abundance and σ the standard deviation of population abundance. At the species scale, we measured for each species i in each site the inverse of the coefficient of variation (σ_i/μ_i) of the species abundance through the six years. We verified that the relationship between μ and σ was linear (Supplementary Fig. 14), and hence our metric is appropriate to measure community stability[46], because temporal stability is not merely driven by mean abundance (Supplementary Fig. 15 and Supplementary Information section J).

We quantified species richness (N') with the asymptotic species richness estimator, using package iNEXT in R[47], to avoid the possible influence of sampling effort in determining true species richness.

We quantified species' average synchrony (η) as the mean correlation coefficient between the field abundances A_i of each species i versus the rest of the species j in the community (all A_j except i) following ref. 39 as:

$$\eta = (1/N) \sum_i r\left(A_i, \sum_{j \neq i} A_j\right)$$

and verified that it was not simply a consequence of species' abundances (Supplementary Fig. 16). Note that in this case we use the total number of species (N) to compute the mean and not N'.

Empirical interaction networks
We obtained the network of interactions in each site by aggregating through all the years the identity of the interactions recorded between

plants and pollinators. This ensures a proper characterization of all potential interactions realized in our communities because sample coverage (measured also using package iNEXT in R[47]) was above 0.85 in all sites. To build a model as parsimonious as possible, we only used unweighted interactions in the mutualistic model (that is, the elements in the matrix encoding the empirical mutualistic interactions that we use in our dynamica model are $M_{ij} = 1$ if species i and j interacted in the field and 0 otherwise), as is usually done in this type of model[14,18,29].

The mutualistic model

To quantify the average persistence probability (ω) we employed a standard mutualistic dynamics model[14,18,28,29], using the empirical networks as the skeleton (see below). The equations describing the abundance of plant (P_i) and animal (A_i) species trough time (t) are of the form:

$$\begin{bmatrix} \frac{dP}{dt} \\ \frac{dA}{dt} \end{bmatrix} = \mathrm{diag}\left(\begin{bmatrix} P \\ A \end{bmatrix} \right) \times \left(\begin{bmatrix} \mathbf{r}_P \\ \mathbf{r}_A \end{bmatrix} - \underbrace{\begin{bmatrix} \boldsymbol{\alpha}_P & -\boldsymbol{\gamma}_P \\ -\boldsymbol{\gamma}_A & \boldsymbol{\alpha}_A \end{bmatrix}}_{A} \begin{bmatrix} P \\ A \end{bmatrix} \right) \quad (1)$$

with parameters accounting for intrinsic growth rate (r), intraguild competition (α) and mutualistic benefit (γ). We considered mean field intraguild competition ($\alpha_{ii}^P = \alpha_{ii}^A = 1, \alpha_{ij}^P = \alpha_{ij}^A = \alpha$) and used the empirical networks to parameterize the mutualistic benefit as follows: $\gamma_{ij} = (\gamma_0 M_{ij})/(k_i^\delta)$, where $M_{ij} = 1$ if we recorded a plant–pollinator interaction between species i and j in the field and 0 otherwise, γ_0 represents the overall level of mutualistic strength, k the degree of the species i, and δ the mutualistic trade-off. The results in the main text correspond to $\alpha = 0.005, \gamma_0 = 0.1$ and $\delta = 0$, but we checked the robustness of the results in Supplementary Information section L using values of γ_0 below the critical threshold to ensure that all our simulated communities were linearly stable[29]. While improvements can be made (for example, considering nonlinear functional responses[48] or empirically based competition instead of mean field[49]), we chose this model for simplicity and because it is used in many previous theoretical studies.

In order to treat pollinators and plants separately, we worked in an effective interaction framework[14], where the mean field competition between plants and animals is modified by the mutualistic interactions. Diagonalizing the interaction matrix (I in equations (1) and (2)) per block allows going from a set of $N_P + N_A$ entangled equations for the abundances of plants and pollinators in the steady state (equation (2)), to two sets of equations, one for plants (N_P species) and one for pollinators (N_A species), with only intraguild interactions (equation (3)). This is achieved by multiplying by the matrix $T = 1 + \Gamma C^{-1}$ both left sides of equation (2) (see Supplementary Information section H for a more detailed explanation):

$$\begin{bmatrix} r_P \\ r_A \end{bmatrix} = \left(\underbrace{\begin{bmatrix} \alpha^P & 0 \\ 0 & \alpha_A \end{bmatrix}}_{C} - \underbrace{\begin{bmatrix} 0 & \gamma_P \\ \gamma_A & 0 \end{bmatrix}}_{\Gamma} \right)^{I} \begin{bmatrix} P \\ A \end{bmatrix} \quad (2)$$

$$\begin{bmatrix} r'_P \\ r'_A \end{bmatrix} = \begin{bmatrix} \alpha'_P & 0 \\ 0 & \alpha'_A \end{bmatrix} \begin{bmatrix} P \\ A \end{bmatrix} \quad (3)$$

We quantified the expected average persistence probability (ω) using matrices α'_A and α'_P in equation (3) with the code provided in a previous study[29].

To calculate the persistence probability of a particular species in the model community (ω_i), we used the structural forecasting framework[16,20]. We randomly sampled 3,000 directions of growth rate vectors (r) uniformly inside the full parameter space and solved the systems of equation (3) to determine the proportion of cases in which each species was present in the community ($P_i, A_i > 0$).

Nestedness analysis

We quantified the nestedness of the empirical plant–pollinator networks using two metrics: v, following ref. 29, and $\bar{v}$, following ref. 50. This latter metric is a measure of how nested a given interaction network is once the expected nestedness given its degree sequence has been discounted (that is, if the network is more or less nested than what could be expected given the degrees of the species in the network). In this metric, values close to 1 indicate no significant nestedness, while larger values indicate increasing significant nestedness (see Supplementary Information section C).

Disentangling the effect of abundance in determining interaction structure

We tested to what extent the abundance of species could be acting as a potential confounding factor, explaining the results obtained. We implemented the null model presented bin ref. 33 (named 'A'), which generates interaction networks such that the species-specific probabilities of interaction are proportional to species' abundances. We generated 100 randomized versions of each of the empirical interaction networks using the vaz_null_external function of package bipartite in R[51], introducing the empirical species' relative abundances as input, and compared both the cumulative degree distribution (Supplementary Fig. 11) and the expected persistent probabilities (Supplementary Fig. 13) of the randomized networks with those obtained for the empirical networks (see Supplementary Information section I).

Structural features driving structural stability

To assess the importance of network structure in determining structural stability, we compared measurements of that feature on empirical networks with measurements performed on 100 randomized versions of those networks keeping some properties fixed. Apart from the null model already presented (null model 'A'), we used other three different null models, which—going from the least to the most constraining—are as follows: 'B' keeps constant the number of species in each species set and the number of interactions; 'C' adds the constraint of keeping also the degree distribution; and finally 'D' keeps the degree of each node constant but reshuffles the interactions. The expected pollinator average persistence probability (ω) of empirical networks compared with that measured in their randomized counterparts can be seen in Supplementary Fig. 17 (see also Supplementary Information section K).

Correlations and regression estimates

Regression estimates from Figs. 2 and 3 were obtained using package seaborn in Python. All Spearman's rank correlation coefficients were obtained using package scipy in Python. The quantile regressions of Fig. 2 were obtained using package statsmodels in Python.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

A dataset of species interaction and abundances can be accessed via Zenodo[52]. Source data are provided with this paper.

Code availability

The code used in this study can be downloaded from Zenodo[52].

References

1. Ollerton, J., Winfree, R. & Tarrant, S. How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326 (2011).
2. Potts, S. G. et al. Safeguarding pollinators and their values to human well-being. *Nature* **540**, 220–229 (2016).
3. Potts, S. G. et al. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* **25**, 345–353 (2010).

4. Winfree, R., Bartomeus, I. & Cariveau, D. P. Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Syst.* **42**, 1–22 (2011).

5. Dicks, L. V. et al. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.* **5**, 1453–1461 (2021).

6. *The Methodological Assessment Report on Scenarios and Models of Biodiversity and Ecosystem Services* (IPBES, 2016).

7. Dietze, M. & Lynch, H. Forecasting a bright future for ecology. *Front. Ecol. Environ.* **17**, 3 (2019).

8. Grimm, V., Schmidt, E. & Wissel, C. On the application of stability concepts in ecology. *Ecol. Modell.* **63**, 143–161 (1992).

9. Ives, A. R. & Carpenter, S. R. Stability and diversity of ecosystems. *Science* **317**, 58–62 (2007).

10. Domínguez-García, V. et al. Advancing our understanding of ecological stability. *Ecol. Lett.* **22**, 1349–1356 (2019).

11. Donohue, I. et al. On the dimensionality of ecological stability. *Ecol. Lett.* **16**, 421–429 (2013).

12. Meerbeek, K. V., Jucker, T. & Svenning, J.-C. Unifying the concepts of stability and resilience in ecology. *J. Ecol.* **109**, 3114–3132 (2021).

13. Domínguez-García, V., Dakos, V. & Kéfi, S. Unveiling dimensions of stability in complex ecological networks. *Proc. Natl Acad. Sci. USA* **116**, 25714–25720 (2019).

14. Rohr, R. P., Saavedra, S. & Bascompte, J. On the structural stability of mutualistic systems. *Science* **345**, 1253497 (2014).

15. Solé, R. V. & Valls, J. On structural stability and chaos in biological systems. *J. Theor. Biol.* **155**, 87–102 (1992).

16. Medeiros, L. P., Boege, K., del Val, E., Zaldívar-Riverón, A. & Saavedra, S. Observed ecological communities are formed by species combinations that are among the most likely to persist under changing environments. *Am. Nat.* **197**, E17–E29 (2021).

17. Godoy, O., Bartomeus, I., Rohr, R. P. & Saavedra, S. Towards the integration of niche and network theories. *Trends Ecol. Evol.* **33**, 287–300 (2018).

18. Song, C., Rohr, R. P. & Saavedra, S. A guideline to study the feasibility domain of multi-trophic and changing ecological communities. *J. Theor. Biol.* **450**, 30–36 (2018).

19. Song, C., Rohr, R. P. & Saavedra, S. Why are some plant–pollinator networks more nested than others? *J. Anim. Ecol.* **86**, 1417–1424 (2017).

20. Saavedra, S., Medeiros, L. P. & AlAdwani, M. Structural forecasting of species persistence under changing environments. *Ecol. Lett.* **23**, 1511–1521 (2020).

21. Tabi, A., Petchey, O. L. & Pennekamp, F. Warming reduces the effects of enrichment on stability and functioning across levels of organisation in an aquatic microbial ecosystem. *Ecol. Lett.* **22**, 1061–1071 (2019).

22. Bartomeus, I., Saavedra, S., Rohr, R. P. & Godoy, O. Experimental evidence of the importance of multitrophic structure for species persistence. *Proc. Natl Acad. Sci. USA* **118**, e2023872118 (2021).

23. Allen-Perkins, A., García-Callejas, D., Bartomeus, I. & Godoy, O. Structural asymmetry in biotic interactions as a tool to understand and predict ecological persistence. *Ecol. Lett.* **26**, 1647–1662 (2023).

24. Chacoff, N. P. et al. Evaluating sampling completeness in a desert plant–pollinator network. *J. Anim. Ecol.* **81**, 190–200 (2011).

25. Ponisio, L. C., Gaiarsa, M. P. & Kremen, C. Opportunistic attachment assembles plant–pollinator networks. *Ecol. Lett.* **20**, 1261–1272 (2017).

26. Peralta, G. et al. Trait matching and phenological overlap increase the spatio-temporal stability and functionality of plant–pollinator interactions. *Ecol. Lett.* **23**, 1107–1116 (2020).

27. Gaiarsa, M. P., Kremen, C. & Ponisio, L. C. Pollinator interaction flexibility across scales affects patch colonization and occupancy. *Nat. Ecol. Evol.* **5**, 787–793 (2021).

28. Bastolla, U. et al. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018–1020 (2009).

29. Saavedra, S., Rohr, R. P., Olesen, J. M. & Bascompte, J. Nested species interactions promote feasibility over stability during the assembly of a pollinator community. *Ecol. Evol.* **6**, 997–1007 (2016).

30. Blanchard, G. & Munoz, F. Revisiting extinction debt through the lens of multitrophic networks and meta-ecosystems. *Oikos* (2022).

31. Gravel, D., Guichard, F., Loreau, M. & Mouquet, N. Source and sink dynamics in meta-ecosystems. *Ecology* **91**, 2172–2184 (2010).

32. García-Callejas, D., Bartomeus, I. & Godoy, O. The spatial configuration of biotic interactions shapes coexistence-area relationships in an annual plant community. *Nat. Commun.* **12**, 6192 (2021).

33. Vázquez, D. P. et al. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* **116**, 1120–1127 (2007).

34. Olito, C. & Fox, J. W. Species traits and abundances predict metrics of plant–pollinator network structure, but not pairwise interactions. *Oikos* **124**, 428–436 (2014).

35. Taylor, S. J. S., Evans, B. S., White, E. P. & Hurlbert, A. H. The prevalence and impact of transient species in ecological communities. *Ecology* **99**, 1825–1835 (2018).

36. Clark, T. & Luis, A. D. Nonlinear population dynamics are ubiquitous in animals. *Nat. Ecol. Evol.* **4**, 75–81 (2020).

37. Tilman, D., Reich, P. B. & Knops, J. M. H. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632 (2006).

38. Tilman, D. Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350–363 (1995).

39. Gross, K. et al. Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *Am. Nat.* **183**, 1–12 (2014).

40. Lázaro, A., Gómez-Martínez, C., González-Estévez, M. A. & Hidalgo, M. Portfolio effect and asynchrony as drivers of stability in plant–pollinator communities along a gradient of landscape heterogeneity. *Ecography* **3**, e06112 (2022).

41. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA* **96**, 1463–1468 (1999).

42. Potts, S. et al. *Proposal for an EU Pollinator Monitoring Scheme* (Publications Office of the European Union, 2020).

43. Woodard, S. H. et al. Towards a U.S. national program for monitoring native bees. *Biol. Conserv.* **252**, 108821 (2020).

44. Bascompte, J., Jordano, P., Melian, C. J. & Olesen, J. M. The nested assembly of plant–animal mutualistic networks. *Proc. Natl Acad. Sci. USA* **100**, 9383–9387 (2003).

45. Kendall, L. K. et al. The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology* **103**, e3809 (2022).

46. Reckling, M. et al. Methods of yield stability analysis in long-term field experiments. A review. *Agron. Sustain. Dev.* **41**, 27 (2021).

47. Hsieh, T. C., Ma, K. H. & Chao, A. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* **7**, 1451–1456 (2016).

48. Cenci, S. & Saavedra, S. Structural stability of nonlinear population dynamics. *Phys. Rev. E* **97**, 012401 (2018).

49. García-Callejas, D. et al. Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities. *Ecol. Lett.* **26**, 831–842 (2023).

50. Jonhson, S., Domínguez-García, V. & Muñoz, M. A. Factors determining nestedness in complex networks. *PLoS ONE* **8**, e74025 (2013).

51. Dormann, C. F., Gruber, B. & Fruend, J. Introducing the bipartite package: analysing ecological networks. *R News* **8**, 8–11 (2008).

52. Domínguez-García, V., Molina, F. P., Godoy, O. & Bartomeus, I. Data and code corresponding to the article "Interaction network structure explains species temporal persistence in empirical plant–pollinator communities". *Zenodo* https://doi.org/10.5281/zenodo.10083504 (2023).

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Author contributions

V.D.-G., O.G. and I.B. designed research; F.P.M. and I.B. did fieldwork and F.P.M. identified species; V.D.-G. developed code and analysed data; V.D.-G. and I.B. performed research; and V.D.-G., O.G. and I.B. wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	None
Data analysis	Python (3.11.0) packages: scipy 1.10.0, seaborn 0.12.2, statsmodels 0.13.5. R (4.2.2) Packages: iNext 3.0.0.

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Dataset of species interaction and abundances can be accessed via Zenodo (https://doi.org/10.5281/zenodo.10083504)

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Policy information about studies with <u>human participants or human data</u>. See also policy information about <u>sex, gender (identity/presentation), and sexual orientation</u> and <u>race, ethnicity and racism</u>.

Reporting on sex and gender	NA
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Recruitment	NA
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Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Using empirical plant-pollinator networks to understand species persistence in the field using the structuralist aproach.
Research sample	12 independent sites across a landscape fragmentation gradient in southern spain
Sampling strategy	Transect sampling
Data collection	Data on species population and interaction strength has been gathered during empirical observations through six consecutive years
Timing and spatial scale	In each site, and during each round, we walked a 100 m straight line for 30 minutes in which we wrote down every plant-pollinator
Data exclusions	None
Reproducibility	12 different sites were sampled.
Randomization	Use of 4 different null models.
Blinding	None

Did the study involve field work?   ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	12 independent sites in a landscape fragmentation gracient
Location	South of Spain
Access & import/export	No special efforts were made. The sites are easy to access upon contacting land owners.
Disturbance	weather

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
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☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	the study did not involved laboratory animals
Wild animals	Data on species population and interaction strength has been gathered during empirical observations of transects. Bees that we were unable to identify in situ were collected for later identification.
Reporting on sex	No
Field-collected samples	Bees were caught by hand-netting and preserved in a freezer at -20ºC until they could be pinned and labeled in the lab. Those specimens which identification was unclear were sent to taxonomic experts.
Ethics oversight	No ethical approval was needed.

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☒	☐	Enable evasion of diagnostic/detection modalities
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☒	☐	Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	No
Novel plant genotypes	NA
Authentication	NA