Pollinator interaction flexibility across scales affects patch colonization and occupancy

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Global change alters ecological communities and may disrupt ecological interactions and the provision of ecosystem functions. As ecological communities respond to global change, species may either go locally extinct or form novel interactions. To date, few studies have assessed how flexible species are in their interaction patterns, mainly due to the scarcity of data spanning long time series. Using a ten-year species-level dataset on the assembly of mutualistic networks from the Central Valley in California, we test whether interaction flexibility affects pollinators' colonization and persistence and their resulting habitat occupancy in a highly modified landscape. We propose three metrics of interaction flexibility associated with different scales of organization within ecological communities and explore which species' traits affect them. Our results provide empirical evidence linking species' ability to colonize habitat patches across a landscape to the role they play in networks. Phenological breadth and body size had contrasting effects on interaction flexibility. We demonstrate the relationship between mutualistic networks and species' ability to colonize and persist in the landscape, suggesting interaction flexibility as a potential mechanism for communities to maintain ecosystem function despite changes in community composition.

Locally and globally, human activity is altering ecological communities, disrupting species interactions and causing failures in ecosystem service provision[1,2]. As community composition shifts and some species are lost, interaction partners may either go locally extinct[3] or form novel interactions[4,5]. Such flexibility of interactions could enable species to respond to changing ecological contexts[6–8], which may increase species' ability to persist between years[5] and over thousand-year timescales[9]. However, little is known about what enables species to be flexible in their interaction patterns and the effects of interaction flexibility on species' ability to colonize and persist in different habitat patches, partially because of a scarcity of long-term datasets of interactions at the community level across a landscape. If, for example, species that are highly flexible in their interaction patterns are able to colonize more habitat patches and persist for longer in the landscape, communities containing these species would be more robust to both species and interaction loss, and to changes in resource availability[10]. Thus, unravelling the relationship between interaction flexibility and species' ability to colonize and persist in different habitat patches in the landscape may allow the identification of key species necessary to prevent not only the loss of other species, but also of ecosystem functions and services[11,12].

Species are embedded in networks of interactions within ecological communities[13] and interaction flexibility has ramifications across different community scales—from the microscale pairwise interactions between specific species to the macroscale structural patterns of the entire community. First, at the microscale, we can investigate interaction flexibility by looking at how a species' direct interaction partners change through time or the consistency with which two species interact[14,15]. Second, at an intermediate community scale, we can go one step further and incorporate indirect interactions and the role that species play within interaction

networks[16–18]. Lastly, at a broader macroscale, we can explore whether species vary in how much they contribute to the maintenance of network structure[19,20]. Variability at one scale may further translate to other community scales and may also vary across space[10]. For example, as species switch their direct interaction partners at a microscale, it is unclear if these changes translate to species' network roles, whether new roles result in changes in species' contribution to the network organization at a macroscale and whether these patterns shift in space[10]. Thus, considering interaction flexibility at these different scales allows us to unravel whether species' behavioural changes translate across scales and may help to identify key species in maintaining community robustness to environmental changes[10,19,21,22].

There are, however, limits to how flexible species can be in their interactions. Interactions are determined by ecological traits that, in turn, restrict interactions[8,23,24]. Ecological theory points to several traits that enable interactions at different scales[7,25–27]. For example, pollinators that have longer phenologies[7,28] and greater abundance[24,29] interact with a larger number of plant species and thus may have greater potential for interaction flexibility. Similarly, body size has also been linked to bees' foraging ability[30,31], which in turn may affect the range of plant species available for interaction[32]. In addition, the spatial context also varies depending on the plant and pollinator community composition at a site, showcasing the importance of incorporating spatial variability when exploring species traits[10]. In this sense, traits that enable a species to be flexible within a season will probably also confer greater partner flexibility between years and across seasons and space.

Here we use a ten-year species-level dataset on the assembly of mutualistic networks to introduce three measures of interaction variability at different network scales (Fig. 1). Together these metrics represent a species interaction flexibility. We then test whether

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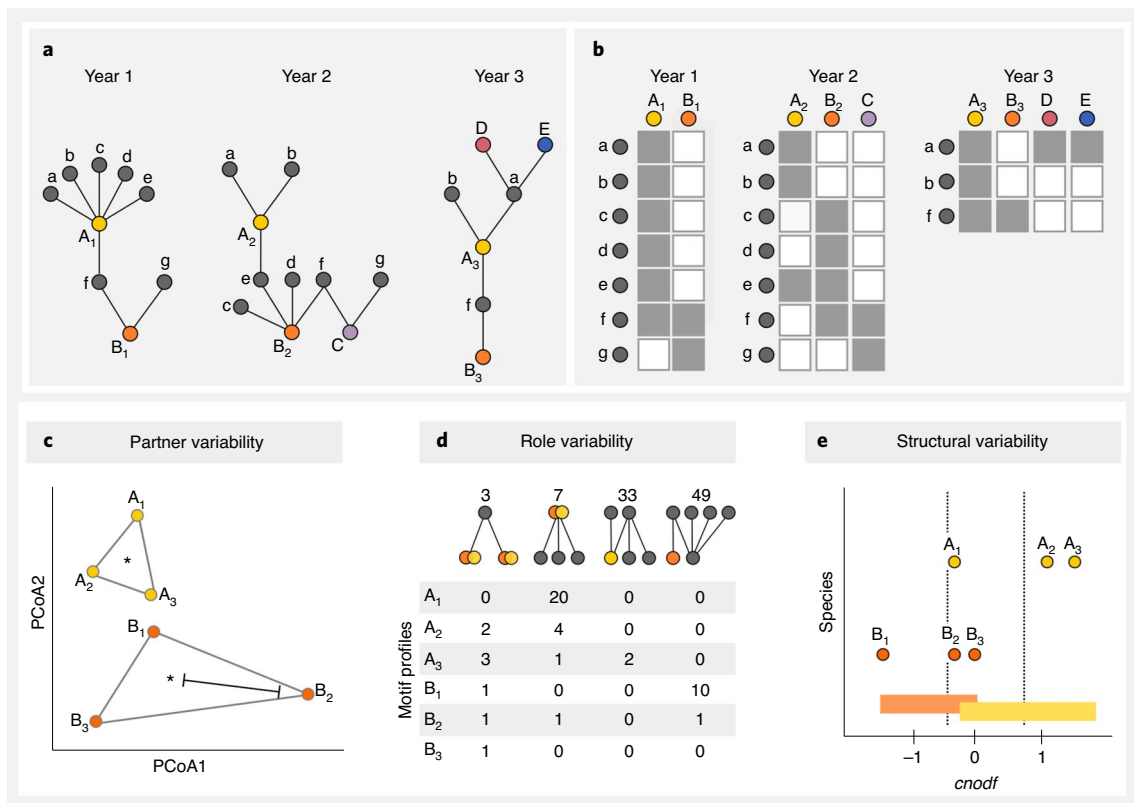
Fig. 1 | Diagram representing the different scales for which we calculated interaction flexibility. a–e, Each lower case letter and grey circle represents a plant species, and capital letters and coloured circles represent bee species (A: yellow; B: orange; C: purple; D: pink; E: blue). **a,b,** We represent the same hypothetical community in a site across three different years as interaction networks (**a**) and interaction matrices (**b**). **c–e,** Here we illustrate how we calculated each interaction flexibility measure for focus species A and B. **c,** We calculated partner variability as the variation in pollinator visitors of each plant species at each site over time, using a modified β-diversity dissimilarity metric adjusted for species richness. The symbol '*' represents the community centroid for species A and B. For clarity, we only represent the distance between species B in year 2 (B_2) and the community centroid (PCoA, Principal Coordinates Analysis). **d,** We calculated network role variability from the number of times each species appeared in each one of the 46 unique node positions available for quantitative motifs. For clarity, in **d** we only illustrate four motif positions (3, 7, 33 and 49). Each line represents how many times each species (A or B) was present in each motif in each year. We then quantified the dissimilarity in motif position between years and calculated role variability as the distance to the community centroid. **e,** We calculated structural variability as how much each species varied in its contribution to network nestedness. In **e**, dashed lines represent the means and the shaded horizontal bars represent the coefficient of variation for species A and B (*cnodf*, contribution to nestedness). We only considered species that were seen at least three times, so in this example interaction flexibility is calculated for species A and B. Refer to Methods for further details.

interaction flexibility affects pollinators' ability to colonize and persist in different sites, which would, in turn, result in a higher proportion of occupied habitat patches across the landscape. Because interactions are fundamentally determined by species traits[8,24,25], we also examine which ecological traits contribute to interaction flexibility and thus indirectly to species' colonization and persistence across a highly modified landscape.

Results
We included 31 species that were seen in at least three years at a site in the flexibility analyses (Supplementary Table 2). Interaction flexibility varied across different network organization scales and across species and sites (Fig. 2). We provide empirical evidence demonstrating that species' ability to change their network role increases the proportion of colonized sites in the landscape (Fig. 3 and Supplementary Table 4) with a strong positive effect on the proportion of occupied sites (Fig. 3 and Supplementary Table 5). Moreover, we also found strong support of a negative effect of partner variability on colonization and persistence (Fig. 3 and Supplementary Table 4), resulting in a strong negative effect on the proportion of occupied sites in the landscape (Supplementary Table 5). We found

no effect of structural variability on either species colonization or persistence (Fig. 3 and Supplementary Table 4).

We then examined the relationship between interaction flexibility and ecological traits, specifically abundance, floral diet breadth, phenological breadth, pollen specialization (known as lecty in bees) and mean body size. We found a strong negative effect of phenological breadth and mean body size on partner variability (Supplementary Fig. 2a and Supplementary Table 6) and a strong positive effect of phenological breadth on structural variability (Supplementary Fig. 2c and Supplementary Table 6). Interestingly, none of the traits had an effect on role variability (Supplementary Fig. 2b and Supplementary Table 6). As expected, phenological breadth and abundance had a consistent positive effect on diet breadth (Supplementary Fig. 2 and Supplementary Table 6).

Discussion
We explored interaction flexibility using a ten-year dataset of pollination networks and showed that species are highly flexible in their interactions across different network scales. We found contrasting effects of pollinators' interaction flexibility on the colonization and persistence of habitat patches in a highly modified landscape. Our
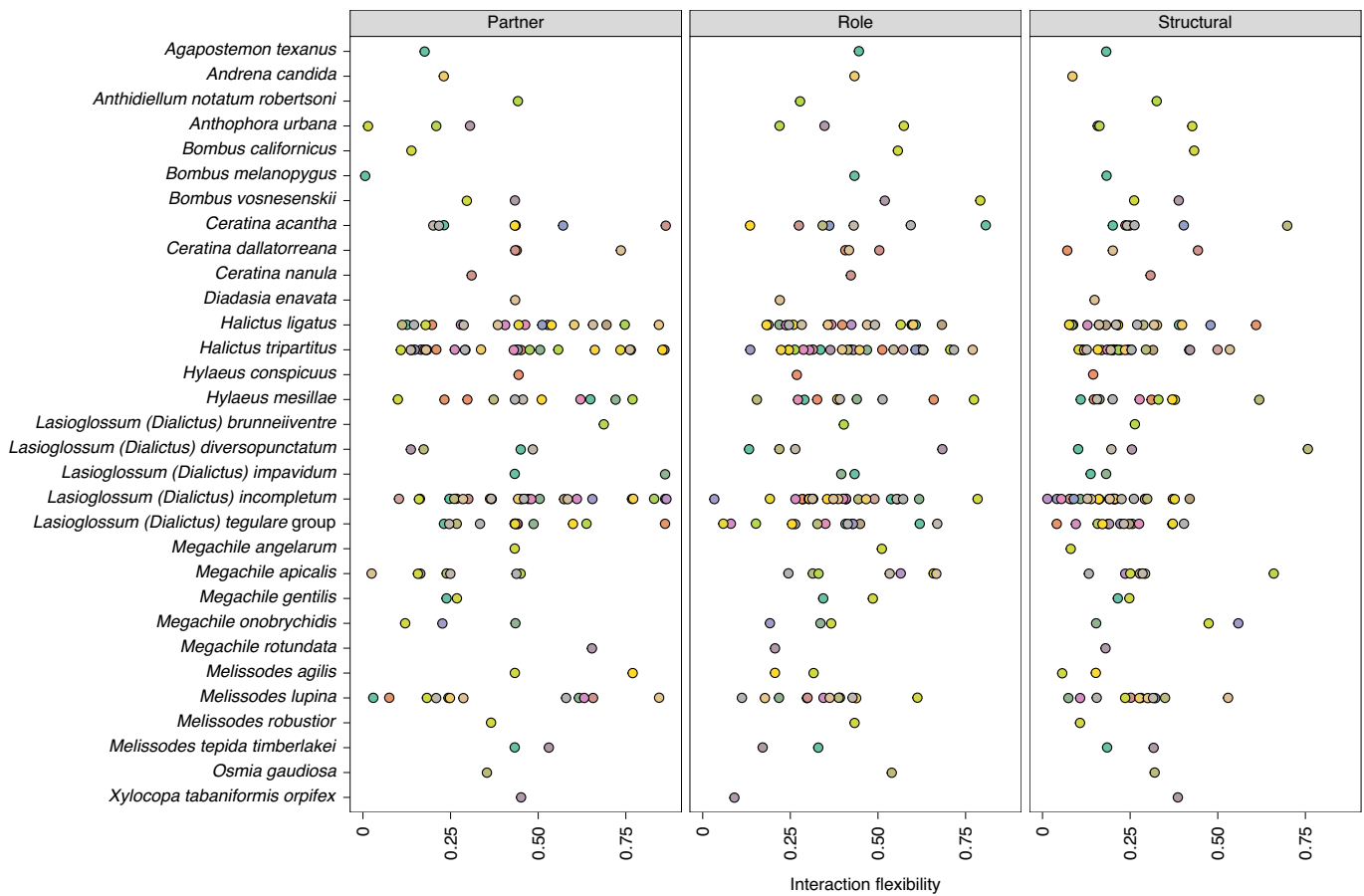
Fig. 2 | Partner, role and structural flexibility for the 31 species seen more than three times at a site included in the analyses. Each point represents a species' coefficient of variation in a site, across years, for partner, role and structural variability; colours represent the different sites.
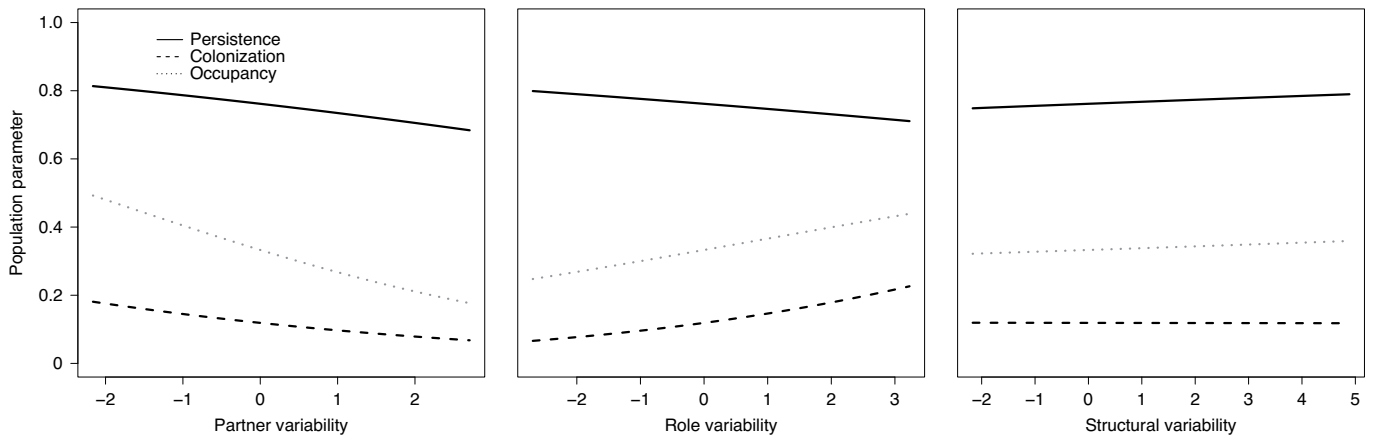

Fig. 3 | The effect of partner variability, role variability and structural variability on persistence (solid line), colonization (dashed line) and proportion of occupied patches (dotted line) across the landscape. We found strong support of a negative effect of partner variability on colonization and occupancy, and of a positive effect of role variability on colonization and the resulting occupancy. We found no support for an effect of structural variability. Refer to Supplementary Tables 4 and 5 for confidence intervals.

results are threefold. First, we found a positive effect of network role variability on species colonization in the landscape, resulting in a higher proportion of habitat patches being occupied. Second, we found a strong negative effect of partner variability on species' colonization and persistence. Third, phenological breadth had opposing effects on partner and structural variability, and no effect on role

variability. Our findings show that ecological networks are highly variable, illustrating the importance of including temporal dynamics in the study of mutualistic networks.

We calculated role variability using a network motif approach. Motifs are structural representations of how species come together to form ecological assemblages[33]. Motifs go beyond species' direct

interaction partners to explicitly incorporate indirect interactions. Our results add to the growing literature showcasing how including motifs when analysing mutualistic networks can provide insights into relevant aspects of network dynamics[17,33,34]. Specifically, we explored the temporal variability of species' motif profiles and found that motif role variability had a strong positive effect on species colonization, which resulted in more habitat patches being occupied by the species in the landscape. Species with high role variability are present in different motif positions across years and are thus able to fill different network roles over time[17]. We can speculate that a possible mechanism for the relationship between colonization and motifs is that high role variability signals a species' ability to adapt to changing ecological contexts, such as resource availability or the abundance of competitors. Ability to adapt to a changing ecological context translates to higher colonization and occupancy rates across the landscape[6,7,17,18,35]. For example,[34] we compared the motif profile of two co-occurring super-generalist bee species and showed that while one species interacts primarily with generalist plant species, the other interacts primarily with specialized plant species. Likewise, we can hypothesize that pollinators with high role variability will preferentially forage on plant species for which there is less competition, either direct or apparent. This pattern in turn would improve species' ability to colonize more habitat patches in the landscape, resulting in a positive effect on the overall landscape patch occupancy.

In a highly modified landscape like the one in our study system, resources are often unpredictable and competition may be high for the most abundant plants[32,36]. In these agricultural habitats, the boom and bust cycle of mass-flowering crops alters the competition dynamics of pollinators[36]. While competition for crop flowers is high, competition may be lower for less abundant resources, resulting in a fitness trade-off in resource use[37,38]. Species that are able to use resources for which there is potentially less competition may be at an advantage[39-41]. The strong negative effect of partner variability on colonization and persistence supports the hypothesis that, when there is high competition for abundant resources, species that are able to explore less abundant resources for which there is less competition might have an advantage in relation to super-generalists. This pattern would be even stronger if less abundant plants also have higher floral rewards[42]. When we examine the species with higher partner variability, all of them interact primarily with the highly abundant plant species of the genus *Brassica*, a common, non-native species in the Central Valley. In contrast, none of the species with smaller partner variability interact with *Brassica*. Instead, although these species with lower partner variability interact with a smaller range of plant partners, the majority of the other species in their site did not interact with the same plants, indicating that there is potentially less competition for these resources. Taken together, our results suggest that species that consistently interact with the same set of plants across years, and thus are less flexible in their partners in a specific site, may have a competitive advantage[38,39], which translates into greater colonization and persistence in this highly modified landscape. Given the existence of a trade-off between quantity and quality of available floral resources[7,43], and their effect on both foraging distance and pollinator fitness, an exciting avenue for future studies would be to test for differences between the nutritional qualities of nectar and pollen from super-abundant plant species that are visited by a wide variety of bee species and those from less abundant, less visited plant species.

Species interactions depend on both phenological matching and the populations of each species being large enough so that their individuals are likely to meet[44,45]. Thus, to be able to interact, two species must overlap in space and time—phenological mismatch precludes interaction occurrence[44]. Wider phenological breadth, however, broadens the window of opportunity for interactions to occur[7,28]. If species are active for longer periods of the year they may have a greater number of interaction partners, which generally results in wider diet breadths[7]. By consistently finding a strong positive effect of phenological breadth on diet breadth (Supplementary Fig. 2), our results empirically suggest that the phenotypic and behavioural traits that enable species to have greater abundances, and to be active for longer periods of the year, also enable species to have wider diet breadths[7,28,29,45].

Moreover, both phenological breadth and mean body size had a negative effect on partner variability. Phenology has been shown to have an important effect in interaction occurrence at smaller timescales, such as weekly[7], and our results suggest that it is also important in the annual scales considered here. The negative effect of phenological breadth on partner variability suggests that species which are active for longer periods of time exhibit little partner turnover and are thus encountered interacting with the same array of partners across the years. In contrast, a species with small phenological breadth is usually seen a small number of times per year. If each time a bee species is encountered it is interacting with a different plant partner, this species would present high partner variability across seasons. As for the negative effect of body size on partner variability, one of the largest species we analysed, *Bombus melanopygus*, is also the one that had one of the smallest values of partner variability. Along the same lines, species from the smallest genus, *Lasioglossum*, are among the species with the largest partner variability values. These results reinforce the importance of considering both temporal and spatial variation in species interactions[10,22], as species may seem specialized in a specific site at a particular point in time, but may accumulate other plant partners over longer sampling periods[12].

Phenological breadth also had a strong positive effect on structural variability, calculated as a species' variability in their contribution to nestedness (*cnodf*). A nested pattern arises when there is asymmetry in the way species interact—that is, when generalist species interact with specialized species[46]. This asymmetry has been shown to increase partner fidelity—the probability that two co-occurring species will interact[15]—while also promoting species coexistence by minimizing effective competition[47]. It has been shown that specialist species have the greatest nestedness contribution[19]. If we hypothesize that this pattern will be recurrent across seasons, specialist species will consistently have a high *cnodf*, resulting in small structural variability across years. Together with the positive effect of phenological breadth on diet breadth that we found, our results suggest that species with shorter phenologies, which also have smaller diet breadths (specialist species), have consistent nestedness contributions and thus present small structural variability across seasons. Interestingly, the lack of a correlation between role and structural variability suggests that species' ability to occupy different positions on network motifs does not scale up to changes in the overall network structure. Given that we found a strong effect of role variability but not of structural variability on species colonization and persistence, future studies could explore how these two structural patterns give rise to the overall observed network patterns. Assuming that nestedness contributes to community stability at the seasonal scale[3,13,48] (but see refs. [49,50]), our results suggest that communities predominantly composed of species with wider phenological breadths will be better able to maintain network structure across seasons, resulting in communities more robust to species extinction and better able to maintain ecosystem function[19,29,51].

Connecting network structure—the architecture of biological interactions—to species colonization and persistence in the landscape is crucial to understanding future trajectories of ecological communities. To our knowledge, empirical evidence linking the roles species play in their networks to species' ability to colonize habitat patches in a highly modified landscape has not been previously explored. If species network roles are evolutionarily conserved[33], we can hypothesize that sister species of highly flexible

species may also be flexible in their interaction patterns, even as environments change. Our results contribute to the growing literature illustrating the temporal variability of ecological networks and suggest that different mechanisms may be acting at different organizational scales to modulate interaction flexibility[22,52]. The existence of species' interaction flexibility across spatial and temporal scales is one potential mechanism that may enable communities to maintain function despite shifts in community composition, competitive interactions and global environmental changes.

Methods

Study sites and data collection. Our study sites were located in the Central Valley of California in Yolo, Colusa and Solano Counties, an area characterized by intensively managed agriculture. The complete dataset is composed of 63 sites, ~16,600 bee specimens from 157 bee species and 152 plant species, totalling ~1,150 interactions. Five of these sites were native plant restoration sites (hedgerows) on the border of large crop fields (ca. 30 hectares), where we monitored community assembly from pre-instalment up to ten years postrestoration (from 2006−2015, Supplementary Table 1; mean 7.4 years of sampling per site). We concurrently monitored ten matched control sites over the same time period, as well as 48 other sites for varying periods, including mature hedgerows. The complete dataset is composed of 251 networks (site–year combinations). Each hedgerow was 3−6 m wide and approximately 350 m long. Mean distance between monitoring sites was 15 km and the minimum distance between sites sampled in the same year was 1 km. The entire area surveyed spanned almost 300 km². We did not sample the sites in 2010 due to logistical constraints. See ref. [53] for more details on data collection and sites.

We sampled the sites up to five times per year between April and August (Supplementary Table 1; mean 3.4 surveys per site, per year sampled). In each sampling round we randomized site sampling order and conducted surveys under bright conditions when the temperature was above 21°C and the wind speed was below 2.5 metres per second. During each sampling round, we hand-netted flower visitors for one hour of active search time, pausing the timer while specimens were handled. We collected all insect flower visitors that touched floral reproductive parts and recorded the identity of the plant for each collected specimen. Here we focus only on wild bees, which are the most abundant and effective flower visitor taxon in the system[54–56]. We did not include honey bees (*Apis mellifera*) because, as managed pollinators whose hives are constantly placed near pollinator-dependent crops, they are widespread throughout this landscape and were present at every site in similarly high abundances, and are thus relatively independent of changes in the ecological context. Expert taxonomists identified bee specimens to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*).

From the field data, we constructed interaction networks for each combination of site and year, totalling 251 networks. Because the number of sampling rounds varied between years (Supplementary Table 1), we used the mean number of plant–pollinator interactions within a year to represent interaction frequency (mean number of visits) for each network. Given that our goal is to explore how species' interaction patterns change through time, we filtered the data as follows. First, we only included in the analysis networks (combinations of site and year) composed of at least five plants and five pollinators (similar to ref. [34]), resulting in 140 networks ranging from 10 to 44 species (mean network size = 18.4). Moreover, we only considered sites that were sampled in at least three different years, resulting in 26 sites that were sampled on average 3.42 times per year, for 4.61 years (Supplementary Table 1). Finally, for the variability and occupancy analysis (below) we only included species that were seen at a site in at least three different years, resulting in 31 species analysed (Supplementary Table 2). For each of the 31 species at each site and each year, we then calculated three measures of interaction flexibility representing three different, complementary, community scales: partner variability (microscale), network role variability (mesoscale) and network structural variability (macroscale) (Fig. 1).

Partner variability. To quantify the variability of interaction partners for each species at each site across years, we modified methods for calculating β-diversity (Fig. 1a,c). Instead of calculating the variation in community composition across sites within a year, for each of the 31 species we estimated interaction turnover across years within a site[5]. First, we calculated the pairwise dissimilarity between survey years at a site using the Chao dissimilarity estimator that incorporates species abundances while also accounting for unobserved species[57,58]. Following ref. [5], we used null models that constrained species richness and the number of interactions of each species to estimate the extent to which the observed dissimilarity deviated from that which would be expected under a random process. With the corrected dissimilarity values we calculated the multivariate dispersion of interaction partner communities for each species[59,60], across years, for each site. We then measured partner variability as the coefficient of variation of the distance from the centroid (Fig. 1c) for each species at each site.

Role variability. To characterize the roles that species can play in their networks, we employed a network motifs approach[17,33] (Fig. 1d). Motifs are considered as the

building blocks of ecological networks[33,61], and each motif represents a specific way in which a set of species interact, encompassing indirect interactions within the network[17,33,61]. As a result, motifs comprise more information than other traditional network metrics[34].

For bipartite networks with quantitative data (interaction frequency), it is currently possible to calculate species positions (nodes) for up to five-species motifs, resulting in 46 unique motif positions for each species[34]. To calculate network role variability at each site for each year, we first counted the number of times each species appeared in each motif position considering the mean of all link strengths for each species' motif occurrence. Thus, for each species j at each site, a vector represents the role of species j in n-dimensional motif space in one year, in which each dimension is the occurrence frequency of species j in a particular position within a motif (Fig. 1d). To control for the fact that species with more interactions tend to appear in more motif positions, we normalized the data by dividing the position measure for each species by the total number of times that species appeared in any motif position. We used the package bmotif[62] to calculate species position within motifs.

We then used a permutational multivariate analysis of variance (PERMANOVA) to test the null expectation that the centroids of motif positions are random with respect to species and site[17,58,63,64]. We used the adonis function in the vegan package and ran 9,999 permutations. PERMANOVA results indicated that sites and species' identity explained a significant amount of variation in motif profiles ($F_{25,6.10}$, $P < 0.001$ and $F_{30,3.32}$, $P < 0.001$, respectively). Having seen that motif profiles are indeed related to species and sites, we characterized species' role variability as the dissimilarity of motif profiles across years for each species at each site. Because we had interaction frequency data, we used the altGower index[60] in the vegdist function[58] to calculate dissimilarity and then quantified the multivariate dispersion of motif positions. Finally, we calculated motif role variability as the coefficient of variation of the distance from the centroid for each species at each site.

Structural variability. To describe species' variability in their relative importance in maintaining the community structure, we used nestedness[46], given the relationship between nestedness and community robustness[3,48,65] (but see ref. [49]). Nestedness is a ubiquitous pattern in mutualistic networks[13,46], in which a core group of generalists interacts with both specialist and generalist species. In our dataset, despite undergoing major structural reorganizations, networks were consistently more nested than the null expectation[5]. Thus, looking at how variable species are in how much they contribute to nestedness may help us understand the importance of structural variability in species' ability to colonize and persist in different habitat patches across the landscape. For each site in a year, we computed each species' contribution to nestedness (cnodf[9], Fig. 1e), a species-level metric. By randomizing only the interactions of the species of interest, cnodf quantifies how much a species' individual contribution to network nestedness compares to what would be expected at random, using a null model[46]. We used the bipartite package[66] to calculate contribution to nestedness. We then calculated species' structural variability as the coefficient of variation of nestedness contribution of each species at each site across years.

Occupancy model. We used a multi-season, multi-species occupancy model (ref. [67], adapted from ref. [68]) to test the effect of each interaction flexibility metric on species' colonization and persistence in the landscape. First, for each site and year, observed occurrences of each species are modelled as a function of a species-specific detection probability that can vary over the years. The model then accounts for imperfect detection and calculates the occurrence probability as a function of species colonization and persistence. The occupancy model allows us to include the uncertainty associated with species detectability when estimating occupancy[67,69]. After accounting for imperfect detection, the model calculates species' true probability of occurrence as a function of both colonization and persistence at each site. We modelled the probability of occupancy for species i at site j as a function of colonization (γ_{ij}) and persistence (ϕ_{ij}). After checking that none of the flexibility metrics were strongly correlated (Supplementary Table 3), we included species-specific and site-specific intercepts and explanatory variables for interaction flexibility (partner variability, role variability and structural variability) for each species at each site. We then calculated average occupancy across the landscape as $\gamma_{ij} / (1 - \phi_{ij} + \gamma_{ij})$[68].

We used Bayesian inference and Markov chain Monte Carlo (MCMC) to estimate model parameters. To improve the sampling efficiency, we used sequential likelihood calculations (filtering) to estimate probability of all detection histories through time at one site, removing the need for many latent states[70]. We ran the MCMC chains for 2×10^5 iterations after an initial burn-in of 2×10^3 iterations using NIMBLE[71]. We used uninformative priors, Norm(0, 10³) for the means of the distributions of the top-level parameters and Unif(0, 10²) for the variances. We calculated posterior probability densities to estimate the support for each parameter and considered strong support when 95% of the posterior was greater than or less than zero.

Structural equation models. Finally, to understand which species traits are related to the different measures of interaction flexibility, we used mixed model

structural equation models[72]. To avoid circularity in this analysis, we only considered a subset of the data, composed of the five hedgerow sites that were followed from pre-instalment of restoration for ten years, at which communities were assembling[73]. We used the remaining portion of the dataset, comprised of 58 sites, to approximate as much as possible the fundamental niches of pollinators in the landscape. We considered five different traits for each species: specialization, abundance, phenological breadth, diet breadth and mean body size.

We characterized specialization as the diversity of pollen that adults feed their larvae (lecty), using published literature and expert opinion[74]. To calculate abundance we used the median number of the total observations per species across all years and sites. Similarly, we calculated phenological breadth as the median number of days between the first and last observation of a species across all years and sites. Finally, we quantified diet breadth as a rarefied measure of the number of plants a pollinator species was seen foraging on[29] across all years and sites, and mean body size as mean intertegular distance of five specimens[74].

The data from the five sites considered in the mixed model structural equation models included 24 species seen at least three times in each of the five assembling restoration sites (Supplementary Table 2), resulting in 53 unique species–site combinations. The restoration sites were sampled 3.37 times per year on average and between six and nine years in total (mean 7.4 years, Supplementary Table 2). Mixed model structural equation modelling[72] enables us to account for the direct and indirect relationships among traits and to estimate the direct and indirect effects of traits on partner, role and structural variability (Supplementary Fig. 1). Because diet breadth has been shown to be affected by other ecological traits[29,45], we modelled all traits as having a direct effect on diet breadth and on each of the measures of interaction flexibility (Supplementary Fig. 1) and we also included random effects for site and species[75]. We used R v.4.0.2 (ref. [76]) to conduct all the above analyses. All data and code used in the analyses are available in Zenodo and Github (https://github.com/Magaiarsa/intFlex).

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

Data availability
Data describing plant–pollinator interactions as well as data generated in this study are available in Github (https://github.com/Magaiarsa/intFlex) and Zenodo (https://zenodo.org/record/4485996#.YE9dzGRKhhF).

Code availability
Code is deposited in Github (https://github.com/Magaiarsa/intFlex) and Zenodo (https://zenodo.org/record/4485996#.YE9dzGRKhhF).

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Author contributions

M.P.G. and L.C.P. designed the analysis. C.K. designed the field study. L.C.P. and C.K. collected data. M.P.G. and L.C.P. developed the metrics for interaction flexibility, which M.P.G. implemented. L.C.P. wrote the first version of the occupancy models, which M.P.G. modified and refined for this study. M.P.G. wrote the manuscript, performed analyses and prepared the figures. All authors contributed to revisions.

Competing interests

The authors declare no competing interests.

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n/a	Confirmed	
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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	No software was used to collect the data.
Data analysis	We used R version 3.5.1 to ran all analysis. We describe the packages in the main text. All code will be available in GitHub, as well as a write-up describing the analyses.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

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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	We show for the first time how interaction flexibility contributes to population persistence and occupancy, using data from the longest contemporary species-level temporal dataset on the assembly of mutualistic networks. First, we develop a novel conceptual framework and introduce three measures of interaction flexibility to capture effects across interaction scales, from pairwise interactions to community-level interaction structure. Then we apply this framework to 10 years of data using these metrics to test whether population dynamics of pollinator species are affected by the flexibility of their ecological interactions. We also examine which ecological traits contribute to interaction flexibility. We provide the first empirical evidence showing that interaction flexibility affects dynamic measures of species' persistence in the landscape, linking population dynamics to species' flexibility of the role they play in ecological networks.
Research sample	Our study sites were located in the Central Valley of California in Yolo, Colusa, and Solano Counties, an area characterized by intensively managed agriculture. We used data previously published in other papers, which is why there was no field work involved for this study. The complete dataset is composed of 63 sites, 16,600 bee specimens from 157 different bee species, and 74 152 plant species, totaling ~1, 150 interactions.
Sampling strategy	Sites were sampled up to five times per year, between April and August, for 10 years (2006-2015). In each sampling round we always randomized site sampling order.
Data collection	We only collected data under sunny conditions when the temperature was above 21C and wind speed was below 2.5 meters/second. During each sampling round, we hand-netted flower-visitors for one hour of active search time (we paused the timer while handling specimens). We collected all insect flower visitors that touched flowers' reproductive parts, and recorded the identity of the plant that each specimen was caught on.
Timing and spatial scale	Data was collected between April and August, for 10 years (2006-2015). Sites were not sampled in 2010 due to logistical constraints. Refer to Table S1 for details on the number of sampling rounds between years for each site.
Data exclusions	We did not collect honey bees (Apis mellifera) because, as managed pollinators whose hives are constantly placed near pollinator-dependent crops, they are widespread throughout this landscape in high abundances and are thus, relatively independent of changes in the ecological context.
Reproducibility	Data was collected the same way at the same sites for 10 years.
Randomization	In each sampling round we always randomized site sampling order.
Blinding	Not relevant.

Did the study involve field work?   ☐ Yes   ☒ No

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.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

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

Animals and other organisms

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Laboratory animals	This study did not involve laboratory animals.
Wild animals	We used data from wild animals collected on previously published in other papers, which is why there was no field work involved for this study.
Field-collected samples	See above.
Ethics oversight	No ethical approval was necessary (see above).

Note that full information on the approval of the study protocol must also be provided in the manuscript.