

## Review

Predicting plant–pollinator interactions:  
concepts, methods, and challenges

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Plant–pollinator interactions are ecologically and economically important, and, as a result, their prediction is a crucial theoretical and applied goal for ecologists. Although various analytical methods are available, we still have a limited ability to predict plant–pollinator interactions. The predictive ability of different plant–pollinator interaction models depends on the specific definitions used to conceptualize and quantify species attributes (e.g., morphological traits), sampling effects (e.g., detection probabilities), and data resolution and availability. Progress in the study of plant–pollinator interactions requires conceptual and methodological advances concerning the mechanisms and species attributes governing interactions as well as improved modeling approaches to predict interactions. Current methods to predict plant–pollinator interactions present ample opportunities for improvement and spark new horizons for basic and applied research.

### The importance of predicting interactions

**Species interactions** (see [Glossary](#)) constitute key determinants of ecological community structure and functions [1]. Therefore, understanding and predicting ecological interactions represents an essential asset for advancing ecological knowledge and for decision-making in environmental management, conservation, and restoration [2–5]. Forecasting which species will interact under certain conditions and in future ecological scenarios becomes especially important given anthropogenic pressures on ecosystems and the need for effective interventions to protect species, their interactions, and the essential ecosystem functions and services that they provide to humanity [6,7]. Furthermore, species interactions might serve as an early warning system for biodiversity conservation, as they can be lost before the species themselves [8,9]. For example, predictions indicating that certain species would lose their interactions under future land use or climate change would provide valuable information for conservation planning and actions. Likewise, predicting with reasonable certainty the interactions between resident species and new species entering a community (resulting, for example, from range shifts due to climate change, biological invasions, or community restoration [10,11]) would allow forecasting the impacts of the colonizer on the resident community. Predictive models also represent useful alternatives to experiments that ecologists cannot conduct in the field. For instance, predictive models allow simulating species introductions or extinctions to understand spatial and temporal population and community dynamics. Furthermore, deviations of model predictions from empirical observations point toward incomplete knowledge and help to generate new hypotheses and theories [12].

In natural ecosystems, plants and pollinators engage in ephemeral interactions in which flowers provide food resources to floral visitors, which in turn often provide essential pollination services

### Highlights

Our success in predicting general community-level interaction patterns contrasts with our limitations to predict pairwise plant–pollinator interactions.

Limitations to predict pairwise interactions come from multiple gaps in our understanding of plant–pollinator interactions, model implementations, and data.

Different phenomenological and mechanistic modeling approaches attempt to predict plant–pollinator pairwise interactions, although we still lack an equitable comparison between these different approaches to accurately determine differences in their predictive ability.

Model predictive ability could be improved by accounting for heterogeneous detection probabilities of interactions resulting from sampling effects, estimating interaction predictors with greater accuracy and building models with more plausible assumptions.

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to plants [13,14]. Although forecasting pollination success might be the ultimate goal in ecology, the first necessary step is to predict **plant–pollinator interactions**. Despite our current understanding of how and why plants and pollinators interact, including our relative success in predicting the structure of **plant–pollinator interaction networks** [15,16], our ability to predict specific pairwise interactions within these networks still represents a major scientific challenge. Several mechanisms have been identified as responsible for community-level interaction patterns [17] and allow the development of reasonable predictions of interaction network structure. However, the poor prediction of pairwise interactions poses a conundrum, as predictive models use biological mechanisms assumed to influence pairwise interactions. Specifically, if we fail to predict pairwise interactions, we might be predicting community interaction patterns correctly but neglecting the underlying mechanisms [17] and the consequences for ecosystem functioning. In addition, predicting pairwise interactions involves particular species with specific traits and functional roles, which represents a better target to manage populations, community structure, and ecosystem functions [18].

Existing models vary widely in their success to predict pairwise plant–pollinator interactions, although it still remains unclear what drives model predictive ability: the type of model, the attributes included in the model for prediction, and/or the methods and datasets used to estimate such attributes. In this review, we provide an overview of the approaches and methods currently available to predict pairwise plant–pollinator interactions, discuss the challenges in measuring **species attributes**, and identify the paths forward to improve model predictive ability.

### Methods for predicting plant–pollinator interactions

**Mechanistic models** and **phenomenological models** are used to understand and predict noisy and hugely complex ecological systems. Mechanistic models focus on the underlying processes deemed ecologically relevant to drive patterns in the data with biologically meaningful parameters that can typically be measured empirically. For instance, existing mechanistic models for predicting plant–pollinator interactions usually encompass one or a combination of species attributes that represent processes assumed to influence interactions. These attributes include species abundances, traits, spatial and temporal distributions, and phylogenies (e.g., [12,19]). Alternatively, phenomenological models attempt to reproduce empirically observed patterns based on the statistical fitting of parameters that best describe the data. Phenomenological models used for plant–pollinator interaction prediction do not explicitly focus on the underlying mechanisms or processes that drive interactions but rather intend to reproduce observed interaction patterns (e.g., [20,21]).

Mechanistic models that directly represent the matching of plant and pollinator attributes can be fitted to the data in a probabilistic way [12,19,22]. For instance, the tapnet framework [22] generates interaction probabilities from abundance (where abundant species have a higher probability of interacting), **trait matching** (with flexible **trait-matching functions**), and phylogenies (modeled as latent traits). This approach combines the species pairwise interaction probabilities generated by the different matching attributes to obtain a unique species pairwise interaction probability. The fact that species interactions within a community do not occur independently from each other poses a challenge for this method, requiring a sophisticated formulation of the likelihood.

Although not strictly mechanistic, **generalized linear models** (GLMs) are used in predicting plant–pollinator interactions (Table S1 in the supplemental information online), where parameters can be constrained by priors to positive or negative values, representing the direction of an assumed causal effect. Dredging through predictors by model selection is not compatible with

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a mechanistic use of GLMs. With GLMs, one or several variables predict the occurrence or frequency of interactions. For example, the abundance of flowers of a plant species may predict the number of interactions with its pollinators. Straightforward to implement, GLMs can encompass a variety of model structures, distributions, and assumptions, such as non-normal responses, and can be extended to incorporate random effects [generalized linear mixed models (GLMMs)]. For instance, including plant and pollinator species identities as random effects allows fitting species-specific unknown effects, such as the nonindependence of interactions within species [23]. Thus, GLMMs can account for the fact that the occurrence and frequency of an interaction between a plant and a pollinator species pair depend not only on the particular attributes included as fixed factors in the model (e.g., abundance) but also on unmeasured attributes and additional interactions that these species have with other species in the community. Furthermore, some extensions of these models, such as structural equation models, allow estimating indirect effects among multiple predictor variables, a useful feature to deal with more complex causal structures, such as the effects of climate conditions or predators [24–26].

Alternatively, among phenomenological models, **machine learning models** use algorithms to recognize patterns of interactions in a training dataset and then use this information to predict new interactions. Several studies have used machine learning methods to predict plant–pollinator interactions, including *k*-nearest neighbor (KNN), random forest, and neural networks [20,21]. Some machine learning algorithms, such as KNN, compute similarities between species (e.g., based on traits and phylogenies) and predict new interactions for a given species based on its traits and phylogenetic position [20]. In contrast, random forest models use decision trees to learn the combination of interacting species attributes that characterize an interaction to predict other interactions [27,28]. Neural networks, however, represent a collection of interconnected units (neurons or processors) in which each unit receives multiple input data, combines them linearly, and passes it onto the next unit until obtaining the final output [20]. Although these data-driven approaches may make successful predictions [20], they do not necessarily represent scientific understanding of the mechanisms driving plant–pollinator interactions, and they assume independence of the observed interactions. An additional limitation of machine learning approaches comes from their need for large amounts of data, which may exceed data available from empirical studies.

The previously-mentioned models for predicting species interactions may differ in the attributes of interactions that they attempt to predict; some predict the occurrence (presence–absence) of interactions, while others predict interaction frequencies. Although interaction occurrence constitutes a first goal in the prediction of interactions, interaction frequencies contain additional information, as they can inform about the strength of the effect of one species on another [29,30] and interaction-dependent ecosystem functions [23]. Furthermore, to make robust predictions, all the aforementioned modeling approaches require a substantial number of observations and, hence, sufficient sampling effort.

### Species attributes used to predict plant–pollinator interactions

Ideally, we aim to predict interactions based on species attributes: tell me about you, and I will tell you who you go with. Previous studies attempting to predict plant–pollinator interactions from species attributes have used species abundances, morphological traits, phenologies, spatial and temporal distributions, and phylogenies [31]. Part of the challenge in predicting interactions from these attributes lies in their multiple (sometimes conflicting) definitions, the methodological differences in their quantification, and in the selection of a single or a combination of species attributes that link to interaction probability (Figure 1). Although the attributes discussed are population

### Glossary

**Forbidden links:** species pairwise interactions that do not occur due to biological constraints.

**Generalized linear model:** statistical technique where a response variable is expressed as a linear combination of predictor variables.

**Machine learning model:** an algorithm used to flexibly represent data to which it is trained.

**Mechanistic model:** mathematical representation of relationships among variables, where its parameters are defined based on biological definitions. Mechanistic models focus on the underlying processes deemed ecologically relevant for driving patterns in the data, with biologically meaningful parameters.

**Phenomenological model:** mathematical representation of relationships among variables where the parameters are defined to best represent the relationship. Phenomenological models used for the prediction of plant–pollinator interactions do not explicitly focus on the underlying mechanisms or processes that drive interactions but rather intend to reproduce interaction patterns with the help of ‘big data’.

**Phylogeny:** representation of a hypothesis about the evolutionary history and relationships among a group of taxa.

**Plant–pollinator interaction networks:** webs of mutualistic interactions between a set of plant species and a set of pollinator species.

**Plant–pollinator interactions:** interactions between flower reproductive parts and their animal visitors.

**Sampling effects:** deviation from reality in the observation or representation of nature due to artifacts in the collection of samples.

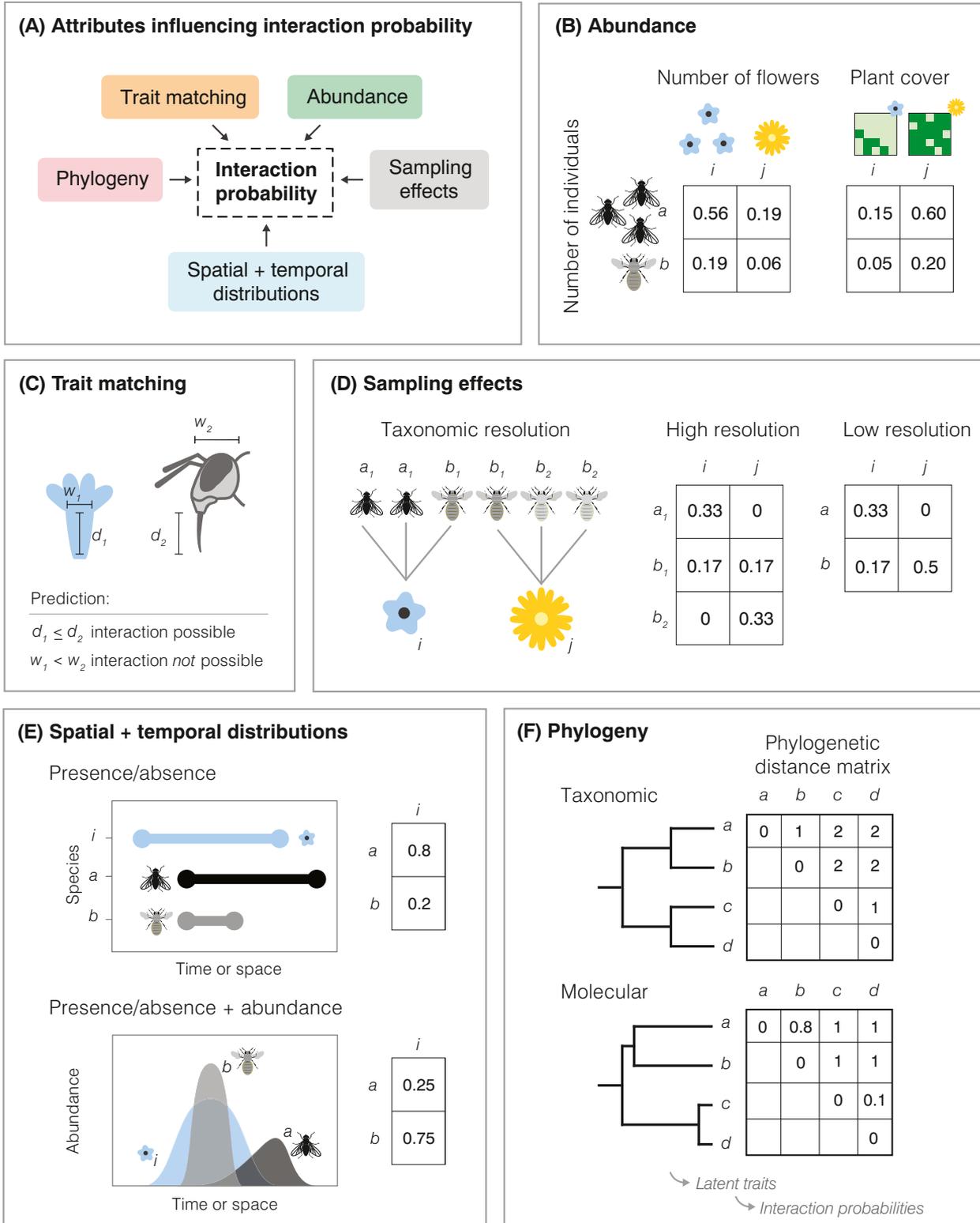
**Species attributes:** qualities or features characteristic of a species.

**Species distribution:** temporal and/or spatial (geographic) arrangement of species.

**Species interactions:** relationships among organisms that have positive, negative, or neutral effects on each other.

**Species traits:** morphological, physiological, and behavioral characteristics of organisms.

**Trait matching:** alignment of the morphological (or physiological or behavioral) traits of species.



attributes, we refer to them as species attributes as the aim is to predict interactions among different species present in a local community.

### Abundance

Plant and pollinator abundance influences the random encounter probability among species. Abundant species will tend to encounter and interact more frequently and with more species [19,32]. When quantifying abundance to predict plant–pollinator interactions, our abundance measurements should capture the availability of pollinators as pollen vectors and the availability of plants as floral food resources [12]. Unfortunately, however, obtaining accurate estimates of abundance represents a challenge. For instance, researchers usually estimate pollinator abundance as the number of flowers visited by a certain pollinator species, hence conflating abundance with activity [17]. This measure of pollinator abundance reflects interaction frequency, which might correlate with species relative abundance in a community [33], although not necessarily strongly [34], as other factors beyond abundance can determine interaction frequency, including **species traits** and pollinator behavior and preferences. Therefore, to avoid confounding the influence of abundance on interactions with that of other attributes (e.g., species preferences and traits), ideally, we should estimate abundance independently from interactions. A better measure of pollinator abundance would therefore assess the number of individuals of a particular pollinator species within a community with methods that do not involve sampling plant–pollinator interactions. However, different sampling methods, such as pan traps, transect walks, or timed observations at flowers, often lead to dramatically different results even within the same taxonomic group [34–36] and ecosystem, thus rendering conflicting estimates of pollinator abundance. This issue arises especially when comparing different pollinator groups, such as birds, bats, and various insect taxa, as they require different methodological approaches to estimate their abundance, such as daytime versus nocturnal sampling and fixed mist nets versus transect walks.

In studies of plant–pollinator interactions, estimates of plant abundance usually include the number of plant individuals, the number of flowers or inflorescences, or the relative cover of flowers. Arguably, measuring abundance in terms of flowers and their resources represents a measure of functional abundance more meaningful for this type of interaction than the number of individuals or biomass (given the high variation among plant species in the number of flowers per individual or unit biomass), which does not necessarily have a clear functional interpretation. Because pollinators search for pollen, nectar, and other floral rewards, estimating plant abundance in terms of nectar or pollen abundance [37] might prove more informative for predicting plant–pollinator interactions (but see [38]). Importantly, plant reward abundance varies greatly through time, imposing high turnover in functional species abundance. For example, flowers of some plant species may offer copious nectar and pollen resources in the morning but few in the afternoon [39] in response to consumption by pollinators or to other environmental factors [40,41]. Furthermore, flower or

#### Trait-matching functions:

mathematical expressions involving two or more variables that define the way in which trait matching is mapped to interaction probability.

**Figure 1. The influence of species attributes and sampling effects on the prediction of plant–pollinator interactions.** (A) Different methods used to measure or estimate attributes will influence interaction probabilities. (B) The abundance of plant species can be estimated as the number of plant individuals, the number of flowers or inflorescences, or the relative cover of flowers. To calculate interaction probabilities, we multiply the relative abundances of each pair of interacting species. For instance, pollinator species *a* has a relative abundance of  $3/4 = 0.75$ , while plant species *i* also has a relative abundance of  $3/4 = 0.75$ ; thus, these two species have a probability of interacting with each other of  $0.75 \times 0.75 = 0.56$ . (C) The selection of plant and pollinator traits used to assess trait matching may determine our predictive performance. Traits of plants and pollinators jointly determine interaction probabilities following particular trait-matching rules (Box 1). (D) Sampling effects include insufficient sampling effort, low taxonomic resolution, and unequal probabilities of recording species and their interactions. For example, under low taxonomic resolution, taxa  $b_1$  and  $b_2$  are both identified as *b*, which affects the estimation of plant–pollinator interaction probabilities. Additionally, (E) representing the overlap in the spatial and temporal distributions of interacting species based on species presence/absence or accounting for species abundances leads to different interaction probabilities. Finally, (F) the phylogenies of plants and pollinators can also influence their interaction probabilities. Differences in the type of data used to construct phylogenies (taxonomic versus molecular) influence estimates of phylogenetic rate of change and hence the phylogenetic distances among plants and pollinators, which in turn influences the estimation of latent traits and plant–pollinator interaction probability.

inflorescence size represents a perching area for visitors, defining a physical constraint [42] and potentially a measure of reward amount [43] per flower unit. Therefore, combining flower density with resource quantity per flower and flower size may constitute a better estimate of plant abundance from a pollinator's perspective, capturing resource abundance more effectively than the abundance of individual plants while focusing on the flower as the packaging unit for pollen and nectar resources [12].

#### Morphological, chemical, and behavioral traits

The morphological, physiological, and behavioral traits of organisms may represent barriers for interactions, determining their occurrence probability. Floral visual and olfactory signals and floral rewards attract pollinators [44,45], and pollinator traits determine their responses to different flower attractants [46,47]. For example, volatiles attractive to pollinators often repel floral antagonists such as ants and other arthropods, thus shaping the interaction probabilities between flowers and their different visitors [48]. Morphological traits, such as corolla width and depth, pollinator proboscis or bird beak width and length, and body size, can also affect plant–pollinator interaction probability [23,49,50]. Although relatively straightforward to measure using calipers or software associated with a microscope, deciding which plant and pollinator traits to measure and their functional interpretation poses a challenge. Furthermore, some traits can be challenging or idiosyncratic (hairs adapted to a certain pollen type, buzzing ability, facial structures for scraping pollen, and nutritional status), which makes measuring them unfeasible for the whole community. In addition, when it comes to using traits to predict interactions, we should consider how trait matching operates. Different available methods compare interacting species traits, which will define interaction probabilities (Box 1).

#### Spatial and temporal distributions

For a plant and a pollinator species to interact, partners need to co-occur in space and time [23,51]. Furthermore, plant and pollinator species abundances, traits, and species degree of generalization can vary across the spatial and temporal **species distribution** [52,53], affecting their interaction probability. For example, species abundances tend to vary widely across their geographic range [54]; similarly, the abundance of plant and pollinator species is likely to be lowest at the beginning and the end of their flowering/flight period. Therefore, plant–pollinator interaction probability relies on the degree of spatial and temporal overlap between the interacting partners.

Incorporating spatial co-occurrence in models predicting plant–pollinator interactions requires data on geographic range sizes. Although for most plant and pollinator species obtaining even coarse estimates of their geographic ranges poses a challenge, national flora and fauna mapping schemes or species distribution models or records could provide useful information [55,56]. An alternative to estimate the spatial overlap of interacting partners is to focus on finer spatial scales, such as assessing the presence of plant and pollinator species in a set of sites sampled in the study area [12].

Likewise, incorporating species temporal distribution to predict plant–pollinator interactions requires phenological data, such as flowering times and pollinator diel and seasonal activity patterns [57]. Species phenology is usually inferred from field surveys, museum collections [58,59], or phenological models that predict flowering and insect emergence [60]. Although phenology is sometimes estimated from data on first flowering date/first emergence date, more robust phenological descriptors include the weighted mean of flowering dates or smoothing techniques, such as generalized additive models. Finally, plant and pollinator phenologies can vary in response to temperature, day length, rainfall, nutrient availability, timing of snowmelt, and

biotic interactions, all of which may vary both naturally and in response to global environmental change [61–63].

### Phylogeny

A **phylogeny** represents the evolutionary history and relationships among groups of organisms, such as species. Although we cannot infer ecological mechanisms through phylogenies, they may help predict species interactions as they can act as surrogates for unknown or unmeasured ("latent") traits that influence the occurrence of interactions [22,64,65]. However, to predict interactions from phylogenies, we need to assume that trait similarity results from evolutionary relatedness, such that traits of closely related species are more alike than those of distantly related species, even though they could also emerge from evolutionary convergence.

Molecular, morphological, and taxonomic data allow the reconstruction of phylogenies of varying resolution. Different methods can also deal with incomplete phylogenies, for example, combining taxonomic trees with diversification times from molecular phylogenies [66–68]. Furthermore, methods used to construct a phylogeny influence its branch lengths, which in turn determines the cophenetic distances among species (Figure 1). The increasing availability of highly resolved phylogenetic trees allows using phylogenies to predict interactions for some groups, particularly plants, birds, and other animals [69,70], although for some of the most widely studied pollinators, such as most insects, we still lack complete, fully resolved phylogenies.

### Sampling effects on the prediction of interactions

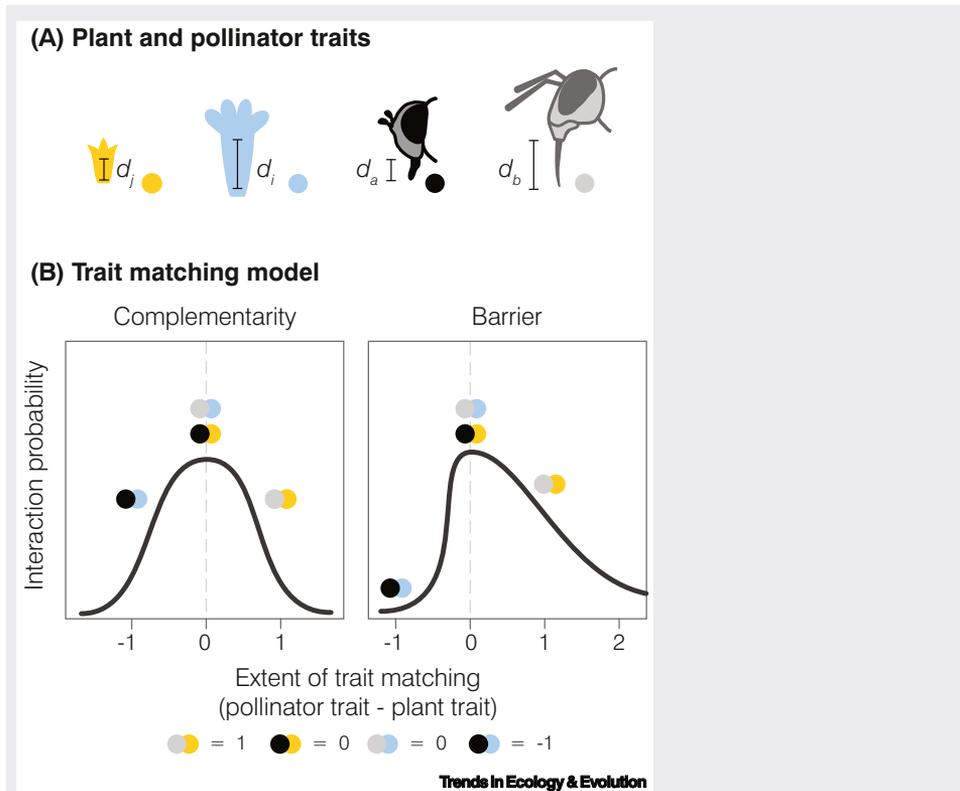
The way we perceive interactions with our observations may be blurred by several types of **sampling effects** resulting from insufficient sampling effort, low taxonomic resolution, and unequal detection probabilities of species and their interactions, which can influence interaction prediction. Although we probably never record all the plant–pollinator interactions that truly occur, insufficient sampling effort hinders the detection of interactions and leads to a far less

#### Box 1. Trait-matching rules

Multiple models used to predict species interactions incorporate the idea of alignment of interacting species traits, usually referred to as trait matching. Trait matching can influence the occurrence of plant–pollinator interactions through two main mechanisms: exploitation barriers and trait complementarity [92]. The similarity in the traits of interaction partners defines the level of barrier/complementarity (Figure 1). For instance, nectar tube length may impose a barrier to pollinators with shorter proboscises, preventing them from reaching the reward. In turn, trait complementarity means that plant and pollinator species with reciprocal trait values will have a greater probability of interacting.

Trait matching is usually estimated from one pair of traits [93,94], albeit multiple traits operate simultaneously in more complex ways, such as simultaneously matching pollinator body size and proboscis length with flower nectar tube length. Currently available methods [22] allow matching multiple pollinator traits against flower traits by building multiple trait-matching matrices, each with a different trait combination, and multiplying them to estimate interaction probabilities. For instance, we can obtain interaction probabilities by combining a matrix representing the match between pollinator proboscis width and corolla tube width with another matrix representing the match between pollinator body size and corolla tube width. However, when using multiple traits for the aforementioned estimation, the nonindependence between trait-matching matrices estimated from the same traits, or from correlated traits, could bias our estimates of interaction probabilities.

An alternative, albeit phenomenological, approach that allows the simultaneous use of multiple nonindependent traits involves calculating trait congruence among interacting species in multivariate space [23]. Specifically, the fourth-corner analysis [95,96] uses similarities among a suite of plant and pollinator traits to estimate whether these traits predict plant–pollinator interactions. Applying this method to different sets of traits could help identify the most relevant traits that determine interactions. Furthermore, multivariate trait space approaches can also incorporate proxy traits not directly linked to the interaction. For instance, we can superimpose the position of pollinator species on their multivariate trait space with the positions of their interaction centroids in plant multivariate trait space [97]. Statistical methods such as Procrustes analysis can be used to maximize this superimposition, and the resulting distances among the corresponding points in the different ordinations (trait space of pollinators and trait space of plants) indicate the trait-matching magnitude, which could be used to predict interactions.



**Figure 1.** Trait complementarity and barrier mechanisms affecting plant–pollinator interaction probability. (A and B) The difference between pollinator and plant traits (A) determines the extent of trait matching among interacting species, which, in turn, influences species interaction probability through trait complementarity and barrier mechanisms (B). Trait complementarity assumes that plant and pollinator trait similarity determines species interaction probability. For instance, a difference of zero between pollinator proboscis length and nectar tube length maximizes species interaction probability, whereas greater differences in traits of interacting partners result in lower interaction probabilities. The barrier mechanism assumes that morphological constraints, such as a proboscis shorter than a nectar tube, result in **forbidden links**.

complete representation of the realized interactions [12,31]. Consequently, some species characteristics, such as their interaction breadth and the properties of interaction networks, can change substantially with sampling effort [71,72]. In turn, low taxonomic resolution may result in the aggregation of species whose taxonomic identities remain unresolved, influencing observed interaction patterns [73]. Low taxonomic resolution may also apply to the intraspecific level, as males and females of the same pollinator species sometimes interact with different plant species [74], influencing the prediction of their interactions.

The biased representation of plant–pollinator interactions in a community can also result from unequal recording probabilities for species and their interactions, coming from skewed distributions of abundances, geographic ranges, phenologies, and trait values. For instance, interactions involving rare species should have lower probabilities of being recorded than interactions involving abundant species [75], whereas traits, such as large body size or diurnal flight time, make some species and their interactions more conspicuous than others [12]. Furthermore, in

most studies, data collection involves sampling from the perspective of a focal group, such as plants (e.g., observing flowers) or pollinators (e.g., collecting pollen from bee bodies), which may also introduce a bias in the interaction data [76–78]. While focusing on one group may improve the detection of interactions for that group, it may not represent the interactions in nonfocal groups well. For example, plant–pollinator interaction data coming from visitation records likely lead to more complete sampling of interactions for plants than for flower visitors. Furthermore, studies focusing solely on a particular subgroup, such as bees, exclude other pollinator groups, offering a partial representation of the community interaction pattern.

### Gaps, challenges, and the way forward to predict interactions

Although we have taken important steps in our quest to predict interactions, we still have a long way to go in this predictive endeavor. First, we need to account for heterogeneous detection probabilities of interactions resulting from sampling effects. Potential ways to solve this problem include increasing the number of replicates in time and space to improve sampling completeness and prediction of spatio-temporal variability of interactions. To avoid focal group bias and improve sampling completeness, we can combine species interaction data [79] collected using different methodologies, such as flower visitation, pollen loads [78,80], and emerging approaches, such as DNA metabarcoding [81,82]. Additionally, we should use statistical methods to estimate interactions occurring in nature but not present in our observations [83,84] and methods that take into account sources of bias such as species abundance [84]. Furthermore, we should measure attributes of species recorded in our study systems, even those not observed interacting, as this information potentially carries predictive value.

Second, we need to improve our estimates of the predictors of interactions (abundance, spatio-temporal distributions, traits, and phylogenies) and how they combine to determine interactions. For instance, we need to record abundances independently from interactions if we want to understand the role abundance plays in predicting interaction frequencies [85]. Moreover, for plants, we should focus not only on the abundance of flowers but also on floral rewards, which play a key role in attracting pollinators. In addition to collecting information on the morphological traits of the interacting species and data relevant for the interactions to occur, many other understudied chemical and behavioral traits, such as floral scent, pollen nutrition, nectar sugar composition, and pollinator sensory and cognitive abilities, also seem essential to predict interaction probabilities. However, we acknowledge that measuring all these traits simultaneously may be unfeasible and that trait values may change with environmental conditions [86]. Stronger collaborative efforts might provide an alternative to increase the amount of data collected. Furthermore, the application of standardized data collection protocols across studies could allow model evaluation under different local scenarios.

Third, from a modeling perspective, we have multiple issues to tackle. To start, we should conduct a thorough comparison of the predictive ability of the different available approaches using the same attributes and datasets. Ideally, comparing model outcomes from multiple datasets, collected in different geographical locations and with different sample sizes, would allow us to determine the generality of model predictions. Moreover, most models make several simplifying assumptions, including that different traits weigh equally for all species, operate simultaneously and independently from each other, and assume no intraspecific variation (one trait value per species). However, these assumptions seem unrealistic as, for example, different traits might contribute differently to interactions for different species pairs, depending on other attributes [87,88], the population's demographic stage (e.g., the reproductive stage), or predominant environmental conditions [89]. Intraspecific trait variability could also play a key role in determining realized interactions [90], yet, we currently have a limited understanding of how intraspecific trait variability affects plant–pollinator

interactions. Furthermore, selecting traits might pose a challenge when trying to predict interactions from dissimilar pollinator groups, such as birds and bees. Novel approaches address these issues in a functional context by using the partners' traits to define the functional space of a species [91]. In addition, the lack of comparative data has prevented us from using behavioral attributes, such as foraging, to predict plant–pollinator interactions. Although we do not know which, if any, of these additional attributes will improve our predictive ability of interactions, they all make biological sense and represent avenues for future research.

### Concluding remarks

Ecology has increasingly become a predictive science in response to the need to understand natural environments and predict how they respond to human activities. This need is pushing ecologists toward improving methods for predicting species interactions. Numerous methods are available to predict pairwise plant–pollinator interactions based on species attributes. All methods present ample opportunities for improvement and spark new horizons for research (see [Outstanding questions](#)). Improving plant–pollinator interaction prediction will allow us to increase our knowledge of interactions and boost a more meaningful ecological understanding of plant–pollinator interaction networks.

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### Author contributions

All authors contributed to discussions, development of ideas, and paper conceptualization. G.P., D.R., C.N.K.B., T.M.K., J. R., and D.P.V. established the general structure of the paper. G.P., P.J.C., D.R., J.F., M.P.P.T., C.F.D., L.A.B., C.N.K.B., and D.P.V. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

### Declaration of interests

The authors declare no competing interests.

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### References

- Eisenhauer, N. *et al.* (2019) A multitrophic perspective on biodiversity–ecosystem functioning research. *Adv. Ecol. Res.* 61, 1–54
- Simmons, B.I. *et al.* (2020) Estimating the risk of species interaction loss in mutualistic communities. *PLoS Biol.* 18, e3000843
- Campbell, A.J. *et al.* (2019) Pollinator restoration in Brazilian ecosystems relies on a small but phylogenetically-diverse set of plant families. *Sci. Rep.* 9, 17383
- Carvalheiro, L.G. *et al.* (2008) Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. *J. Appl. Ecol.* 45, 1419–1427
- Raimundo, R.L.G. *et al.* (2018) Adaptive networks for restoration ecology. *Trends Ecol. Evol.* 33, 664–675
- Bascompte, J. and Scheffer, M. (2023) The resilience of plant–pollinator networks. *Annu. Rev. Entomol.* 68, 363–380
- Goulson, D. (2019) The insect apocalypse, and why it matters. *Curr. Biol.* 29, R967–R971
- Valiente-Banuet, A. *et al.* (2015) Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307
- Jordano, P. (2016) Chasing ecological interactions. *PLoS Biol.* 14, e1002559
- Parra-Tabla, V. and Arceo-Gómez, G. (2021) Impacts of plant invasions in native plant–pollinator networks. *New Phytol.* 230, 2117–2128
- Richman, S.K. *et al.* (2020) Asynchronous range shifts drive alpine plant–pollinator interactions and reduce plant fitness. *Glob. Chang. Biol.* 26, 3052–3064
- Vázquez, D.P. *et al.* (2009) Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology* 90, 2039–2046
- Garibaldi, L.A. *et al.* (2021) Time to integrate pollinator science into soybean production. *Trends Ecol. Evol.* 36, 573–575
- Wei, N. *et al.* (2021) Pollinators contribute to the maintenance of flowering plant diversity. *Nature* 597, 688–692
- Valdovinos, F.S. (2019) Mutualistic networks: moving closer to a predictive theory. *Ecol. Lett.* 22, 1517–1534
- Strydom, T. *et al.* (2021) A roadmap towards predicting species interaction networks (across space and time). *Philos. Trans. R. Soc. B* 376, 20210063

### Outstanding questions

How should predictive models incorporate trait variability?

Do predictions of plant–pollinator interactions improve by including plant reward abundance (e.g., nectar or pollen quantity) compared with using flower density or flower abundance metrics that incorporate flower size as proxies for attractiveness?

Do we need to incorporate population dynamics to improve the prediction of species interactions?

Can we tease apart sampling effects from true ecological mechanisms driving species interactions?

How do we improve the definitions of species attributes, their selection, quantification, and matching for prediction?

17. Vázquez, D.P. *et al.* (2009) Uniting pattern and process in plant–animal mutualistic networks: a review. *Ann. Bot.* 103, 1445–1457
18. Harvey, E. *et al.* (2017) Bridging ecology and conservation: from ecological networks to ecosystem function. *J. Appl. Ecol.* 54, 371–379
19. Olito, C. and Fox, J.W. (2015) Species traits and abundances predict metrics of plant–pollinator network structure, but not pairwise interactions. *Oikos* 124, 428–436
20. Pichler, M. *et al.* (2020) Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks. *MEE* 11, 281–293
21. Stock, M. *et al.* (2021) Pairwise learning for predicting pollination interactions based on traits and phylogeny. *Ecol. Model.* 451, 109508
22. Benadi, G. *et al.* (2022) Quantitative prediction of interactions in bipartite networks based on traits, abundances, and phylogeny. *Am. Nat.* 199, 841–854
23. Peralta, G. *et al.* (2020) Trait matching and phenological overlap increase the spatio-temporal stability and functionality of plant–pollinator interactions. *Ecol. Lett.* 23, 1107–1116
24. Benoit, A.D. and Kalisz, S. (2020) Predator effects on plant–pollinator interactions, plant reproduction, mating systems, and evolution. *Annu. Rev. Ecol. Syst.* 51, 319–340
25. Oglivie, J.E. *et al.* (2017) Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecol. Lett.* 20, 1507–1515
26. Junker, R.R. *et al.* (2010) Intra-floral resource partitioning between endemic and invasive flower visitors: consequences for pollinator effectiveness. *Ecol. Entomol.* 35, 760–767
27. Ormai, A. and Keasar, T. (2020) Floral complexity traits as predictors of plant–bee interactions in a mediterranean pollination web. *Plants* 9, 1432
28. Sydenham, M.A.K. *et al.* (2022) MetaComNet: a random forest-based framework for making spatial predictions of plant–pollinator interactions. *MEE* 13, 500–513
29. Vázquez, D.P. *et al.* (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* 8, 1088–1094
30. Vázquez, D.P. *et al.* (2012) The strength of plant–pollinator interactions. *Ecology* 93, 719–725
31. Vázquez, D.P. *et al.* (2022) Ecological interaction networks. What we know, what we don't, and why it matters. *Ecol. Austral* 32, 670–697
32. de Manincor, N. *et al.* (2020) Does phenology explain plant–pollinator interactions at different latitudes? An assessment of its explanatory power in plant–hoverfly networks in French calcareous grasslands. *Oikos* 129, 753–765
33. Vázquez, D.P. *et al.* (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116, 1120–1127
34. Thompson, A. *et al.* (2021) Pollinator sampling methods influence community patterns assessments by capturing species with different traits and at different abundances. *Ecol. Indic.* 132, 108284
35. Tepedino, V.J. and Portman, Z.M. (2021) Intensive monitoring for bees in North America: indispensable or improvident? *Insect Conserv. Divers.* 14, 535–542
36. O'Connor, R.S. *et al.* (2019) Monitoring insect pollinators and flower visitation: the effectiveness and feasibility of different survey methods. *MEE* 10, 2129–2140
37. Tew, N.E. *et al.* (2021) Quantifying nectar production by flowering plants in urban and rural landscapes. *J. Ecol.* 109, 1747–1757
38. Maruyama, P.K. *et al.* (2014) Morphological and spatio-temporal mismatches shape a Neotropical savanna plant–hummingbird network. *Biotropica* 46, 740–747
39. Schwarz, B. *et al.* (2021) Within-day dynamics of plant–pollinator networks are dominated by early flower closure: an experimental test of network plasticity. *Oecologia* 196, 781–794
40. Domingos-Melo, A. *et al.* (2023) A negative association between nectar standing crop and pollen transfer suggests nectar functions as a manipulator of pollinating bats. *Ann. Bot.* 131, 361–372
41. Hemberger, J.A. *et al.* (2023) Experimental heatwaves disrupt bumblebee foraging through direct heat effects and reduced nectar production. *Funct. Ecol.* 37, 591–601
42. Carvalheiro, L.G. *et al.* (2014) The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecol. Lett.* 17, 1389–1399
43. Ortiz, P.L. *et al.* (2021) Do visual traits honestly signal floral rewards at community level? *Funct. Ecol.* 35, 369–383
44. Reinhard, J. *et al.* (2004) Scent-triggered navigation in honeybees. *Nature* 427, 411
45. Hempel de Ibarra, N. *et al.* (2022) The role of colour patterns for the recognition of flowers by bees. *Philos. Trans. R. Soc. B* 377, 20210284
46. Stang, M. *et al.* (2009) Size-specific interaction patterns and size matching in a plant–pollinator interaction web. *Ann. Bot.* 103, 1459–1469
47. Smolla, M. *et al.* (2016) Copy-when-uncertain: bumblebees rely on social information when rewards are highly variable. *Biol. Lett.* 12, 20160188
48. Junker, R.R. *et al.* (2010) Responses to olfactory signals reflect network structure of flower–visitor interactions. *J. Anim. Ecol.* 79, 818–823
49. Klumpers, S.G.T. *et al.* (2019) Foraging efficiency and size matching in a plant–pollinator community: the importance of sugar content and tongue length. *Ecol. Lett.* 22, 469–479
50. De Luca, P.A. *et al.* (2019) Does body size predict the buzz-pollination frequencies used by bees? *Ecol. Evol.* 9, 4875–4887
51. Duchenne, F. *et al.* (2020) Phenological shifts alter the seasonal structure of pollinator assemblages in Europe. *Nat. Ecol. Evol.* 4, 115–121
52. CaraDonna, P.J. and Waser, N.M. (2020) Temporal flexibility in the structure of plant–pollinator interaction networks. *Oikos* 129, 1369–1380
53. Zoller, L. *et al.* (2020) Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer. *Sci. Rep.* 10, 21187
54. Dallas, T.A. *et al.* (2020) Weighing the evidence for the abundant-center hypothesis. *Biodivers. Inform.* 15, 81–91
55. Sydenham, M.A.K. *et al.* (2022) Neutral processes related to regional bee commonness and dispersal distances are important predictors of plant–pollinator networks along gradients of climate and landscape conditions. *Ecography* 2022, e06379
56. Waser, S.K. *et al.* (2001) Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *N. Z. J. Ecol.* 25, 1–17
57. Vázquez, D.P. *et al.* (2023) Phenological mismatches and the demography of solitary bees. *Proc. R. Soc. B* 290, 20221847
58. Belitz, M.W. *et al.* (2023) Phenological research based on natural history collections: practical guidelines and a lepidopteran case study. *Funct. Ecol.* 37, 234–247
59. Dorian, N.N. *et al.* (2023) Ecological traits explain long-term phenological trends in solitary bees. *J. Anim. Ecol.* 92, 285–296
60. Nietschke, B.S. *et al.* (2007) A developmental database to support insect phenology models. *Crop Prot.* 26, 1444–1448
61. Rafferty, N.E. *et al.* (2020) Changing climate drives divergent and nonlinear shifts in flowering phenology across elevations. *Curr. Biol.* 30, 432–441
62. Fisogni, A. *et al.* (2020) Urbanization drives an early spring for plants but not for pollinators. *Oikos* 129, 1681–1691
63. Rosbakh, S. *et al.* (2021) Siberian plants shift their phenology in response to climate change. *Glob. Chang. Biol.* 27, 4435–4448
64. Rezende, E.L. *et al.* (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448, 925–928
65. Pearse, I.S. and Altermatt, F. (2013) Predicting novel trophic interactions in a non-native world. *Ecol. Lett.* 16, 1088–1094
66. Liu, H. *et al.* (2021) Geographic variation in the robustness of pollination networks is mediated by modularity. *Glob. Ecol. Biogeogr.* 30, 1447–1460
67. Encinas-Viso, F. *et al.* (2022) Pollen DNA metabarcoding reveals cryptic diversity and high spatial turnover in alpine plant–pollinator networks. *Mol. Ecol.* 32, 6377–6393
68. Lomáscolo, S.B. *et al.* (2019) Inferring coevolution in a plant–pollinator network. *Oikos* 128, 775–789
69. Webb, C.O. and Donoghue, M.J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Mol. Ecol. Notes* 5, 181–183

70. Jetz, W. *et al.* (2012) The global diversity of birds in space and time. *Nature* 491, 444–448
71. Banasek-Richter, C. *et al.* (2004) Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *J. Theor. Biol.* 226, 23–32
72. Schwarz, B. *et al.* (2020) Temporal scale-dependence of plant-pollinator networks. *Oikos* 129, 1289–1302
73. Hemprich-Bennett, D.R. *et al.* (2021) Assessing the impact of taxon resolution on network structure. *Ecology* 102, e03256
74. Roswell, M. *et al.* (2019) Male and female bees show large differences in floral preference. *PLoS ONE* 14, e0214909
75. Vázquez, D.P. and Aizen, M.A. (2003) Null model analyses of specialization in plant-pollinator interactions. *Ecology* 84, 2493–2501
76. Jordano, P. (2016) Sampling networks of ecological interactions. *Funct. Ecol.* 30, 1883–1893
77. de Manincor, N. *et al.* (2020) How biased is our perception of plant-pollinator networks? A comparison of visit- and pollen-based representations of the same networks. *Acta Oecol.* 105, 103551
78. Zhao, Y.-H. *et al.* (2019) The topological differences between visitation and pollen transport networks: a comparison in species rich communities of the Himalaya-Hengduan Mountains. *Oikos* 128, 551–562
79. Quintero, E. *et al.* (2022) Methodological overview and data-merging approaches in the study of plant-frugivore interactions. *Oikos* 2022, e08379
80. Olesen, J.M. *et al.* (2011) Missing and forbidden links in mutualistic networks. *Proc. R. Soc. B* 278, 725–732
81. Gous, A. *et al.* (2021) Floral hosts of leaf-cutter bees (Megachilidae) in a biodiversity hotspot revealed by pollen DNA metabarcoding of historic specimens. *PLoS ONE* 16, e0244973
82. Bell, K.L. *et al.* (2022) Plants, pollinators and their interactions under global ecological change: the role of pollen DNA metabarcoding. *Mol. Ecol.* 32, 6345–6362
83. M'Gonigle, L.K. *et al.* (2015) Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. *Ecol. Appl.* 25, 1557–1565
84. Weinstein, B.G. and Graham, C.H. (2017) Persistent bill and corolla matching despite shifting temporal resources in tropical hummingbird-plant interactions. *Ecol. Lett.* 20, 326–335
85. Vizentin-Bugoni, J. *et al.* (2014) Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird-plant network. *Proc. R. Soc. B* 281, 20132397
86. Vaudo, A.D. *et al.* (2022) Impacts of soil nutrition on floral traits, pollinator attraction, and fitness in cucumbers (*Cucumis sativus* L.). *Sci. Rep.* 12, 21802
87. Peralta, G. *et al.* (2020) Strength of niche processes for species interactions is lower for generalists and exotic species. *J. Anim. Ecol.* 89, 2145–2155
88. González-Varo, J.P. and Traveset, A. (2016) The labile limits of forbidden interactions. *Trends Ecol. Evol.* 31, 700–710
89. Klomberg, Y. *et al.* (2022) Spatiotemporal variation in the role of floral traits in shaping tropical plant-pollinator interactions. *Ecol. Lett.* 25, 839–850
90. Liang, H. *et al.* (2021) Evolutionary and ecological factors structure a plant-bumblebee network in a biodiversity hotspot, the Himalaya-Hengduan Mountains. *Funct. Ecol.* 35, 2523–2535
91. Dehling, D.M. *et al.* (2022) The contribution of mutualistic interactions to functional and phylogenetic diversity. *Trends Ecol. Evol.* 37, 768–776
92. Santamaría, L. and Rodríguez-Gironés, M.A. (2007) Linkage rules for plant-pollinator networks: trait complementarity or exploitation barriers? *PLoS Biol.* 5, e31
93. Zhao, Y.-H. *et al.* (2022) Morphological trait-matching in plant-Hymenoptera and plant-Diptera mutualisms across an elevational gradient. *J. Anim. Ecol.* 91, 196–209
94. Dalsgaard, B. *et al.* (2021) The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird-plant networks. *Funct. Ecol.* 35, 1120–1133
95. Legendre, P. *et al.* (1997) Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78, 547–562
96. Legendre, P. *et al.* (2002) A statistical test for host-parasite coevolution. *Syst. Biol.* 51, 217–234
97. Dehling, D.M. *et al.* (2016) Morphology predicts species' functional roles and their degree of specialization in plant-frugivore interactions. *Proc. R. Soc. B* 283, 20152444