Plant–pollinator interactions and the assembly of plant communities

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Most studies of plant community assembly have focused on how the abiotic aspects of a habitat (e.g. soil moisture or mineral composition) or direct interactions among plants in a community (e.g. competition for space or nutrients) influence which species establish and persist, but they have tended to neglect indirect interactions such as those mediated by pollinators. We address three types of plant–pollinator interactions — filtering, facilitation and competitive exclusion — and their predicted impacts on communities. The few available studies that address how pollinator-mediated interactions limit or promote plant species establishment and persistence provide support for many of these predictions. An integrated framework for understanding plant community assembly needs to incorporate abiotic and biotic interactions, including plant–pollinator and other plant–animal interactions.

Introduction: Integrating plant–animal interactions and community assembly

The degree to which ecological traits, such as leaf and seed characteristics [1], influence the distribution and abundance of species is a contentious issue. The field is divided as to whether communities tend to be a product of random assembly processes [2] versus repeatable, trait-based assembly processes [3]. Consequently, interest in community assembly is currently growing [4], with many empirical advances and novel methods, such as the incorporation of evolutionary history into hypothesis testing [5]. Recent studies have tested the predictions that niche overlap, degree of trait (especially ecophysiological) similarity, and phylogenetic distance between species influence patterns of species co-occurrence [6]. However, the field of plant community assembly has rarely considered the role of plant–animal interactions in this process. Conversely, the study of plant–animal interactions has tended to focus on the direct, pair-wise interactions (see Glossary) between plants and animals, with insufficient attention to the greater community context [7].

Using plant–pollinator interactions as a case study, we hope to show that combining the principles of community assembly with the insight gained from studies of species interactions can enhance our understanding of the role of mutualisms in shaping patterns of species coexistence. We consider the three processes — namely, filtering, facilitation and competition (see Glossary) — most likely to

influence patterns of plant community assembly through plant–pollinator interactions, and we then address the potential role of phylogenetic approaches in this area.

Three main processes by which plant-animal interactions influence community assembly
Habitat filtering

Ecological sorting, or habitat filtering (see Glossary), predicts that the environmental influences of a particular site or community determine which species can establish [8]. The environment acts as a 'filter', keeping some species out and allowing only those with particular adaptations to persist. A classic example of a habitat filter is the serpentine soil type, in which the mineral content and poor nutrient availability tends to filter out species that cannot tolerate harsh edaphic conditions [9]. One key prediction of habitat filtering is that it tends to result in communities of species that share similar traits [5], a phenomenon known as trait (or phenotypic) clustering (Table 1; see Glossary).

The local pollinator community can operate as a habitat filter if the absence of a particular pollinator prevents the establishment of a plant species in a community. Such filtering can be direct, as when a plant species cannot

Glossary

Competition for pollination: any interaction in which co-occurring plant species (or phenotypes) suffer reduced reproductive success because they share pollinators. The reduction in reproductive success could occur either because the pollinator pool is a limiting resource or because interspecific pollen transfer interferes with pollination.
Diffuse facilitation: the combined effects of many species having a positive influence on the fitness of a target species (contrast with pairwise facilitation).
Habitat filtering: filtering of species that can persist within a community on the basis of their tolerance of the local environment.
Mutualist network: a set of organisms interacting in a jointly beneficial manner.
Pair-wise facilitation: probability of a plant species' establishment is increased by the presence of another plant species, owing to facilitative interactions between them (contrast with diffuse facilitation).
Phylogenetic signal: degree to which phylogenetically related organisms tend to resemble each other.
Plant–pollinator network: an assembly of plants and pollinators potentially interacting as a system.
Pollen limitation: the failure of a plant to set a full complement of seeds owing to insufficient pollen receipt.
Pollination mode: the specific means by which a plant disseminates and receives pollen (could be abiotic or biotic).
Pollination syndrome: a set of floral traits typically associated with the attraction and utilization of a specific type (or group) of pollinator(s).
Pollinator isolation: pollinator fidelity in a mixed population.
Trait clustering: species in a community have more similar traits than expected by chance; also called phenotypic clustering.
Trait evenness: species in a community have traits that are more divergent than expected by chance; also called phenotypic overdispersion.

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Table 1. Conceptual framework: how plant–pollinator interactions and phylogenetic signal might influence community assembly

Dominant community process	Description	Phenotypic community pattern	Phylogenetic trait pattern	Community phylogenetic pattern	Refs
Pollinator facilitation or filtering	Plant species that share pollinators are more likely to establish and persist in coexistence	Plants in the community have more similar pollinator syndromes than expected by chance	Conserved (Figure 3a)	Clustered (communities consist of closely related plants that share pollinators) (illustrated in Figure 3a,ii)	[28,32, 60,67]
			Not conserved (Figure 3b)	Even (communities consist of distantly related plants that share pollinators) (illustrated in Figure 3b,ii)	[68,69]
Pollinator-mediated competition	Plants that use different pollinator resources establish more easily (limiting similarity)	Plants in the community are more divergent in their pollinator syndromes than expected by chance	Conserved (Figure 3a)	Even (communities consist of unrelated plants with divergent pollinator use) (illustrated in Figure 3a,iii)	[18]
			Not conserved (Figure 3b)	Random (communities consist of closely or distantly related species with divergent pollinator use) (illustrated in Figure 3b,iii)	[44]

reproduce in an area because there are no suitable pollinators [10]. Alternatively, the physical environment itself (e.g. light spectrum, climate, water availability) might influence the interaction between a plant and its pollinators, determining which pollination systems can persist.

Studies of agricultural systems demonstrate that the existence of a suitable habitat is critical for the maintenance of native crop pollinators (Box 1). For example, the frequency of visits to grapefruit flowers by native stingless and solitary bees declines with distance from the forest edge, presumably because the primary forest is their preferred habitat [11]. Similarly, pesticide use can impact pollinator survival and disrupt native plant–pollinator interactions, preventing plants that rely on those pollinators from establishing and/or persisting [12]. Widespread evidence for pollen limitation (see Glossary) [13] indicates that pollinator availability influences the reproductive success of plant species and hence their relative abundance and persistence in a community.

Examples from the invasive-species literature support the idea that successful invaders are able to co-opt the services of existing pollinators, often to the detriment of native plants (Box 1). However, our general understanding of how the local pollinator community influences plant species establishment is poor. Large-scale, comparative studies indicate that shifting or declining pollinator populations can negatively impact plant species reproduction and persistence [14], but local scale studies that isolate cause and effect are still needed. Species in the genus *Ficus,* which have evolved extremely specialized relationships with pollinating fig wasps, offer a compelling example of the pollination environment acting as a filter. In Florida, two formerly sterile ornamental species, *Ficus altissima* and *Ficus microphylla*, recently became invasive only after their specialist pollinator was accidentally introduced [15]. Similarly, in New Zealand, two *Ficus* species were cultivated for many years without ever setting seed, owing to the lack of their pollinating wasp species [16].

Several studies illustrate how the abiotic environment can influence the interaction between plants and pollinators, thus favoring species with particular pollination modes (see Glossary). For example, habitat light availability alters color perception and the efficacy of different flower colors for pollinator attraction. Light reflectance depends on both illumination and background, and flower color (as perceived by an animal pollinator) can vary from invisible to conspicuous under different light regimes [17]. For example, in low-light habitats, a green flower might be less visible against a green background, whereas white, red and orange flowers offer signal contrast and are most visible in low-light conditions against green backgrounds. Indeed, white-flowered species are over-represented in shaded, understory habitats when compared with open habitats such as meadows and deserts [18]. Similarly, arctic plant communities tend to be composed of species exhibiting corolla colors that reflect best under high intensity light conditions [19]. Moreover, flower color is associated with pollinator specificity [20], and a change in perceived color can influence the ability of a plant to attract a suitable pollinator. If plants are unable to attract appropriate pollinators owing to poor visibility and/or variation in perception by pollinators, persistence in that habitat is less likely.

Light availability can also influence which species establish in an area by influencing nectar production. Plants living in poorly lit habitats are constrained to a lower rate of photosynthesis, which could prevent the establishment of plant species with energetically costly floral displays or high nectar production. For example, it has been suggested that hummingbird-pollinated plants, which tend to produce much higher quantities of nectar than insect-pollinated species [21], should be less common in the understory [22,23]. Similar effects could result from metabolic differences among pollinator species that influence their ability to tolerate regional, seasonal and/or diurnal temperature conditions. Whether plants with costly floral displays are more common in habitats with low light availability or cooler climate regimes has yet to be determined.

Box 1. Invasive species and agricultural introductions: community assembly in action?

Plant invasions and human-assembled agricultural plant communities offer a rare opportunity to observe community assembly as it occurs.

Examples from invasive species

Invasions represent natural experiments in community assembly. Where invasive species succeed, we gain valuable information about the ecological factors that influence the establishment of a species in a community. A study of invasive grasses in California suggests that successful invaders are more distantly related to the existing species in a community than would be expected by random chance [61], suggesting a role for limiting similarity in community assembly. However, we lack data demonstrating whether the establishment of an invader could be influenced by competitive exclusion and/or habitat-filtering based on pollinator resources. Nevertheless, several case studies offer insight into the role plant–pollinator interactions can play in community assembly:

- Plant communities artificially invaded by the alien plant *Impatiens glandulifera* had significantly more pollinators, more species of pollinators, and higher visitation rates to existing species. Moreover, *I. glandulifera* was more likely to be visited by generalist insects, suggesting that it does not require specialist pollinators to invade a community. The results of this study suggest that native pollinators, especially generalists, can enhance alien plant establishment [62].
- Introducing purple loosestrife *Lythrum salicaria* to plots draws pollinators away from its congener *Lythrum alatum*, suggesting the possibility that the native species facilitates the establishment of the invader by providing an established pollinator community, and that competition for pollinators negatively influences seed set in a native species [63].
- Introduction of the alien plant *Phacelia tanacetifolia* to communities of native *Melampyrum pratense* increased overall pollinator visitation to experimental plots. Interestingly, the two plants appear to place pollen on different parts of their bumblebee pollinators, which might reduce interspecific pollen transfer and enhance the possibility of coexistence [64].

Agricultural examples

Farmers have long relied on introduced or naturally occurring pollinators to fertilize seed and fruit crops. Recently, in the face of pollinator population declines, the value of native pollinators as an 'ecosystem service' has been highlighted [12]. These managed communities might provide clues about how natural communities assemble:

- Fruit set was reduced in the tropical crops *Macadamia integrifolia* and *Dimocarpus longan* with distance from natural rainforest, suggesting that these crop species experience a reduction in fitness when removed from native pollinators [65]. This finding is consistent with diffuse facilitation; high diversity forests are required to maintain pollinators.
- Similarly, coffee yields have been found to decline with distance from forest remnants, possibly owing to a reduction in pollinator diversity and, hence, pollination services [66].

Facilitation

The role of facilitation and other positive plant–plant interactions in community assembly has recently received increased attention [24–27]. If successful establishment of a species is influenced by the availability of a particular pollinator community, plants should benefit from living in close proximity to other plants that attract the same pollinators. Pollinator-mediated facilitation resembles a filtering process, because the success of the plant species is promoted by the presence of appropriate pollinators. However, we feel that it should be recognized as a distinct process, consistent with general treatments in ecological theory, because it is not directly dependent on interactions with the abiotic environment. Several studies have demonstrated that a plant species might indirectly enhance pollinator visitation to a neighboring species by increasing visitation or activity levels of shared pollinators [28–30]. Per flower visitation has been shown to increase with the density of plants in a homogeneous (i.e. single species) patch [31]. This effect extends to heterospecific patches; visitation by specialist bees to *Clarkia xantiana* increased by 93% in the presence of pollinator-sharing congeners [28,32], supporting the idea that pollinator-mediated facilitation can exist within and among species (Figure 1). As with filtering, species occupying communities shaped by direct facilitation are predicted to exhibit floral trait similarities (Table 1).

Tension exists between the benefits and costs of pollinator facilitation; plants benefit from increased visitation but might suffer fitness declines due to the increased incidence of heterospecific pollen transfer. Plants in small, isolated communities have the most to gain from pollinator facilitation [31]. Fine-scale adjustments in flowering phenology, spatial clustering of conspecifics, and divergence in pollen placement are three mechanisms that might enable coexisting species to reap the benefits of sharing pollinators while reducing their exposure to heterospecific pollen [32].

The extent to which co-occurring plants share pollinators is currently unknown for most communities. Indeed, the degree to which plant species tend towards specialization on a single pollinator (or group of pollinators) versus generalization on several species of pollinators is currently under debate [33]. New insights from studies that describe plant–pollinator networks (see Glossary) suggest that the sharing of pollinators among plants in a community is more common than previously thought [34]. Studies that measure plant fitness in response to changes in the identity and visitation rates of pollinators are needed to better assess the degree to which a plant's neighboring species influence its establishment and persistence in a particular location.

Facilitative interactions can be quite 'diffuse' (see Glossary), whereby the presence of a certain species or set of species positively influences pollinator visitation and reproduction for multiple co-occurring species (Figure 1). For example, staggered flowering phenology by species in a community can operate as a form of diffuse facilitation by maintaining a consistent pollinator community throughout the flowering period [35–37]. Interestingly, the aggregation of flowering schedules among plant species in a community has also been reported, which could function as pollinator-mediated facilitation if pollinator attraction at the community level is improved by the mass flowering [38]. Ultimately, whether the community-level flowering pattern tends to be staggered or aggregated is likely to be a joint outcome of the processes of facilitation and competition [36].

Competitive exclusion

Perhaps because the tremendous variety of floral forms catches the eye of the human observer, pollination biologists
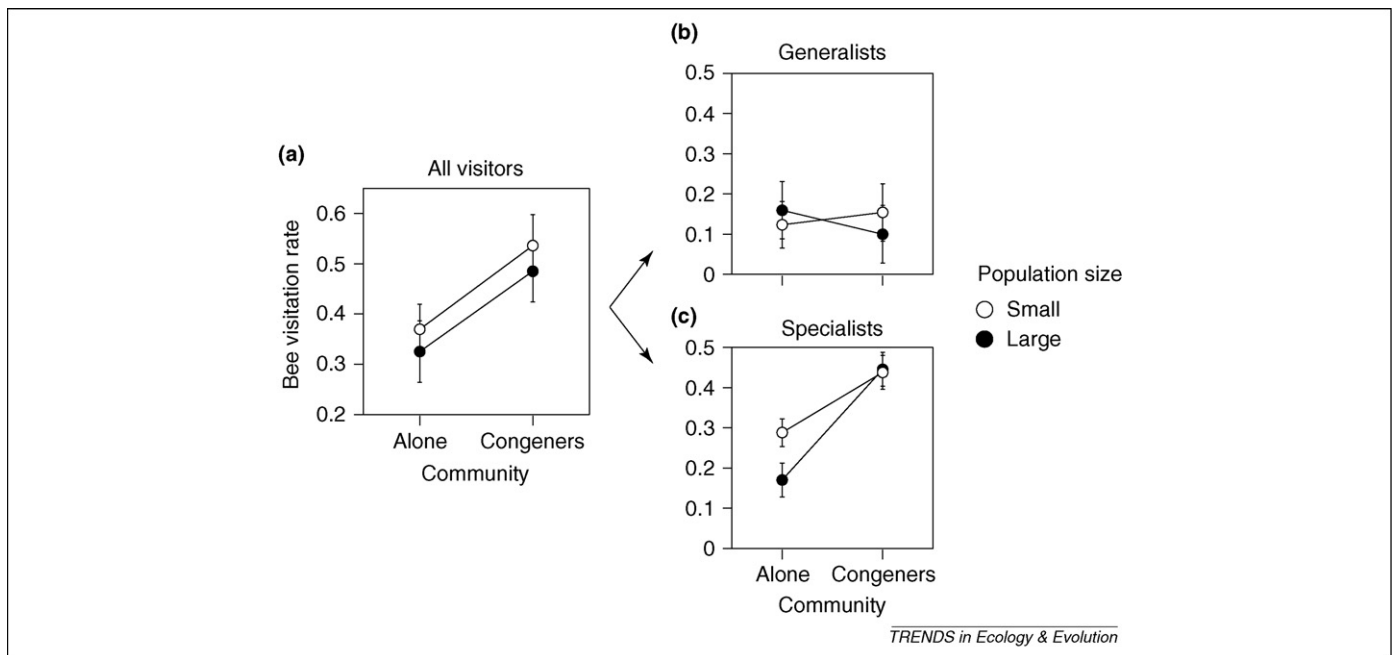
Figure 1. The *Clarkia* species studied extensively by Moeller and Geber [28,32,60] in the southern Sierra Nevada offer a compelling system for examining community assembly through pollinator interactions. Populations of *Clarkia xantiana* can be found in isolation or coexisting sympatrically with congeners *Clarkia cylindrica*, *Clarkia unguiculata* and/or *Clarkia speciosa*. Moeller and Geber [28] demonstrated that the co-occurrence of pollinator-sharing congeners increases pollinator visitation to *C. xantiana* and relaxes selection on traits associated with self-fertilization (which is not expected to be adaptive when interactions are facilitative). Interestingly, their investigationsrevealed that the overall pattern of increased visitation in the presence of congeners, illustrated in (a), is driven largely by differential visitation by specialist, but not generalist, bee species (compare (b) and (c)). Furthermore, population size did not significantly influence bee visitation rate. Moeller and Geber's research in this system strongly supports the hypothesis that coexistence of pollinator-sharing *Clarkia* species might be promoted by facilitative interactions with pollinators. Figure reproduced with permission from reference [28].

have tended to neglect processes that result in community-wide trait similarities, and have instead focused on diversity and differentiation of floral traits among co-occurring species. In general, phenotypically similar species are more likely to compete for pollinator services, and therefore communities structured by competition are expected to exhibit a diversity of pollination syndromes (see Glossary). This can occur through competitive exclusion and/or through character displacement, whereby natural selection drives divergence in floral traits, reducing the intensity of competition and facilitating species coexistence [39]. It can be difficult to discern whether a pattern of species coexistence is the result of past competitive exclusion or of character displacement. One hallmark of character displacement is that trait divergence is more exaggerated among sympatric populations than among allopatric populations, owing to the additional influence of competition on trait divergence [40].

Pollinator-mediated competition can impose negative fitness consequences through two distinct processes: competition for pollinator preference and competition through interspecific pollen transfer [41]. In the first, a limited supply of pollinators means that one or both species suffer reduced visitation. In the second, pollinators may or may not be limiting, but interspecific pollen transfer results in lower reproductive success [42]. When interactions with a particular pollinator are likely to deliver incompatible pollen, plants that use an alternate, more specialized pollinator have a higher probability of persistence [43]. Both forms of 'competition' are predicted to result in communities that exhibit a diversity of pollination modes [41,44].

Although there is evidence demonstrating that competition for pollinators with co-flowering species has negative

consequences for plant fitness [45,46], few studies have directly examined the influence of pollination mode on species establishment, local extinction, or community assembly. Perhaps the best evidence to date comes from Fishman and Wyatt [42], who demonstrated that the evolution and maintenance of self-fertilization in the single-flowered sandwort *Arenaria uniflora* probably evolved to alleviate the negative effects of heterospecific pollen transfer upon secondary contact with its congener, the mountain sandwort *Arenaria glabra*.

Much of the research on the influences of plant–pollinator interactions at the community level has been motivated by the question of whether plants that share pollinators tend to stagger their flowering phenology to avoid competition for pollinators [47]. Indeed, evidence suggests that animal-pollinated plants tend to exhibit greater variation in their flowering schedules when compared with wind-pollinated species [48]. Phenotypic selection analysis has also shown strong fitness effects of earlier or later flowering, within individual species [49]. However, we know of no examples of studies that have explicitly tested whether flowering phenology influences species persistence in a particular community, and thus we lack a clear understanding of the role of flowering time in community assembly. Because reproductive phenology responds to shifts in temperature and moisture, a thorough understanding of its role in community assembly could be crucial in predicting how communities will respond to global climate change scenarios [50].

To test whether the community assembly process has been influenced by competition for pollinators, many researchers have examined the species and floral trait composition of existing plant communities and compared
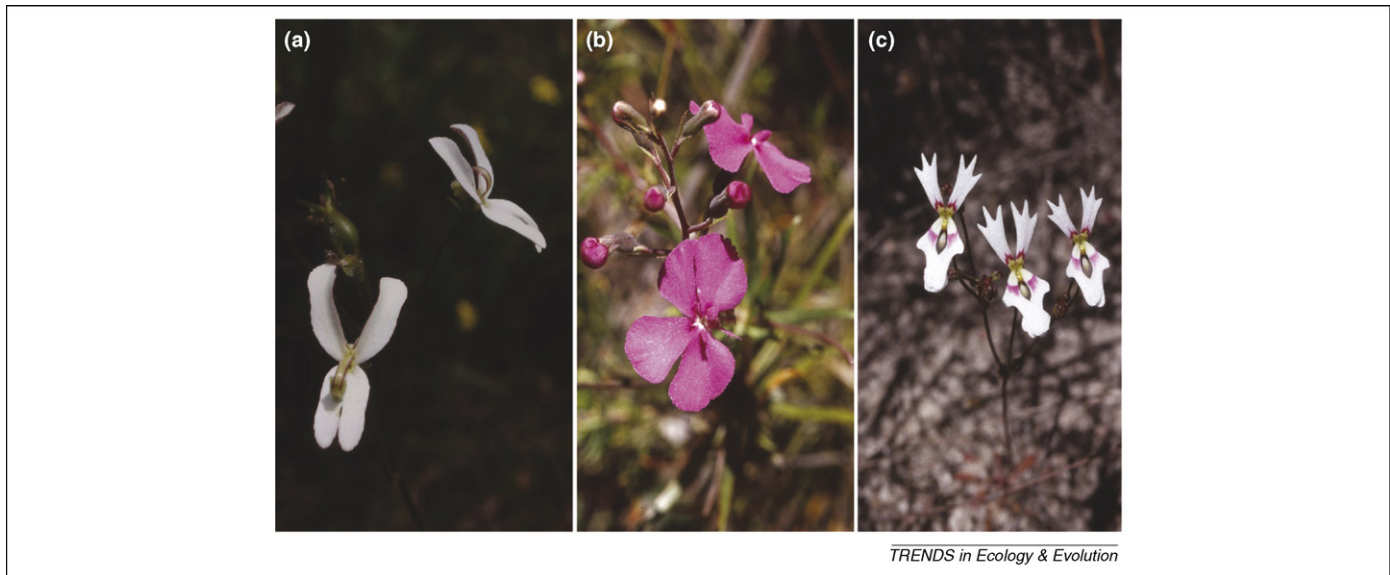
Figure 2. Three sympatric species of Triggerplants (genus *Stylidium*) found in Western Australia. Armbruster and colleagues [44] used null models to examine whether species of Triggerplants are assembled non-randomly with respect to pollination mode. Their research strongly suggests that communities are assembled in a manner that reduces range overlaps between species using similar pollination modes. Furthermore, their analyses support the hypothesis that character displacement has facilitated coexistence. The panels illustrate three divergent modes of pollination coexisting at a single site. In **(a)**, *Stylidium schoenoides* exhibits pollen placement on the dorsal part of the pollinator, in **(b)** *Stylidium scandens* exhibits lateral pollen placement, and in **(c)**, *Stylidium calcaratum* exhibits ventral pollen placement. Photographs kindly provided by W.S. Armbruster, Institute of Arctic Biology, University of Alaska, Fairbanks.

them with a null expectation. These studies offer mixed support for the hypothesis of community assembly through pollinator-mediated competition. Armbruster *et al*. [44] used a null model approach and concluded that the distribution and overlap of traits associated with pollen placement in 31 species of Triggerplants (*Stylidium*) in Western Australia was consistent with post assembly character displacement (Figure 2). More recently, van der Niet *et al*. [51], in a study of animal-pollinated species in the Cape Flora, found that edaphic shifts are more likely to be associated with pollinator shifts when sister taxa have overlapping distributional ranges, but not when sister pairs are found in allopatry. They argued that this pattern is most consistent with the hypothesis that pollinator shifts are operating as agents of reinforcement. Interestingly, their data are also consistent with a process whereby prior divergence in an isolating trait (pollinator syndrome) enables sister taxa to coexist sympatrically.

In summary, our current understanding of the role of plant–pollinator interactions in community assembly comes largely from studies that focused on patterns of trait diversity in communities, rather than patterns of trait clustering. Studies that infer assembly processes from existing patterns are by far the most prevalent (although see [46]), whereas those that use an experimental approach are less common [39]. It would be particularly constructive to shift the field toward studies that examine the consequences of specific plant trait combinations on the persistence of existing species in communities, as well as the establishment of new species, whether these are desired natives as in restoration or aliens that may be the targets of control efforts.

Phylogenetic considerations
Phylogenetic approaches allow questions about community assembly to be framed in the context of the

evolutionary history of the species being studied. Phylogenetic methods make it possible to test whether trait divergence between sister taxa is greater than expected, given a background rate of evolutionary change. Thus, phylogenetic relationships provide a null expectation, allowing us to test hypotheses about the relationship between community assembly and trait evolution [52]. Patterns of phylogenetic community structure reflect the cumulative action of multiple processes, and can provide an effective means of integrating the joint effects of plant–environment, plant–plant and plant–animal interactions.

Recent research in community assembly has considered the tendency for related species to resemble each other in their traits (phylogenetic signal; see Glossary), which can be used to predict whether closely related species are likely to coexist [52]. Filtering and facilitation are predicted to yield communities with phenotypically similar species; if closely related species share pollinators, then these communities will also be composed of species that are more closely related than expected by chance alone (Table 1, Figure 3). Conversely, the process of competitive exclusion is predicted to generate communities of species less closely related than those in communities formed by random assembly, again in the case where there is high phylogenetic signal for pollination modes. These ideas have been used to better understand how ecophysiological traits influence community assembly [5,6], but to our knowledge they have yet to be applied to floral traits at the community level.

Phylogenetic information has recently been applied to examine whether close relatives tend to exhibit similarities in the structure of their mutualist networks (see Glossary). In their exploration of 36 plant–pollinator networks, Rezende and colleagues [53] found mixed support for their hypothesis that the number of pollinator species that a plant species interacts with is phylogenetically conserved. Their findings have implications for our un-
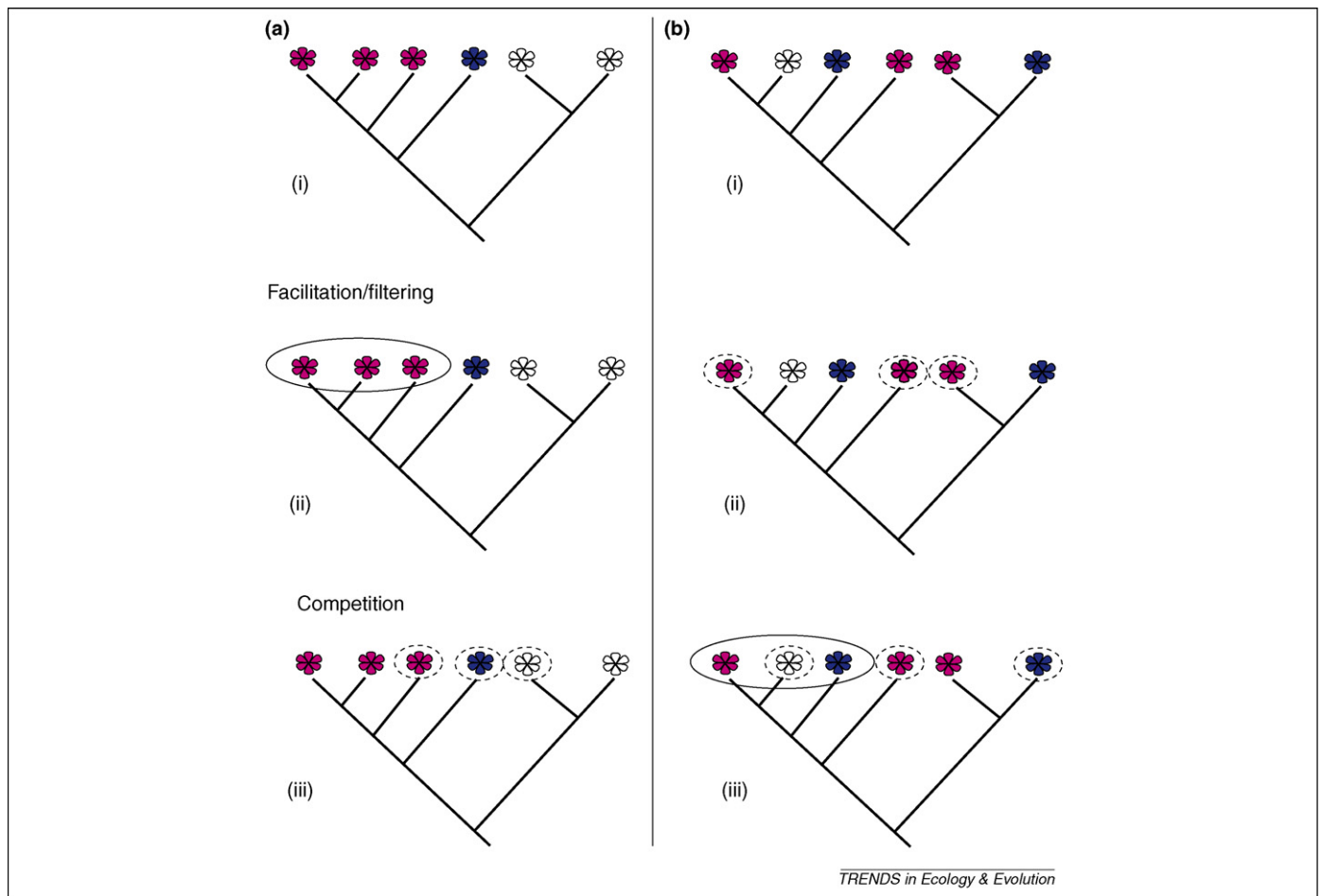
Figure 3. The pattern of trait distribution on a phylogeny influences the predicted phylogenetic relatedness of species in a community (see Table 1). In panel **(a)**, the flower color trait pattern is evolutionarily conserved, whereas in **(b)** it is not conserved. Ovals indicate potential three-species communities that are assembled either through the process of facilitation and/or filtering (ii) or through competition (iii). Depending on the trait distribution, the two processes can result in communities of close relatives (solid ovals), as in (a) (ii), communities of distant relatives (dashed ovals) as in (b) (ii) and (a) (iii), or either, as illustrated in (b) (iii).

derstanding of how community structure evolves; if interaction networks are evolutionary labile, as their results suggest, this implies that community structure is also evolutionary labile (because species are unlikely to experience the same interaction network as their ancestors).

Phylogenetic studies play a valuable role in understanding the relationships among speciation, trait evolution and community assembly. One striking pattern in the New World is the number of flowering plant lineages in which the evolution of hummingbird pollination appears to be followed by an increased rate of speciation [54]. In many of these lineages it has been demonstrated that hummingbird pollination arose multiple times independently [55,56]. Furthermore, prezygotic pollinator isolation (see Glossary) appears to facilitate sympatry of congeners, vastly improving the ability of close relatives to coexist [57]. However, many neotropical plant lineages have no specialized hummingbird-pollinated species [54], illustrating that differences in traits and community structure are influenced not only by environmental differences but also by intrinsic differences among lineages.

In another example from the Neotropics, congeners in the animal-pollinated plant lineage Sinningieae (Gesneriaceae) often exhibit overlapping distributions, suggesting that community structure might be a result

of sympatric speciation. However, upon reconstructing the phylogeny of the lineage, Perret *et al.* [58] concluded that, for most clades, the data were more consistent with range shifts following allopatric speciation. Furthermore, the authors were able to use the phylogeny to identify whether divergence in floral traits was associated with the current degree of sympatry between sister species; it was not. Thus, understanding the phylogenetic history of a lineage can help to discern whether species co-occurrence is the result of random shifts in species ranges over time, sympatric speciation, or ecological sorting processes operating against a background of speciation and evolutionary divergence [59].

Although our ability to trace the evolutionary history of community structure and interaction networks is still in its infancy, this field has great potential for improving our understanding of how ancestral community structure has influenced present day community structure and phylogenetic diversity.

Future directions
The examples above highlight a variety of processes by which plant–pollinator interactions can influence plant species establishment and persistence, and hence impact the assembly and structure of plant communities. Recent

concern over the worldwide decline of pollinator species stresses the importance of understanding the impact of these interactions on plant species and plant communities [14]. The ideas presented here could easily be extended to make predictions based on other biotic interactions (e.g. herbivores, parasites, seed dispersers, etc.). We believe that the role of species interactions and reproductive traits has received insufficient attention in the development of community assembly theory, and that there is great potential for future research in this area. It is important that researchers in both fields recognize that community assembly processes do not act in isolation. Ultimately, the establishment and persistence of a species in a community reflect the outcome of interactions with the biotic and abiotic aspects of the environment. By taking these into consideration, a more complete picture of the processes that drive plant community assembly will emerge.

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