Received: 18 April 2025 | Accepted: 5 May 2025

DOI: 10.1002/ecs2.70492

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Seed mix performance and species network roles as a framework to select candidate key resources for pollinator habitat

Uta Müller[1,2] | **Katherine Borchardt**[1,3] | **Anna Britzman**[1,4] | **Neal M. Williams**[1]

[1]Department of Entomology and Nematology, University of California Davis, Davis, California, USA

[2]Department of Entomology, University of Minnesota, Saint Paul, Minnesota, USA

[3]Department of Biology, University of Massachusetts Amherst, Amherst, Massachusetts, USA

[4]US Forest Service, Mcclellan, California, USA

Correspondence
Uta Müller
Email: uta_mue@posteo.de

Funding information
Foundation for Food and Agriculture Research, Grant/Award Number: 549032 sub 5805-UCD-FFAR-9032; KIND Foundation (KIND Healthy Snacks)

Handling Editor: Sunshine A. Van Bael

Abstract

Current native bee declines have been attributed in part to loss of habitat and floral resources. Mitigation approaches include trying to establish or enhance bee habitat by planting wildflowers, which is often done by using seed mixes. Most assessments of plant performance in pollinator seed mixes are based on the abundance and diversity of visitors they support, which might be key elements of community interactions such as supporting specialized links within plant–pollinator networks or changes in core position within networks across seasons. Therefore, the selection of "candidate key pollinator resources" could be usefully extended to include assessment of species network roles. In two different experiments, we independently assessed the performance of a set of 28 native California wildflowers, first in seed mix applications over three years and second in standardized mono-specific plantings of the same plant species. Within seed mixes, plant species' performance according to maximum floral area and phenological coverage clearly differed with certain taxa found to dominate, or only establish short term or not be competitive at all. Only a small set of 5 species persisted with high performance over the whole three years. Based on mono-specific plot studies quantifying species network roles, as opposed to simply abundance-diversity metrics, we identified network core species and species supporting ecologically specialized pollinators. Both species roles are characteristic in natural plant–pollinator networks and therefore could present key characteristics for choosing plants with the aim of restoring mutualistic plant–pollinator networks with wildflower habitat plantings. Plant species' network roles changed over the seasons within a year arguing for the inclusion of seasonality when choosing candidate key pollinator resources for plant mixes. Only a subset of species in networks proved to be successful in seed mix applications where plants needed to perform under competition. The results emphasize the need to evaluate wildflower plantings and prioritize species of high performance for multiple criteria in current and future applications.

KEYWORDS
bee conservation, habitat plantings, pollinator habitat restoration, pollinator networks, seed mixes

INTRODUCTION

Recent evidence from collections worldwide suggests that numerous species of native bees are declining (Zattara & Aizen, 2021). Although a variety of interacting factors contribute to these declines (LeBuhn & Vargas Luna, 2021), one increasingly well-documented mechanism is the reduction in abundance and continuity of floral resources that are critical to the persistence of diverse bee communities (Nicholson et al., 2021). Loss of continuity over the season creates gaps or curtailment in resources at critical times (Timberlake et al., 2019) that may increase adult mortality and also reduce the numbers of offspring that can be provisioned. Both factors can decrease population growth rates and increase the probability of local extinction (Burkle et al., 2013). The loss of reliable floral resources is particularly acute in intensive agricultural landscapes in which conversion of land from natural habitat to crop fields, simplification and homogenization of crops and fields (e.g., Ollerton et al., 2014; Scheper et al., 2014), and weed management reduce noncrop floral resources and their phenological diversity.

Enhancing flowering habitat by planting wildflower meadows, flower-rich field borders or hedgerows can help to bolster floral resource abundance and diversity and restore flowering continuity between periods of crop flowering within agricultural landscapes (Balzan et al., 2014; Gill et al., 2016; Hardman et al., 2016; Schulte et al., 2017). Flower plantings generally benefit pollinator diversity (Lane et al., 2020) and abundance (Albrecht et al., 2020; Balzan et al., 2014; Lowe et al., 2021); however, the value of high-diversity plantings is not universal and may depend on the choice of plant species. For example, the presence of certain plant species that are particularly attractive and/or provide higher quality pollen rewards than others (Vaudo et al., 2020) can have a greater impact for supporting pollinators than the overall diversity of the mix in both agricultural (Warzecha et al., 2018) and natural ecosystems (Harmon-Threatt & Hendrix, 2015). From a set of 94 tested plant species, Warzecha et al. (2018) found that 14 were most used by the pollinator community, and the top four species supported 80% of all flower visitors (Warzecha et al., 2018). Similar results have been shown in other systems as well (Nichols et al., 2019). Thus, it is possible that diverse plantings with few attractive species benefit bee communities less than simpler mixes with crucial plant species included (Lowe et al., 2021; Williams & Lonsdorf, 2018). Moreover, when targeting pollinator species of conservation concern, tailored selection of host plant species may be essential for seed mix design (Purvis et al., 2021).

The concept of keystone species—those that exert a disproportionate influence on the patterns of species occurrence, distribution, and density in a community (de Visser et al., 2012)—applies here. Within the context of habitat restoration for pollinators and pollination service, keystone plant species have been broadly described as plant species supporting a high abundance and diversity of species within the pollinator community (Zych et al., 2007). We like to emphasize that we decided to use the term "candidate key species" to account for the caveat of not being able to include information on the effects of biomass or removal as required for the canonical definition of a keystone species (Paine, 1995). In practice, the value of a plant species for supporting bees is often evaluated and/or ranked based on the frequency, abundance, and diversity of pollinators it attracts relative to other available floral species (Harmon-Threatt & Hendrix, 2015; Lundin et al., 2017; Nichols et al., 2019; Tuell et al., 2014). Although choosing individual plant species that support disproportionate bee diversity is a logical approach to selecting individual plants for restoration and pollinator conservation, the logic can break down when designing plant communities to support diverse bee communities for at least two reasons. First, different plant species may be strongly redundant in the bees they support, and although redundancy provides other benefits for bolstering stability and resilience (Burkle et al., 2020), it is inefficient for promoting bee diversity. Instead, plant species that support complementary sets of bees offer greater benefit. The point is easily understood with respect to plants that bloom at different times of the year. Choosing a spring and a summer blooming species is likely to offer greater benefit for bees than two otherwise similar species that both bloom in spring. Second, pollinator conservation may also target rare species or those of particular importance. In this case, understanding plants with specific functional characteristics, for example, supporting crop pollinators versus total diversity may inform their value. Mallinger et al. (2019) found that *Phacelia* spp. were frequented predominantly by social generalists, whereas sunflowers supported rare and specialist species (Mallinger et al., 2019). Expanding the concept of keystone plant species to include characteristics that, on the one hand, more comprehensively represent their species role within plant–pollinator community interactions (e.g., Russo et al., 2013) across seasons and, on the other hand, capture their performance within mixed plantings could promote the inclusion of plant species for pollinator plantings that support diverse, resilient pollinator communities.

Defining candidate key plant species for pollinator plantings

Pollinator visitation characteristics

Within a community context, plants and pollinators form interaction networks where flowers are linked to flower visitors based on patterns of visitation (Warzecha et al., 2018), or use of resources (e.g., pollen collected; Ballantyne et al., 2015). Taking a network perspective to plant selection can capture general characteristics like the centrality metric *degree*—the number of interactions per species—which itself is a component of biodiversity and essential for ecosystem services such as pollination (Tylianakis et al., 2010). In addition, species can be characterized using species network metrics (Blüthgen et al., 2006; González et al. 2010). For example, plant–pollinator networks often are composed of core generalist plant species that are hubs of interactions and can support more ecologically specialized bee species. These characteristics are encompassed by *centrality*, which describes the central core of the network (Bascompte et al., 2003). High centrality of some plants is crucial to support a high proportion of the pollinator community, but also enhances the robustness of a network and its resilience to disturbances if extinctions are simulated from lowest to highest degree. If extinction is simulated from high to low, affecting the few central species, a network is more vulnerable to extinction (Bascompte, 2007; Memmott et al., 2004). As such, a high centrality score may better represent the qualities of a true candidate keystone species than a simple measure of high pollinator richness. Network analysis also can be used to identify the floral preferences of bee taxa that are more specialized (Blüthgen et al., 2006) via specialization indices, like *degree*, which can then be used to determine a plant species' importance for supporting ecologically specialized pollinator taxa.

As such, a network perspective for plant selection provides a way to help identify the central candidate keystone plant species that promote a robust community structure and support pollinator diversity to create a resilient community of interactions in the face of changes to species richness and abundance (Valiente-Banuet et al., 2015). In addition, by expanding from the central core species, additional plants can be chosen to support specialized plant–pollinator interactions that would not necessarily be conserved by targeting only the candidate keystone plants.

The importance of network analysis has been emphasized for the conservation of interactions (Borchardt et al., 2021; Tylianakis et al., 2010); however, few studies have explored its use for the selection of plant species to include in pollinator habitat plantings (Maia et al., 2019; Russo et al., 2013). Approaches include the identification of core plant species that support stability for community interactions (Maia et al., 2019; Russo et al., 2013) as well as the identification of connective species that link different modules at one point in time or between seasons (Larson et al., 2014). Such species bolster phenological stability of interactions and their persistence over time (e.g., "node duration"; Russo et al., 2013).

Plant-flowering performance characteristics

In order for a plant species to become a pollinator resource, it must successfully establish and bloom within the context of the plant mix (Scheper et al., 2015). Thus, in addition to the properties of its interactions with pollinators, establishment and competitiveness in terms of flowering performance are critical characteristics for plant selection. Floral display area is one definitive trait to assess plant establishment and performance with respect to supporting pollinators (Haaland et al., 2011; Nayak et al., 2015; Tuell et al., 2014; Williams et al., 2015). Although vegetative performance is undoubtedly important in restoration and pollinator plantings (Wilkerson et al., 2014), it may not simply translate to attracting and supporting pollinators. In addition to flower abundance, flowering duration critically affects a plant's ability to support pollinators. Longer flowering periods tend to support a greater diversity of visitors with different phenologies and strongly contribute to the seasonal continuity of flower resources (Sutter et al., 2017; Williams et al., 2015). Finally, the few existing studies of pollinator mix establishment suggest that, generally, some plant species come to dominate over two to three years (Wilkerson et al., 2014), whereas others can struggle to establish, fail to flower, or get outcompeted (Schmidt et al., 2020). Therefore, assessment of performance across multiple years is needed.

Benefits of integrating two datasets

Assessment of plant importance whether through simple attractiveness or more comprehensive network-based metrics can be biased by flower abundance or display area. Attempts to correct this bias by including plant relative abundance can still overestimate and underestimate the importance of individual species (Fründ et al., 2016). No study that we are aware of has independently evaluated plant species independent of establishment and flowering performance in mixes in order to disentangle and control for the influence of relative abundance/dominance. To address these knowledge gaps, we combine two datasets: one on pollinator visitation using standardized arrays of monospecific plots of equal area for all plant species and another assessing plant flowering performance and phenology through the season for three years from mixed-species plantings of the same plants grown at varying densities and richness (Müller et al., 2024). We use the combination to identify candidate keystone species for supporting native bee communities based on plants' species network roles and flowering performance in mixed plantings. We specifically addressed two research questions: (1) Which plant species are candidate keystone pollinator resources that could support a diverse pollinator community according to species network roles in comparison to abundance- and richness-based metrics? (2) How do these potential candidate keystone pollinator resources perform in seed mix applications according to maximum floral area and phenological coverage?

MATERIALS AND METHODS

Experimental setup

We consolidated data from two independent studies: one that examined native bee visitation to arrays of standard-area monospecific plots for 27 Northern California native wildflowers and another that quantified the flowering performance of these species in replicate mixed species plots.

Plant–pollinator visitation

For the native bee visitation data, the 27 native wildflower species also included in the seed mixes were planted in individual 1 m^2 monospecific plots within four replicate blocks. The plot design was sown identically in 2014 and again in 2018 and grown over multiple years at two locations: University of California, Davis Bee Biology Research Facility (2015–2017; 38.536439 N, 121.788142 W) and at Hedgerow Farms, Inc. (2018–2019; 38.623742 N, 121.98938 W). The monospecific plot design allowed us to control for resource availability and removed differences in establishment success among the different plant species by providing standardized flowering areas per plant species for sampling of bee visitation data. Plots were regularly trimmed to maintain plot area, and all nontarget plant species were removed by hand weeding throughout the season. Plots were separated by 1-m alleyways covered with weed cloth. At both sides, plots were only watered if monthly rainfall was below the average of the previous 10 years as assessed from data from https://cimis.water.ca.gov with Davis, CA (Davis Bee Biology Research Facility) and Esparto, CA (Hedgerow Farms) as the selected data resource.

Data collection

Bee sampling was conducted weekly over the entire blooming season (March–October/November) in the years 2015–2017 (UC Bee Biology) and 2018–2019 (Hedgerow Farms). A total of 28–37 sample rounds were used depending on interannual variation in phenology. We netted all bees that touched the reproductive part of a flower during a 30-second observation at each plot in bloom (for a total of 2 min per species among the four blocks per site). These observations were repeated once in the morning and once in the afternoon. Morning and afternoon samples were a minimum of 3 h apart to capture expected variation in visitation throughout the day. The observation design allowed to account for local as well as temporal variability in capturing flower visits per species as feasible within the time available. We used stopwatches, pausing them while a bee was netted so that specimen processing was not included in the 30-s observation period. All netted bees were identified to species by taxonomic experts using reference collections housed at the Williams Lab and Bohart Museum of Entomology, UC Davis. All collected specimens are curated at the University of California Davis. On the bee sampling day, we also counted individual flowers (floral abundance) per plot and measured corolla areas of 5 individuals for each species from which we calculated floral area per plot for each weekly sampling round.

Flowering performance study

The seed mix experiment was carried out between 2018 and 2021 at the UC Davis student farm (38°32′11″ N, 121°47′18″ W), USA. The experimental setup comprised 120 2 m × 2 m plots in a 20 × 6 grid with treatments located randomly. Plots were separated by 1-m alleyways covered with weed cloth (Dewitt 3.2 oz. Ground Cover). The seed mix design included a fully blocked crossing of three diversity and three density treatments. It also added the inclusion or exclusion of grasses at the lower two density treatments (Table 1) (Müller et al., 2024).

The sown plant species comprised the 27 forb species in the mono-specific plots and two grass species, all native to California. Forbs were included in approximately equal numbers of early (spring, Feb–April), mid (early summer, May–Jun), and late (late summer–fall, July–Oct) blooming species. Both annual and perennial species were included (Appendix S1: Table S1). In order to account for the effects of plant identity on mix performance, we varied the plant species composition of a mix across 7–10 replicates for each treatment. Within each replicate, forb species were randomly drawn from the pool of species represented in the monospecific plots while meeting the requirements for seasonal stratification (Müller et al., 2024).

All plots were regularly trimmed around the perimeter to maintain equal area. Any plant other than the target species for that plot was weeded out. As was done for the monoplots, these mixed species plots were only watered if monthly rainfall was below the average of the previous 10 years as assessed from data from https://cimis.water.ca.gov with Davis, CA, as the selected data resource.

Data collection—Flowering performance study

Flower counts of sown plant species, percent cover of grass, and weeds were assessed in two randomly chosen 1 m^2 quarters of each study plot every three weeks from March to October for a total of 8–11 sample rounds per year over three consecutive years. Corolla areas were measured annually for all forb species during peak bloom (Müller et al., 2024).

DATA ANALYSIS

Candidate key plants—Abundance/diversity metrics

Apis mellifera was excluded from the analysis. The frequency of native bee visits to flower species showed a strong correlation among all years (Spearman correlation, all $p > 0.001$, R: 0.54–0.64); thus the data were pooled among years for final analysis. Although this choice excludes measuring variability in plant performance among years, it substantially increases the data supporting main plant-level patterns and streamlines interpretations. Abundance of native bee visits was calculated as the proportion of total native bee visits per sampling event on each plant species summed across the four blocks. Species richness was calculated as the cumulative number of native bee species identified on each plant species during each part of the season. Abundance and richness were calculated within early, mid, late parts of the season for each year using the same designations as described above for selecting plants for the seed mix experiment and to match the temporal units used in the network analysis (see below).

Candidate key plants—Network metrics

We identified candidate key plant species for supporting pollinators based on traditional abundance and diversity metrics, as well as two complementary characteristics in plant–pollinator networks. The first metric was core/central position as a resource for bees within bee-plant visitation networks and the second, ability to support specialized bees. Native bee abundance, species richness, and species-level network indices were calculated for all 27 plant species included in the seed mix experiment based on visitation data. Native bee visits per flower were first used to generate quantitative plant–pollinator networks with the *bipartite* package in R (Dormann et al., 2021). We created separate

TABLE 1 Overview of seed mix design experiment (120 plots).

Total seeding density (seeds/m^2)	Forb:Grass treatment	Sown forb species richness: Low (9)	Sown forb species richness: Medium (12)	Sown forb species richness: High (24)
Low (242 seeds)	Forb	10	7	7
	Forb + grass	10	7	7
Medium (484 seeds)	Forb	10	7	7
	Forb + grass	10	7	7
High (968 seeds)	Forb	10	7	7
	Forb + grass	NA	NA	NA

Abbreviation: NA, not applicable.

networks for early, mid, and late season as described above for selecting plants for the seed mix experiment. Subsequent metrics for each plant species were calculated based on these separate season-specific networks. Centrality position for each target plant species was calculated using the individual-level network metrics *betweenness centrality*, which measures the importance of a species as a connector in the community, and *closeness centrality*, which describes proximity as a measure through closed linkage pathways to other species in the community (González et al. 2010). To classify plant species that could form a network core, we used the 4-year mean for the metrics *betweenness* and *closeness centrality*. Plant species exceeding upper quartiles for betweenness and closeness centrality in the same season were considered central candidate key species. To assess support for specialist bees, we first calculated d' for each bee species, where d' describes reciprocal specialization by accounting for interaction frequency with regard to the abundance of the interaction partner. We then determined the mean of d' for all bee species visiting each plant species weighted by visitation frequency. Plant species ranking above the upper quartile of mean d' were considered candidate key for supporting specialist bees (candidate specialist keystone species). Similar upper quartiles for "abundance" and "richness" of visiting bees were determined for each plant and used to identify them as candidate key species. As such, our focus is on species as contextual ecological specialists rather than specifically intrinsic oligolectic bees (Cane & Sipes, 2006), although the former will undoubtedly contain some of the latter.

Flowering performance in seed mixes

To assess the performance of focal plant species growing within mixed-species plots, we evaluated the two independent criteria, *maximum floral area* and *seasonal phenological coverage* for each plant species. We determined maximum floral area as the highest floral area covered in any sample round from any plot in which the focal species was sown. This approach provided a metric independent of phenological coverage. To calculate seasonal phenological coverage, we first calculated the average floral area per species for each season over all plots in which it was sown and used it as a seasonal threshold. Species cover was then coded as a binary variable for each sample round depending on whether its floral area exceeded the species-specific seasonal threshold (1) or did not (0). Phenological coverage comprised the number of sample rounds in which the floral area of a species exceeded its seasonal threshold. In order to test for the sensitivity of results to our choice of seasonal categories, the analysis was repeated with the median instead of the mean and with the upper SD of the mean applied as thresholds.

We calculated means for maximum floral area and phenological coverage separately for each year and selected a group of 12 "best-performing" species with an above median performance within the community for maximum floral area and phenological coverage in at least two out of three years. Finally, the potential pollinator resources from the network analysis were compared with the best-performing species in seed mixes.

The relationship between maximum floral abundance and phenological coverage was tested using linear mixed-effects models within the package *lme4* (Bates, 2007). In the models, phenological coverage was included as the predictor, maximum floral cover as the response variable, and plant species as a random effect. All models were checked for homoskedasticity of residuals with diagnostic plots by the package *DHARMa* (Hartig, 2021). All analyses were performed in R version 4.0.3.

RESULTS

Candidate key plant species

Overall, we identified 10 plant species that were in the upper quartile of centrality scores within at least one seasonal network (central candidate key species) and 15 plant species that were in the upper quartile of weighted mean d' for visitors and thus candidate key for supporting specialist bees in at least one season. In addition, 9 species ranked in the upper quantile within at least one seasonal network for abundance and 11 species for richness (Figures 1–4; Appendix S1: Figure S2). All plant species ranking highest in abundance were also identified as central candidate key species. Plant species receiving highest visitor richness were all categorized as central candidate key species or candidate key for supporting specialist species except *Lasthenia fremontii* and *Malacothrix saxatilis* (Figure 4). However, abundance and richness metrics alone failed to consistently identify plant species supporting specialized bee interaction as identified with the network approach. Such species supporting specialists included *Heterotheca grandiflora*, *Achillea millefolium*, *Clarkia unguiculata*, *Lupinus densiflorus*, and *Madia elegans* (Figures 1–3).

In the early season, *Phacelia ciliata*, *Phacelia tanacetifolia*, *Phacelia campanularia*, *Eriophyllum lanatum*, and *Eschscholtzia californica* ranked in the upper quartiles for both betweenness and closeness centrality and thus were classified as central candidate keystone species. *P. ciliata* and *E. lanatum* scored particularly high. Plants

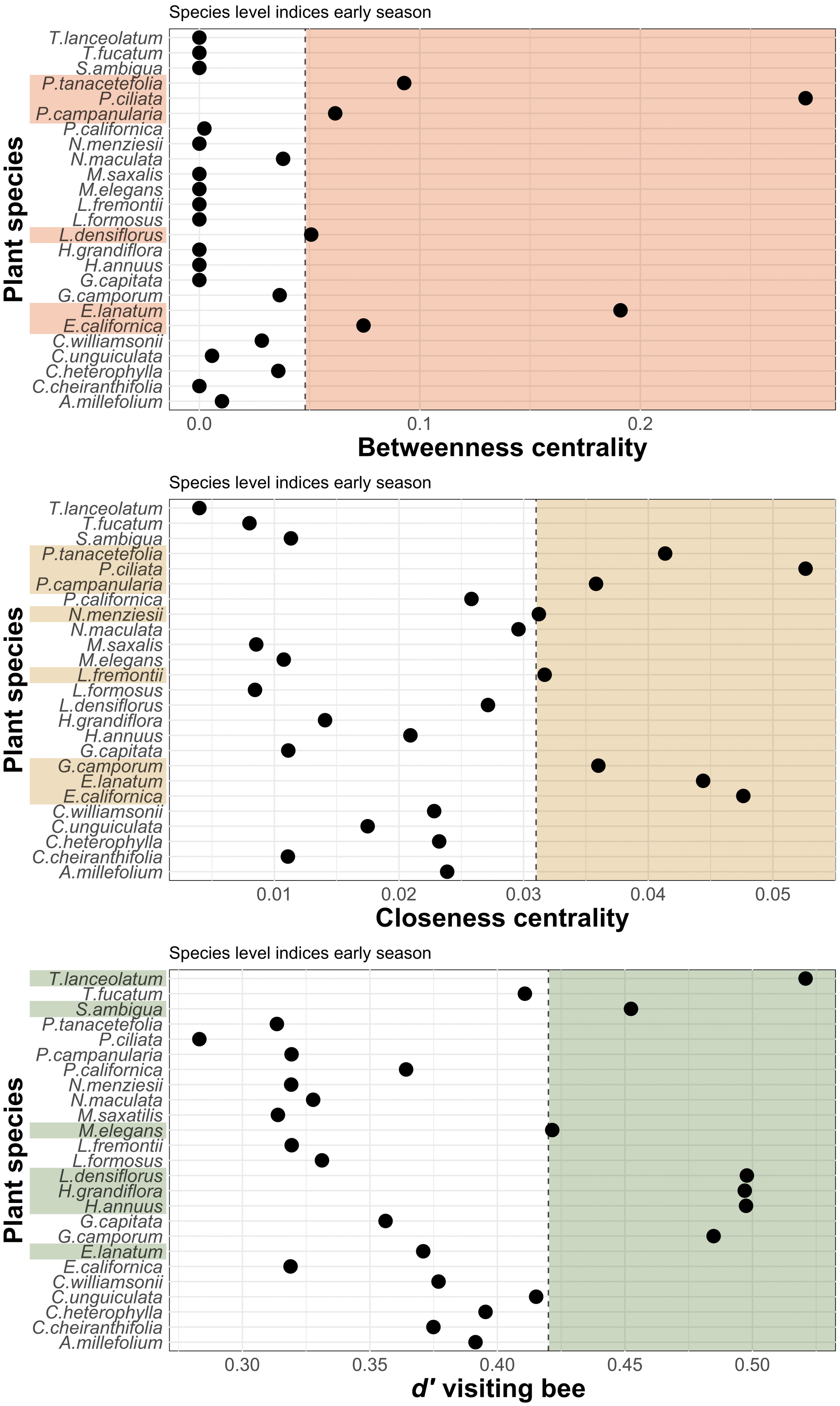

FIGURE 1 Centrality indices (betweenness centrality and closeness centrality) and specializations (d' of visiting bees) of visiting bees for early-season networks. Highlighted plant species are ranging above upper quartiles (25%) and are represented as colored areas.

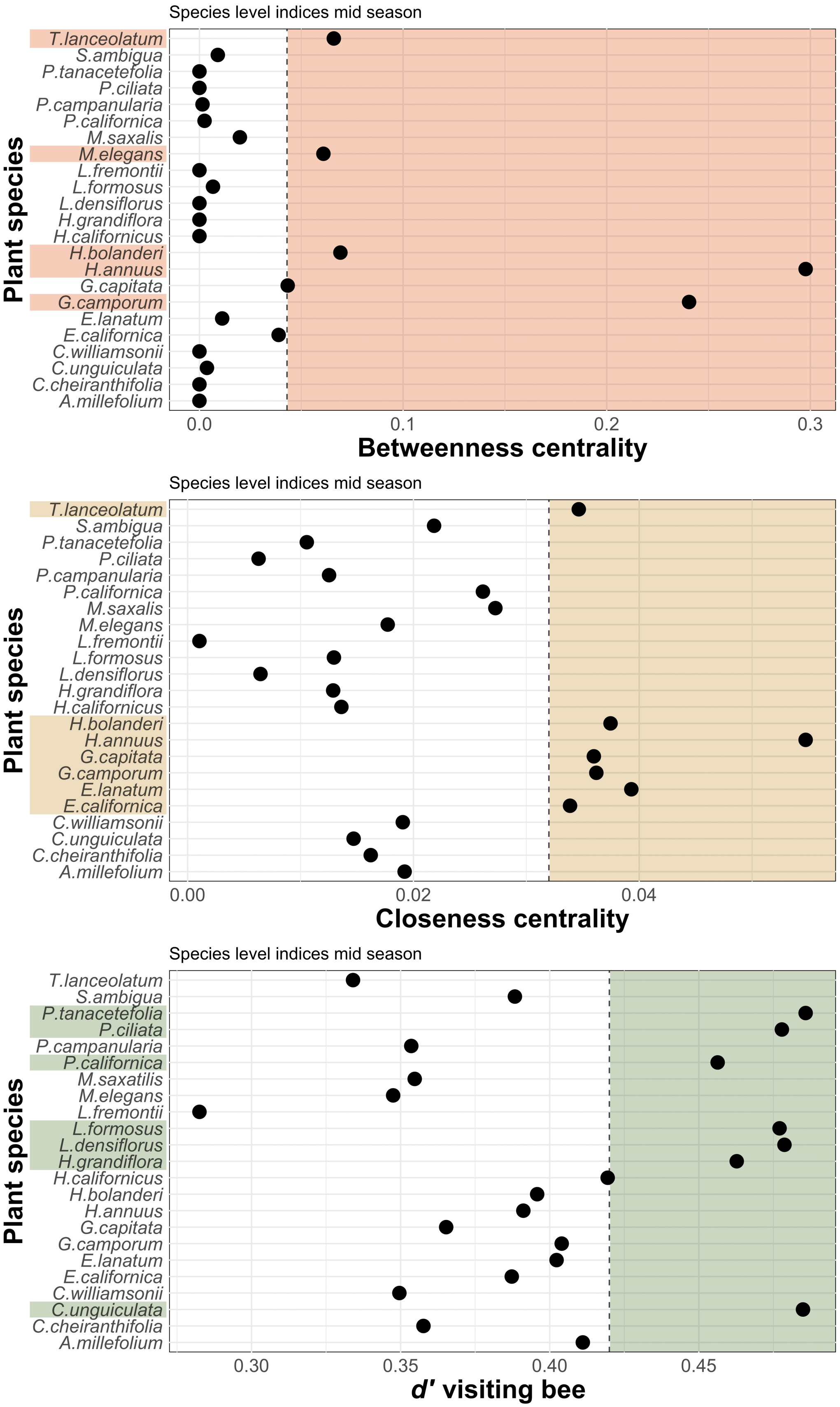

FIGURE 2 Centrality indices (betweenness centrality and closeness centrality) and specializations (*d*′ of visiting bees) of visiting bees for mid-season networks. Highlighted plant species are ranging above upper quartiles (25%) and are represented as colored areas.

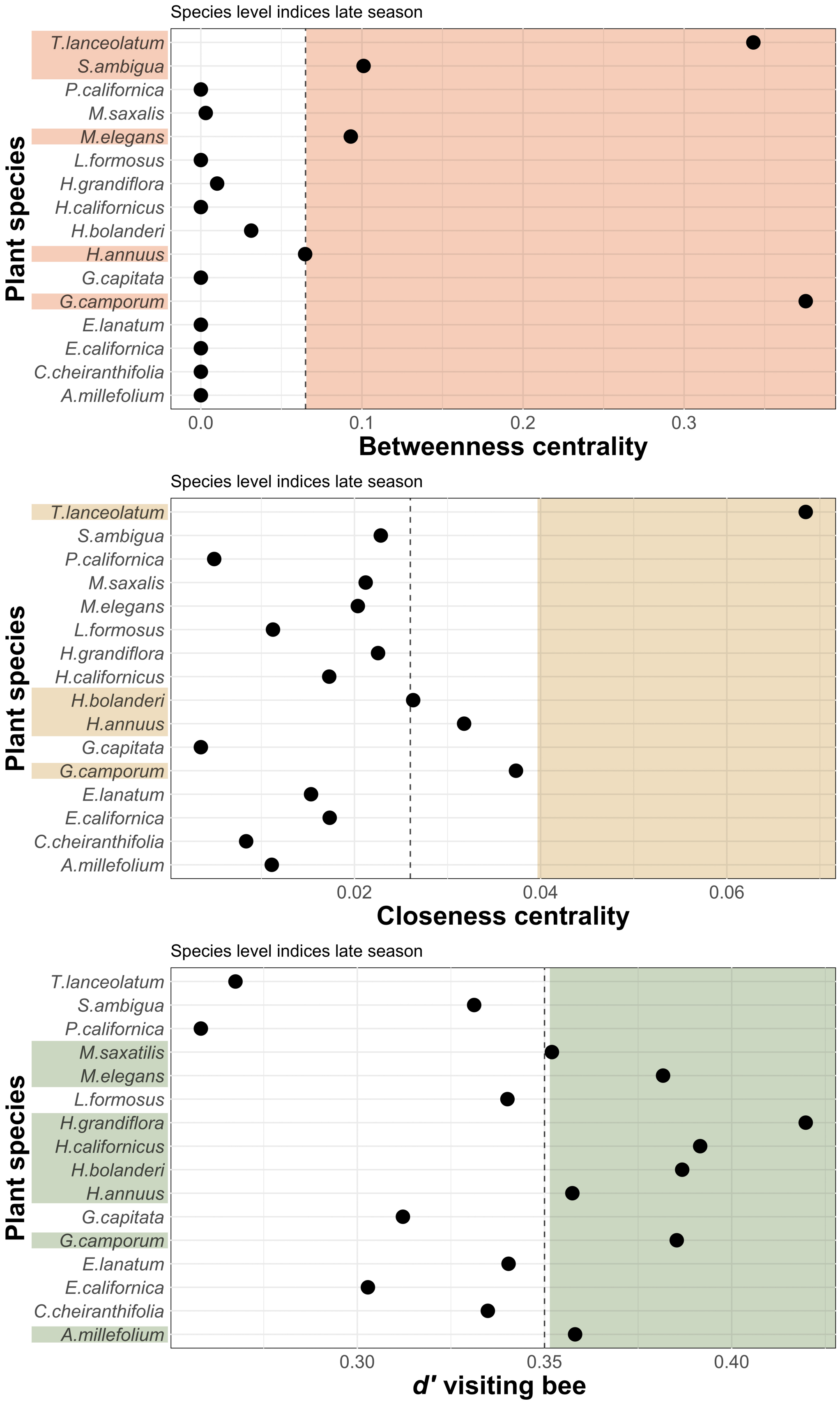

FIGURE 3 Centrality indices (betweenness centrality and closeness centrality) and specializations (d' of visiting bees) of visiting bees for late-season networks. Highlighted plant species are ranging above upper quartiles (25%) and are represented as colored areas.

FIGURE 4 All plant species sown in seed mixes. Species highlighted are those best performing in seed mixes with an above median seed mix performance for maximum floral area and phenological coverage in at least two out of three years, central candidate key species in networks, candidate key species for supporting specialized interactions, species of high abundance and richness of visiting native bees. Photo credit: Neal Williams Lab.

important for specialists included *Trichostema lanceolatum*, *Sphaeralcea ambigua*, *Lu. densiflorus*, *Het. grandiflora*, *Helianthus annuus*, and *Grindelia camporum*. Candidate keystone species based on visiting bee abundance included *P. ciliata*, *P. tanacetifolia*, and *P. campanularia*, *E. lanatum*, *E. californica*, and *Gr. camporum*. Based on visitor richness, *P. ciliata*, *P. tanacetifolia*, *E. californica*, *E. lanatum*, and *La. fremontii* all had richness values within the upper quartile. *P. ciliata* was a standout with distinctively high abundance and richness of visiting native bees (Figure 1; Appendix S1: Figure S2).

In the mid-season, *T. lanceolatum*, *Helianthus bolanderi*, *Hel. annuus*, *Gr. camporum*, *Gilia capitata* and, marginally, *E. californica* ranked as central key species. Of these, H. annuus notably was high for both metrics. Candidate key supporters for specialists included *P. tanacetifolia*, *P. ciliata*, *Phacelia californica*, *Lupinus formosus*, *Lu. densiflorus*, *Het. grandiflora*, and *C. unguiculata*. Highest visiting bee abundances were observed on *Hel. annuus*, *Hel. bolanderi*, and *Gr. camporum*. *E. lanatum*, *E. californica*, *Gi. capitata*, and *T. lanceolatum* also ranked in the upper quartile for visitor abundances. *Gr. camporum* attracted notably higher bee richness than others, although *Gi. capitata*, *S. ambigua*, *Hel. annuus*, *Mal. saxatilis*, and *Hel. bolanderi* all ranked in the upper quartile (Figure 2; Appendix S1: Figure S3).

In the late season network, *Mad. elegans* and *Gr. camporum* were the two most prominent species with regard to both centrality and support of specialized interactions. *T. lanceolatum* and *Hel. annuus* ranked as candidate central key species with additional relevance of *S. ambigua*. Unlike in the early- and mid-season, *Mal. saxatilis* and *Ac. millefolium* emerged with high importance for specialized interactions. Specialist bees were further supported by the sunflowers *Hel. bolanderi* and *Helianthus californica*. *T. lanceolatum*, *Hel. annuus*, *Hel. bolanderi*, and *Gr. camporum* ranked highest in abundances and richness of visiting bees; *S. ambigua* ranked high in visiting bee richness (Figure 3; Appendix S1: Figure S4).

Interestingly, plants with long phenology often changed roles among seasons. For example, of those species present in all three seasons, *E. californica* showed a central role in the network with both centrality values above upper quantile thresholds in early and mid-season but not in the late season, whereas *Gr. camporum* and *T. lanceolatum* supported ecologically specialized bees in the early season, but in the mid- and late season both became central. Other plant species with long phenologies were candidate key species for a short period (*E. lanatum*, *Gi. capitata*) or important for specialized bees only in one season (*Ac. millefolium*). *Het. grandiflora* showed consistent support of specialized native bees over all three seasons.

Flowering performance in seed mixes

Over the three years of the seed mix experiment, the numbers of blooming plant species decreased substantially. Of the 27 sown species, 26 flowered during the first year, 23 in the second, and 18 in the third. Nonetheless, there was a positive linear relationship between maximal floral area and phenological coverage of a plant species for all three years (linear mixed model, t value 0.764, $p < 0.01$; Figure 5a–c).

The best-performing plant species in seed mixes according to the criteria of exceeding the medians for both maximal floral area and phenology changed over the three years. Most turnover occurred after the first year, with more consistency between the second year and third year. In the first year, *E. californica*, *Nemophila maculata*, *Nemophila menziesii*, *Hel. annuus*, *C. unguiculata*, *Clarkia williamsonii*, and *P. tanacetifolia* were most abundant and phenologically persistent. *Hel. annuus*, *Hel. bolanderi*, and *N. maculata* vanished by the second year during which *E. lanatum*, *Ac. millefolium*, *Collinsia heterophylla*, *Lu. densiflorus*, and *Gr. camporum* dominated the blooming plant community. Even though *Gr. camporum* was highly persistent, its floral area fell right at the median. *Clarkia williamsonii* and *Mad. elegans* also performed above the median but were much less dominant. By the third year, three species, *E. californica*, *Ac. millefolium*, and *Gr. camporum*, clearly dominated. Several other species including *Lu. densiflorus*, *N. menziesii*, *C. heterophylla*, *E. lanatum*, and *P. tanacetifolia* still persisted at levels above the median. When considering all three years, only five species consistently performed above the median for both maximum area and phenological coverage: *E. californica*, *N. menziesii*, *C. unguiculata*, *C. williamsonii*, and *P. tanacetifolia* (Figure 5a–c).

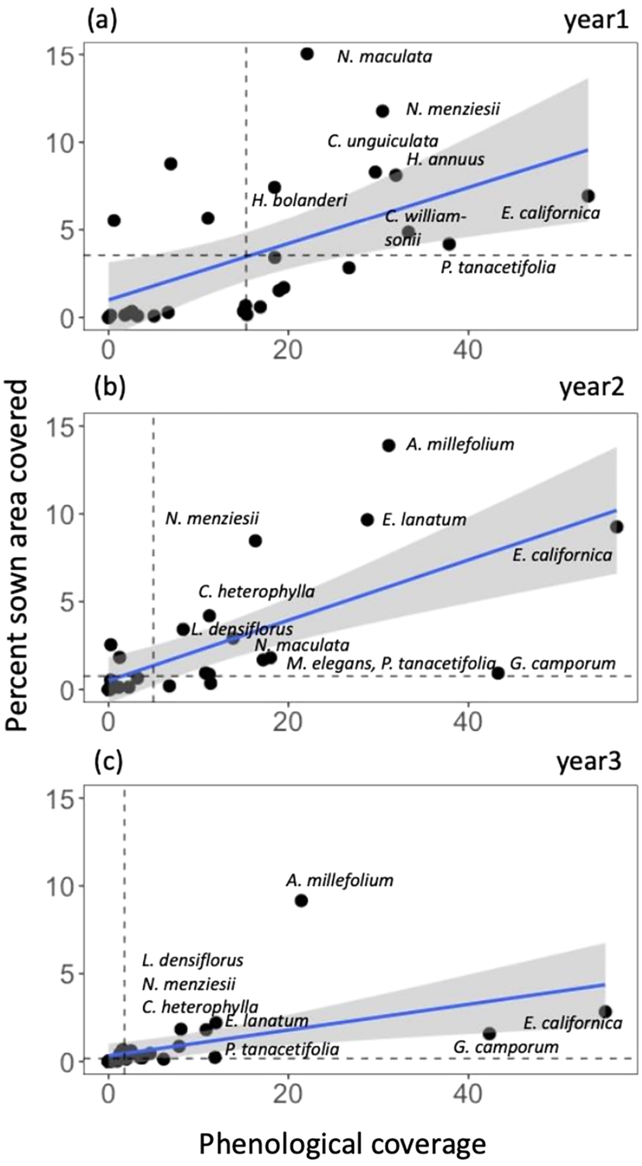

FIGURE 5 Maximum floral area (proportion of sown area covered with flowers during its peak sample round) and phenological coverage (rounds over seasonal threshold) for plant species in each of the three years; dashed lines indicate the medians for each variable. Each point represents one plant species.

Taken together, the results from network analysis and performance in mixes revealed several plant species of high function in supporting bees and competitiveness in mixed planting: *E. californica* outperformed all other species by being of central and specialized importance in the early- and mid-season networks and of consistently high-performing species in mixed plantings. *P. tanacetifolia*, which was of central and specialized importance in the network, performed well in the first year of seed mix applications, although it tapered off subsequently. Other plant species with potential for high function in supporting bees had temporal limitations in seasonal and yearly performance and would require specific management to grow well in mixed species applications. *T. lanceolatum*, for example, which showed high seasonal centrality and importance for specialized bees (Figures 1–3), performed poorly in seed mixes in the first year and did not establish thereafter. *Hel. annuus*, *Hel. bolanderi*, and *Het. grandiflora*, which were of high temporal importance both as central candidate key species and for supporting specialized pollinators, declined after the first year and might require some additional management to persist. *Ac. millefolium* emerged as one of the few dominating species only after the second year and supported specialized interactions in the late season.

In combination, the two evaluations yielded a selection of 8 species with important network roles and strong flowering performance in mixed plantings. Each exceeded overall median metrics in at least two out of three years of the experiment. *Gr. camporum*, *E. lanatum*, *P. tanacetifolia*, and *E. californica* are particularly important candidates. All four were also selected when using abundance and richness metrics. Additional species with high seed mix performance and specialist roles in the network (*Ac. millefolium*, *C. unguiculata*, *Lu. densiflorus*, and *Mad. elegans*) were not selected when exclusively using abundance and richness of visiting bees as selection criteria (Figure 4).

DISCUSSION

Re-evaluating candidate key species selection for pollinator habitat plantings

Flowering habitats grown from seed mixes are widely implemented to support bees and other pollinators (Albrecht et al., 2020; Lowe et al., 2021). In general, the value of different plants for supporting pollinators for such actions is assessed from mixed species plantings (Lundin et al., 2017; Nichols et al., 2019; Warzecha et al., 2018). In this context, plant species' abilities to support pollinators can be conflated with their competitive performance in plant mixtures because more competitive species likely produce larger floral displays that are more attractive to bees (Winfree et al., 2015). As such, some high-functioning plant species would likely be missed using assessments made in mixed plantings because they poorly establish or compete with others. These species could be functionally important for supporting bees and other pollinator species with specific management to establish and maintain them. By separating the assessment of pollinator support from performance in mixes using two complementary datasets, we robustly identified a set of plant species as pollinator foraging resources, as well as species that could be high-performing if managed appropriately. For example, in our study, *T. lanceolatum*, which ranked highly in abundance–richness metrics as well as in importance in network assessment, failed to establish or flower in mixed plantings grown from seed mixes. Thus, for practical purposes, including it in a seed-based wildflower planting would require more elaborate management actions to promote its growth and persistence. In this case, *T. lanceolatum* could have high impact because its role was not duplicated by other plant taxa. After separate tests of attraction and performance, consolidating plant species evaluation criteria improves the effectiveness of conservation measures and also potentially reduces costs as wildflower seeds are expensive (Williams & Lonsdorf, 2018).

We also highlight that species network roles provide a usefully more discrete approach for informing plant choices for seed mixes, or other types of plantings, by identifying central candidate keystone species and species that support specialized bee interactions. Particularly, the latter are inadequately detected by the simpler visitation metrics commonly used as criteria for selecting key pollinator resources (Harmon-Threatt & Hendrix, 2015; Lundin et al., 2017; Nichols et al., 2019; Tuell et al., 2014).

Potential of network approach: Species network roles versus abundance–richness metrics

Supporting and/or restoring plant–pollinator networks as part of restoration actions aims to replicate communities whose interaction patterns resemble natural ones. This goal anchors the species' role in a network as an important selection criterion in conservation efforts (Maia et al., 2019; Russo et al., 2013). Targeting networks with natural characteristics by providing selected floral resources builds on several assumptions. First, this assumes that species' network roles are conserved after introduction in novel communities (Maia et al., 2019). Second, since pollinator species are expected to reassemble at floral resources as long as source populations are present in the local environment (Forup et al., 2008; Potts et al., 2003), it assumes that pollinator community assembly will not be impacted by facilitation and competition (Rathcke, 1983) and interaction patterns are reasonably fixed (Kaiser-Bunbury et al., 2010). Additional evidence is required to confirm what these few case studies have shown so far.

Because simpler metrics like visitor abundance and richness are still commonly used to evaluate plants for inclusion in seed mixes, we compared traditional metrics against emerging network-based metrics across plant species. Traditional and network methods often produced congruent results. Plant species that supported high abundance and species richness of visiting pollinators were among those with the highest centrality scores (core species, see also, Maia et al., 2019). However, it is also important to keep in mind that such core species also have caveats such as being of low floral rewards due to intense competition (Valdovinos et al., 2010, 2013, 2016) or hubs for pathogen transmission (Piot et al., 2020). Furthermore, they may not support all targeted pollinators (Howlett et al., 2021). A desire to select plant species that contribute most to supporting pollinator communities requires a more comprehensive look at species interactions (Borchardt et al., 2021). Our comparison revealed that plant species can play an important role in the network despite low abundance and richness of flower visitors—in particular through their support of specialized pollinators such as oligolectic bees collecting pollen of a specialized range of plant species as demonstrated by *C. unguiculata*, *Lu. densiflorus*, *Ac. millefolium*, and *Mad. elegans*.

Many specialist bees are of high conservation concern due to reported declines (Bartomeus et al., 2013; Burkle et al., 2013) despite a scarcity of data for many taxa and geographic regions (Zattara & Aizen, 2021). Such declines are also concerning for the conservation of whole plant–pollinator networks because specialized interactions are important for the floral structure and evolution (Mathiasson & Rehan, 2020). If specialized interactions go undetected and the plants supporting them are not incorporated in wildflower plantings, this could exacerbate species declines. In general, wildflower plantings often support common generalists rather than rare or threatened species taxa (Arathi et al., 2019; Kleijn et al., 2015; Korpela et al., 2013), perhaps because the design principles used to create them focus on supporting highly attractive plant species (i.e., those that support larger numbers and richness of flower visitors) rather than on those that support rarer specialists. In any case, focusing on generalist bee species alone can eventually impair pollination efficiency as a community of generalists might not be able to provide the same level of pollination service as a community with specialists included (Meldrum et al., 2024).

In order to address the problem, seed mixes can additionally be tailored to support specialist taxa (Haaland et al., 2011). Rare and specialized pollinators might depend on minimum population sizes of their specific host plants (Larsson & Franzén, 2007). As such, network-based metrics that identify plants that tend to host specialists could help design seed mixes that support certain pollinator taxa by providing species-specific foraging profiles as outlined by Russo et al. (2013). Plant species hosting generalists can simultaneously host abundant generalists (Tylianakis et al., 2010).

Plant performance in seed mixes

In order to guarantee resource provisioning for pollinators by candidate key plants, performance in plantings also must be assessed and added as a criterion in plant selection. Previous studies have evaluated the performance of individual plant species in applied pollinator seed mixes (Lybbert et al., 2022; Scheper et al., 2021; Wilkerson et al., 2014) and detected differences between sown and established species composition in a mix as well as differences in individual species' performances (Bretzel et al., 2009; Scheper et al., 2015; Schmidt et al., 2020). Using complementary metrics to identify a set of strong performing plant species for a seed mix can facilitate tailoring mixes for different goals because plant species can provide different profiles that have different impacts on the outcomes. For example, if we sought a species with a long bloom period that persisted over multiple years, our data would suggest that *Gr. camporum*, *Lu. densiflorus*, and *E. californica* may be most promising. If we additionally required species that lasted late into the season, then *Gr. camporum* would be best (see also Wilkerson et al., 2014). If instead, the seed mixes were to be resown on a short-time scale (1–2 years), then *P. ciliata* and *P. tanacetifolia* could be prioritized for early-season and *Hel. bolanderi* or *Hel. annuus* for mid-late season floral resources. *Lu. densiflorus* or *Ac. millefolium*, on the other hand, offer long-term phenology and multi-year persistence while supporting specialized interactions.

Implication for pollinator planting applications

The traditional ecological concept of a keystone species can refer to only one or a few candidates for a particular system (Power et al., 1996 and included references); however, restoration ecology deals with novel systems and aims at effectively building stability and sustainability across an entire community. Plant–pollinator networks show high seasonal turnover in which communities can differ significantly from one season to the other. Key species should therefore be designated with a seasonal perspective and can include long- as well as short-term examples. Therefore, we chose a set of plant species from seasonal networks as candidate key species for our system. We also added a set of candidates supporting specialized interactions.

The application of our presented method considers the conflict between scientific management recommendations and practical resource availability. Recording pollinator visitations, taxonomically identifying specimens, and analyzing extensive plant–pollinator visitation datasets like the one used in the present study require resources like time, funding, and scientific expertise that might not be available in planning, implementing, and evaluating practical restoration projects (see also Bruninga-Socolar et al., 2023; Larson et al., 2014). Therefore, it is noteworthy that simple abundance and richness data can identify the most popular plant species for pollinators and be used in the case of resource constraints. However, plant species that play particular roles in communities, such as supporting specialized visitors, can be missed with these simpler metrics. The present results therefore justify the investment in more extensive network analysis approaches if feasible.

Future perspectives on criteria for candidate key pollinator resource selection

Despite the insights made by applying more detailed metrics for identifying candidate key plant species, they nonetheless leave open approaches that characterize more detailed causal mechanisms for choosing particular plants for mixes. Pollinator resources could be identified with newer approaches that focus on nutritional rewards. Species richness in pollen and nectar can attract a high diversity and abundance of common generalist pollinators such as bumble bees (Carvell et al., 2007; Pywell et al., 2006). However, not only quantity but also quality of pollen and nectar elucidates a plant's value. Bees require both nutritional resources to obtain necessary nutrients like carbohydrates, proteins, lipids, and micronutrients (Brodschneider & Crailsheim, 2010) and also depend on different nutrients throughout their life cycles (Filipiak, 2019). Pollen and nectar quality varied between different host plants (Vaudo et al., 2015), which argues for a consideration of a plant's nutritional value when identifying key pollinator resources (Neece et al., 2023). More plant functional traits impacting practical requirements (Sabatino et al., 2021) could be included in future evaluations. Finally, in the face of climate change, pollinator plantings must consider phenological coverage with regard to potential mismatches (Forrest et al., 2015; Rafferty & Ives, 2011) and integrate them in the network perspective.

CONCLUSION

Instead of simply enhancing plant species richness, integration of a selection of evaluated candidate key resources in mixes can increase cost-effectiveness and sustainability of ecological benefits (Lybbert et al., 2022). Although this has been attempted based on simple visitation approaches (e.g., Williams & Lonsdorf, 2018), species network roles can extend the perspective of candidate key pollinator resource selection and enhance the predominantly used metrics of abundance and richness of visitors with regard to specialized plant–pollinator interactions allowing the identification of crucial additive candidates to key species. There is high value in assessing both performance and species network roles when choosing plant species for pollinator mixes with enhanced resilience and sustainability.

AUTHOR CONTRIBUTIONS

Neal M. Williams and Katherine Borchardt designed the experiment. Uta Müller and Anna Britzman collected data and managed the experiment. Uta Müller developed the data analysis, analyzed the data, and led the manuscript writing. All authors contributed to manuscript writing.

ACKNOWLEDGMENTS

We thank Kimiora Ward, Eric Lonsdorf, and Tina Harrison for input on seed mix study design, Katharina Ullmann for support at UC Davis Student Farm, Grace Milburn for commitment in fieldwork, and Bethanne Bruninga-Socolar and Clara Stuligross for helpful comments on the manuscript. The project was supported by Grant 549032 sub 5805-UCD-FFAR-9032 to Neal M. Williams from the Foundation for Food and Agriculture (FFAR). Additional support came from a gift from the KIND Foundation (KIND Healthy Snacks) to Neal M. Williams and the UC Davis Student Farm.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Müller, 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.17362439.

ORCID

Uta Müller https://orcid.org/0000-0001-7476-3834
Neal M. Williams https://orcid.org/0000-0003-3053-8445

REFERENCES

Albrecht, M., D. Kleijn, N. M. Williams, M. Tschumi, B. R. Blaauw, R. Bommarco, A. J. Campbell, et al. 2020. "The Effectiveness of Flower Strips and Hedgerows on Pest Control, Pollination Services and Crop Yield: A Quantitative Synthesis." *Ecology Letters* 23(10): 1488–98.

Arathi, H. S., M. W. Vandever, and B. S. Cade. 2019. "Diversity and Abundance of Wild Bees in an Agriculturally Dominated Landscape of Eastern Colorado." *Journal of Insect Conservation* 23: 187–197.

Ballantyne, G., K. C. R. Baldock, and P. G. Willmer. 2015. "Constructing more Informative Plant–Pollinator Networks: Visitation and Pollen Deposition Networks in a Heathland Plant Community." *Proceedings of the Royal Society B: Biological Sciences* 282(1814): 20151130.

Balzan, M. V., G. Bocci, and A.-C. Moonen. 2014. "Augmenting Flower Trait Diversity in Wildflower Strips to Optimise the Conservation of Arthropod Functional Groups for Multiple Agroecosystem Services." *Journal of Insect Conservation* 18: 713–728.

Bartomeus, I., J. S. Ascher, J. Gibbs, B. N. Danforth, D. L. Wagner, S. M. Hedtke, and R. Winfree. 2013. "Historical Changes in Northeastern US Bee Pollinators Related to Shared Ecological Traits." *Proceedings of the National Academy of Sciences of the United States of America* 110(12): 4656–60.

Bascompte, J. 2007. "Networks in Ecology." *Basic and Applied Ecology* 8(6): 485–490.

Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. "The Nested Assembly of Plant–Animal Mutualistic Networks." *Proceedings of the National Academy of Sciences of the United States of America* 100(16): 9383–87.

Bates, D. M. 2007. "lme4: Linear Mixed-Effects Models Using S4 Classes." version 09975-13. https://cran.r-project.org/web/packages/lme4/

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. "Measuring Specialization in Species Interaction Networks." *BMC Ecology* 6: 1–12.

Borchardt, K. E., C. L. Morales, M. A. Aizen, and A. L. Toth. 2021. "Plant–Pollinator Conservation from the Perspective of Systems-Ecology." *Current Opinion in Insect Science* 47: 154–161.

Bretzel, F., B. Pezzarossa, S. Benvenuti, A. Bravi, and F. Malorgio. 2009. "Soil Influence on the Performance of 26 Native Herbaceous Plants Suitable for Sustainable Mediterranean Landscaping." *Acta Oecologica* 35(5): 657–663.

Brodschneider, R., and K. Crailsheim. 2010. "Nutrition and Health in Honey Bees." *Apidologie* 41(3): 278–294.

Bruninga-Socolar, B., E. V. Lonsdorf, I. G. Lane, Z. M. Portman, and D. P. Cariveau. 2023. "Making Plant–Pollinator Data Collection Cheaper for Restoration and Monitoring." *Journal of Applied Ecology* 60(9): 2031–39.

Burkle, L. A., C. M. Delphia, and K. M. O'Neill. 2020. "Redundancy in Wildflower Strip Species Helps Support Spatiotemporal Variation in Wild Bee Communities on Diversified Farms." *Basic and Applied Ecology* 44: 1–13.

Burkle, L. A., J. C. Marlin, and T. M. Knight. 2013. "Plant-Pollinator Interactions over 120 Years: Loss of Species, co-Occurrence, and Function." *Science* 339(6127): 1611–15.

Cane, J. H., and S. Sipes. 2006. "Floral Specialization by Bees: Analytical Methods and a Revised Lexicon for Oligolecty." In *Plant-Pollinator Interactions: From Specialization to Generalization*, edited by N. M. Waser, and J. Ollerton, 99–122. Chicago, IL: University of Chicago Press.

Carvell, C., W. R. Meek, R. F. Pywell, D. Goulson, and M. Nowakowski. 2007. "Comparing the Efficacy of Agri-Environment Schemes to Enhance Bumble Bee Abundance and Diversity on Arable Field Margins." *Journal of Applied Ecology* 44(1): 29–40.

de Visser, S., E. Thébault, and P. C. de Ruiter. 2012. "Ecosystem Engineers, Keystone Species." In *Ecological Systems: Selected Entries from the Encyclopedia of Sustainability Science and Technology*, edited by R. Leemans, 59–68. New York: Springer New York.

Dormann, C. F., J. Fruend, B. Gruber, M. C. F. Dormann, T. LazyData, and T. ByteCompile. 2021. "Package 'bipartite'." R-Project.

Filipiak, M. 2019. "Key Pollen Host Plants Provide Balanced Diets for Wild Bee Larvae: A Lesson for Planting Flower Strips and Hedgerows." *Journal of Applied Ecology* 56(6): 1410–18.

Forrest, J. R. K., R. W. Thorp, C. Kremen, and N. M. Williams. 2015. "Contrasting Patterns in Species and Functional-Trait Diversity of Bees in an Agricultural Landscape." *Journal of Applied Ecology* 52(3): 706–715.

Forup, M. L., K. S. E. Henson, P. G. Craze, and J. Memmott. 2008. "The Restoration of Ecological Interactions: Plant–Pollinator Networks on Ancient and Restored Heathlands." *Journal of Applied Ecology* 45(3): 742–752.

Fründ, J., K. S. McCann, and N. M. Williams. 2016. "Sampling Bias Is a Challenge for Quantifying Specialization and Network Structure: Lessons from a Quantitative Niche Model." *Oikos* 125(4): 502–513.

Gill, R. J., K. C. R. Baldock, M. J. F. Brown, J. E. Cresswell, L. V. Dicks, M. T. Fountain, M. P. D. Garratt, et al. 2016. "Protecting an Ecosystem Service: Approaches to Understanding and Mitigating Threats to Wild Insect Pollinators." In *Advances in Ecological Research*, edited by G. Woodward, and D. A. Bohan 54, 135–206. Cambridge, MA: Academic Press.

González, A. M. M., B. Dalsgaard, and J. M. Olesen. 2010. "Centrality Measures and the Importance of Generalist Species in Pollination Networks." *Ecological Complexity* 7(1): 36–43.

Haaland, C., R. E. Naisbit, and L. O. U. I. S.-F. É. L. I. X. Bersier. 2011. "Sown Wildflower Strips for Insect Conservation: A Review." *Insect Conservation and Diversity* 4(1): 60–80.

Hardman, C. J., K. Norris, T. D. Nevard, B. Hughes, and S. G. Potts. 2016. "Delivery of Floral Resources and Pollination Services on Farmland under Three Different Wildlife-Friendly Schemes." *Agriculture, Ecosystems & Environment* 220: 142–151.

Harmon-Threatt, A. N., and S. D. Hendrix. 2015. "Prairie Restorations and Bees: The Potential Ability of Seed Mixes to Foster Native Bee Communities." *Basic and Applied Ecology* 16(1): 64–72.

Hartig, F. 2021. "Package DHARMa." R package. https://cran.r-project.org/web/packages/DHARMa/index.html.

Howlett, B. G., J. H. Todd, B. K. Willcox, R. Rader, W. R. Nelson, M. Gee, F. G. Schmidlin, et al. 2021. "Using Non-bee and Bee Pollinator-Plant Species Interactions to Design Diverse Plantings Benefiting Crop Pollination Services." In *Advances in Ecological Research*, Vol. 64, 45–103. Cambridge, MA: Academic Press.

Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Müller, and A. Caflisch. 2010. "The Robustness of Pollination Networks to the Loss of Species and Interactions: A Quantitative Approach Incorporating Pollinator Behaviour." *Ecology Letters* 13(4): 442–452.

Kleijn, D., R. Winfree, I. Bartomeus, L. G. Carvalheiro, M. Henry, R. Isaacs, A.-M. Klein, et al. 2015. "Delivery of Crop Pollination Services Is an Insufficient Argument for Wild Pollinator Conservation." *Nature Communications* 6(1): 7414.

Korpela, E.-L., T. Hyvönen, S. Lindgren, and M. Kuussaari. 2013. "Can Pollination Services, Species Diversity and Conservation be Simultaneously Promoted by Sown Wildflower Strips on Farmland?" *Agriculture, Ecosystems & Environment* 179: 18–24.

Lane, I. G., C. R. Herron-Sweet, Z. M. Portman, and D. P. Cariveau. 2020. "Floral Resource Diversity Drives Bee Community Diversity in Prairie Restorations along an Agricultural Landscape Gradient." *Journal of Applied Ecology* 57(10): 2010–18.

Larson, D. L., S. Droege, P. A. Rabie, J. L. Larson, J. Devalez, M. Haar, and M. McDermott-Kubeczko. 2014. "Using a Network Modularity Analysis to Inform Management of a Rare Endemic Plant in the Northern G Reat P Lains, USA." *Journal of Applied Ecology* 51(4): 1024–32.

Larsson, M., and M. Franzén. 2007. "Critical Resource Levels of Pollen for the Declining Bee Andrena Hattorfiana (Hymenoptera, Andrenidae)." *Biological Conservation* 134(3): 405–414.

LeBuhn, G., and J. Vargas Luna. 2021. "Pollinator Decline: What Do we Know about the Drivers of Solitary Bee Declines?" *Current Opinion in Insect Science* 46: 106–111.

Lowe, E. B., R. Groves, and C. Gratton. 2021. "Impacts of Field-Edge Flower Plantings on Pollinator Conservation and Ecosystem Service Delivery–A Meta-Analysis." *Agriculture, Ecosystems & Environment* 310: 107290.

Lundin, O., K. L. Ward, D. R. Artz, N. K. Boyle, T. L. Pitts-Singer, and N. M. Williams. 2017. "Wildflower Plantings Do Not Compete with Neighboring Almond Orchards for Pollinator Visits." *Environmental Entomology* 46(3): 559–564.

Lybbert, A. H., S. J. Cusser, K.-L. J. Hung, and K. Goodell. 2022. "Ten-Year Trends Reveal Declining Quality of Seeded Pollinator Habitat on Reclaimed Mines Regardless of Seed Mix Diversity." *Ecological Applications* 32(1): e02467.

Maia, K. P., I. P. Vaughan, and J. Memmott. 2019. "Plant Species Roles in Pollination Networks: An Experimental Approach." *Oikos* 128(10): 1446–57.

Mallinger, R. E., J. G. Franco, D. A. Prischmann-Voldseth, and J. R. Prasifka. 2019. "Annual Cover Crops for Managed and Wild Bees: Optimal Plant Mixtures Depend on Pollinator Enhancement Goals." *Agriculture, Ecosystems & Environment* 273: 107–116.

Mathiasson, M. E., and S. M. Rehan. 2020. "Wild Bee Declines Linked to Plant-Pollinator Network Changes and Plant Species Introductions." *Insect Conservation and Diversity* 13(6): 595–605.

Meldrum, J. R., D. L. Larson, T. B. Hoelzle, and J. E. Hinck. 2024. "Considering Pollinators' Ecosystem Services in the Remediation and Restoration of Contaminated Lands: Overview of Research and its Gaps." *Integrated Environmental Assessment and Management* 20(2): 322–336.

Memmott, J., N. M. Waser, and M. V. Price. 2004. "Tolerance of Pollination Networks to Species Extinctions." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271(1557): 2605–11.

Müller, U. 2025. "Utamue86/https-github.com-Utamue86-pollinatorhabitatresources-releases-tag-PollinatorHabitatResources_UMue: Pollinator Key Resources (Pollinator_key_resources)." Zenodo. https://doi.org/10.5281/zenodo.17362439.

Müller, U., B. Bruninga-Socolar, J. Brokaw, J. Schreiber, D. P. Cariveau, and N. M. Williams. 2024. "Successful Pollinator Seed Mixes Include Low Grass Density and High Forb Richness across a Range of Total Seeding Densities." *Restoration Ecology* 32(8): e14262.

Nayak, G. K., S. P. M. Roberts, M. Garratt, T. D. Breeze, T. Tscheulin, J. Harrison-Cripps, I. N. Vogiatzakis, M. T. Stirpe, and S. G. Potts. 2015. "Interactive Effect of Floral Abundance and Semi-Natural Habitats on Pollinators in Field Beans (Vicia Faba)." *Agriculture, Ecosystems & Environment* 199: 58–66.

Neece, J., J. Brokaw, A. Coker, and B. Bruninga-Socolar. 2023. "Seeding Density of Wildflower Mixes Affects Nectar Production in a Focal Plant Species." *Restoration Ecology* 31(7): e13912.

Nichols, R. N., D. Goulson, and J. M. Holland. 2019. "The Best Wildflowers for Wild Bees." *Journal of Insect Conservation* 23(5): 819–830.

Nicholson, C. C., J. J.-M. Hayes, S. Connolly, and T. H. Ricketts. 2021. "Corridors through Time: Does Resource Continuity Impact Pollinator Communities, Populations, and Individuals?" *Ecological Applications* 31(3): e02260.

Ollerton, J., H. Erenler, M. Edwards, and R. Crockett. 2014. "Extinctions of Aculeate Pollinators in Britain and the Role of Large-Scale Agricultural Changes." *Science* 346(6215): 1360–62.

Paine, R. T. 1995. "A Conversation on Refining the Concept of Keystone Species." *Conservation Biology* 9: 962–64.

Piot, N., G. Smagghe, and I. Meeus. 2020. "Network Centrality as an Indicator for Pollinator Parasite Transmission Via Flowers." *Insects* 11(12): 872.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. "Linking Bees and Flowers: How Do Floral Communities Structure Pollinator Communities?" *Ecology* 84(10): 2628–42.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. "Challenges in the Quest for Keystones." *BioScience* 46: 609–620.

Purvis, E. E. N., L. R. Best, and P. Galpern. 2021. "Identifying Key Forage Plants to Support Wild Bee Diversity and a Species at Risk in the Prairie Pothole Region." *Insect Conservation and Diversity* 14(6): 851–861.

Pywell, R. F., E. A. Warman, L. Hulmes, S. Hulmes, P. Nuttall, T. H. Sparks, C. N. R. Critchley, and A. Sherwood. 2006. "Effectiveness of New Agri-Environment Schemes in Providing Foraging Resources for Bumblebees in Intensively Farmed Landscapes." *Biological Conservation* 129(2): 192–206.

Rafferty, N. E. and A. R. Ives. 2011. "Effects of Experimental Shifts in Flowering Phenology on Plant-Pollinator Interactions." *Ecology Letters* 14(1): 69–74.

Rathcke, B. J. 1983. "Competition and Facilitation among Plants for Pollination." In *Pollination Biology*, edited by L. A. Real. Orlando, FL: Academic Press.

Russo, L., N. DeBarros, S. Yang, K. Shea, and D. Mortensen. 2013. "Supporting Crop Pollinators with Floral Resources:

Network-Based Phenological Matching." *Ecology and Evolution* 3(9): 3125–40.

Sabatino, M., A. Rovere, and P. Meli. 2021. "Restoring Pollination Is Not Only about Pollinators: Combining Ecological and Practical Information to Identify Priority Plant Species for Restoration of the Pampa Grasslands of Argentina." *Journal for Nature Conservation* 61: 126002.

Scheper, J., M. Reemer, R. van Kats, W. A. Ozinga, G. T. J. van der Linden, J. H. J. Schaminée, H. Siepel, and D. Kleijn. 2014. "Museum Specimens Reveal Loss of Pollen Host Plants as Key Factor Driving Wild Bee Decline in The Netherlands." *Proceedings of the National Academy of Sciences of the United States of America* 111(49): 17552–57.

Scheper, J., R. Bommarco, A. Holzschuh, S. G. Potts, V. Riedinger, S. P. M. Roberts, M. Rundlöf, et al. 2015. "Local and Landscape-Level Floral Resources Explain Effects of Wildflower Strips on Wild Bees across Four European Countries." *Journal of Applied Ecology* 52(5): 1165–75.

Scheper, J., T. Bukovinszky, M. E. Huigens, and D. Kleijn. 2021. "Attractiveness of Sown Wildflower Strips to Flower-Visiting Insects Depends on Seed Mixture and Establishment Success." *Basic and Applied Ecology* 56: 401–415.

Schmidt, A., A. Kirmer, K. Kiehl, and S. Tischew. 2020. "Seed Mixture Strongly Affects Species-Richness and Quality of Perennial Flower Strips on Fertile Soil." *Basic and Applied Ecology* 42: 62–72.

Schulte, L. A., J. Niemi, M. J. Helmers, M. Liebman, J. G. Arbuckle, D. E. James, R. K. Kolka, et al. 2017. "Prairie Strips Improve Biodiversity and the Delivery of Multiple Ecosystem Services from Corn–Soybean Croplands." *Proceedings of the National Academy of Sciences of the United States of America* 114(42): 11247–52.

Sutter, L., P. Jeanneret, A. M. Bartual, G. Bocci, and M. Albrecht. 2017. "Enhancing Plant Diversity in Agricultural Landscapes Promotes both Rare Bees and Dominant Crop-Pollinating Bees through Complementary Increase in Key Floral Resources." *Journal of Applied Ecology* 54(6): 1856–64.

Timberlake, T. P., I. P. Vaughan, and J. Memmott. 2019. "Phenology of Farmland Floral Resources Reveals Seasonal Gaps in Nectar Availability for Bumblebees." *Journal of Applied Ecology* 56(7): 1585–96.

Tuell, J. K., A. K. Fiedler, D. Landis, and R. Isaacs. 2014. "Visitation by Wild and Managed Bees (Hymenoptera: Apoidea) to Eastern US Native Plants for Use in Conservation Programs." *Environmental Entomology* 37(3): 707–718.

Tylianakis, J. M., E. Laliberté, A. Nielsen, and J. Bascompte. 2010. "Conservation of Species Interaction Networks." *Biological Conservation* 143(10): 2270–79.

Valdovinos, F. S., B. J. Brosi, H. M. Briggs, P. de Moisset Espanés, R. Ramos-Jiliberto, and N. D. Martinez. 2016. "Niche Partitioning Due to Adaptive Foraging Reverses Effects of Nestedness and Connectance on Pollination Network Stability." *Ecology Letters* 19(10): 1277–86.

Valdovinos, F. S., P. de Moisset Espanés, J. D. Flores, and R. Ramos-Jiliberto. 2013. "Adaptive Foraging Allows the Maintenance of Biodiversity of Pollination Networks." *Oikos* 122(6): 907–917.

Valdovinos, F. S., R. Ramos-Jiliberto, L. Garay-Narváez, P. Urbani, and J. A. Dunne. 2010. "Consequences of Adaptive Behaviour for the Structure and Dynamics of Food Webs." *Ecology Letters* 13(12): 1546–59.

Valiente-Banuet, A., M. A. Aizen, J. M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M. B. García, et al. 2015. "Beyond Species Loss: The Extinction of Ecological Interactions in a Changing World." *Functional Ecology* 29(3): 299–307.

Vaudo, A. D., J. F. Tooker, C. M. Grozinger, and H. M. Patch. 2015. "Bee Nutrition and Floral Resource Restoration." *Current Opinion in Insect Science* 10: 133–141.

Vaudo, A. D., J. F. Tooker, H. M. Patch, D. J. Biddinger, M. Coccia, M. K. Crone, M. Fiely, et al. 2020. "Pollen Protein: Lipid Macronutrient Ratios May Guide Broad Patterns of Bee Species Floral Preferences." *Insects* 11(2): 132.

Warzecha, D., T. Diekötter, V. Wolters, and F. Jauker. 2018. "Attractiveness of Wildflower Mixtures for Wild Bees and Hoverflies Depends on some Key Plant Species." *Insect Conservation and Diversity* 11(1): 32–41.

Wilkerson, M. L., K. L. Ward, N. M. Williams, K. S. Ullmann, and T. P. Young. 2014. "Diminishing Returns from Higher Density Restoration Seedings Suggest Trade-Offs in Pollinator Seed Mixes." *Restoration Ecology* 22(6): 782–89.

Williams, N. M., and E. V. Lonsdorf. 2018. "Selecting Cost-Effective Plant Mixes to Support Pollinators." *Biological Conservation* 217: 195–202.

Williams, N. M., K. L. Ward, N. Pope, R. Isaacs, J. Wilson, E. A. May, J. Ellis, et al. 2015. "Native Wildflower Plantings Support Wild Bee Abundance and Diversity in Agricultural Landscapes across the United States." *Ecological Applications* 25(8): 2119–31.

Winfree, R., and C. Kremen. 2009. "Are Ecosystem Services Stabilized by Differences among Species? A Test Using Crop Pollination." *Proceedings of the Royal Society B: Biological Sciences* 276(1655): 229–237.

Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. "Abundance of Common Species, Not Species Richness, Drives Delivery of a Real-World Ecosystem Service." *Ecology Letters* 18(7): 626–635.

Zattara, E. E., and M. A. Aizen. 2021. "Worldwide Occurrence Records Suggest a Global Decline in Bee Species Richness." *One Earth* 4(1): 114–123.

Zych, M., P. Niemczyk, and R. Niemirski. 2007. "Umbellifers as Potential Keystone Species in Restoration Projects." *Acta Agrobotanica* 60(2): 45–49.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Müller, Uta, Katherine Borchardt, Anna Britzman, and Neal M. Williams. 2025. "Seed Mix Performance and Species Network Roles As a Framework to Select Candidate Key Resources for Pollinator Habitat." *Ecosphere* 16(12): e70492. https://doi.org/10.1002/ecs2.70492