Received: 17 March 2025 | Accepted: 21 October 2025

DOI: 10.1111/1365-2664.70216

Journal of Applied Ecology

RESEARCH ARTICLE

Flowers for habitat enhancement primarily benefit common insect pollinators across temperate grasslands

Will Glenny[1,2] | Jose B. Lanuza[1,3] | Demetra Rakosy[1,2,4] | Emma Ladouceur[1,5,6,7] | Yuping Zhong[1,2] | Tiffany M. Knight[1,2,8,9]

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; [2]Department of Species Interaction Ecology, UFZ-Helmholtz Centre for Environmental Research, Halle, Germany; [3]Mediterranean Institute for Advanced Studies (IMEDEA, UIB-CSIC), Mallorca, Balearic Islands, Spain; [4]Thünen Institute of Biodiversity, Braunschweig, Germany; [5]Department of Biology, University of Prince Edward Island, Charlottetown, Prince Edward Island, Canada; [6]Canadian Centre for Climate Change and Adaptation, University of Prince Edward Island, St. Peter Bay, Prince Edward Island, Canada; [7]School of Climate Change and Adaptation, University of Prince Edward Island, Charlottetown, Prince Edward Island, Canada; [8]Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany and [9]National Tropical Botanical Garden, Kalaheo, Hawaii, USA

Correspondence
Will Glenny
Email: willglenny@gmail.com

Funding information
Alexander von Humboldt-Stiftung; Martin-Luther-Universität Halle-Wittenberg

Handling Editor: Fabrice Requier

Abstract

1. Pollinator habitat enhancement typically relies on flowering species that are possible to cultivate and produce in large quantities, instead of species that fulfil valuable functional roles for plant–pollinator interaction diversity.
2. Using plant–pollinator interaction data from 673 plant–pollinator networks within 17 different studies in temperate grasslands of Europe, we evaluated if native plant genera that are readily available from commercial seed suppliers frequently occur across plant–pollinator networks, are attractive to pollinators and support pollinator assemblages that occupy complementary functional roles in interaction space.
3. Readily available flowers frequently occurred across plant–pollinator networks and were attractive to pollinators. On average, only 8.29 (SE = 0.90) readily available plant genera were required to support most of the pollinator species across all the studies analysed here, compared to 11.53 (SE = 1.64) plant genera with limited availability. However, they fulfilled redundant functional roles within communities by supporting overlapping assemblages of abundant pollinators. Simulated flower mixes of native plant genera that frequently occurred across pollinator networks supported fewer rare and less-selective pollinators than a random selection of plant genera, indicating that revegetation may result in the functional homogenization of pollinator communities.
4. *Synthesis and applications*: Flowers that are attractive and occupy a complementary position in interaction space could be prioritized in flower mixes to recover rare and specialized pollinators. By defining the ecological roles of readily available plants in plant–pollinator networks, particularly those that receive high visitation rates from complementary pollinator communities, this study provides a

practical guide for conserving pollinators with ecologically informed restoration practices.

KEYWORDS
community assembly, complementarity, flower mixes, habitat enhancement, mutualism, pollinator, restoration

1 | INTRODUCTION

Constraints of the seed supply chain limit the plants that can be used to enhance habitats by their suitability to large-scale production, instead of their ability to recover community stability or ecosystem function (Haaland et al., 2011; Kaul et al., 2023; Ladouceur et al., 2018; Zinnen, Barak, et al., 2025; Zinnen & Matthews, 2022). The constraints of the seed supply chain are particularly relevant for flowering plant species that enhance landscapes for pollinators by revegetating areas with plants to provide more pollen and nectar resources (Ranalli et al., 2025). While some seed mixes in Europe favour legumes for the production of nectar, or aim to maximize flower species richness (Müller et al., 2024; Scheper et al., 2013), few are based on quantitative evidence to understand the functional role of flowering plants to improve pollinator diversity (Garbuzov & Ratnieks, 2014; Menz et al., 2011). Consequently, flower mixes for pollinator habitat enhancement are often informed by a combination of best judgement, practical considerations and cost (Rowe, 2010), instead of the functional role of flower species to recover pollinator diversity.

Enhancing pollinator habitats with flowering plants can increase local species richness but may lead to the functional homogenization of pollinator communities across the landscape by supporting pollinators that perform similar ecological roles across interaction networks. Flowering plants that occur across more local populations, have complementary phenologies and an overall longer activity period, and consequently overlap with a wide range of generalist and specialist pollinators (Chacoff et al., 2018; Peralta et al., 2020; Resasco et al., 2021). Enhancing landscapes by introducing a few flowering plant species that establish across many pollinator networks could increase floral cover, and consequently, the chances that floral resources are available to most of the pollinator species. However, enhancing landscapes with the same subset of flowering plant species across local communities potentially leads to the biotic homogenization of floral communities (Holl et al., 2022), with unknown effects on the structure of plant–pollinator interaction networks. Homogenous plant communities may strengthen interactions with species from the overall community that share pollination behaviours, leading to the reciprocal biotic homogenization of higher trophic levels. Flowering plants that are attractive to pollinators from a wide range of taxonomic and functional groups can enhance habitats to support diverse pollinator communities.

Land managers often face the challenge of maximizing outcomes of habitat enhancement while balancing the cost of plant materials, making it important to prioritize flowers in mixes that support complementary pollinator assemblages (Williams & Lonsdorf, 2018). A flowering plant occupies a position in interaction space depending on the composition of pollinator visitors, relative to other flowering plants in a community. Flowers that are 'original' attract pollinators that are far from the community average in interaction space, while plants that are 'unique' are visited by pollinators that are different from the next most similar plant species in interaction space (Buisson et al., 2013; Burkle et al., 2020; Figure 1). Given the limited number of flower species that can be included in mixes, prioritizing flower species with non-overlapping pollinator assemblages—like those that attract original or unique pollinator assemblages—can enhance pollinator diversity and rebuild interaction network structure in line with specific goals (Blüthgen & Klein, 2011; Devoto et al., 2012; Ladouceur et al., 2022). Understanding the relationship between how frequently flowers appear in pollinator networks, and the uniqueness and originality in interaction space, could improve flower mix design to enhance landscapes for pollinators at appropriate spatial scales.

We used seed supply data from Ladouceur et al. (2018) to identify flowering plant genera that are readily available from seed suppliers in Europe, and integrated these data with a European database of plant–pollinator interaction studies (Lanuza et al., 2025b) to evaluate whether flowering plants for pollinator habitat enhancement also occur frequently across pollinator networks, and if the frequency of occurrence influences pollinator visitation patterns to these flowers. We hypothesized that readily available flowers occurred more frequently across pollinator networks and supported more pollinator species, than flowers that are less available from seed suppliers (Cavender-Bares et al., 2020; Zinnen & Matthews, 2022). Even though frequently occurring flowers may interact with a wide range of pollinator species, they potentially decrease pollinator community diversity by strengthening interactions with a similar subset of the pollinator community (Carstensen et al., 2016; Peralta et al., 2020; Vazquez et al., 2009). Thus, we hypothesized that there was a negative association between the occurrence of flowers across pollinator networks, and originality in interaction space, because these flowers strengthened interactions with functionally similar subsets of mainly generalist pollinators (Buisson et al., 2013; Parra et al., 2022; Peralta et al., 2020). Lastly, pollinator visitation data was compared between simulated flower mixes of plants that occur frequently in pollinator networks, to a random selection of flowers, to understand if habitat enhancements for pollinators supported fewer

Journal of Applied Ecology

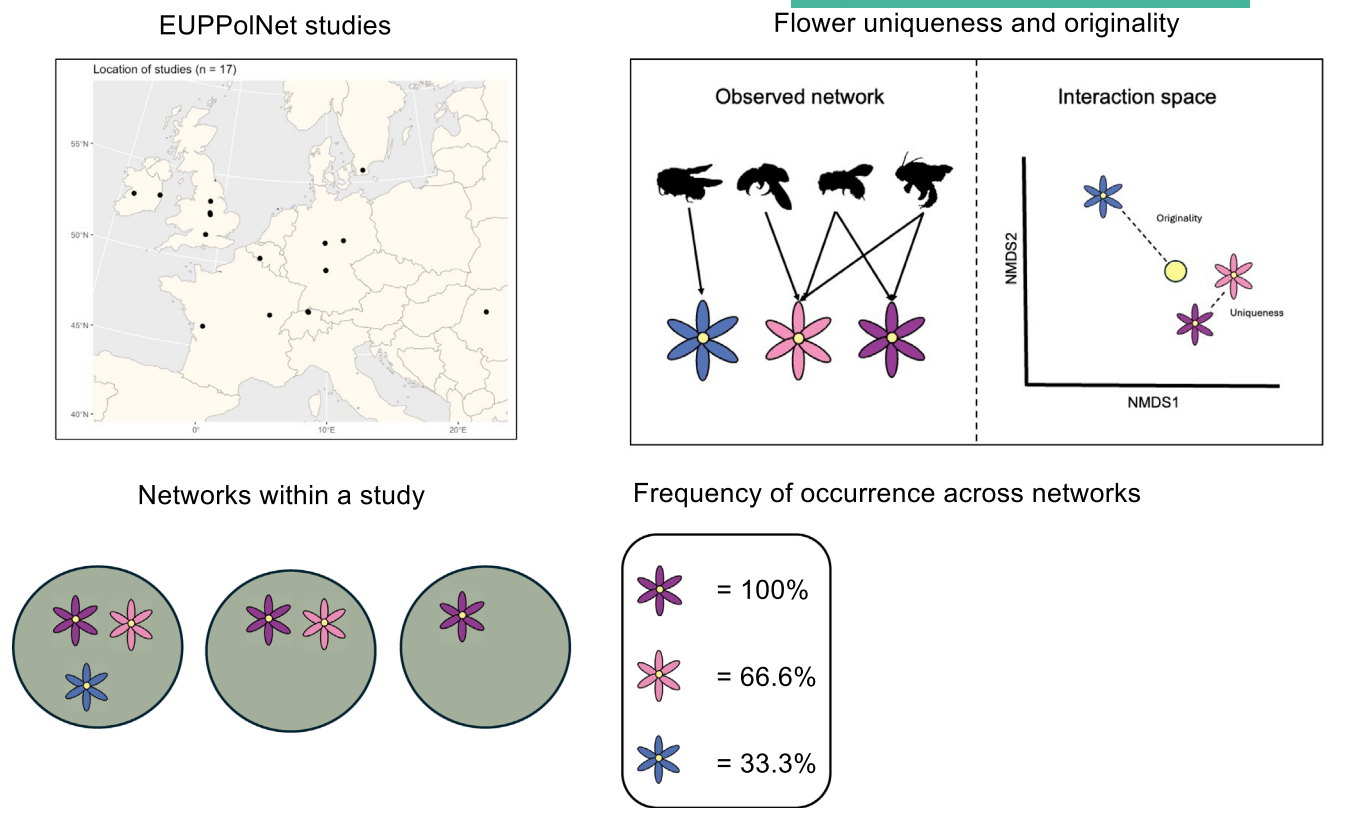

FIGURE 1 Within each study of the EuPPollNet database, the frequency of occurrence across networks was calculated for each flower species. Based on the identity and abundance of pollinators visiting a flower species in a study (right), originality is the distance of a flower from the community mean (left; yellow dot) in interaction space, and uniqueness is the distance to the nearest neighbour in interaction space.

rare and less specialized pollinator species. Results indicate that readily available flowers occur frequently across pollinator networks and support taxonomically diverse pollinator species. However, mixes of frequently occurring flowers are likely to support fewer rare and less selective pollinators, potentially leading to the functional homogenization of pollinator communities. To increase the availability of flowers that support rare pollinators, we highlight a number of flower genera that have high visitation rates and uniqueness as candidates to improve flower mixes for whole pollinator communities.

2 | MATERIALS AND METHODS

2.1 | Readily available plant genera in Europe

The plant species list from Ladouceur et al. (2018) was used to identify flowering plant genera that are native to the EU and readily available from commercial seed suppliers in Europe. In brief, a list of native plant species cultivated by commercial operations was compiled through a literature search and surveying seed suppliers in Europe ($n = 17$ suppliers, $n = 1122$ plant species). Seed suppliers were from 17 countries (Ladouceur et al., 2018) and spanned all major biogeographical regions of the European continent and islands. Flowering plant genera were readily available if they were defined in Ladouceur et al. (2018) as 'commercially available' and produced by more than 40% of seed suppliers. We used 40% as a cut-off so that *Trifolium*, which is a genus that is known to be ubiquitous for commercial applications worldwide, was included as a readily available genus. This selection criteria resulted in 44 readily available plant genera (Table S1), with genera representing 3.95 species/genus (SE = 0.49). While we acknowledge that interspecific variation within genera exists in plant traits, the genus level is considered the most practical for pollinator enhancement recommendations because most species within the genus have similar benefits for pollinators (Garbuzov & Ratnieks, 2014).

2.2 | Plant–pollinator visitation data

Pollinator visitation patterns and the frequency of plant genera across plant–pollinator networks were described using the European Plant-Pollinator Networks database (EuPPollNet; Lanuza et al., 2025b). EuPPollNet contains 623,476 plant–pollinator interactions from 1522 local plant–pollinator networks across the European continent. These networks belong to 54 independent studies conducted between 2004 and 2021 that document interactions of the main insect floral visitors occurring in Europe.

To ensure that pollinator visitation patterns to plant genera were reliably sampled and comparable across studies, EuPPollNet was filtered by studies that sampled plant–pollinator interactions using a transect method, had more than 10 distinct local networks and targeted entire pollinator communities. Only studies from the Continental or Atlantic bioregion were included to standardize the interaction data to temperate grasslands of Europe. Only interactions from individuals belonging to three of the main orders of European pollinators were included (Hymenoptera, Diptera and Lepidoptera) (Willemstein, 1983), and honeybees (*Apis mellifera*) were excluded because the abundance of these species within communities is mainly dependent on anthropogenic activities (60.0% of all interactions in EuPPollNet). As a result of this selection criteria, there are $n = 17$ studies with $n = 673$ total local networks, and the number of local networks per study ranged between 12 and 113 (median = 21) (Table S2; Figure S1).

2.3 | Flower frequency across pollinator networks

Flower frequency across pollinator networks was assigned to each plant genus within a study based on the number of local networks where a plant genus was detected, relative to the plant genus that was detected in the most local networks (Mouillot et al., 2013; Simpson et al., 2022). Standardized flower frequency ranged between 0.01 and 1.00, but was also defined categorically to establish an easily identifiable benchmark for land managers. Plant genera with a standardized frequency in pollinator networks of 50% or more were considered 'frequent', which was 17.6% of plant genera across all studies (Figure S2).

2.4 | Pollinator assemblages visiting plant genera

To describe the position of flower genera in interaction space, pollinator visitations to a plant genus were aggregated across all local networks within a study into a single regional-level metaweb. Aggregating interactions across a study was required to record the full range of pollinator species that visit a plant genus. We excluded any plant genus from a study that received fewer than five total visitations within the regional-level metaweb, because there was not enough data to reliably describe the pollinators these plants support (range = 27.5%–66%, median = 42% of plant genera in a study). Our results are robust to this visitation threshold because the extremely long right-tailed distribution of total visitations to plant genera does not change despite excluding plants with low pollinator visitation (Figure S3).

The rarity and specialization of pollinator species were estimated within each study, to understand if plant genera that frequently occur across pollinator networks are likely to support taxonomic and functionally diverse pollinator assemblages. Rare pollinators were defined as any species accounting for less than 1% of total interactions in a study (Simpson et al., 2022). Specialization of pollinators was calculated using the weighted metric d' (Blüthgen et al., 2006) and unweighted metric normalized degree (ND) to fully characterize the diet breadth of species.

2.5 | Analyses

2.5.1 | What plant genera frequently occur across pollinator networks?

We tested the hypothesis that readily available plants frequently occur across local pollinator networks, by comparing the mean standardized frequency in networks between readily available plant genera and plant genera with limited availability using a *t*-test. To ensure that the result was robust against our decision on how to define a readily available plant, we manipulated the threshold and re-ran the analysis. Next, we tested the hypothesis that readily available plant genera support more pollinator species, than plant genera with limited availability. Using the species accumulation curves of plant genera that are readily available or have limited availability within each study, we measured pollinator species richness supported by an equivalent number of plant genera in each group, which was defined by the number of readily available genera in a study. A *t*-test with study as a random effect was used to compare means.

2.5.2 | How is frequency of occurrence related to originality and uniqueness in interaction space?

Originality is the difference in interaction space between a plant and the average position of other co-occurring plants in the community (Figure 1) (Buisson et al., 2013; Burkle et al., 2020). To estimate the originality of each plant genus within a study, a distance and dissimilarity matrix was made based on the observed plant–pollinator interactions. Some networks were large and contained many plants that did not share any pollinator species Extended dissimilarities were thus required to estimate dissimilarity between plant genera. A Principal Coordinates Analysis (PCoA), with the distance of each plant genus to the overall community centroid was used to estimate originality.

Uniqueness is the distance in interaction space between a plant and the next most similar plant genus co-occurring in a community (Figure 1) (Buisson et al., 2013; Burkle et al., 2020). Based on the PCoA from above, we calculated the mean distance to all other plant genera in NMDS space within a study.

We used a Pearson's correlation to exclude a potential correlation between originality and uniqueness (Pearson's correlation = 0.11). Following a non-significant correlation, separate linear mixed effects models were used to investigate the relationship between the frequency of a flower across networks and status as a readily available plant, on pollinator uniqueness and originality. Originality and uniqueness were both response variables, with plant frequency and status as a readily available plant as main effects. Study and

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology

plant genus were separate crossed random effects to account for repeated sampling of the same plant genera across studies and different plant genera within the same study. Originality and frequency of occurrence across pollinator networks were log transformed to ensure normality. Separate two-way ANOVAs were used to test for a significant association between covariates and response variables, followed by a *t*-test using Satterthwaite's method to approximate degrees of freedom.

2.6 | Flower mixes for pollinator habitat enhancement

Flower mixes support an increasing number of pollinators with more species but based on the cost constraints of purchasing plant materials, flower species richness has limiting returns for pollinator diversity (Harmon-Threatt & Hendrix, 2015; M'Gonigle et al., 2017; Otto et al., 2017; Williams et al., 2015). We aimed to understand if flower mixes of plants that occur frequently across pollinator networks support specialized and rare pollinator species, by comparing the mean generalization and rare species richness of pollinator assemblages between 10 frequent and randomly selected plant genera. We acknowledge that flower mixes can include more or less than 10 flower genera depending on the resources available to land managers but believe this is a realistic number based on published evidence (Harmon-Threatt & Hendrix, 2015; M'Gonigle et al., 2017; Otto et al., 2017; Williams et al., 2015). Only studies that had 10 or more plant genera that frequently occurred across networks ($n = 9$ studies) were included for this exercise. Within each study, 10 frequently occurring plant genera were randomly drawn without replacement to represent a flower mix, and the associated pollinator interactions were included to represent the pollinator community supported by the flower mix. For each random draw of plant genera, we calculated the mean normalized degree (ND; number of unique plant genera relative to the total plant genera in a network) and selectivity (d') of all pollinator species and the number of rare species per interaction. The richness of rare pollinators was divided by the total interactions associated with the 10 randomly selected plant genera (random species seed mix), to understand how well plants that frequently occur across pollinator networks support rare pollinators standardized by interaction frequency. This process was then repeated with 10 randomly selected plant genera. The selection of 10 frequently occurring and random plant genera was repeated 100 times for each study.

The direction and magnitude of the effects of flower mixes with frequently occurring plants on mean pollinator ND, selectivity and rare species richness were compared by calculating *Z*-score standardized effect sizes. For each study, the mean pollinator value (richness of rare species, ND and selectivity) from each run of the random-species flower mix was subtracted from the mean value of each run of the frequently occurring species flower mix, and then divided by the standard deviation of the pollinator value across all runs of the random-species flower mix. The mean and 95% confidence intervals were plotted. Based on the density distribution of rare pollinators across all studies (Figure S4), we re-ran this analysis when categorizing pollinators as rare if they participated in 0.5% (as opposed to 1%) of interactions and compared the results finding no differences (Figure S5). Additionally, we manipulated the threshold to define frequent plants and re-ran the analysis to determine how sensitive the results were to our decisions.

2.7 | Recommendations for attractive and unique flower genera

To provide recommendations for flowers that are attractive and unique within flower mixes, we identified all the cases of plant genera in the top 15th, 25th, 35th and 45th percentiles of visitation rates and uniqueness values. We report the mean number of plant genera that were attractive and unique as a proportion of all plant genera within a family at the 25th percentile, to identify families with the most realistic potential to reach restoration end goals for commercial cultivation. No ethical approval was required for this study.

3 | RESULTS

3.1 | What flower genera frequently occur across pollinator networks?

Pollinator visitation was observed in 169/332 (50.9%) plant genera provided by seed producers, and only 17.2% of these plant genera are readily available. Readily available flower genera occurred in more pollinator networks than flower genera with limited availability (Figure 2a). Across all studies, the mean frequency of occurrence in pollinator networks of readily available flower genera was 0.86 times greater than that of flower genera with limited availability (*t*-test, SE = 0.17, $t\text{-value}_{df=254} = 5.9$, $p < 0.001$) (Figure S6) and was robust against the threshold to define readily available genera (Figure S7). On average, the same number of readily available flower genera supported 18.59 more pollinator species (LMER *t*-test, SE = 4.95, $t\text{-value}_{12.47} = 12.47$, $p = 0.003$) than less available plant genera (Figure 2b).

3.2 | How is frequency of occurrence related to originality and uniqueness in interaction space?

There was no association between the originality and uniqueness of flower genera (Figure 3a). Originality was negatively associated with the frequency of occurrence across networks (LMER *t*-test, est = −0.06, SE = 0.005, $t\text{-value}_{860} = -13.09$, $p < 0.001$) but not with the availability from seed suppliers (LMER *t*-test, est = 0.003, SE = 0.01, $t\text{-value}_{109} = 0.32$, $p = 0.73$) (Figure 3b). Uniqueness was not associated with the frequency of occurrence across pollinator networks (LMER *t*-test, est = 0.02, SE = 0.03, $t\text{-value}_{782} = 6.82$, $p = 0.47$),

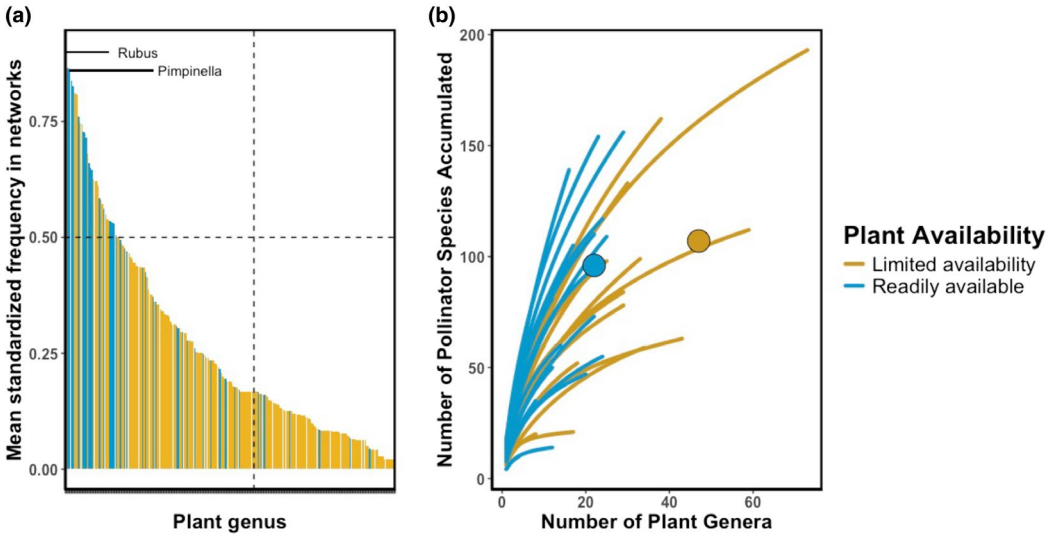

FIGURE 2 (a) Bar plot illustrating the distribution of the mean frequency of occurrence (*y*-axis) of readily available (blue) and limited availability (gold) plant genera (*x*-axis). Bar height represents the mean frequency of occurrence of a plant genus across all studies where it was detected. Dashed lines are the 50th percentile. (b) Species accumulation curves of the number of pollinator species (*y*-axis) for readily available (blue) and limited availability (gold) plant genera (*x*-axis). Points indicate the mean number of flower genera and number of pollinator species accumulated across all studies.

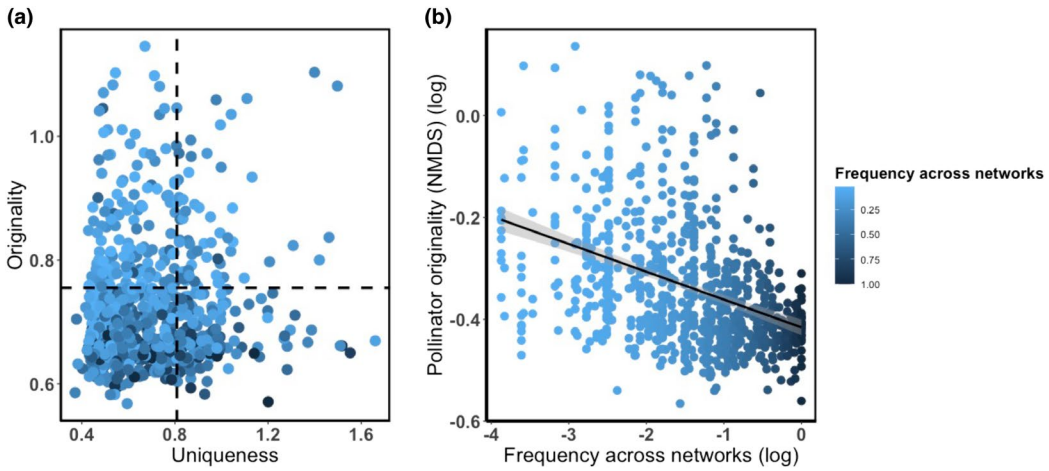

FIGURE 3 (a) Relationship between the visiting pollinator assemblage uniqueness (*x*-axis) and originality (*y*-axis) for plant genera in a study. Darker blue points are plant genera that occur across more pollinator networks. Dashed lines are the 50th percentile of uniqueness and originality. (b) The pollinator assemblage originality (*y*-axis) declines as plants occur more frequently across pollinator networks (*x*-axis).

or the availability from seed suppliers (LMER *t*-test, est = 0.02, SE = 0.02, $t\text{-value}_{772} = -1.30$, $p = 0.21$).

3.3 | Flower mixes for pollinator habitat enhancement

Flower mixes of plants that frequently occur across pollinator networks supported less-selective pollinators in 7/9 of studies and had a lower richness of rare pollinator species in 8/9 studies (Figure 4). This effect was stronger on the taxonomic diversity compared to the selectivity of the pollinator community, with a 50.3% stronger reduction in rare species richness compared to pollinator selectivity. Plants that frequently occur across networks were visited by more- or less-generalized pollinators in 5/9 studies. Less-restrictive thresholds (i.e. 20%) result in a higher number of flower genera that are common, and flower mixes are more likely to resemble the pollinator assemblage visiting random flowers (Figure S8).

3.4 | Recommendations for attractive and unique flower genera

Across all studies, there were only 47 cases where a plant genus was in the top 25th percentile of pollinator uniqueness and visitation

Journal of Applied Ecology

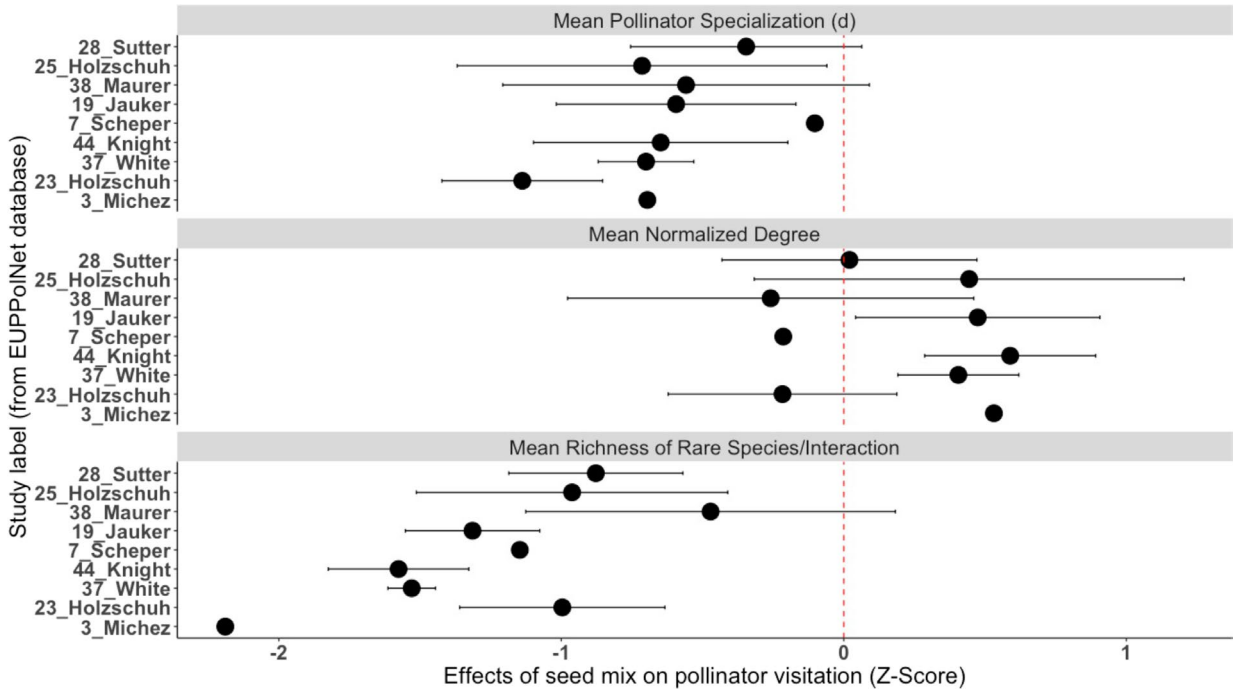

FIGURE 4 Standardized Z-scores for the effects of flower mixes of frequently occurring plants on pollinator selectivity (*d′*; top), normalized degree (middle) and mean richness of rare species (bottom). For each study (*y*-axis), the magnitude and direction of the effects of flower mix was measured using standardized Z-scores (*x*-axis). The red dashed line indicates the population mean of the response variable centred at zero. A result was considered significantly different than random if the 95% error bars did not overlap with zero.

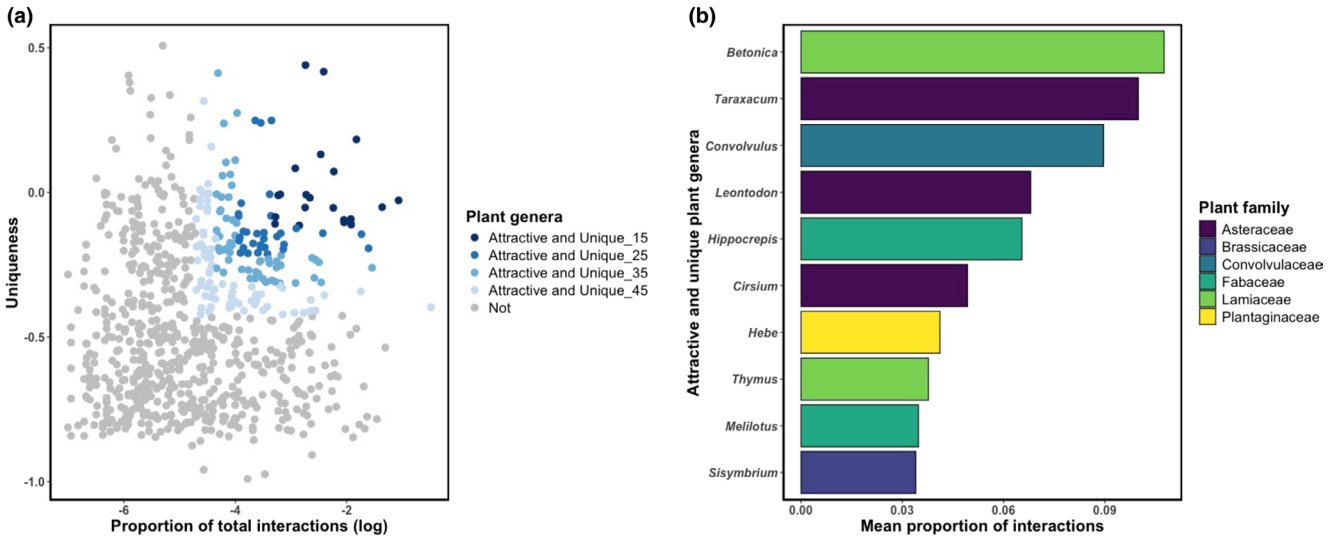

FIGURE 5 (a) Flower genera that are in the top 15th, 25th, 35th and 45th percentiles of attractive (*x*-axis) and uniqueness (*y*-axis). (b) Ten of 25 Flower genera (*y*-axis) that are in the top 25th percentile of attractive and uniqueness but have limited availability from seed suppliers. Bars are coloured depending on the family of the plant genus.

rate (Figure 5a). Among plant genera with limited availability for restoration but are attractive to unique pollinator assemblages, seed suppliers may consider plant genera from six families for production (Figure 5b). Specifically, 27.5% of the most attractive and unique flower genera belong to the Asteraceae family (Figure S9a). As a percentage of the flower genera within the family visited by pollinators, Convolvulaceae, Geraniaceae and Ranunculaceae, had the most genera that were attractive and unique (Figure S9b).

4 | DISCUSSION

We aimed to understand if flowers that are readily available from commercial seed suppliers occur frequently across local pollinator networks, and whether these flowers strengthen interactions with functionally similar subsets of generalist pollinator species. We found that readily available plant genera from European seed suppliers were also taxa that occur frequently across local pollinator networks.

Naturally widespread plants may have traits that are conducive to the commercial seed supply chain, like long-lived seeds that readily germinate, and aesthetically pleasing flowers with a reliable market demand. Readily available flowers that occur frequently across pollinator networks supported more pollinator species than plants with limited availability. This may be because flowers that persist across time and space receive high pollinator visitation by sharing activity periods with many pollinator species (Chacoff et al., 2018; Resasco et al., 2021; Vázquez et al., 2007), and only a few readily available flower genera are required to support most of the pollinators in a community. However, the originality of flowers in interaction space declined as flowers occurred more frequently across networks, suggesting that these plants may serve as hubs of network modules, and strengthen interactions with similar subsets of the pollinator community (Olesen et al., 2007). Additionally, rare pollinator richness and selectivity were lower for flower mixes composed of plants that frequently occur across pollinator networks compared to a random selection of plants in the community. Readily available plant genera may strengthen interactions with common and less-selective pollinator species, but neglect rare specialists which are often a target of conservation (Nichols et al., 2022; Wood et al., 2017). Therefore, recovering pollinator diversity may depend on the capacity to identify, cultivate and incorporate plant materials into seed mixes that support rare and specialized pollinator assemblages.

Readily available flower genera from commercial seed suppliers in Europe occurred frequently across plant–pollinator interaction networks and supported many pollinator species, indicating that increasing floral cover benefits pollinator abundance and richness. Plants that occupy many local communities have complementary activity periods and provide consistent floral resources for pollinators across space and time by persisting across the landscape (Havens & Vitt, 2016; Ogilvie & Forrest, 2017; Zinnen, Barak, et al., 2025). Our study demonstrates that plants which occur frequently across networks form more interactions, likely because species interact proportionally to their abundances (Vázquez et al., 2007). For these reasons, it takes proportionally fewer frequently occurring plant species to support a majority of the pollinator community, which is consistent with other flower mixes (Burkle et al., 2020; Glenny et al., 2023; Nichols et al., 2023; Warzecha et al., 2018). Pollinator habitat enhancements could benefit species richness simply by improving flower cover. By contrast, most flowers are rare and receive low pollinator visitation. It could be that specialized flowers also have a narrow range of habitat requirements. As the number of flowers within mixes increases, so does the overall pollinator species richness, with an increasing likelihood that some pollinator species are rare.

Only 17.2% of all plant genera visited by insect pollinators are readily available from commercial seed suppliers in Europe. This finding is consistent with previous studies reporting a limited diversity of all the potential plant species available for restoration (i.e. 'the restoration species pool') (Kaul et al., 2023; Ladouceur et al., 2018; White et al., 2018; Zinnen, Chase, et al., 2025; Zinnen & Matthews, 2022). Hay transfer, the translocation of plant material harvested from species-rich donor sites, or spontaneous colonization can increase the potential number of species colonizing local sites but may still be insufficient to fully recover diversity in local communities. Hay transfer excludes rare species with unique germination requirements (Wagner et al., 2021), donor sites may be unavailable and seed banks in Europe may be depauperate due to a legacy of disturbance, over-fertilization and climate change pressures (Auffret et al., 2023). Improving cold stratification, embryo development and seed longevity techniques may expand the pool of species that can practically be used in pollinator habitat enhancement projects to include plants with unique germination requirements (Jiménez-Alfaro et al., 2016).

Originality was negatively associated with the frequency of flowering plants in pollinator networks, indicating that plants that are rare across local communities form interactions with pollinator species that occupy a distinct niche in functional interaction space. The pollinator assemblage visiting these plants may have unusual morphological or behavioural traits that are not already supported by plant species that occur more across pollinator networks (Kondratyeva et al., 2019), and are frequently neglected by habitat enhancements (Nichols et al., 2022; Wood et al., 2017). Consequently, rare plants occupy an important role in interaction space by supporting pollinators that are complementary to the community average (Blüthgen & Klein, 2011). Plants with high originality in interaction space may be less nested (Resasco et al., 2021; Vázquez et al., 2007), and may be less strongly associated with a network topology that is consistent with community stability (Glenny et al., 2023; Menz et al., 2011). Furthermore, we did not observe an association between the frequency of occurrence and pollinator assemblage uniqueness. Instead, there may be a correlation between uniqueness in floral trait space (visual, olfactory or gustatory cues), and interaction space, to support rare and specialized pollinators (Burkle & Runyon, 2019). Commercial seed supply companies that can cultivate flowers with unique traits in interaction space could improve the availability of functionally important plants for pollinator habitat enhancement.

To aid practitioners in prioritizing plants that maximize pollinator diversity with revegetation seed mixes, we identified flower genera that were both attractive and occupied unique positions in interaction space. Land managers are often restricted by the cost of acquiring plant materials to a limited number of plant genera that can be included within seed mixes for pollinator habitat enhancement and must choose the genera that provide the greatest cost–benefit ratio for pollinators (Harmon-Threatt & Hendrix, 2015; M'Gonigle et al., 2017; Otto et al., 2017; Williams et al., 2015). While the role of plants for pollinator restoration exists along a spectrum, land managers must evaluate their budgets and choose the number of species to meet their end goals. Among the 25th percentile of plants that are unique and attractive, Convolvulaceae, Geraniaceae and Ranunculaceae had the highest percentage of flower genera. While these plant families share flowers that are morphologically similar (radially symmetrical with open anthers), nutritional profiles (Pioltelli et al., 2024; Vaudo et al., 2020) and/or olfactory signals are additional dimensions of flower–pollinator interactions that may determine the

uniqueness of a flower in interaction space. It is also worth noting that our analysis took place at the genus level, when the position of a flower in interaction space may be better resolved by traits that vary more at the interspecific level. By contrast, there were flowers that were frequent and less available by seed suppliers (Supplemental Table 3). Genera like *Ribes*, *Cirsium*, *Carduus* and *Taraxacum* were attractive for pollinators, but could be a nuisance for landowners, and therefore undesirable for habitat enhancements associated with other management goals, like grazing. While we did not consider the role of plants that are ornamental or exotic to the EU for pollinator habitat enhancement, their visually striking floral morphologies and ease of cultivation, could potentially fulfil unique positions in interaction networks. The prioritization of unique plant species in restoration seed mixes may be important to achieve restoration end goals associated with rare and specialized pollinators (Ladouceur et al., 2022).

Selectivity and richness of rare pollinators were lower for mixes of flowers that frequently occur in pollinator networks compared to random, indicating that pollinator habitat enhancement is likely to support a few abundant pollinators that account for most of the interactions in a network. Abundant pollinators with diet flexibility that forage opportunistically have more chances to form interactions with different floral partners. We found contrasting results depending on the use of weighted (*d′*) and unweighted (ND) metrics of specialization. Weighted metrics are influenced by interaction frequency, so plants appear as if they support a generalist pollinator assemblage if generalist pollinators account for most of the visitations to a plant genus. By contrast, unweighted metrics are influenced equally by each pollinator visitor and potentially reduce the importance of abundant pollinators for the interaction patterns to a flower. Consequently, frequently occurring plants are visited heavily by generalist pollinators, but also by a wide range of pollinator species that co-occur in lower abundances. Interestingly, there was a stronger negative association of mixes with frequently occurring plants on rare species richness compared to mean pollinator selectivity, suggesting that taxonomic diversity may decline more rapidly than interaction diversity as a result of revegetation. This may be a result of the flexible and nested nature of plant–pollinator interaction networks where many rare pollinator species can be extirpated while still maintaining the overall structure of interaction networks (Petanidou et al., 2008). Additionally, we only included studies from the Continental and Atlantic bioregions of Europe, which excludes regions like the Mediterranean where beetles likely contribute to network structure (Lanuza et al., 2025b). Flower mixes for pollinator habitat enhancement must balance the cost–benefit ratio of supporting abundant generalists, potentially at the expense of rare specialists.

In conclusion, pollinator habitat enhancement in temperate grasslands of Europe using readily available plants from commercial seed suppliers will likely have congruent effects on the pollinator community by supporting abundant pollinator species. Frequently occurring flowers have high visitation richness and abundance but fulfil redundant functional roles within flower mixes by sharing pollinator assemblages with co-occurring flower genera. Frequently occurring flowers are still likely to support many common pollinators but are less suited to support rare specialists. Seed supply pipelines that emphasize functionally important plants for pollinator community assembly are likely to provide land managers with the materials to restore resilient and stable biotic communities.

AUTHOR CONTRIBUTIONS

Will Glenny conceptualized the study, wrote the first draft, and analysed the data; Jose B. Lanuza contributed to the conceptualization analysis and writing; Demetra Rakosy and Emma Ladouceur contributed data and helpful comments; Tiffany M. Knight contributed to the conceptualization and provided leadership; and Yuping Zhong provided helpful discussions and comments.

ACKNOWLEDGEMENTS

We thank all the contributors to the EUPPolNet database for public access to their data, and Dr. Ignasi Bartomeus and members of the Species Interaction Ecology group at iDiv for important comments to improve this manuscript. Will Glenny was funded by the Alexander von Humboldt Foundation post-doctoral research fellowship, Jose B. Lanuza was funded by Martin Luther University Halle-Wittenberg Support Fund for integrative Biodiversity Research in Saxony-Anhalt (MLU|BioDivFund). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available at Zenodo https://doi.org/10.5281/zenodo.15183272 (Lanuza et al., 2025a).

STATEMENT ON INCLUSION

Our study was a continental synthesis of plant–pollinator interactions, which brings together scientists and data from diverse geographical, socio-economic and cultural regions.

ORCID

Will Glenny https://orcid.org/0000-0002-2522-3775
Jose B. Lanuza https://orcid.org/0000-0002-0287-409X
Emma Ladouceur https://orcid.org/0000-0002-4943-4358

REFERENCES

Auffret, A. G., Vangansbeke, P., De Frenne, P., Auestad, I., Basto, S., Grandin, U., Jacquemyn, H., Jakobsson, A., Kalamees, R., & Koch, M. A. (2023). More warm-adapted species in soil seed banks than in herb layer plant communities across Europe. *Journal of Ecology*, *111*, 1009–1020.

Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, *12*, 282–291.

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*, 1–12.

Buisson, L., Grenouillet, G., Villéger, S., Canal, J., & Laffaille, P. (2013). Toward a loss of functional diversity in stream fish assemblages under climate change. *Global Change Biology*, *19*, 387–400.

Burkle, L. A., Delphia, C. M., & O'Neill, K. M. (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., & Runyon, J. B. (2019). Floral volatiles structure plant–pollinator interactions in a diverse community across the growing season. *Functional Ecology*, *33*, 2116–2129.

Carstensen, D. W., Sabatino, M., & Morellato, L. P. C. (2016). Modularity, pollination systems, and interaction turnover in plant-pollinator networks across space. *Ecology*, *97*, 1298–1306.

Cavender-Bares, J., Padullés Cubino, J., Pearse, W. D., Hobbie, S. E., Lange, A., Knapp, S., & Nelson, K. C. (2020). Horticultural availability and homeowner preferences drive plant diversity and composition in urban yards. *Ecological Applications*, *30*, e02082.

Chacoff, N. P., Resasco, J., & Vázquez, D. P. (2018). Interaction frequency, network position, and the temporal persistence of interactions in a plant–pollinator network. *Ecology*, *99*, 21–28.

Devoto, M., Bailey, S., Craze, P., & Memmott, J. (2012). Understanding and planning ecological restoration of plant–pollinator networks. *Ecology Letters*, *15*, 319–328.

Garbuzov, M., & Ratnieks, F. L. (2014). Listmania: The strengths and weaknesses of lists of garden plants to help pollinators. *BioScience*, *64*, 1019–1026.

Glenny, W., Runyon, J. B., & Burkle, L. A. (2023). Plant selection for pollinator restoration in seminatural ecosystems. *Frontiers in Ecology and the Environment*, *21*, 148–156.

Haaland, C., Naisbit, R. E., & Bersier, L.-F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity*, *4*, 60–80.

Harmon-Threatt, A. N., & Hendrix, S. D. (2015). Prairie restorations and bees: The potential ability of seed mixes to foster native bee communities. *Basic and Applied Ecology*, *16*, 64–72.

Havens, K., & Vitt, P. (2016). The importance of phenological diversity in seed mixes for pollinator restoration. *Natural Areas Journal*, *36*, 531–537.

Holl, K. D., Luong, J. C., & Brancalion, P. H. (2022). Overcoming biotic homogenization in ecological restoration. *Trends in Ecology & Evolution*, *37*, 777–788.

Jiménez-Alfaro, B., Silveira, F. A., Fidelis, A., Poschlod, P., & Commander, L. E. (2016). Seed germination traits can contribute better to plant community ecology. *Journal of Vegetation Science*, *27*, 637–645.

Kaul, A. D., Barash, M., & Albrecht, M. A. (2023). Common, showy, and perennial species dominate a restoration species pool. *Restoration Ecology*, *31*, e13969.

Kondratyeva, A., Grandcolas, P., & Pavoine, S. (2019). Reconciling the concepts and measures of diversity, rarity and originality in ecology and evolution. *Biological Reviews*, *94*, 1317–1337.

Ladouceur, E., Jiménez-Alfaro, B., Marin, M., De Vitis, M., Abbandonato, H., Iannetta, P. P., Bonomi, C., & Pritchard, H. W. (2018). Native seed supply and the restoration species pool. *Conservation Letters*, *11*, e12381.

Ladouceur, E., McGowan, J., Huber, P., Possingham, H., Scridel, D., van Klink, R., Poschlod, P., Cornelissen, J. H. C., Bonomi, C., & Jiménez-Alfaro, B. (2022). An objective-based prioritization approach to support trophic complexity through ecological restoration species mixes. *Journal of Applied Ecology*, *59*, 394–407.

Lanuza, J. B., Knight, T. M., Montes-Perez, N., Glenny, W., Acuña, P., Albrecht, M., Artamendi, M., Badenhausser, I., Bennett, J. M., Biella, P., Bommarco, R., Cappellari, A., Castro, S., Clough, Y., Colom, P., Costa, J., Cyrille, N., de Manincor, N., Dominguez-Lapido, P., & Bartomeus, I. (2025a). Data from: EuPPollNet: A European database of plant-pollinator networks. *Zenodo*. https://doi.org/10.5281/zenodo.15183272

Lanuza, J. B., Knight, T. M., Montes-Perez, N., Glenny, W., Acuña, P., Albrecht, M., Artamendi, M., Badenhausser, I., Bennett, J. M., Biella, P., Bommarco, R., Cappellari, A., Castro, S., Clough, Y., Colom, P., Costa, J., Cyrille, N., de Manincor, N., Dominguez-Lapido, P., … Bartomeus, I. (2025b). EuPPollNet: A European database of plant-pollinator networks. *Global Ecology and Biogeography*, *34*, e70000.

Menz, M. H., Phillips, R. D., Winfree, R., Kremen, C., Aizen, M. A., Johnson, S. D., & Dixon, K. W. (2011). Reconnecting plants and pollinators: Challenges in the restoration of pollination mutualisms. *Trends in Plant Science*, *16*, 4–12.

M'Gonigle, L. K., Williams, N. M., Lonsdorf, E., & Kremen, C. (2017). A tool for selecting plants when restoring habitat for pollinators. *Conservation Letters*, *10*, 105–111.

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., & Mouquet, N. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, *11*, e1001569.

Müller, U., Bruninga-Socolar, B., Brokaw, J., Cariveau, D. P., & Williams, N. M. (2024). Integrating perspectives on ecology, conservation value, and policy of bee pollinator seed mixes. *Frontiers in Ecology and the Environment*, *22*, e2715.

Nichols, R. N., Holland, J. M., & Goulson, D. (2022). Can novel seed mixes provide a more diverse, abundant, earlier, and longer-lasting floral resource for bees than current mixes? *Basic and Applied Ecology*, *60*, 34–47.

Nichols, R. N., Holland, J. M., & Goulson, D. (2023). A novel farmland wildflower seed mix attracts a greater abundance and richness of pollinating insects than standard mixes. *Insect Conservation and Diversity*, *16*, 190–204.

Ogilvie, J. E., & Forrest, J. R. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, *21*, 75–82.

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19891–19896.

Otto, C. R., O'Dell, S., Bryant, R., Euliss, N. H., Jr., Bush, R., & Smart, M. D. (2017). Using publicly available data to quantify plant–pollinator interactions and evaluate conservation seeding mixes in the northern Great Plains. *Environmental Entomology*, *46*, 565–578.

Parra, S. A., Thébault, E., Fontaine, C., & Dakos, V. (2022). Interaction fidelity is less common than expected in plant–pollinator communities. *Journal of Animal Ecology*, *91*, 1842–1854.

Peralta, G., Vázquez, D. P., Chacoff, N. P., Lomáscolo, S. B., Perry, G. L., & Tylianakis, J. M. (2020). Trait matching and phenological overlap increase the spatio-temporal stability and functionality of plant–pollinator interactions. *Ecology Letters*, *23*, 1107–1116.

Petanidou, T., Kallimanis, A. S., Tzanopoulos, J., Sgardelis, S. P., & Pantis, J. D. (2008). Long-term observation of a pollination network: Fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters*, *11*, 564–575.

Pioltelli, E., Guzzetti, L., Larbi, M. O., Labra, M., Galimberti, A., & Biella, P. (2024). Landscape fragmentation constrains bumblebee nutritional ecology and foraging dynamics. *Landscape and Urban Planning*, *247*, 105075.

Ranalli, R., Borghesan, S., Labra, M., & Biella, P. (2025). From cities to refuges for pollinators: Urban practices for enhancing pollinator habitats in changing landscapes. *Journal of Applied Ecology*, *62*, 2874–2881.

Resasco, J., Chacoff, N. P., & Vázquez, D. P. (2021). Plant–pollinator interactions between generalists persist over time and space. *Ecology*, *102*, e03359.

Rowe, H. I. (2010). Tricks of the trade: Techniques and opinions from 38 experts in tallgrass prairie restoration. *Restoration Ecology*, *18*, 253–262.

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G., & Kleijn, D. (2013). Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – A meta-analysis. *Ecology Letters*, *16*, 912–920.

Simpson, D. T., Weinman, L. R., Genung, M. A., Roswell, M., MacLeod, M., & Winfree, R. (2022). Many bee species, including rare species,

are important for function of entire plant–pollinator networks. *Proceedings of the Royal Society B*, *289*, 20212689.

Vaudo, A. D., Tooker, J. F., Patch, H. M., Biddinger, D. J., Coccia, M., Crone, M. K., Fiely, M., Francis, J. S., Hines, H. M., & Hodges, M. (2020). Pollen protein: Lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects*, *11*, 132.

Vazquez, D. P., Bluthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant-animal mutualistic networks: A review. *Annals of Botany*, *103*, 1445–1457.

Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, *116*, 1120–1127.

Wagner, M., Hulmes, S., Hulmes, L., Redhead, J. W., Nowakowski, M., & Pywell, R. F. (2021). Green hay transfer for grassland restoration: Species capture and establishment. *Restoration Ecology*, *29*(S1), e13259.

Warzecha, D., Diekötter, T., Wolters, V., & Jauker, F. (2018). Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conservation and Diversity*, *11*, 32–41.

White, A., Fant, J. B., Havens, K., Skinner, M., & Kramer, A. T. (2018). Restoring species diversity: Assessing capacity in the US native plant industry. *Restoration Ecology*, *26*(4), 605–611.

Willemstein, S. C. (1983). *An evolutionary basis for pollination ecology*. Brill.

Williams, N. M., & Lonsdorf, E. V. (2018). Selecting cost-effective plant mixes to support pollinators. *Biological Conservation*, *217*, 195–202.

Williams, N. M., Ward, K. L., Pope, N., Isaacs, R., Wilson, J., May, E. A., Ellis, J., Daniels, J., Pence, A., & Ullmann, K. (2015). Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. *Ecological Applications*, *25*, 2119–2131.

Wood, T. J., Holland, J. M., & Goulson, D. (2017). Providing foraging resources for solitary bees on farmland: Current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, *54*, 323–333.

Zinnen, J., Barak, R. S., & Matthews, J. W. (2025). Influence of ecological characteristics and phylogeny on native plant species' commercial availability. *Ecological Applications*, *35*, e3070.

Zinnen, J., Chase, M. H., Charles, B., Harmon-Threatt, A., & Matthews, J. W. (2025). Pollinator seed mixes are phenologically dissimilar to prairie remnants. *Restoration Ecology*, *33*, e14352.

Zinnen, J., & Matthews, J. W. (2022). Species composition and ecological characteristics of native seed mixes in the Midwest (USA). *Ecological Restoration*, *40*, 247–258.

SUPPORTING INFORMATION

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

Table S1. Flowering plant genera within the EUSafeNet database, that are commercially available and produced by more than 40% of seed suppliers according to Ladouceur et al. (2018).

Table S2. Studies ($n = 17$) from the EuPPollNet database that fit our selection criteria.

Table S3. Flowering plant genera within the EuPollNet database that are visited in <50% of pollinator networks, but are produced by fewer than 40% of commercial seed suppliers according to Ladouceur et al. (2018).

Figure S1. The geographic center of each study from the EuPPollNet database, included for analysis. Descriptions of the study associated with each point are in Table S2.

Figure S2. Plant genera within a study (*x*-axis) are sorted according to the standardized commonness (*y*-axis), which is the number of local networks where a plant genus is present standardized by the most common plant genus.

Figure S3. Total number of visitations (*y*-axis; color scale) to a plant genus within a study (*x*-axis).

Figure S4. Sensitivity analysis to select the threshold-level of interactions to define rare pollinator species.

Figure S5. Sensitivity analysis to defining the threshold of rare pollinator species at 0.05% of all interactions.

Figure S6. The mean standardized frequency in pollinator networks (*y*-axis) is greater for plant genera that are ready available (blue) from commercial seed suppliers, compared to those plants that have limited availability (gold) (*x*-axis).

Figure S7. Sensitivity analysis manipulating the threshold for readily-available plant genera.

Figure S8. Sensitivity analysis manipulating the threshold for common plant genera.

Figure S9. (a) Plant families (*x*-axis) with the raw counts of plant genera that are attractive to unique pollinator assemblages (*y*-axis). (b) Plant families (*x*-axis) with the percentage of plant genera within a family that are attractive to unique pollinator assemblages (*y*-axis).

How to cite this article: Glenny, W., Lanuza, J. B., Rakosy, D., Ladouceur, E., Zhong, Y., & Knight, T. M. (2026). Flowers for habitat enhancement primarily benefit common insect pollinators across temperate grasslands. *Journal of Applied Ecology*, *63*, e70216. https://doi.org/10.1111/1365-2664.70216