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Temporal variation in the roles of exotic and native plant species in plant–pollinator networks

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Abstract. The role of individual plant species, including those that are rare or invasive, in the structure of plant–pollinator networks will depend on how connected the plants are to pollinator species and when they flower. Plant species visited by a high diversity of pollinators that visit few other species during a particular time period are thought to provide high value to the insect community. Here, we examined the role of plant species in a plant–pollinator network across the entire flowering season and across dune and adjacent woodland habitats in Wisconsin, USA. We found strong turnover of plants, pollinators, and their interactions in time and space. Both native and exotic species play important structural roles in plant–pollinator networks. Simulations reveal that the loss of the early-flowering rare plant, *Cirsium pitcheri*, would result in a disproportionate loss of pollinator species. Furthermore, the critical role that this species plays in the network is not replaced by its exotic relative, *Centaurea stoebe*. Our research demonstrates that consideration of temporal and spatial variability in networks allows for critical plant species to be identified within a plant–pollinator network that might otherwise be overlooked.

Key words: *Centaurea stoebe; Cirsium pitcheri;* invasive plants; phenology; pollination network; rare plants; temporal pollinator dynamics.

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INTRODUCTION

It is currently estimated that one of every five plant species is threatened by extinction (Brummitt et al. 2008), and preventing the loss of these species, and the services they provide are global conservation priorities. There are regulations and treaties at national and international levels designed to protect individual species from extinction, such as the 1992 Convention on Biological Diversity. Because every plant species is embedded in an entangled network of interactions within its community, loss of an individual plant species can lead to extinctions of interacting species in the community (Tylianakis et al. 2010). For example, the loss of a plant species could result in the loss of a critical resource for animal pollinators.

To consider the relationship between plant species and their animal pollinators, a plant–pollinator visitation network can be constructed to describe the animal pollinator species that are

observed to visit flowers of each plant species. Plant species that have many links to animal species are disproportionately important to community structure and stability (Dupont and Olesen 2012). Plant–pollinator networks typically have a nested structure in which specialists interact with generalists and generalists interact with both specialists and generalists (reviewed by Vázquez et al. 2009). In some networks, a few abundant and highly generalized plant species may form the hub of these nested networks (González et al. 2010). The loss of these hub species would be expected to have profound effects on other species in the community, whereas the loss of more peripheral specialized species would have weak effects at the community level (Memmott et al. 2004). It is often observed that abundant plant species form the hub of the network. This pattern can be explained either by sampling effects (i.e., interactions of rare species are more difficult to observe; Winfree et al. 2014) or by biological processes (i.e., abundant plant species are more likely to encounter potential interaction partners; Fort et al. 2016).

Threatened plant species are often the focus of conservation efforts; however, these species typically have low abundance and may be specialized on a few generalized animal pollinators (Ashworth et al. 2004, Gibson et al. 2006, Olesen et al. 2008, Mouillot et al. 2013). Thus, rare plant species often do little to maintain the abundance and diversity of animal pollinators in the community. Further, in some highly invaded communities, invasive exotic plant species are abundant, are highly generalized in their pollination, and play topologically important roles in plant–pollinator networks (Memmott and Waser 2002, Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, Bartomeus et al. 2008, Kaiser-Bunbury et al. 2009, Padrón et al. 2009, Valdovinos et al. 2009, Vilà et al. 2009). These findings create a potential conundrum for conservation. Control of invasive species is typically desirable for conservation purposes; however, invasive plant removal might eliminate an important resource to animal pollinators (Gibson et al. 2006, Carvalheiro et al. 2008) and reduce pollination of some native species (Ferrero et al. 2013). In other invaded systems, invasive plant species negatively affect native plants via competition for shared pollinators (Carvalheiro et al. 2014). Such competition might be more likely if the invasive plant is closely related to native plants and has similar floral traits (Morales and Traveset 2009, Gibson et al. 2012).

Plant–pollinator interactions vary in time and space, due to plant or animal species' preferences for different habitats in a landscape and due to variable patterns in the phenology of flowering and pollinator activity (Ramos-Jiliberto et al. 2018). Understanding the role that individual plant species play in the network thus requires an explicit consideration of this spatial–temporal variation. There are several species-level indices that capture the role of species in a network. Species strength, the sum of the proportions of interactions performed by a given plant species across all its interaction partners, measures the extent to which the pollinators in the system depend on each plant species (Bascompte et al. 2006). High values of species strength indicate that many pollinator species depend on the same focal plant species. Partner diversity is the mean diversity of pollinator species per plant species based on the frequency of each link (Dormann 2011). High values of partner diversity indicate that a focal plant species is highly generalized. Species-level specialization (d') quantifies how interaction frequencies of a given species deviate in relation to the availability of interaction partners in the network, defined by their marginal totals (Blüthgen et al. 2006). High values for d' indicate that the focal plant species has many exclusive interactions with pollinator species.

The number of resulting extinctions of animal pollinators after simulated removal of particular plant species in a plant–pollinator network provides another method to quantify the relative importance of different plant species in the network (Memmott et al. 2004, Kaiser-Bunbury et al. 2010). This approach makes many assumptions, in particular that the resources provided by any given plant species are necessary for the survival of a particular pollinator species and that, therefore, the loss of a pollinator species is directly related to the loss of a plant species. Despite these limitations, this method provides a quantitative measure of the importance of a specific plant species to overall pollinator species diversity. Further, this method considers the disproportionate importance of plant species that flower early in the season—the disappearance of

an important early-flowering species will mean that insects relying on that plant species will not be present in the network later in the growing season.

Of particular interest in this study are two closely related species (tribe Cardueae of the family Asteraceae) that overlap in phenology and provide attractive resources to insect pollinators (Baskett et al. 2011, Inkster 2016, Jolls et al. 2019). *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray, or Pitcher's thistle, is endemic to dune habitats of the Great Lakes of North America, where it can be locally abundant. Globally ranked G2G3, this species is threatened by habitat conversion, invasive seed predators, inbreeding depression (Havens et al. 2012, Jolls et al. 2015), and climate change (Vitt et al. 2010). *Centaurea stoebe* L., or spotted knapweed, is found in a broad range of habitats (Mráz et al. 2012, Otiskova et al. 2014) and has been introduced to North America multiple times, where it is considered a noxious weed in multiple localities (Marrs et al. 2008). The exotic plant, *Ce. stoebe,* can reduce pollinator visits to the native plant, *Ci. pitcheri* (Baskett et al. 2011).

Here, we quantify the roles of exotic and native plant species within a plant–pollinator network with explicit consideration of temporal variation and habitat associations. We quantified the composition of plants, pollinators, and their interactions each month over the entire flowering season (five months) within a landscape that had a dune and adjacent woodland habitat. We then calculated species-level indices for all plant species in the community to determine the species that play the most important structural roles in the network in each month. Finally, we calculated the number of insect visitor species that would be lost from the network as a result of the loss of each plant species through simulation. We use this information to consider the roles of the native and exotic species in this community.

Methods

Study system

We observed the plant–pollinator interactions in the sand dune and adjacent woodland communities at Sturgeon Bay Ship Canal Nature Preserve, Door County, Wisconsin, USA (44.792455°, −87.314349°; Fig. 1). The preserve at Ship Canal is a modified mosaic ridge and swale dune landscape of the coastal Great Lakes of North America that has both woodland habitat and open dune. The preserve is bounded on the north by a man-made canal dug in 1850 to link Sturgeon Bay more directly to Lake Michigan. The land was disturbed by recreational vehicles and foot traffic and unmanaged until purchased by the Door County Land Trust in 2010. The habitat is also heavily invaded by multiple exotic plant species (e.g., *Ce. stoebe*, *Saponaria officinalis* L., *Securigera varia* (L.) Lassen, *Sedum acre* L., and *Hypericum perforatum* L.) with colorful flowers and apparent floral resources including pollen. Control of invasive plant species with herbicide application began in 2011 and has been maintained with periodic hand pulling by volunteers throughout the growing season. As a result of these control measures, exotic species are present and distributed across the site but were not found as dominant monocultures during the study period.

Study plots

On 14 March 2016, prior to the start of the growing season, we randomly selected the locations of 40–10 m diameter circular plots. Plots were systematically located along a curvilinear (meander) transect to capture all habitat types throughout the dunes and adjacent woodland (Fig. 1). The transect design was chosen to minimize distances traveled on foot between plots across sensitive areas of the dune system (i.e., the meander transect runs parallel to the dune and swale formations, rather than perpendicular, which causes local sand collapse of the dune face). Randomization of the plots along the transect was imposed by the distance traveled from the center of one plot to the center of the next. One plot located in the woods overlapped too closely with another and was subsequently removed from the study.

We visited all 39 plots every 7–10 d from 18 April to 22 September 2016, to identify all plant species that were flowering in each plot, to document phenology of plants (based on floral abundance via counts of the number of open flowers for each species), and to observe and record plant–pollinator interactions (see *Plant-pollinator interactions*). Floral abundance for each species was estimated using a tally counter. For species

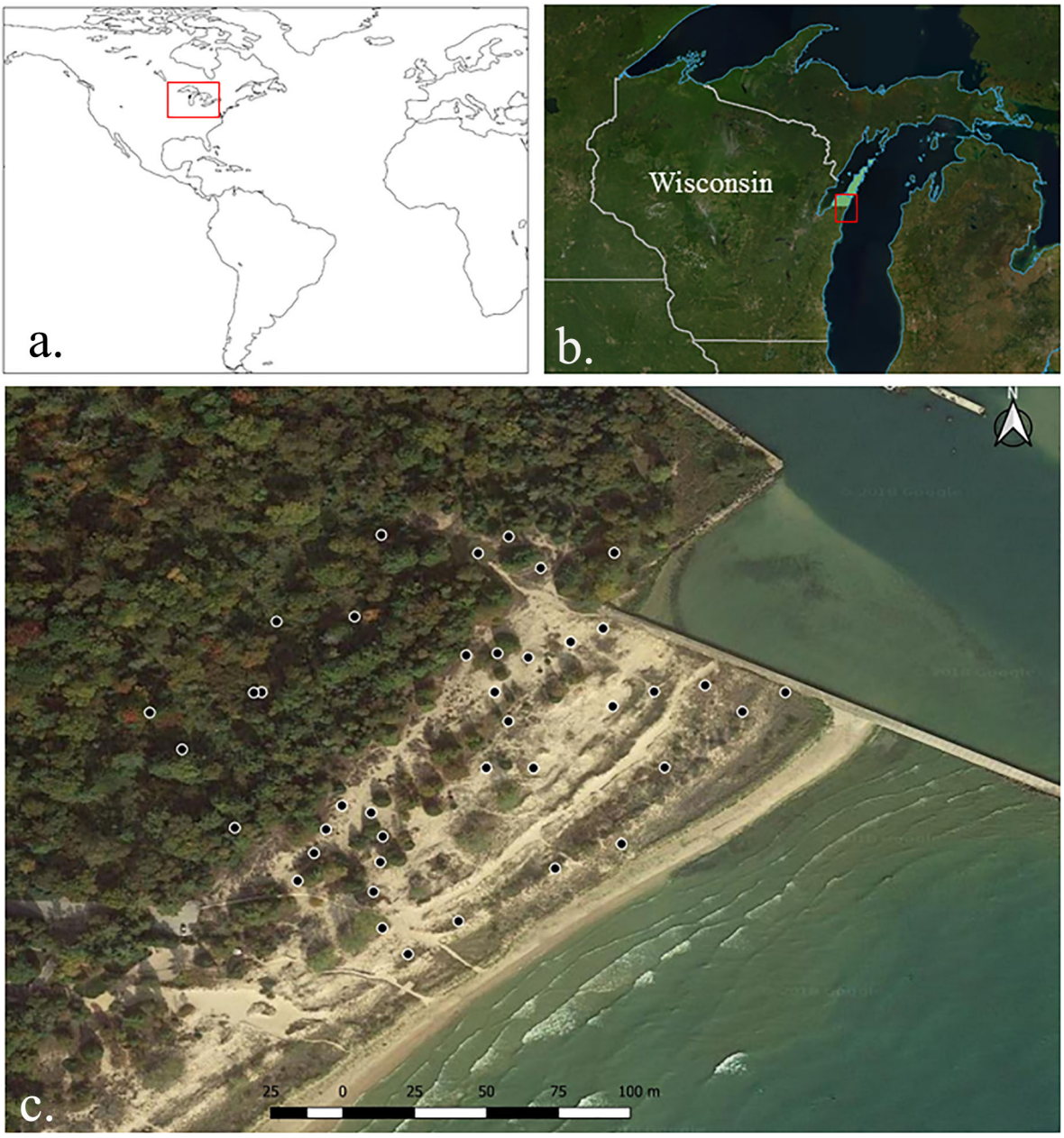


Fig. 1. (a) Map showing the location of the study site in North America, (b) position of the site on the southern Door Peninsula (highlighted in green) in the Great Lakes, and (c) map showing the location of habitats and plots within our study site at the Ship Canal Nature Preserve.

with complex inflorescences (e.g., species in the Asteraceae), we considered each head to be one flower. When head or flower number exceeded 500, the total number was estimated. Floral abundance of two tree species (*Acer rubrum* L. and *Acer spicatum* Lam.) was observed by counting whole inflorescences visible in the canopy above the circular plot via binoculars. Observations occurred between 09:30 and 15:30 local time under conditions of clear skies and low wind to

ensure optimal pollinator activity and consistent sampling conditions throughout the field season.

Flowering plant species

We observed 33 animal-pollinated plant species flowering in our plots over the course of the entire growing season (grasses and wind-pollinated trees were excluded). We considered 26 of these for analyses on plant–pollinator interactions, dropping species which experienced infrequent pollinator visitation, or which were too rare to allow for adequate sampling of plant–pollinator interactions ($N = 7$). For example, the exotic plant *Myosotis sylvatica* Ehrh. was abundant in the woods, with over 4000 flowers counted over six sampling dates; insect visitation, however, was rare with only six visitors recorded over the same time frame. For each of our 26 focal plant species, the species richness of floral visitors observed was within the 95% confidence intervals (or nearly so) of the Chao estimator, indicating that our sampling was adequate (Chacoff et al. 2012; see Appendix S1). We also constructed a phenology curve for these species using our data on number of flowers per species per time point using the R package ggridges (Wilke 2017).

Plant–pollinator interactions

At the start of each observation day, we randomly chose a plot to begin our observations. At each plot, we noted the species that were in flower. For each plot with flowering plants, we observed each plant species for 10 min and recorded the identity of each insect visitor that contacted a flower. We restricted our observations to only floral visitors that came in contact with the reproductive parts of plants (and thus could potentially be performing pollination). Nocturnal interactions are excluded from our network. We recorded only the orders of insects that are likely pollinators (Hymenoptera, Lepidoptera, Diptera, and Coleoptera). Insects that could be identified to species on the wing were not collected (e.g., Monarch [*Danaus plexippus* Linnaeus, 1758], Yellow Swallowtails [*Papilio glaucus* Linnaeus, 1758]). All insects were identified to morphospecies and photographed to document visitation during the field observations. Insect specimens were collected throughout the observation period using a vacuum-powered handheld aspirator (BioQuip model 2820GA, BioQuip Products, Rancho Dominguez, California, USA) and identified to species (or other taxonomic groups for difficult species complexes) by P. Vitt. Insect specimen identification was confirmed by Brian Scholtens, College of Charleston and U. Michigan Biological Station, and by Michael Arduser, Missouri Department of Conservation. These confirmed determinations were used for all analyses. Specimens from this work are vouchered at the Chicago Botanic Gardens Insect Collection.

Plant, insect, and interaction composition

To test how plant composition, pollinator composition, and plant–pollinator interactions vary in time and space, we calculated Jaccard's similarity for each month of the study (May, June, July, August, and September) and for each habitat (dunes, woods). We summed all observations for each month. We had few observations in April, and these were combined with the observations made in May. We used analysis of similarities (ANOSIM) to test for the effects of habitat and month on Jaccard's similarity and multidimensional scaling plots to visualize the results using the R package vegan (Oksanen et al. 2013). Analysis of similarities is a nonparametric test that assesses whether between-group differences in community composition are similar to within-group differences (R value close to 0; the null hypothesis), or if they are larger (R closer to 1). P-values are obtained by comparing the observed R to the distribution of R found in 999 permutations of the group classification.

Species-specific network metrics

To quantify the role of individual plant species in the network, we calculated species strength (which quantifies the extent to which the pollinators in the system depend on the plant species), partner diversity (which quantifies the generalization of the plant species), and species-level specialization (d', which quantifies how many exclusive interactions the plant species has with pollinator species) for each plant species in each monthly network using the R package bipartite (Dormann et al. 2009). We then used ANOVA to determine how native status of plants (exotic vs. native) influenced species-specific metrics for each monthly network (we excluded

consideration of April, May, and September due to inadequate sample size of exotic plants in those months).

Simulated plant extinctions

We simulated the effect that the loss of each plant species would have on pollinator species loss. For each insect and month, we calculated the proportion of visits each pollinator has with each plant. We considered a pollinator species to be vulnerable to extinction if a plant species that was detected to support 100% of its observed visits was lost from the habitat. We also considered less extreme scenarios, in which the pollinator would be vulnerable to extinction from the loss of a plant that supported 60% or 80% of its observed visits. For each plant species, we calculated the number of pollinators that would be lost if the plant was lost. In our simulations, once a pollinator is lost in an early month, it could not be re-lost in a later month. For example, the insect pollinator *Bombus borealis* Kirby, 1837 relies heavily on the plant *Ci. pitcheri* in June and on the plant *H. perforatum* in July. However, the insect's extinction in our simulation would be attributed to *Ci. pitcheri*, because we expect that the lack of resources in June would result in the loss of this insect before *H. perforatum* flowers in July.

This simulation provides a quantitative assessment of the importance of each plant species in supporting pollinator diversity and considers the temporal availability of different plant species to animal pollinators. Such simulations are simplistic and make many assumptions, such as the inability of insect species to change behavior in response to plant species loss, and the necessity of the plant resources for pollinator survival. For example, *B. borealis* is unlikely go locally extinct in our study system in the absence of *Ci. pitcheri*, as *B. borealis* is capable of consuming floral resources from multiple plant species in several plant families, and flying long distances for foraging. However, *Ci. pitcheri* likely provides an important floral resource for *B. borealis* individuals at our site, and without *Ci. pitcheri*, these bees may have poorer nutrition and health or decide to forage and nest elsewhere.

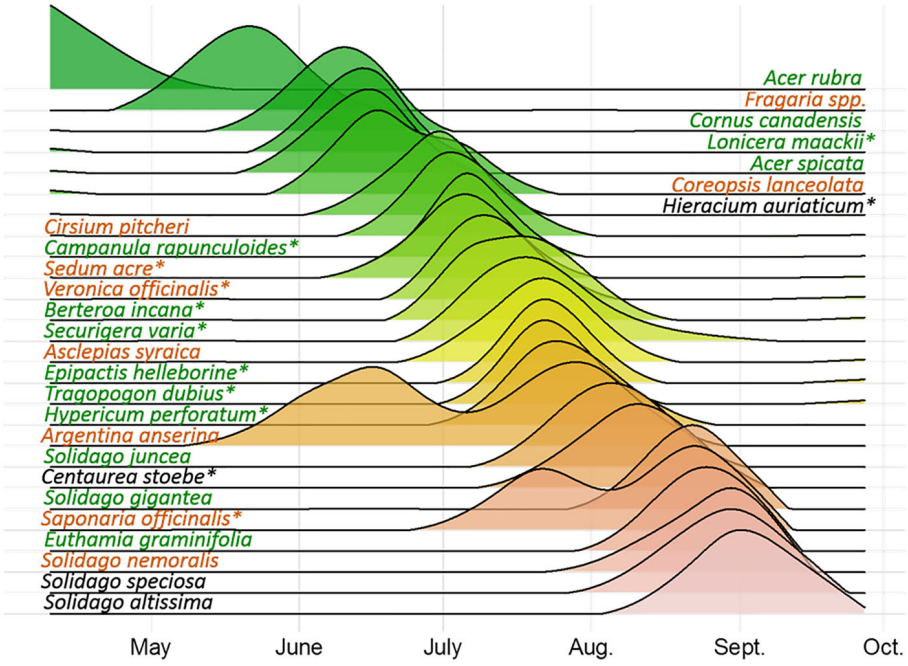


Fig. 2. Phenology of each plant species based on its density of interactions with pollinators. Species names are color-coded based on their habitat associations (green, woods; brown, dune; black, both). Asterisks next to species names indicate non-native plant species. Species are indexed by peak flowering time; curve filling follows the spring (green)-to-fall (peach) timeline.

Results

We observed 2194 interactions among 26 plant species and 43 pollinator species (or morphospecies). Twelve plant species are non-native (Fig. 2). Habitat association and native status (native, exotic) were distributed throughout the phylogeny of these focal plant species (Appendix S2). Most plant species had a unimodal pattern of flowering, but two were bimodal (Fig. 2).

Plant composition was significantly different across habitats (ANOSIM, $r = 0.606$, $P = 0.01$) but not months (ANOSIM, $r = 0.008$, $P = 0.353$; Fig. 3a), with nine plant species occurring only in the dunes, 13 plant species occurring only in the woodland habitat, and four plant species found in both habitats. In contrast, visiting insect composition was significantly different across months (ANOSIM, $r = 0.455$, $P = 0.009$) but not habitats (ANOSIM, $r = -0.012$, $P = 0.521$; Fig. 3b). As a result, plant–visitor interactions vary in time and space (Fig. 3c).

Native and exotic plant species both provide important structural roles in the network (Fig. 4). There was no difference between exotic and native plants in any metric (species strength, partner diversity, species-level specialization) for the June, July, and August networks (ANOVA, all $P > 0.05$; Fig. 5). This is illustrated by our two focal species. In June, native *Ci. pitcheri* has the greatest species strength, whereas exotic *Ce. stoebe* has a high species strength in August (Fig. 5).

Our simulation demonstrates that removal of the native, threatened species, *Ci. pitcheri*, would have the most dramatic effect on insect visitor extinctions (Fig. 6). Many insects are observed to visit this plant almost exclusively during the time in which it is flowering. However, the exotic and early-flowering plant *Lonicera maackii* (Rupr.) Herder was the second most important plant species identified with this approach.

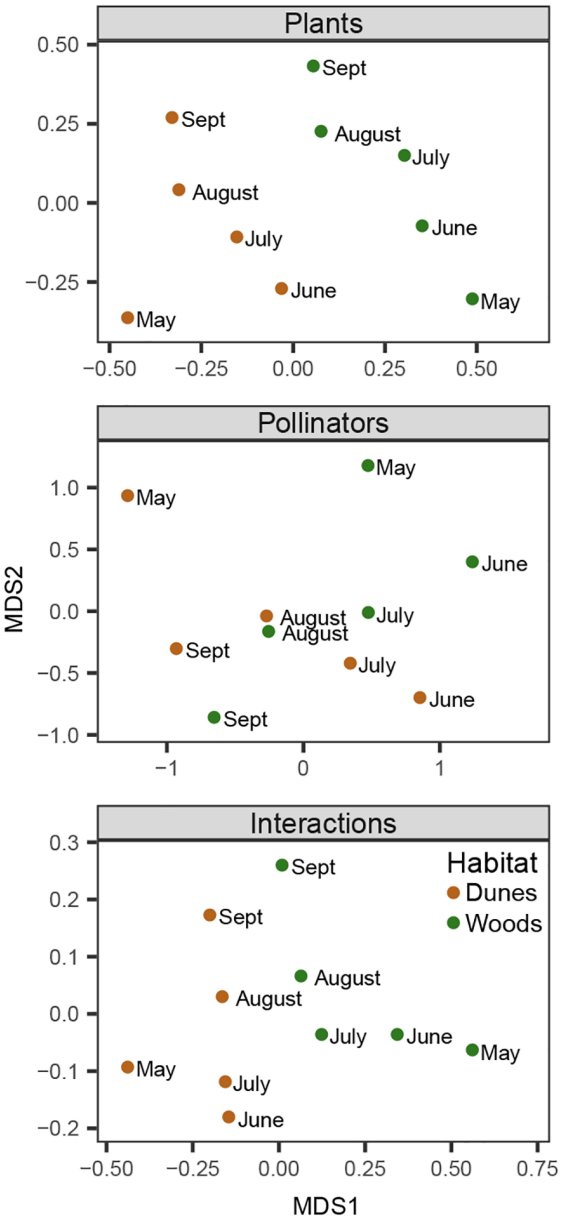


Fig. 3. Multidimensional scaling plots showing Jaccard's similarity between plants, pollinators, and interactions between plants and pollinators across time and space. Points that are closer together are more similar in species (or interaction) composition. Data shown for woods plots in green and dunes plots in brown.

Discussion

Our results show that both phenology and habitat associations can shape the structure of plant–pollinator interactions. Plant species composition was highly spatial at our study site, with most species present in either the dunes or woods, but not across both habitat types. In contrast, the composition of the insect visitors had a stronger temporal than spatial structure,

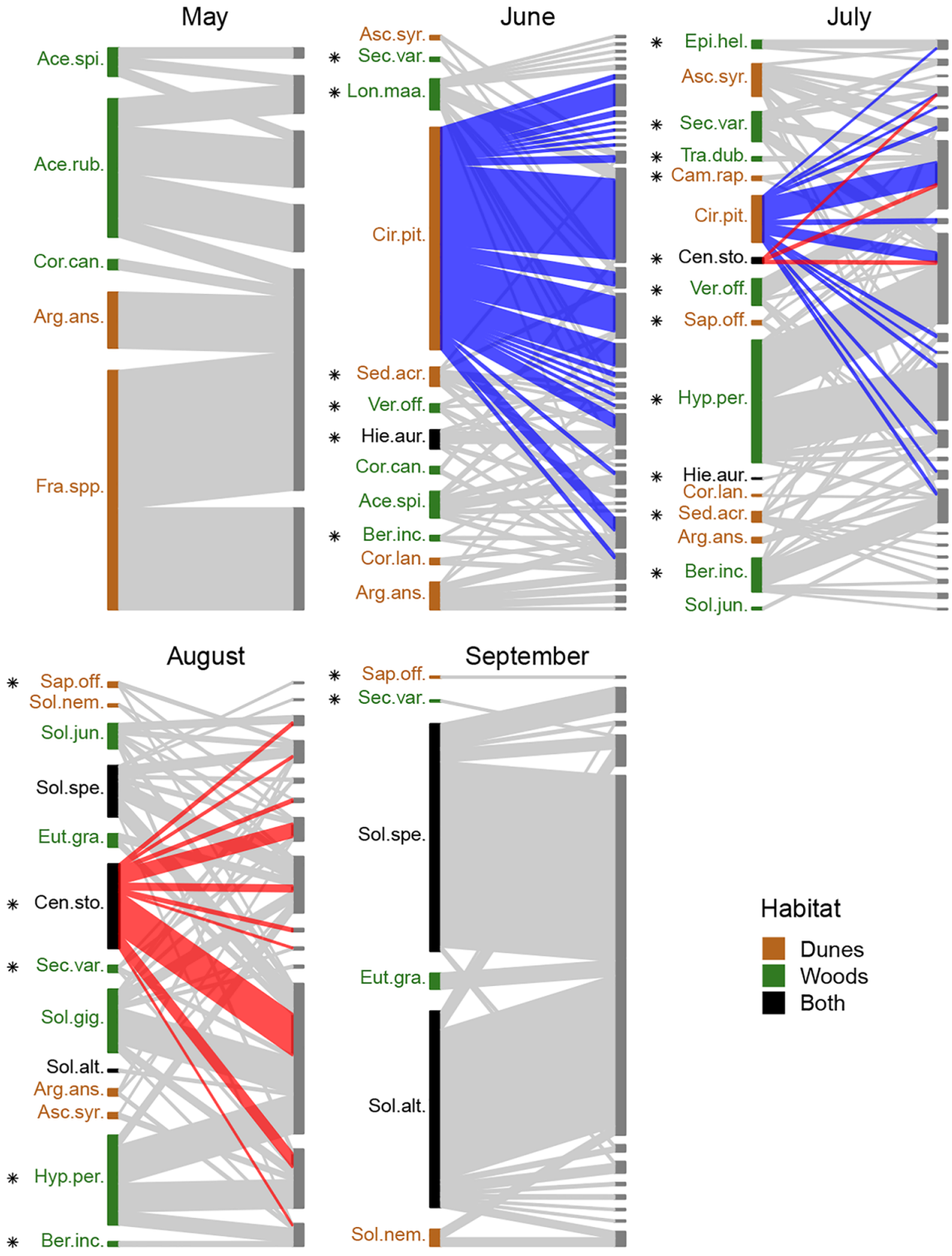


Fig. 4. Monthly plant–pollinator networks. All plants flowering during the monthly study periods are indicated

(Fig. 4. Continued)
on the left, color-coded to indicate habitat. Plant species in the dune habitat are indicated in brown, while those in the woods are green and those in found in both habitats are black. Invasive plant species are indicated using asterisks next to their names. Network connections are shown with gray bands, and the size of the bands reflects the number of visitations observed. The network connections between the native, threatened thistle, *Cirsium pitcheri*, and its pollinator visitors are indicated in blue, while network connections between the exotic knapweed, *Centaurea stoebe*, and its visitors are indicated in red. Species abbreviations are Ace.rub., *Acer rubrum*; Ace.spi., *Acer spicata*; Arg.ans., *Argentina anserina*; Asc.syr., *Asclepias syriaca*; Ber.inc., *Berteroa incana*; Cam.rap., *Campanula rapunculoides*; Cen.sto., *Centaurea stoebe*; Cir.pit., *Cirsium pitcheri*; Cor.can., *Cornus canadensis*; Cor.lan., *Coreopsis lanceolata*; Epi.hel., *Epipactis helleborine*; Eut.gra., *Euthamia graminifolia*; Fra.spp., *Fragaria* spp.; Hie.aur., *Hieracium aurantiacum*; Hyp.per., *Hypericum perforatum*; Lon.maa., *Lonicera maackii*; Sap.off., *Saponaria officinalis*; Sec.var., *Securigera varia*; Sed.acr., *Sedum acre*; Sol.alt., *Solidago altissima*; Sol.gig., *Solidago gigantea*; Sol.jun., *Solidago juncea*; Sol.nem., *Solidago nemoralis*; Sol.spe., *Solidago speciosa*; Tra.dub., *Tragopogon dubius*; and Ver.off., *Veronica officinalis*.

suggesting that these insects move freely between the habitat types. This resulted in plant–pollinator interactions that vary in time and space. Several plant species were shown to play disproportionately important roles in the plant–pollinator network, such as the native plants *A. spicatum* and *Ci. pitcheri*, as well as the exotic plants *Ce. stoebe* and *H. perforatum*. However, plant species' native status did not affect the species-specific metrics for any time period, suggesting that both native and exotic species are important to network structure in this system. These results have implications for documenting ecosystem services provided both by rare and by invasive plant species and for the management of both.

The role that the rare native plant, *Ci. pitcheri*, plays in the network is not easily replaced by other species, even its exotic generalist relative, *Ce. stoebe*. Other studies indicate that closely related invasive plant species, particularly those with similar floral characteristics, may play similar roles in the pollinator network (Morales and Traveset 2009, Gibson et al. 2012). In contrast, we found native *Ci. pitcheri* is critical to pollinators because it provides resources earlier in the season, allowing those pollinators with long activity periods to persist, thrive, and be available for interactions later in the season. This is particularly true for the five *Bombus* species in our system (*B. borealis*, *B. griseocollis* De Geer, 1773, *B. impatiens* Cresson, 1863, *B. rufocinctus* Cresson, 1863, and *B. vagans* Smith, 1854); 131 of their 158 interactions were with *Ci. pitcheri*. Thus, it is important that conservation measures are in place to prevent the extinction of *Ci. pitcheri*. *Cirsium pitcheri* is threatened by habitat conversion, low genetic diversity, and seed predation, primarily by weevils introduced as biocontrol agents for weedy thistles (Havens et al. 2012). Active management is occurring at this study site to remove invasive plant species, including *Ce. stoebe*, which once dominated the habitat.

Nearly half of the plant species in our interaction networks are non-native. Removal of all of the non-native plant species that provide resources for pollinators may decrease the available support for the pollinator community and could lead to declines in pollinator abundance and/or diversity. This could result in a reduction of pollination services to native plant species (Pauw 2007). Alternatively, it is possible that the elimination of invasive plant species will allow other native plant species to become more abundant and provide more resources to the pollinators at this site. Further, restoration activities could include adding species that will provide floral resources to pollinators (Kaiser-Bunbury et al. 2017). Of particular interest are the invasive plants, *L. maackii* and *H. perforatum*, which play important roles in our network but are highly invasive and thus important targets for weed management. As removal proceeds, the response of the pollinator community, in terms of abundance, diversity, and composition, should be monitored as part of the invasive plant species removal program. Optimally, this would be done using an experimental design that allows these factors to be compared between removal and

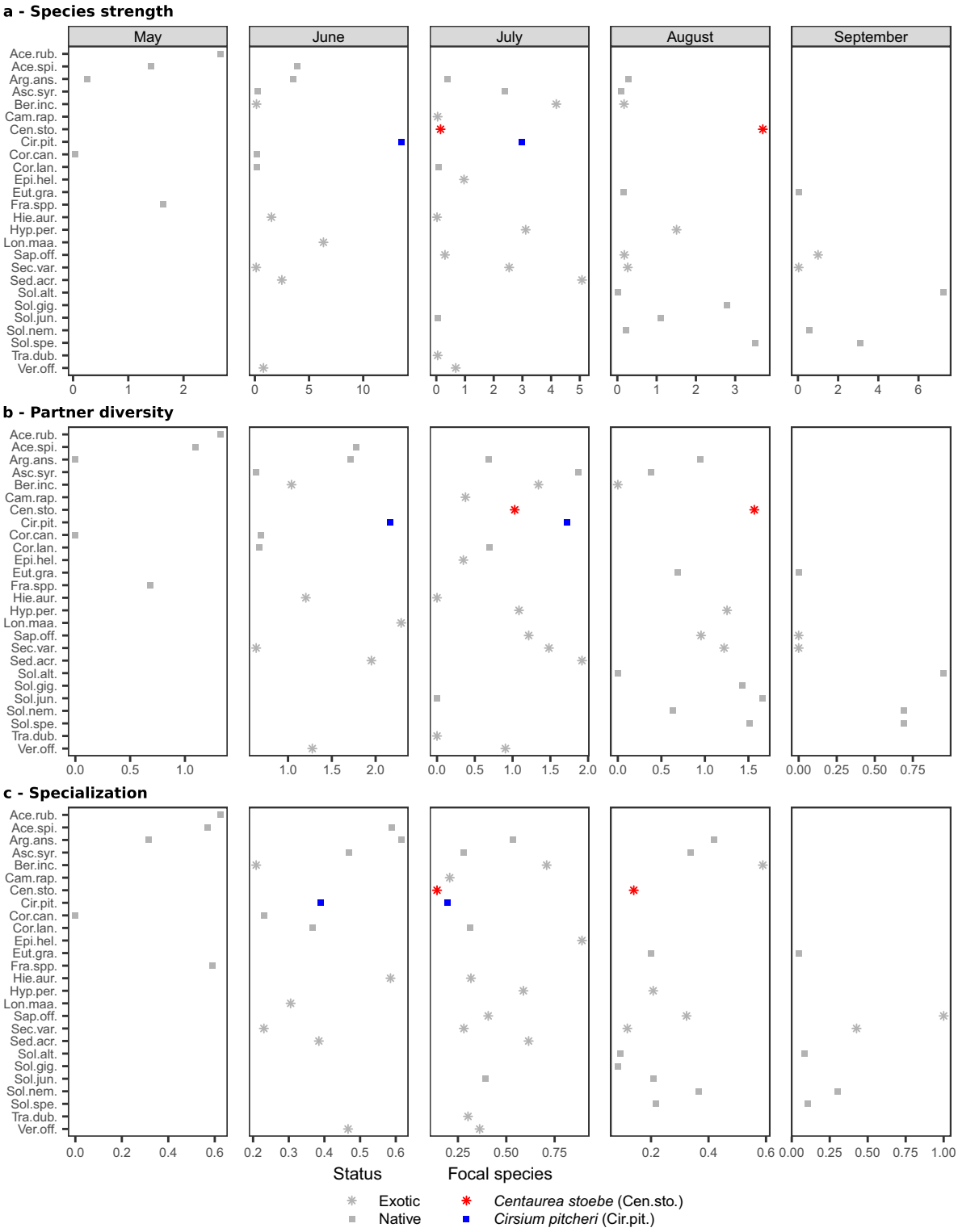


Fig. 5. Species-specific network metrics (*x*-axis) for each plant species and month: (a) species strength, (b) part-

(Fig. 5. Continued)
ner diversity, and (c) species-level specialization. The values for exotic plants are indicated with asterisks and for native plants are shown with square. Values for the native, threatened thistle, *Cirsium pitcheri*, are indicated with a blue square, while metrics for the exotic knapweed, *Centaurea stoebe*, are indicated with a red asterisk. Species abbreviations are the same as in Fig. 4.

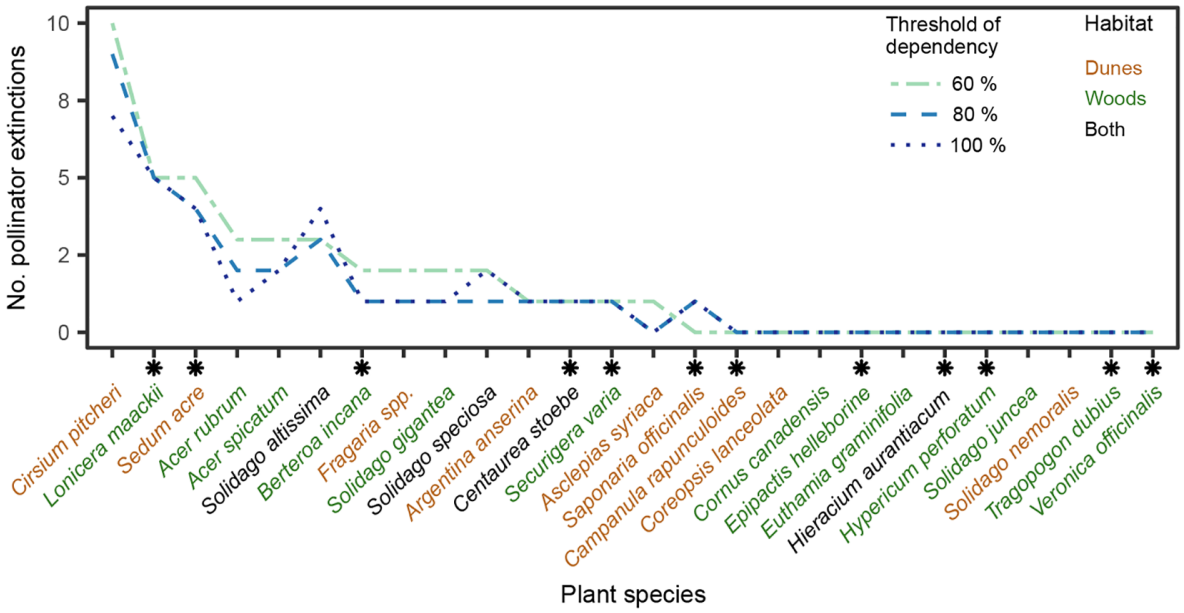


Fig. 6. Number of insect visitor species that would be lost in response to the simulated loss of each plant species. The dark blue dotted line indicates results from simulations that considered a pollinator lost if it has 100% of its visits are to a single plant species during a month-long observation period. The light blue dashed and the turquoise dotted and dashed lines indicate results if 80% and 60% of the visits are to a single plant species, respectively. Asterisk associated with plant species names indicates the species is exotic.

control sites, as well as with and without restoration of native plant species that provide similar resources.

Conservation efforts have largely moved away from the single-species approach to encompass landscape-scale priorities, in part reflecting the importance of species interactions (Tylianakis et al. 2010), and ecosystem services (Chan et al. 2006). Our results presented here highlight the importance of single-species conservation efforts as part of this continuum. Equally important, we have demonstrated that ensuring a broad phenological diversity of pollinator resources (Havens and Vitt 2016), especially early in the season, is critical for supporting the conservation of pollinators such as *Bombus* species.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2981/full

Appendix S1: For each plant species, we show the species richness of floral visitors observed, the species richness expected based on the Chao estimator, one standard error for the Chao estimator, and the lower and upper confidence intervals for the Chao estimator.

Appendix S2: Phylogeny of the 26 plants in our study. Many of our plant species were present on the dated molecular phylogeny of vascular plants created by Zanne et al. (2014). Species not present on the phylogeny were bound into the phylogeny at the genus level using the function congeneric.merge in the pez package of R (Pearse et al. 2015). We used Blomberg's *K* as a measure of the strength of phylogenetic signal of native status and habitat association across these plant species. Our observed Blomberg's *K* values were compared to those generated by random permutations of the data. We found no evidence of a phylogenetic signal in either native status or habitat association.