Global Ecology and Conservation 18 (2019) e00603

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

An endemic plant and the plant-insect visitor network of a dune ecosystem

Claudia L. Jolls [a, c, d, *], Jaclyn N. Inkster [a, b], Brian G. Scholtens [c, e], Pati Vitt [d, f], Kayri Havens [d]

[a] *Department of Biology, Howell Science Complex MS 551, East Carolina University, Greenville, NC, USA*
[b] *Nomad Ecology LLC, Martinez, CA, USA*
[c] *University of Michigan Biological Station, Pellston, MI, USA*
[d] *Chicago Botanic Garden, Glencoe, IL, USA*
[e] *College of Charleston, Charleston, SC, USA*
[f] *Lake County Forest Preserves, Libertyville, IL, USA*

ARTICLE INFO

Article history:
Received 14 November 2018
Received in revised form 26 March 2019
Accepted 26 March 2019

Keywords:
Plant-insect visitor network
Cirsium pitcheri
Rarity
Dune endemics

ABSTRACT

Network theory increasingly is used to quantify and evaluate mutualistic interactions, such as those among plants and their flower-visiting insects or pollinators. Some plant species have been shown to be important in community structure using network metrics; however, the roles of plant taxa, particularly rare species, are not well understood. Pitcher's thistle (*Cirsium pitcheri*), a threatened endemic of Great Lakes shorelines, flowers late-June to early-August, when other floral resources may be less abundant or unavailable. We performed 10 min insect visitor observations on all insect pollinated plants in 44—10 m by 10 m plots at Sturgeon Bay, northern lower MI, USA, during *C. pitcheri* flowering and recorded plant species, number of open flowers, species of insect visiting, and number of visits by insects. Pitcher's thistle received 18.2% of all 600 recorded visits, 61.1% more than the next most visited plant. Pitcher's thistle also received visits from 22 of the 59 different insect species in the network, twice as many as the next most visited plant species. Species-level network analysis metrics showed that Pitcher's thistle was most generalized, with greatest species strength, betweenness, and connectance scores of any other plant taxon, demonstrating network topological importance. Pitcher's thistle received significantly more insect visits relative to its abundance that did any other plant species. Therefore, conservation of *C. pitcheri* and of other rare taxa, particularly in xeric and low diversity systems, can be significant beyond species-level management and may extend to conservation of the plant-insect community.

1. Introduction

A plant-pollinator (or plant-insect visitor) network is defined as the cumulative interactions between plants and their animal visitors (potential pollinators) in an ecosystem. Network analysis has been used to assess the topological importance, or the level of support in network stability, of individual species within ecological networks (Jordán et al., 2008). Such

* Corresponding author. Department of Biology, Howell Science Complex MS 551, East Carolina University, Greenville, NC, USA
E-mail address: jollsc@ecu.edu (C.L. Jolls).

https://doi.org/10.1016/j.gecco.2019.e00603

networks focus on multi-way interactions within conventional food webs, i.e., gathering of food resources, not just the one-way transfer of pollen and resultant seed set (pollination). Also, confirmation of effective pollination is not always possible. Insect visitation to flowers is more often observed and such interactions are termed “plant-flower visitor” or “plant-insect visitor” networks (e.g., Koski et al., 2015, conventions we adopt here). Flowering plants that attract a wide variety of visitors (several orders of insect or animal) are considered generalists, as opposed to specialists, which attract few visitors (one order of insect or a few specific species) (Waser et al., 1996). Plants are considered generalists based not only on the number of visiting insect species, but also on the number of visits of each interaction relative to the rest of the network (Blüthgen et al., 2006; Sahli and Conner, 2006). The extinction of highly connected species has the potential to result in a cascade of secondary extinctions of species, including loss of generalist pollinators such as Hymenoptera and Lepidoptera, and ultimately imperil pollination networks (Memmott et al., 2004).

A keystone species was originally defined as a predator species that holds other species in check that would otherwise dominate the system (Paine, 1969). Recent usage of the keystone concept has been extended to refer to a species whose effect is disproportionately large in relation to body size and abundance (Power et al., 1996). While the term is beset by ambiguities and controversy, the concept may be useful in its application in conservation (Mills et al., 1993). This concept has been applied to plant-flower visiting insect interactions (keystone host mutualists) by analyzing the number of connections and the strength of those connections to other species (Martín Gonzáles, 2010; Pocock et al., 2011). Other species-level metrics (connectedness, betweenness, measures of species generality or specificity, and species strength) have been used to identify potentially important plants in plant-insect networks (Martín Gonzáles, 2010; Pocock et al., 2011; Robson, 2014; Koski et al., 2015).

Even rare plants, those with limited geographic distribution, local abundance, and habitat specificity (Rabinowitz, 1981), can be important members of flower-insect visitor networks (Memmott et al., 2004; Severns and Moldenke, 2010). Rare endemic plants of oceanic island networks can have higher linkage to pollinators than do non-endemics and robustness of this network (ability to withstand perturbation) can be partially attributed to the presence of native plant species (Olesen et al., 2002). Similarly, a rare clover endemic to the sand dunes of Manitoba and Saskatchewan (*Dalea villosa* var. *villosa* (Nutt.) Spreng., Fabaceae) is an important nectar and pollen resource for insects, with significantly higher visitation rates than all the other plant species present (Robson, 2014). Rare species, particularly in low diversity communities such as dunes, similarly may have major roles in plant-flower visitor networks. Although identification of “keystone” taxa is best confirmed through removal of these species followed by quantification of community response, this is rarely possible with protected taxa or those with intractable life histories (large size, long-lived, slow-growing). Network analysis of plant-flower visitor interactions is particularly useful for these rare species and their contributions to ecosystem function (Mouillot et al., 2013; Leitao et al., 2016).

Pitcher's thistle (*Cirsium pitcheri* (Torr.) Torr. & A. Gray, Asteraceae) is a federally threatened species, endemic to the sand dunes and cobble shores of the western Great Lakes. This herbaceous perennial grows for 4–8 yr as a vegetative rosette. In its last year of life, the plant bolts, flowers, producing approximately 30 floral heads per plant on average (Havens et al., 2012; Inkster, 2016) before it sets seed and then dies (monocarpic). Pitcher's thistle has no means of vegetative reproduction and relies solely on seed set for reproduction. Bagged inflorescences (heads or capitula) do produce seed, confirming potential for self-pollination within a head in the absence of an insect visit (autogamy). However, insect transfer of pollen is important for seed set, as is true for many Asteraceae. Selfing can occur via pollinator movements within and among heads on the same plant (geitonogamy), but more seeds per head are produced with insect-mediated outcrossing (Loveless, 1984).

Pitcher's thistle flowers from late June to early August, a long (2 mo) period, when other floral resources in the dune ecosystem may not be present or as abundant (Voss and Reznicek, 2012; Goodwillie and Jolls, 2014). Fig. 1 presents flowering phenology for plant species co-occurring with Pitcher's thistle for which flowering period is well-documented. This flowering plant is primarily pollinated by members of the genus *Bombus* and the bee family Halictidae, but visits from other solitary

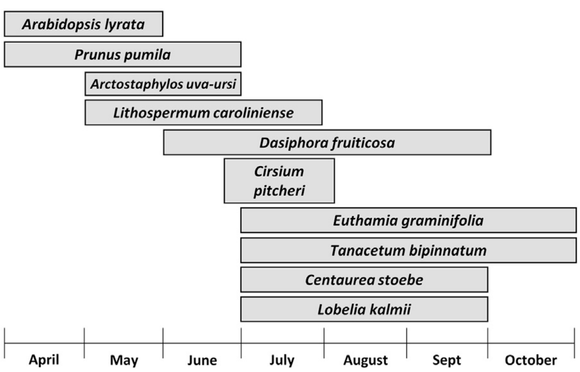

Fig. 1. Phenology of flowering periods of Great Lakes dune insect pollinated plant species. Flowering period data are from floras (Voss, 1972; Ownbey and Morley, 1991; Flora of North America Editorial Committee, 1993; Chadde, 2013). Width of the box for each species reflects the length of flowering season.

bees, butterflies, flies and beetles have also been documented (Keddy and Keddy, 1984; Loveless, 1984; Baskett et al., 2011). This diversity of insect visitors suggests *C. pitcheri* may be a generalist and could function as an important floral resource in the Great Lakes natural dune ecosystem. Although this plant is threatened and limited in its distribution, we hypothesized that *C. pitcheri* is a valuable floral resource to the insect fauna of the local dune ecosystem during its flowering period.

2. Materials and methods

2.1. Field study

We observed insect visitation on all insect-pollinated flowering plants in randomly selected plots at Sturgeon Bay, Wilderness State Park, Emmett County, northwestern lower MI. The site is a large west-facing complex of parallel beach-dune ridge complex on the east shore of Lake Michigan (Lichter, 1998). Sturgeon Bay suffers comparatively minimal negative impacts from human use of the coastal shoreline. Floral diversity is higher than neighboring sites. Pitcher's thistle populations here are relatively large, associated with the primary and secondary dunes near the lake, characterized by strong winds, sand erosion and deposition, low organic matter, and low vegetation cover.

We randomly selected 60 points in a 0.255 km^2 polygon around the dune ecosystem along 2461.5 m (2.46 km) of shoreline polygon using ArcGIS 10.1 software (ESRI, 2013) and satellite imagery. These randomly-selected points represented the center of 60–10 m by 10 m plots for sampling to be sufficiently robust for network analysis (Granovetter, 1976). All plots were located windward of the secondary dune and not within the forested inland community. Plots were selected randomly to determine which plot was visited on each day of observation; each plot was observed once during the sampling period. We then performed 10 min observations (JNI as the sole observer) during warm, low wind weather from 1000 to 1500 h on all the insect-pollinated flowering plants during the *C. pitcheri* flowering season, 26 June-5 August 2015. Insect-pollinated taxa were assumed to be those with showy flowers. If there were no flowering plants in a plot, no observations were performed. We recorded plant species, number of open flowers (or flowering units), insect species visitors, and number of each visit. Each flowering individual in that plot was observed for a single 10 min period. For plants in the family Asteraceae, the head (inflorescence) was considered one flowering unit (Memmott, 1999). A visit was counted if the insect made contact with floral parts of the plant (i.e., petals, stamens, stigmas). If not identifiable in the field, insects were collected for later identification. When individual plants of the same species occurred within 1 m of one another, multiple plants were observed for visits at the same time to reduce the field time spent in a single plot. A total of 14,010 min of observation with 600 insect visits was recorded in 44 plots. Taxonomy follows that of Voss and Reznicek (2012) for vascular plants and the Integrated Taxonomic Information System on-line database for the insects (http://www.itis.gov, retrieved 02/20/2019).

2.2. Network analysis

We classified the plant-flower visitor network as directed (one-way), i.e., only plants and insects interact with one another. We constructed the network using 30 plant species that were visited by insects; the nine plant species that never received visits were not included in the network. Three species of crab spiders (Aranae, Thomisidae), sit-and-wait predators that use flowers as a habitat structure (Morse, 1979), were observed on two plant species. These spiders are at a higher trophic level than the insects visiting flowers for pollen and nectar resources and were removed from the final network. We retained the insect predator *Nabicula subcoleoptrata* Kirby (Hemiptera, Nabidae) in the network since it has also been recorded visiting related *Cirsium* genus members for pollen and nectar resources in neighboring Wisconsin (Williams, 2015). Some *Bombus* species are particularly difficult to identify, particularly on the wing; recorded observations of some species were identified to genus only as *Bombus* sp. for network analysis. These unknown *Bombus* visitors may have been *B. bimaculatus* Cresson (Hymenoptera, Apidae), *B. borealis* Kirby, *B. vagans* Smith, and/or *B. griseocollis* (De Geer) (the latter more typical of forested sites), all of which occur in the area. However, these unknown *Bombus* sp. were not confused with the other two distinctive *Bombus* species (*B. impatiens* Cresson and *B. ternarius* Say) during the field-based on-the-wing observations.

To assess the relative importance of each plant species, we computed seven species-level indices using the R statistical software package Bipartite (Dormann et al., 2008; R Core Team, 2013). Normalized degree (ND) is the number of insect species that visited a plant divided by the number of potential insect visitors in the network. Species strength (SS) is a sum of the insect visitor dependencies on the plant species. Complementary measures of centrality include betweenness (B) and closeness (C). Betweenness is a measure of centrality for nodes in the network that quantified the number of times a plant bridges the shortest path between two other nodes, or the species importance as a connector. Closeness (C) similarly describes the proximity of a species to the rest of the network by quantifying the length of each path to the rest of the nodes (Martín Gonzalés et al., 2010). Both betweenness and closeness values can be unweighted (consider only the presence and absence of interactions) and weighted (BW and CW which consider the frequency of interactions weighted by the number of visits the plant species received in the entire network) (Soares et al., 2017). The metric *d'* is an index of specialization scaled from 0 (most generalized) to 1 (most specialized), measured by the number of visitors a plant has (Blüthgen et al., 2006). Betweenness, closeness, and *d'* species-level indices all have been used to theoretically identify topologically important species in other networks (Martín González et al., 2010; Pocock et al., 2011).

3. Results

The plant-flower visitor network at Sturgeon Bay dunes consisted of 21 plant species visited and 59 insect species (Appendix). There were six orders of insects in the entire network; 23 Hymenoptera (bees, wasps, ants) represented the largest group. Hymenopterans also performed over half the visits to plants (376 visits of 600 total). The insect taxon with the most visits was the unconfirmed *Bombus* sp. (Hymenoptera, Apidae; 95 visits) with the ant *Formica argentea* Wheeler (Hymenoptera, Formicidae; 91 visits) at a close second (Table 1, Fig. 2, Appendix). These bees and ants also performed the most visits to individual plants. The strongest interaction in the network was between the ant, *F. argentea* and *Anticlea elegans* (Pursh) Ryd. (Melanthiaceae) with 53 total visits, although this was likely nectar foraging and not effective pollination. The second strongest interaction in the network was between *Bombus* sp. and *Centaurea stoebe* L. (spotted knapweed, Asteraceae) with 50 total visits (Table 1; Appendix). These frequent insect visitors also were observed on *C. pitcheri* flowering heads (Table 2).

Pitcher's thistle was the most visited plant species: 22 different insect taxa (37.3% of all observed) and 109 (18.2%) of all the visits in the entire network. The two species with the second greatest number of insect visitors (11 taxa) were shrubby cinquefoil (*Dasiphora fruticosa* (L.) Rydb., Rosaceae) and the Lake Huron tansy (*Tanacetum bipinnatum* (L.) Sch. Bip., Asteraceae). The invasive spotted knapweed (*C. stoebe*) had the second greatest number of visits (68), roughly 60% of Pitcher's thistle visits (Table 1, Fig. 2). Pitcher's thistle also received a greater variety of insect visitors compared to other plant species (22 insect representatives from each of the six orders). Visitors to Pitcher's thistle included eight species of Hymenoptera (six bee and two ant types), five fly species (Diptera), three beetle species (Coleoptera), three butterflies (Lepidoptera), two true bugs (Hemiptera), and *Trimerotropis huroniana* E.M. Walker (Lake Huron locust; Orthoptera, Acrididae) a state-listed threatened insect in MI, WI, and Canada (Rankin and Crispin, 1994, Table 2*)*. We also observed three insect taxa that visited Pitcher's thistle exclusively: a Cleridae beetle (Coleoptera), *Stomoxys calcitrans* (L.) (Diptera, Muscidae), *Anatrytone logan* (W.H. Edwards) (Lepidoptera, Hesperidae) and *Polites mystic* (W.H. Edwards) (Lepidoptera, Hesperidae) (Appendix). These insect visitors were infrequent, are widely distributed taxa (Cleridae), only incidentally visit for nectar (*Stomoxys*), and are generalist feeders, including on common milkweed (*Polites* and *Atrytone* on *Asclepias syriaca* L., Apocynaceae).

Nearly all the species level network indices showed Pitcher's thistle to be the most topologically important plant in this network (ND, SS, BW, C, and CW; Table 3). The SS value of 9.525 is 61% larger than the next largest SS value of 5.65 for *D.*

Table 1
Counts and percentages of insect species visitors (species richness) and total number of visits to each plant taxon in the Sturgeon Bay dune flowering plant-insect visitor network. Insect species percentages were derived from the 59 total insect taxa in the network. Insect visits percentages were computed from the 600 total observed.

Plant	Abbreviation	Insect Species		Insect Visits	
		Number	Percent	Number	Percent
Apocynaceae					
Asclepias syriaca L.	ASSY	6	10.2	23	3.8
Asteraceae					
Centaurea stoebe L.	CEST	8	13.6	68	11.3
Cirsium pitcheri (Torr.) Torr. & A. Gray	CIPI	22	37.3	109	18.2
Coreopsis lanceolata L.	COLA	3	5.1	5	0.8
Eupatorium perfoliatum L.	EUPE	4	6.8	5	0.8
Euthamia graminifolia (L.) Nutt.	EUGR	10	17	44	7.3
Hieracium piloselloides Vill.	HIPI	1	1.7	1	0.2
Leucanthemum vulgare Lam.	LEVU	6	10.2	27	4.5
Solidago ohioensis Riddell	SOOH	8	13.6	30	5
Tanacetum bipinnatum (L.) Sch. Bip.	TABI	11	18.6	19	3.2
Boraginaceae					
Lithospermum caroliniense (Walter) MacMill.	LICA	10	17	37	6.2
Brassicaceae					
Arabidopsis lyrata (L.) O'Kane & Al-Shehbaz	ARLY	5	8.5	9	1.5
Cakile edentula (Bigelow) Hook.	CAED	1	1.7	1	0.2
Campanulaceae					
Lobelia kalmii L.	LOKA	6	10.2	66	11
Hypericaceae					
Hypericum kalmianum L.	HYKA	6	10.2	12	2
Lamiaceae					
Clinopodium arkansanum (Nutt.) House	CLAR	1	1.7	6	1
Lentibulariaceae					
Utricularia cornuta Michx.	UTCO	4	6.8	8	1.3
Melanthiaceae					
Anticlea elegans (Pursh) Rydb.	ANEL	5	8.5	64	10.7
Onagraceae					
Oenothera oakesiana (A. Gray) S. Watson & J.M. Coult.	OEOA	6	10.2	11	1.8
Rosaceae					
Dasiphora fruticosa (L.) Rydb.	DAFR	11	18.6	50	8.3
Potentilla anserina L.	POAN	2	3.4	5	0.8

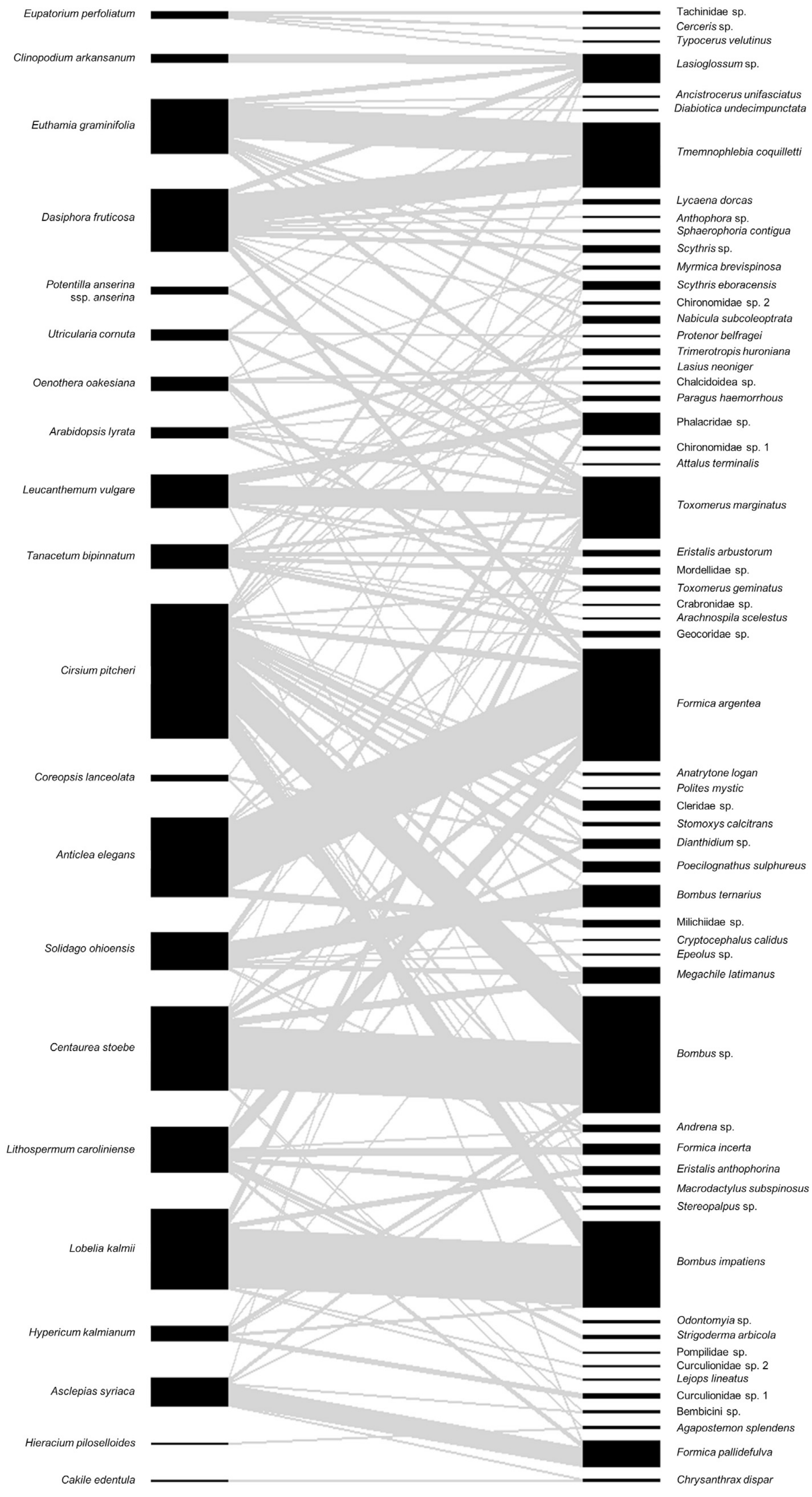

Fig. 2. The Sturgeon Bay dunes plant-insect visitor network as sampled during the *Cirsium pitcheri* flowering season in summer 2015. The right hand bars represent the insect visitors; the left represent the plants. Width of the respective bars depicts the total number of visits performed or number of visits received for insects and plants, respectively. The width of each gray bar shows the strength of the connection between each pair of plants and insects.

Table 2
Insect visitors and number of visits to *Cirsium pitcheri* in the Sturgeon Bay dune plant-insect visitor network surveyed during the 2015 *C. pitcheri* flowering season.

Species/Morphospecies	Family	Order	Visits
Anatrytone logan (W.H. Edwards)	Hesperiidae	Lepidoptera	1
Bombus impatiens Cresson	Apidae	Hymenoptera	20
Bombus sp.	Apidae	Hymenoptera	37
Bombus ternarius Say	Apidae	Hymenoptera	2
Chironomidae sp.	Chironomidae	Diptera	1
Cleridae sp.	Cleridae	Coleoptera	7
Dianthidium sp.	Megachilidae	Hymenoptera	2
Formica argentea Wheeler	Formicidae	Hymenoptera	5
Formica incerta Buren	Formicidae	Hymenoptera	3
Geocoridae sp.	Geocoridae	Hemiptera	1
Lasioglossum sp.	Halictidae	Hymenoptera	4
Macrodactylus subspinosus (F.)	Scarabaeidae	Coleoptera	1
Megachile latimanus Say	Megachilidae	Hymenoptera	4
Nabicula subcoleoptrata Kirby	Nabidae	Hemiptera	1
Poecilognathus sulphureus (Loew)	Bombyliidae	Diptera	8
Polites mystic (W.H. Edwards)	Hesperiidae	Lepidoptera	1
Scythris sp.	Scythrididae	Lepidoptera	2
Stereopalpus sp.	Anthicidae	Coleoptera	2
Stomoxys calcitrans (L.)	Muscidae	Diptera	3
Tmemnophlebia coquilletti (Johns.)	Bombyliidae	Diptera	2
Toxomerus geminatus (Say)	Syrphidae	Diptera	1
Trimerotropis huroniana E.M. Walker	Acrididae	Orthoptera	1

fruitcosa. The index *d'*, a measure of species specialization, indicates that Pitcher's thistle is the most generalized (0.362) plant taxon. The two species with only one visit (*Cakile edentula* (Bigelow) Hook., Brassicaceae and *Hieracium piloselloides* Vill., Asteraceae) were the most specialized (0.864). Betweenness (B), in contrast, showed *Asclepias syriaca* as the most topologically important species; however, when the index was weighted by number of visits (BW), Pitcher's thistle far exceeded *A. syriaca* (Table 3).

C. pitcheri also had many more visits relative to its abundance on the dune landscape than did other plant species present. e.g., *Lobelia kalmii* L. (Campanulaceae) (Fig. 3A and B). There were 123 open flower heads on a total of 44 Pitcher's thistle plants observed during the entire sampling period, yet *C. pitcheri* still received the most visits by insects. In contrast, Carolina puccoon, *Lithospermum caroliniense* (J.F. Gmel.) MacMill. (Boraginaceae), had 1874 flowers on 54 plants, over 15 times the number of heads of Pitcher's thistle, yet received only 37 total visits from insects (Fig. 3A, Table 1). The plant that received the most total observation time was *Lobelia kalmii* with 4390 min (439 plants). Despite this abundance, *L. kalmii* received only 60.5% (66) as many visits as Pitcher's thistle (Fig. 3B, Table 1).

Table 3
Species level network indices for the Sturgeon Bay dune flowering plant-insect visitor network. The indices are normalized degree (ND), species strength (SS), betweenness (B), weighted betweenness (BW), closeness (C), weighted closeness (CW) and *d'*, a measure of specialization.

Plant	Normalized Degree	Species Strength	Betweenness	Weighted Betweenness	Closeness	Weighted Closeness	*d'*
Anticlea elegans	0.085	2.094	0.008	0.043	0.050	0.033	0.704
Arabidopsis lyrata	0.085	2.311	0.004	0.000	0.049	0.016	0.627
Asclepias syriaca	0.102	2.293	0.212	0.132	0.043	0.023	0.722
Cakile edentula	0.017	0.500	0.000	0.000	0.026	0.005	0.848
Centaurea stoebe	0.136	2.482	0.299	0.209	0.058	0.028	0.554
Cirsium pitcheri	0.373	9.525	0.078	0.310	0.055	0.029	0.362
Clinopodium arkansanum	0.017	0.261	0.000	0.000	0.041	0.019	0.669
Coreopsis lanceolata	0.051	0.817	0.010	0.000	0.043	0.009	0.698
Dasiphora fruticosa	0.186	5.366	0.038	0.056	0.053	0.028	0.505
Eupatorium perfoliatum	0.068	3.043	0.000	0.000	0.041	0.011	0.765
Euthamia graminifolia	0.169	4.559	0.003	0.003	0.052	0.028	0.626
Hieracium piloselloides	0.017	0.500	0.000	0.000	0.031	0.005	0.848
Hypericum kalmianum	0.102	1.392	0.034	0.000	0.051	0.016	0.404
Leucanthemum vulgare	0.102	1.785	0.048	0.048	0.047	0.029	0.603
Lithospermum caroliniense	0.169	5.620	0.076	0.076	0.052	0.027	0.537
Lobelia kalmii	0.102	3.578	0.005	0.119	0.049	0.029	0.686
Potentilla anserina	0.034	0.125	0.038	0.000	0.053	0.016	0.378
Oenothera oakesiana	0.102	2.557	0.028	0.000	0.049	0.018	0.471
Solidago ohioensis	0.136	3.860	0.014	0.000	0.050	0.024	0.759
Tanacetum bipinnatum	0.186	5.186	0.044	0.004	0.054	0.019	0.661
Utricularia cornuta	0.068	1.146	0.075	0.000	0.055	0.018	0.317

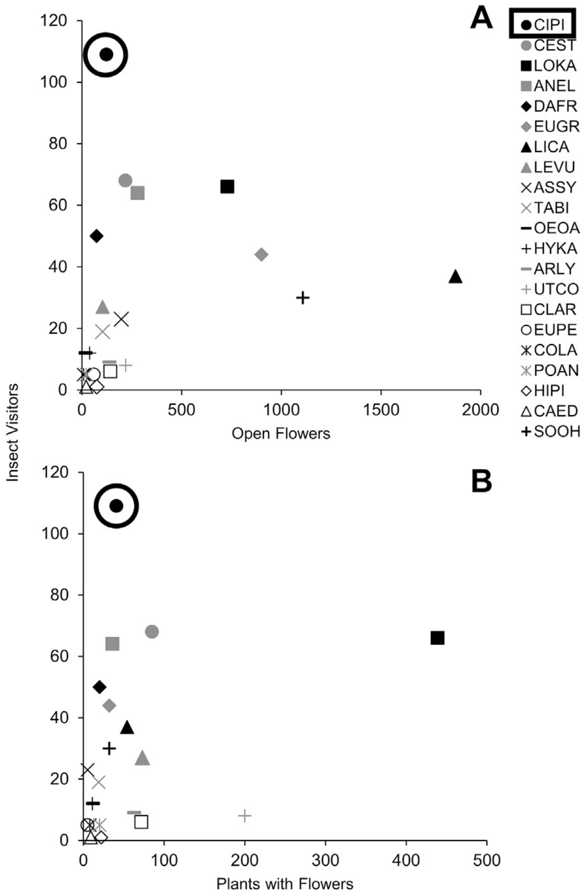

Fig. 3. Number of insect visits each species received relative to abundances of the A) the total number of open flowers and B) the total number of plants that were observed for insect visits in the dune network. Legend names correspond to the first two letters of the genus and specific epithet of each plant taxon. *Cirsium pitcheri* (highlighted with black outline) received the greatest number of insect visits of any other plant taxon in flower, independent of floral display or flowering plant abundance.

4. Discussion

The Great Lakes endemic *Cirsium pitcheri* is an important floral resource for insect visitors. We observed many of the same insect visitors to Pitcher's thistle as have others, including the same members of the families Apidae (*Bombus impatiens*), Bombyliidae, Formicidae, Halictidae (*Lasioglossum* sp.), Hesperidae, Megachilidae (*Megachile latimanus* Say), Nymphalidae, Scarabaeidae (*Strigoderma arbicola* (F.)) (Keddy and Keddy, 1984; Loveless, 1984; Baskett et al., 2011). Hymenopterans were most common in this network, typical of other systems, particularly xeric habitats (Carson et al., 2016; Lance et al., 2017). This diversity of insects that visit Pitcher's thistle reported by others suggests the potential of this plant species as an important floral resource in other dune and cobble shore habitat throughout its range. We found that Pitcher's thistle had many more visits from more types of insects than did any other plant species in the dune network. The species-level network metrics also point to the possible role of Pitcher's thistle as a key plant species supporting the network structure. We observed high BW and CW scores, measures of how much each member contributes to network structure, suggesting that Pitcher's thistle may mediate insect visits to other plant species (Martín González et al., 2010; Pocock et al., 2011). *C. pitcheri* was the most generalized plant in the dune network (*d'*, Table 3), receiving insect visits from the six insect orders in the network (Table 2). Generalists are usually very important for maintenance of network structure (Memmott et al., 2004; Sahli and Conner, 2006) and also are more likely to be considered keystone species in these same networks (Martín González et al., 2010; Pocock et al., 2011).

In the plant-insect visitor network literature, network analysis species-level indices typically are used to identify topologically important species (their "keystoneness", Jordán, 2009), but these indices do not take into account relative abundance (Robson, 2014; Koski et al., 2015). We have shown that *Cirsium pitcheri* has many insect visits relative to abundance of flowers and reproductive plants in the network, many more than other plant species that were similarly abundant (Fig. 3). Plant-flower visitor networks are classically under-sampled (Petanidou et al., 2008; Bosch et al., 2009), particularly temporally. Studies report high proportions of species with one or few links, an observation in contrast to widely accepted view that generalization, not specialization, is the norm in pollination systems. Typically, construction of plant-flower visitor networks is based on observations of focal plants. This approach limits our view of interactions among rare plants and pollinators, which may be the majority in most communities (Bosch et al., 2009). Opportunistic foraging is well-documented, particularly in bees of the genus *Bombus* (Waser et al., 1996). Also, some nodes are difficult to identify taxonomically, e.g., *Bombus* on the wing. Studies typically address these taxonomic challenges by focusing on resource interaction rather than taxonomic identify (e.g., solitary or colonial bees that gather nectar and pollen, Campos-Navarrete et al., 2013). We could not differentiate *Bombus* sp. among three congeners known from the dune ecosystem. Although not presented here, distributing *Bombus* sp. visits into three different taxa did not change any network metric more than 0–3% on average, nor did this change the interpretation of the network. Pitcher's thistle still received the greatest number of visits and type of visitors compared to any other co-blooming plant species. That said, ecological importance of species may change over time (Power et al., 1996; Bosch et al., 2009) and annual variation in topology has been documented for other plant-flower visitor networks (Petanidou et al., 2008; Chacoff et al., 2018). This variation argues for repeated, longer-term documentation of these networks.

One question that arises from our results is why do so many different insect species visit Pitcher's thistle more frequently relative to other co-occurring plants in flower? Higher insect visitation rates may be related to presentation of nectar and pollen resources by Pitcher's thistle relative to other co-flowering taxa, based on size of floral display, duration, and timing of the presentation of these resources. The flowering units of Pitcher's thistle (the head or capitulum inflorescence) offer significant amounts of pollen and nectar to insect visitors. Floral displays of other taxa (e.g., *Lithospermum caroliniense* or *Lobelia kalmii* during our observation period, Fig. 3) can be much smaller than those presented by the capitula of *C. pitcheri*. Insects do not visit single florets, but rather whole inflorescences or heads; other plant-flower visitor networks also use inflorescences of plant families Asteraceae and Apiaceae as the flowering unit for quantification (Memmott, 1999). Few plant-flower visitor network studies compare resource availability (pollen, nectar) among species. Pollen data harvested from insect visitors also can offer perspectives on rare plant species that might be missed by floral observation alone (Bosch et al., 2009). Another obvious next step is to document resource availability, including energy and nutrient flow through ecosystems, as possible mechanisms to explain network structure.

The importance of a plant species in an interaction also relates to its phenology relative to other available resources. For example, fig species (*Ficus* spp., Moraceae) in tropical rainforests of southeastern Asia support frugivores at times of year when other fruits are scarce, providing critical nutritional resources for many vertebrate species (Lambert and Marshall, 1991). Our network analysis did not attempt to analyze the importance of the dune floral resources through the entire growing season, rather we sought to quantify the relative importance of plants during the Pitcher's thistle flowering period. Pitcher's thistle flowers late-June to late-July, after abundant spring floral resources such as bearberry (*Arctostaphylous uva-ursi* L., Ericaceae) and sand cherry (*Prunus pumila* L. Rosaceae), and before fall flowering resources such as Houghton's goldenrod (*Solidago houghtonii* Torr. & A. Gray, Asteraceae) and Ohio goldenrod (*Solidago ohioensis* Riddell, Asteraceae) (Voss, 1972, Fig. 1). High insect visitation to Pitcher's thistle also may be mediated in part by its flowering morphology: heads mature in a determinate corymbose array. After the initial terminal, heads below it flower, often resulting in a flowering period of almost a month on any given individual. A bimodal presentation of colorful, non-green flowers early in the growing season and then in later August occurs in forested and prairie communities (Goodwillie and Jolls, 2014). The timing of Pitcher's thistle flowering may help contribute to its role to the dune pollinator network, despite its rarity.

Future studies should explore the relative importance of rare taxa in more degraded, less diverse ecosystems. Environmental extremes and abundance of invasives can alter community networks, including lower connectedness of native plants with the pollination network (Lindsay et al., 2011; Lance et al., 2017). Baskett et al. (2011) showed that insect diversity and visits to Pitcher's thistle increased in areas after invasive species such as baby's breath (*Gypsophila paniculata* L., Caryophyllaceae) and spotted knapweed (*C. stoebe*) were removed. In the Sturgeon Bay dune system, similar Hymenoptera visit both Pitcher's thistle and spotted knapweed extensively (Appendix). Spotted knapweed also has been shown to be heavily visited by bees in old-field and common garden experiments (Carson et al., 2016). Recent work also suggests that density of this invasive and its phenology relative to native plant taxa can determine impact on plant-flower visitor interactions in other ecosystems (Herron-Sweet et al., 2016). With the removal of knapweed, we might expect to see increased and stronger visitation of Hymenoptera to Pitcher's thistle.

Our study has shown that in relatively pristine and protected Great Lakes dune habitats, Pitcher's thistle is an important resource for flower-visiting insects. The resilience of networks (their ability to tolerate loss of plants or insect pollinators) may be higher in xeric communities such as dunes that are dominated by bees as pollinators, particularly if plants like Pitcher's thistle are well-linked (Lance et al., 2017). Better understanding of plant-flower visitor mutualisms involving rare taxa as well as their roles in the community are needed. Like other rare taxa, Pitcher's thistle populations suffer many threats including coastal habitat degradation (Rankin and Crispin, 1994), herbivory (Phillips and Maun, 1996; Stanforth et al., 1997; Bevill et al., 1999; Rowland and Maun, 2001), low germination in the field (Hamzé and Jolls, 2000), low genetic diversity (Fant et al., 2014), invasive species encroachment (Baskett et al., 2011; Emery et al., 2013), climate change-induced habitat narrowing (Vitt et al., 2010), natural succession in the absence of disturbance (Jolls et al., 2015), and most recently non-target impacts from biological control agents (Havens et al., 2012; Hakes and Meunier, 2018). We do not know how tolerant these dune systems will be to climate change, however. Small populations of Pitcher's thistle are at high risk of extinction or significant population decline (Nantel et al., 2018). Increasing anthropogenic threats that risk loss of important species may destabilize entire networks, leading to a cascade of secondary extinctions (Memmott et al., 2004).

Our data also suggest that this rare endemic thistle may play a significant role in the dune ecosystem. Pitcher's thistle is not the only threatened or narrowly endemic plant species that appears to be ecologically important to the plant-insect network. Rare plants offer important ecosystem services in addition to pollinator resources and habitat, e.g., dispersal by the rare Peruvian palm, *Ceroxylon echinulatum* Galeano (Anthelme et al., 2011) and even carbon cycling, particularly if locally abundant (Álvarez-Yépiz and Dovčiak, 2015). The majority of literature is focused on the rarity of rare species, perhaps at the expense of their ecosystem roles, even though they may contribute significantly to ecosystem function (Rabinowitz et al., 1986; Álvarez-Yépiz and Dovčiak, 2015). Although rare species may represent 30–50% of all taxa in a community, their importance is hard to establish (Tscharntke et al., 2005). Better understanding of plant-flower visitor mutualisms involving rare taxa as well as their other roles in the community are needed. Pitcher's thistle and other rare taxa may help maintain larger community networks, which argues for their conservation, not because they are rare but because they are important.

5. Conclusions

Pitcher's thistle is an important floral resource for the insect species visitors in the dune network, offering important ecosystem services, as suggested for other rare species. Network analysis species-level indices also show Pitcher's thistle is topologically important for the network structure. Although abundance of *C. pitcheri* is low compared to other plants in the network, this endemic thistle is visited by greater abundances of a greater diversity of insect visitors, compared to the other dune plants. Although rare, Pitcher's thistle may function as a keystone species in the dune network for floral insect visitors in mid-summer, increasing the importance of conservation efforts for this and possibly other rare plant species.

Author contributions

JI, CJ, PV, KH conceived and designed the research; JI, CJ, BS acquired the data; JI, CJ, BS, PV, KH analyzed and interpreted the data; CJ, JI drafted and prepared the manuscript; CJ, JI, BS PV, KH, revised and edited the manuscript.

Acknowledgements

We acknowledge support from US Fish and Wildlife Service Great Lakes Restoration Initiative to KH, CJ, and PV, and the Ann Arbor Woman's Farm and Garden Association to JI. Special thanks to G. Beatty, R. Christian, I. Culver, E. Dietrick, E. Fegley, R. Fortner, C. Goodwillie, M. C. Ho, J. Johnson, J. Luczkovich, K. O'Brien, A. Reznicek, and C. Tate for assistance in field, lab, and with analyses, as well as to our anonymous reviewers and editorial staff for comments on the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gecco.2019.e00603.

References

Álvarez-Yépiz, J.C., Dovčiak, M., 2015. Enhancing ecosystem function through conservation: threatened plants increase local carbon storage in tropical dry forests. Trop. Conserv. Sci. 8, 999–1008. https://doi.org/10.1177/194008291500800410.

Anthelme, F., Lincango, J., Gully, C., Duarte, N., Montúfar, R., 2011. How anthropogenic disturbances affect the resilience of a keystone palm tree in the threatened Andean cloud forest? Biol. Conserv. 144, 1059–1067. https://doi.org/10.1016/j.biocon.2010.12.025.

Baskett, C.A., Emery, S.M., Rudgers, J.A., 2011. Pollinator visits to threatened species are restored following invasive plant removal. Int. J. Plant Sci. 172, 411–422. https://doi.org/10.1086/658182.

Bevill, R.L., Louda, S.M., Stanforth, L.M., 1999. Protection from natural enemies in managing rare plant species. Conserv. Biol. 13, 1323–1331. https://doi.org/10.1046/j.1523-1739.1999.98450.x.

Blüthgen, N., Menzel, F., Blüthgen, N., 2006. Measuring specialization in species interaction networks. BCM Ecol. 6, 9. https://doi.org/10.1186/1472-6785-6-9.

Bosch, J., Martín González, A.M., Rodrigo, A., Navarro, D., 2009. Plant-pollinator networks: adding the pollinator's perspective. Ecol. Lett. 12, 409–419. https://doi.org/10.1111/j.1461-0248.2009.01296.x.

Campos-Navarrete, M.J., Parra-Tabla, V., Ramos-Zapata, J., Díaz-Castelazo, C., Reyes-Novelo, E., 2013. Structure of plant-hymenoptera networks in two coastal shrub sites in Mexico. Arthropod-Plant Interact. 7, 607–617. https://doi.org/10.1007/s11829-013-9280-1.

Carson, B.D., Bahlai, C.A., Gibbs, J., Landis, D.A., 2016. Flowering phenology influences bee community dynamics in old fields dominated by the invasive *Centaurea stoebe*. Basic Appl. Ecol. 17, 497–507. https://doi.org/10.1016/j.baae.2016.04.004.

Chadde, S., 2013. Wisconsin Flora: an Illustrated Guide to the Vascular Plants of Wisconsin. CreateSpace Publishing; Charleston, South Carolina.

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. https://doi.org/10.1002/ecy.2063.

Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the Bipartite package: analysing ecological networks. R. News 8, 8–11.

Emery, S.M., Doran, P.J., Legge, J.T., Kleitch, M., Howard, S., 2013. Aboveground and belowground impacts following removal of the invasive species baby's breath (*Gypsophila paniculata*) on Lake Michigan sand dunes. Restor. Ecol. 21, 506–514. https://doi.org/10.1111/j.1526-100X.2012.00915.x.

ESRI, 2013. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, California.

Fant, J.B., Havens, K., Keller, J.M., Radosavljevic, A., Yates, E.D., 2014. The influence of contemporary and historic landscape features on the genetic structure of the sand dune endemic, *Cirsium pitcheri* (Asteraceae). Heredity 12, 519–530. https://doi.org/10.1038/hdy.2013.134.

Flora of North America Editorial Committee, 1993. In: Flora of North America North of Mexico. 19 Vols. New York and Oxford.

Goodwillie, C., Jolls, C.L., 2014. Mating systems and floral biology of the herb layer: a survey of two communities and the state of our knowledge. In: Gilliam, F.S., Roberts, M.R. (Eds.), The Herbaceous Layer in Forests of Eastern North America, second ed. Oxford University Press, New York, pp. 109–129.

Granovetter, M., 1976. Network sampling: some first steps. Am. J. Sociol. 81, 1287–1303. https://www.jstor.org/stable/i329012.

Hakes, A.S., Meunier, Z.D., 2018. Nonhost neighborhood increases biocontrol weevil damage to the nontarget, federally threatened Pitcher's thistle (*Cirsium pitcheri*). Global Ecol. Conserv. 13 e00376. https://doi.org/10.1016/j.gecco.2018.e00376.

Hamzé, S.I., Jolls, C.L., 2000. Germination ecology of a federally threatened endemic thistle, *Cirsium pitcheri*, of the Great Lakes. Am. Midl. Nat. 143, 141–153. http://www.jstor.org/stable/3082990TAG.
Havens, K., Jolls, C.L., Marik, J.E., Vitt, P., McEachern, A.K., Kind, D., 2012. Effects of a non-native biocontrol weevil, *Larinus planus*, and other emerging threats on populations of the federally threatened Pitcher's thistle, *Cirsium pitcheri*. Biol. Conserv. 155, 202–211. https://doi.org/10.1016/j.biocon.2012.06.010.
Herron-Sweet, C.R., Lehnhoff, E.A., Burkle, L.A., Littlefield, J.L., Mangold, J.M., 2016. Temporal- and density-dependent impacts of an invasive plant on pollinators and pollinator services to a native plant. Ecosphere 7 e01233. https://doi.org/10.1002/ecs2.1233.
Inkster, J.N., 2016. The antagonistic and mutualistic plant-insect interactions of Pitcher's thistle (*Cirsium pitcheri* (Torr. ex EaTorr. & A. Gray, Asteraceae), a federally threatened Great Lakes dune and cobble shore endemic plant. Masters of Science Thesis. East Carolina University, Greenville, North Carolina.
Jolls, C.L., Marik, J.E., Hamzé, S.I., Havens, K., 2015. Population viability analysis and the effects of light availability and litter on populations of *Cirsium pitcheri*, a rare, monocarpic perennial of Great Lakes shorelines. Biol. Conserv. 187, 82–90. https://doi.org/10.1016/j.biocon.2015.04.006.
Jordán, F., 2009. Keystone species and food webs. Philos. Trans. R. Soc. B 365, 1733–1741. https://doi.org/10.1098/rstb.2008.0335.
Jordán, F., Okey, T.A., Bauer, B., Libralato, S., 2008. Identifying important species: linking structure and function in ecological networks. Ecol. Model. 216, 75–80. https://doi.org/10.1016/j.ecolmodel.2008.04.009.
Keddy, C., Keddy, P., 1984. Reproductive biology and habitat of *Cirsium pitcheri*. Mich. Bot. 23, 57–67.
Koski, M.H., Meindl, G.A., Arceo-Gómez, G., Wolowski, M., LeCroy, K.A., Ashman, T., 2015. Plant–flower visitor networks in a serpentine metacommunity: assessing traits associated with keystone plant species. Arthropod-Plant Interact. 9, 9–21. https://doi.org/10.1007/s11829-014-9353-9.
Lambert, F.R., Marshall, A.G., 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. J. Ecol. 79, 793–809. http://www.jstor.org/stable/2260668.
Lance, R.F., Bailey, P., Lindsay, D.L., Cobb, N.S., 2017. Precipitation and the robustness of a plant and flower-visiting insect network in a xeric ecosystem. J. Arid Environ. 144, 48–59. https://doi.org/10.1016/j.jaridenv.2017.03.015.
Leitao, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Mendonça, F., Mouillot, D., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. Proc. R. Soc. B 283, 20160084. https://doi.org/10.1098/rspb.2016.0084.
Lichter, J., 1998. Primary succession and forest development on coastal Lake Michigan sand dunes. Ecol. Monogr. 68, 487–510. https://doi.org/10.2307/2657151.
Lindsay, D.L., Bailey, P., Lance, R.F., Clifford, M.J., Delph, R., Cobb, N.S., 2011. Effects of a nonnative, invasive lovegrass on *Agave palmeri* distribution, abundance, and insect pollinator communities. Biodivers. Conserv. 20, 3251–3266 doi 10.1007s10531-011-0133-x.
Loveless, M.D., 1984. Population biology and genetic organization in *cirsium pitcheri*, an endemic thistle. Ph.D. Dissertation, University of Kansas, Lawrence, Kansas.
Mills, L.S., Soulé, M.E., Doak, D.F., 1993. The keystone-species concept in ecology and conservation. Bioscience 43, 219–224. https://doi.org/10.2307.
Martín González, A.M., Dalsgaard, B., Olesen, J.M., 2010. Centrality measures and the importance of generalist species in pollination networks. Ecol. Complex. 7, 36–43. https://doi.org/10.1016/j.ecocom.2009.03.008.
Memmott, J., 1999. The structure of a plant-pollinator food web. Ecol. Lett. 2, 276–280. https://doi.org/10.1046/j.1461-0248.1999.00087.x.
Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. Proc. Roy. Soc. Lond. B. 271, 2605–2611. https://doi.org/10.1098/rspb.2004.2909.
Morse, D.H., 1979. Prey capture by the crab spider *Misumena calycina* (Araneae: Thomisidae). Oecologia 39, 309–319. https://doi.org/10.1007/BF00345442.
Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmeli-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J.,, Thuiller, W., 2013. Rare species support vulnerable functions in high diversity ecosystems. PLoS Biol. 11, e1001569. https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.1001569.
Nantel, P.L., Jones, J., Drake, C., 2018. Viability of multiple populations across the range of a species at risk: the case of Pitcher's thistle, *Cirsium pitcheri*, in Canada. Global Ecol. Conserv. 16, e00445. https://doi.org/10.1016/j.gecco.2018.e00445.
Olesen, J.M., Eskildsen, L.I., Venkatasamy, S., 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. Divers. Distrib. 8, 181–192. https://doi.org/10.1046/j.1472-4642.2002.00148.x.
Ownbey, G.B., Morley, T., 1991. Vascular Plants of Minnesota. University of Minnesota Press, Minneapolis, Minnesota.
Paine, R.T., 1969. A note on trophic complexity and community stability. Am. Nat. 103, 91–93. https://doi.org/10.1086/282586.
Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P., Pantis, J.D., 2008. Long-term observation of a pollination network: fluctuation in species interactions, relative invariance of network structure and implications for estimates of specialization. Ecol. Lett. 11, 564–575. https://doi.org/10.1111/j.1461-0248.2008.01170.x.
Phillips, T., Maun, M.A., 1996. Population ecology of *Cirsium pitcheri* on Lake Huron sand dunes I. Impact of white-tailed deer. Can. J. Bot. 74, 1439–1444. https://doi.org/10.1139/cjb-2015-0032.
Pocock, M.J.O., Johnson, O., Wasiuk, D., 2011. Succinctly assessing the topological importance of species in flower-pollinator networks. Ecol. Complex. 8, 265–272. https://doi.org/10.1016/j.ecocom.2011.06.003.
Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones: identifying keystone species is difficult but essential to understanding how loss of species will affect ecosystems. Bioscience 46, 609–620. http://www.jstor.org/stable/1312990.
R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.
Rabinowitz, D., 1981. Seven forms of rarity. In: Synge, H. (Ed.), Biological Aspects of Rare Plant Conservation. John Wiley and Sons Ltd., New York, pp. 205–2017.
Rabinowitz, D., Cairns, S., Dillon, T., 1986. Seven forms of rarity and their frequency in the flora of the British Isles. In: Soule, M.E. (Ed.), Conservation Biology. The Science of Scarcity and Diversity. Sinauer, Sunderland, Massachusetts, pp. 182–204.
Rankin, J.D., Crispin, S.R., 1994. The conservation of biological diversity in the Great Lakes ecosystem: issues and opportunities. The Nature Conservancy, Great Lakes Program, Chicago, Illinois.
Robson, D.B., 2014. Mutualistic and antagonistic networks involving the rare silky prairie-clover (*Dalea villosa* var. *villosa*) and its co-flowering plants and insect visitors. Botany 92, 47–58. https://doi.org/10.1139/cjb-2013-0231.
Rowland, J., Maun, M.A., 2001. Restoration ecology of an endangered plant species: establishment of new populations of *Cirsium pitcheri*. Restor. Ecol. 9, 60–70. https://doi.org/10.1046/j.1526-100X.2001.009001060.x.
Sahli, H.F., Conner, J.K., 2006. Characterizing ecological generalization in plant-pollination systems. Oecologia 148, 365–372. https://doi.org/10.1007/s00442-006-0396-1.
Severns, P.M., Moldenke, A.R., 2010. Management tradeoffs between focal species and biodiversity: endemic plant conservation and solitary bee extinction. Biodivers. Conserv. 19, 3605–3609. https://doi.org/10.1007/s10531-010-9897-7.
Soares, R.G.S., Ferreira, P.A., Lopes, L.E., 2017. Can plant-pollinator network metrics indicate environmental quality? Ecol. Indicat. 78, 361–370. https://doi.org/10.1016/j.ecolind.2017.03.037.
Stanforth, L.M., Louda, S.M., Bevill, R.L., 1997. Insect herbivory on juveniles of a threatened plant, *Cirsium pitcheri*, in relation to plant size, density and distribution. Ecoscience 4, 57–66. http://www.jstor.org/stable/42900699.
Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, Theis, C., 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol. Lett. 8 https://doi.org/10.1111/j.1461-0248.2005.00782.x, 857-784.
Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D., Yates, E., 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. Biol. Conserv. 143, 18–27. https://doi.org/10.1016/j.biocon.2009.08.015.
Voss, E.G., 1972. Michigan Flora. Part I. Gymnosperms and Monocots. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Voss, E.G., Reznicek, A.A., 2012. Field Manual of Michigan Flora: A Comprehensive Guide to Michigan's Wild-Growing Seed Plants. University of Michigan Press, Ann Arbor.
Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in pollination systems, and why it matters. Ecology 77, 1043–1060. https://doi.org/10.2307/2265575.
Williams, A.H., 2015. Feeding records of true bugs (Hemiptera: heteroptera) from Wisconsin, supplement. Great Lakes Entomol. 48, 192–198.