Historical Bee Species Diversity and Current Plant-Bee Pollination Networks on Plummers Island, Maryland

7 authors, including:

Sam Droege
United States Geological Survey
67 PUBLICATIONS **8,742** CITATIONS

John T. Lill
George Washington University
83 PUBLICATIONS **3,832** CITATIONS

BioOne COMPLETE

A Plant-Bee Visitation Network for Plummers Island, MD

Authors: Oppenheimer, Robert L., and Lill, John T.

A PLANT-BEE VISITATION NETWORK FOR PLUMMERS ISLAND, MD

ROBERT L. OPPENHEIMER AND JOHN T. LILL

(RLO, JTL) Department of Biological Sciences, The George Washington University, Washington, DC, USA (e-mail: roblouopp@gmail.com; e-mail: lillj@gwu.edu)

Abstract.—Plummers Island is a small island located in the Potomac River in Montgomery Co., MD. Bees have been collected and cataloged from Plummers Island since 1909, but their floral associations have not been thoroughly described. As bees are important pollinators of natural and managed terrestrial ecosystems, monitoring their floral host choices is an important step towards proper land management and conservation practices. We collected bees from flowering plants on and adjacent to Plummers Island over two seasons and characterized their interactions using a bipartite plant-bee visitation network. Seven hundred and forty individual bees visited 30 species of flowering plants currently classified in 17 different genera. The resulting network was characterized by nested, asymmetrical interactions, but did not show strong evidence of either extreme generalization or specialization. The plant with highest interaction frequency score (species strength) was the invasive poison hemlock, *Conium maculatum* (Apiaceae), while the common sweat bee, *Augochlora pura* (Halictidae) had the highest interaction strength for the bees. We discuss these results considering species phenology and potential sampling biases and compare them to previous records for the island.

Key Words: Plant-pollinator interactions, Ecological networks, Specialization, Invasive plants, Rare species

---

There are approximately 20,000 species of extant bees worldwide (Danforth et al. 2013, Sann et al. 2018) most of which are dependent on plant pollen to provision their young. The diet breadth of different bees ranges from specialization on the pollen of one or a few plant species (oligolecty), to generalization on a wide variety of species or plant families (polyletcy), to kleptoparasitism, in which bees lay their eggs in the already provisioned nests of host bees (Michener 2007). As spillover of wild bees from natural ecosystems provides significant pollination of agricultural crops, documenting and monitoring wild bee communities and their floral associations is important for informing conservation policy surrounding both the bees and the wild plants on which they depend (Kremen 2008).

Attempts to understand wild bee communities and their floral associations typically employ analyses of these interactions as bipartite (two-group) ecological networks. Ecological networks help ecologists to better understand how species interactions create structured and

resilient communities (Bascompte et al. 2006, Dormann et al. 2017). Plant-visitation (or plant-pollinator) networks can be used to visualize the presence and strength of interactions between plants and pollinators (i.e., the frequency of occurrence of interactions)(Memmot 1999). They take into account species abundance and can be used to test hypotheses related to foraging strategies (Sazatornil et al. 2016) or plant community composition (Seitz et al. 2020), to document temporal changes in interactions and interaction frequencies (Petanidou et al. 2008, Burkle et al. 2013, Sajjad et al. 2017) or differences between disturbed and restored habitat (Forup et al. 2008), or to test hypotheses concerning the resilience of systems to species loss (Memmott et al. 2004, Saavedra et al. 2011, Brosi et al. 2017).

Analyses of plant-pollinator interactions using ecological networks have shown that most networks are characterized by uneven, asymmetrically distributed interactions (Bascompte et al. 2003). Such asymmetrical network topography is considered nested: a subset of species with fewer interactions are connected to the network through interactions with a subset of species with more interactions (Bascompte et al. 2003, Jordano et al. 2003, Vazquez and Aizen 2004, Nielsen and Bascompte 2007, Vázquez et al. 2009). Theoretically, this structure allows for the persistence of rare, pair-wise interactions by providing a rich pool of more general interactions that serve to connect rarer, or more specialized, outliers to the network (Bascompte et al. 2006).

Plummers Island is a small (4.8 ha) island located 14.5 km northwest of the Washington, DC metropolitan area. The island is accessible by foot and is separated from the mainland by the Rock Run Culvert, which is only ~10 meters at its widest point. The topography of Plum-

mers Island supports a diverse flora within a relatively small area; over 800 plant species and more than 2000 insect species have been documented in three different plant communities (riparian, terrace, and upland forest) on the island since 1901when members of the Washington Biological Field Club began sampling the island's biodiversity (Stains 2004, Brown 2005, Shetler et al. 2006).

The bees of Plummers Island have been documented with various techniques (pan traps, hand nets) since 1909. Noted hymenopterist, Karl V. Krombein, compiled a thorough checklist, tallying 163 species from 37 genera, including 9 species documented from the adjacent mainland (Krombein 1985). While Krombein (1985) noted many bee-floral associations he observed on the island, no quantitative plant-bee networks have been previously constructed. Due to the extensive sampling history of Plummers Island we set out to characterize its summer plant-bee community by sampling bees from flowers using aerial nets over the course of two summers. We briefly characterize the resultant network and highlight some of its notable characteristics. Additionally, we address limitations of our sampling efforts, how those limitations are reflected by network metrics, and discuss these metrics within an ecological context. The interaction matrix underlying this network has been submitted to the Interaction Web Database (https://iwdb.nceas.ucsb.edu/resources.html) and the Web of Life Database (http://www.web-of-life.es/map.php). We hope this dataset will be useful for future ecological research conducted on Plummers Island.

MATERIALS AND METHODS

Bees were collected from May 31 to August 13, 2012 and from June 5

through August 20, 2013 one to three times per week, on sunny days between 10 AM and 3 PM. For each sampling period, the amount of time spent at each plant species each day was recorded. No more than 2 hours and no less than 30 minutes each day were spent at a focal flowering plant, which was typically surveyed in a single patch. This method was used to maximize the number of plants sampled and bees collected. Samplings were typically done by a single individual, and if no pollinator activity was observed after 30 minutes, the individual moved on to a different plant species. This was continued until either the end of anthesis or the end of the yearly sampling period. Bees were collected using an aerial net from flowering plants if contact was made by the bee and the reproductive organs of the plant. Collected bees were immediately killed by placing them in individual vials of 95% EtOH. Bees were identified by Sam Droege at the USGS Patuxent Wildlife Research Center. Plants were identified using field-guides (Brandenburg 2010) and a dichotomous key (Radford et al. 1964) and were cross referenced against the Plummers Island flora (Shetler et al. 2006). The bees and voucher plant specimens are stored at the George Washington University Biology Department.

The plant-bee network (and associated metrics) was constructed using the "bipartite" package in R Studio (Dormann et al. 2008, RStudio Team 2020). For each plant and bee species, we computed the following network metrics: degree, strength, and Bluthgen's specialization index. We also computed the network level specialization index H_2'. Degree (k) is the total number of bee species that were recorded visiting a given plant, or the total number of plant species a given bee was recorded visiting

and does not account for the frequency of these interactions. Strength (S) accounts for interaction frequency and is calculated by first creating a dependency matrix: the frequency of each interaction for each species is divided by the total number of interactions for that species. Strength is the sum of those dependencies and represents the importance of a species for members of the other trophic level (Dormann 2011). As sampling bias can significantly affect network structure (Blüthgen et al. 2006, 2008), Bluthgen's specialization index (d') and the network-level specialization index (H_2') are useful because they are unaffected by network size (Blüthgen et al. 2008). Bluthgen's d' and H' are based on Shannon's diversity index and measure specialization at the species and network levels respectively. Both indices increase with increased specialization and take on a value between 0 and 1(Blüthgen et al. 2006). R Studio was also used to assess whether the number of hours spent at each flowering plant predicted the degree, interaction strength, and d' for each plant-pollinator relationship using simple linear regression.

Nestedness (N) of the network was calculated using the online program BINMATNEST (Rodríguez-Gironés and Santamaría 2006). BINMATNEST calculates the nestedness temperature of a binary matrix and compares this temperature to a series of n randomly created matrices. A network's temperature is inversely related to its nestedness calculation such that a higher temperature characterizes a less nested network. BINMATNEST returns the average temperature of the hypothetical random matrices as well as a probability that the temperatures of these random matrices are significantly greater than that of the observed empirical matrix. A perfectly nested network will have a temperature

of 0, while networks characterized by disorder have a maximum temperature value of 100. We used the null model 3 to test significance (Rodríguez-Gironés and Santamaría 2006).

RESULTS

A total of 740 bees representing 42 species, 17 genera, and 5 families were collected from 30 flowering plant species (representing 156 unique interactions; Tables 1 and 2; Figure 1). Twenty-five individual bees could be identified to genus, but not species, due to either missing or destroyed morphological features. These individuals are likely species already in our collection (S. Droege, pers. comm.), but we conservatively placed them as unidentified species in their representative genera (*Ceratina* sp. (n = 10), *Hylaeus* sp. (n = 12), and *Lasioglossum* sp. (n = 3) (Table 2)). Nine of the identified species we collected were not recorded in Krombein's (1985) checklist (Table 2). Six of these nine species were Halictid sweat bees, four of which came from the genus *Lasioglossum*. *Andrena confederata* Viereck, *Bombus perplexus* Cresson, and *Melissodes bimaculatus* Lepeletier are the remaining three new species recorded. These nine rare species also had somewhat low strength (Fig. 1 asterisks) as eight of them were in the lower 2nd quartile range for overall strength values. However, these species do not appear to be generally restricted in their diet breadth (Fig. 3 asterisks), as none of them fall into the upper 3rd quartile range for d' values.

A total of 442 of the sampled bees were female and 298 were male. The floral associations of collected bees are given in Table 2, while the strengths of those interactions are depicted in Figure

1 as a bipartite web. The web displays species according to decreasing strength values, with species with higher strength values at the top of the web; interaction strength between plants and bees are represented by the thickness of each connecting line. The strongest (i.e., most connected) plants in the network were *Conium maculatum* L. (Apiaceae), *Cephalanthus occidentalis* L. (Rubiaceae), and *Lapsana communis* L. (Asteraceae); the strongest bees were *Augochlora pura* Say (Halictidae), *Ceratina calcarata* Robertson (Apidae) and *Bombus impatiens* Cresson(Apidae).

Combined over the two years of sampling, an average of 4.10 hours (± 2.84 SD) was spent at each focal plant species (total sampling hours = 123 hrs) (Table 1). Time spent at each plant over 2 years significantly affected the degree (r^2_{adj} = 0.23, p < 0.01), and interaction strength (r^2_{adj} = 0.11, p < 0.05), but did not significantly correlate with d' (r^2_{adj} = -0.02, p = 0.53).

The average d' for bees (0.34, 0.30–0.40 95% CI) in the network was not significantly different from the average d' for plants (0.37; 0.30–0.45 95% CI; Welch's t = -0.7, df = 59.9, p = 0.47). The network for Plummers island had a nestedness temperature of 8.4 which significantly differed from the null model (null model average temperature= 20.2 ±7.7 VAR, p<0.0001). The network level specialization index H_2' was 0.50.

Figures 2 and 3 depict the specialization index (d') for plants (2) and bees (3). The plant species with the highest d' value was *Asclepias syriaca* L. (Apocynaceae). *Bombus griseocollis* Degeer had the highest d' value for bees, followed by *Ptilothrix bombiformus* Cresson, a pollen specialist on *Hibiscus* spp. across its range (Rudy 1980, Sampson et al. 2016). Twenty-two of 26 visits by

Table 1. List of host plants for the bees of Plummers Island. Plant names are organized alphabetically by family. Native status indicates whether plants are native to North America; sex ratio indicates the ratio of male to female bees collected; n = total number of interactions; D = degree or the number of species interactions; Hours = hours spent observing each plant over two seasons.

Plant Species	Family	Native Y/N	Sex Ratio (M:F)	n	D	Hours
Conium maculatum	Apiaceae	N	0.17	30	13	6.50
Apocynum cannabinum	Apocynaceae	Y	0.50	10	5	9.91
Asceplias syriaca	Apocynaceae	Y	0.50	58	7	7.75
Aster lanceolatus	Asteraceae	Y	0.35	23	7	2.92
Eupatorium coelestinum	Asteraceae	Y	0.33	12	4	3.92
Eupatorium purpureum	Asteraceae	Y	0.50	21	5	3.75
Helianthus decapetalus	Asteraceae	Y	0.67	9	4	0.50
Lapsana communis	Asteraceae	N	0.06	17	7	4.25
Polymnia uvedalia	Asteraceae	Y	0.42	60	4	3.50
Rudbeckia hirta	Asteraceae	Y	0.00	4	2	1.25
Rudbeckia laciniata	Asteraceae	Y	0.60	40	6	1.50
Solidago sp.	Asteraceae	Y	0.90	21	3	1.50
Verbesina alternifolia	Asteraceae	Y	0.67	15	4	1.50
Campsis radicans	Bignoniaceae	Y	0.00	1	1	1.17
Erysimum cheiranthoides	Brassicaceae	N	0.14	7	4	8.17
Commelina erecta	Commelinaceae	Y	0.25	4	2	2.75
Calystegia sepium	Convulvaceae	Y	0.50	4	3	2.00
Hypericum prolificum	Hypericaceae	Y	0.00	45	5	1.42
Lycopus rubellus	Lamiaceae	Y	0.25	8	3	2.00
Satchys tenuifolia	Lamiaceae	Y	0.94	18	5	4.83
Lindernia dubia	Linderniaceae	Y	0.13	16	5	3.42
Hibiscus laevis	Malvaceae	Y	0.28	43	9	5.83
Oxalis stricta	Oxalidaceae	Y	0.29	7	5	4.84
Polygonum amphibium	Polygonaceae	Y	0.10	10	2	3.33
Lysimachia nummularia	Primulaceae	N	0.00	1	1	0.50
Cephalanthus occidentalis	Rubiaceae	Y	0.43	79	16	7.24
Scrophularia marilandica	Scrophulariaceae	Y	0.59	34	5	3.75
Solanum carolinense	Solanaceae	Y	0.00	28	3	9.82
Verbena hastata	Verbenaceae	Y	0.41	59	6	3.42
Verbena urticifolia	Verbenaceae	Y	0.61	56	10	9.83

P. bombiformus were made to *Hibiscus laevis* All., which received a total of 43 visits by 9 different bee species.

DISCUSSION

Network Structure

The nine species newly-recorded from Plummers Island were represented by a range of 1–11 individuals collected (Table 2) over two summer sampling periods. Low frequencies for species in a network analysis may be indicators of sampling bias such as a focus on large, showy species (Chacoff et al. 2012). The fact that these species were not recorded in a previous checklist, however, suggests that they may indeed be rare species for Plummers Island and accurately depicted in the visitation network.

As is predicted for ecological networks, the Plummers network was significantly nested and characterized by asymmetrical interaction frequency ordered around a subset of species which interact with most

Table 2. List of bees for Plummers Island collected over two summers from 30 flowering plants. Bees are listed alphabetically by family. The numbers of individual female and males collected are listed above their respective host plants. Krombein 1985 indicates whether bees were present in a previous checklist. If species were present under a synonymous name, then synonyms are listed.

	Krombein 1985
Andrenidae	
Andrena banksi Malloch	Yes
♀- 1 ♂- 0	
Conium maculatum	
Andrena confederata Viereck	No
♀- 2 ♂- 0	
Conium maculatum	
Andrena hilaris Smith	Yes
♀- 1 ♂- 0	
Conium maculatum	
Andrena imitatrix Cresson	Yes
♀- 1 ♂- 0	
Conium maculatum	
Andrena perplexa Smith	Yes
♀- 3 ♂- 0	
Conium maculatum	
Andrena spiraeana Roberston	Yes
♀- 1 ♂- 0	
Cephalanthus occidentalis	
Andrena vicina Smith	Yes
♀- 2 ♂- 0	
Conium maculatum	
Apidae	
Anthophora abrupta Say	Yes
♀- 0 ♂- 1	
Asclepias syriaca	
Apis mellifera Linnaeus	Yes
♀- 8 ♂- 0	
Cephalanthus occidentalis	
Verbena urticifolia	
Bombus auricomus Robertson	Yes
♀- 2 ♂- 0	
Cephalanthus occidentalis	

Table 2. Continued.

	Krombein 1985
Bombus bimaculatus Cresson	Yes

♀- 2 ♂- 14
Asclepias syriaca *Cephalanthus occidentalis*

Cephalanthus occidentalis	*Conium maculatum*
	Stachys tenuifolia
	Aster lanceolatus
Bombus griseocollis Degeer	Yes

♀- 29 ♂- 36
Asclepias syriaca *Apocynum cannabinum*
Hibiscus laevis *Asclepias syriaca*
Solanum carolinense *Cephalanthus occidentalis*
Stachys tenuifolia

Bombus impatiens Cresson	Yes

♀- 84 ♂- 26
Cephalanthus occidentalis *Cephalanthus occidentalis*
Eupatorium coelestinum *Eupatorium purpureum*
Eupatorium purpureum *Helianthus decapetalus*
Hibiscus laevis *Hibiscus laevis*
Hypericum prolificum *Polymnia uvedalia*
Polymnia uvedalia *Stachys tenuifolia*
Rudbeckia laciniata *Verbesina alternifolia*
Solanum carolinense

Bombus perplexus Cresson	No

♀- 0 ♂- 8
Cephalanthus occidentalis
Verbena urticifolia

Ceratina calcarata Robertson	Yes

♀- 91 ♂-22
Asclepias syriaca *Eupatorium coelestinum*
Calystegia sepium *Hibiscus laevis*
Cephalanthus occidentalis *Lindernia dubia*
Eupatorium coelestinum *Polygonum amphibium*
Eupatorium purpureum *Polymnia uvedalia*
Helianthus decapetalus *Stachys tenuifolia*
Hypericum prolificum *Aster lanceolatus*
Lindernia dubia *Verbena hastata*
Lycopus rubellus
Oxalis stricta
Polymnia uvedalia
Rudbeckia hirta
R. laciniata
Scrophularia marilandica
Stachys tenuifolia
Aster lanceolatus
Verbena hastata
Verbena urticifolia
Verbesina alternifolia

Table 2. Continued.

		Krombein 1985
Ceratina sp.		NA
♀- 6	♂-4	
Helianthus decapetalus	*Lindernia dubia*	
Solidago sp.	*Verbena hastata*	
Aster lanceolatus		
Verbena hastata		
V. urticifolia		
Ceratina strenua Smith		Yes
♀- 4	♂-0	
Oxalis stricta		
Rudbeckia hirta		
Solidago sp.		
Aster lanceolatus		
Melissodes bimaculatus (Lepeletier)		No
♀- 0	♂-1	
	Hibiscus laevis	
Ptilothrix bombiformus Cresson	Oligolectic on *Hibiscus*	Yes
♀- 24	♂-3	
Cephalanthus occidentalis	*Calystegia sepium*	
Hibiscus laevis	*Cephalanthus occidentalis*	
	Hibiscus laevis	
Colletidae		
Colletes thoracicus Smith		Yes
♀- 5	♂- 0	
Conium maculatum		
Hylaeus sp.		Yes
♀- 7	♂- 5	
Cephalanthus occidentalis	*Cephalanthus occidentalis*	
Conium maculatum	*Conium maculatum*	
Halictidae		
Agapostemon virescens (Fabricius)		No
♀- 0	♂- 1	
	Polymnia uvedalia	
Augochlora pura (Say)		Yes
♀- 56	♂- 149	
Cephalanthus occidentalis	*Apocynum cannabinum*	
Commelina erecta	*Calystegia sepium*	
Conium maculatum	*Cephalanthus occidentalis*	
Eupatorium coelestinum	*Commelina erecta*	
Erysimum cheiranthoides	*Eupatorium coelestinum*	
Eupatorium purpureum	*Erysimum cheiranthoides*	
Hibiscus laevis	*Eupatorium purpureum*	
Lapsana communis	*Helianthus decapetalus*	

Table 2. Continued.

		Krombein 1985
Polymnia uvedalia	*Hibiscus laevis*	
Rudbeckia laciniata	*Lycopus rubellus*	
Scrophularia marilandica	*Oxalis stricta*	
Aster lanceolatus	*Polymnia uvedalia*	
Verbena hastata	*Rudbeckia laciniata*	
V. urticifolia	*Scrophularia marilandica*	
Verbesina alternifolia	*Solidago* sp.	
	Verbena hastata	
	V. urticifolia	
	Verbesina alternifolia	
Augochlorella aurata (Smith)		Yes
♀- 48	♂- 9	
Commelina erecta	*Lapsana communis*	
Erysimum cheiranthoides	*Verbena hastata*	
Hibiscus laevis	*V. urticifolia*	
Hypericum prolificum		
Lapsana communis		
Polygonum amphibium		
Scrophularia marilandica		
Verbena hastata		
V. urticifolia		
Verbesina alternifolia		
Augochloropsis metallica (Fabricius)		No
♀- 11	♂- 0	
Apocynum cannabinum		
Hibiscus laevis		
Rudbeckia laciniata		
Solanum carolinense		
Verbena urticifolia		
Halictus confusus (Smith)		Yes
♀- 0	♂- 2	
	Cephalanthus occidentalis	
	Verbena urticifolia	
Lasioglossum birkmani (Curtis)		Yes-*Evylaeus birkmani*
♀- 7	♂- 1	
Conium maculatum	*Asclepias syriaca*	
Lapsana communis		
Lysimachia nummularia		
Lasioglossum cressonii Robertson		Yes-*Dialictus cressonii* (Robertson) and *D. delectatus* (Mitchell)
♀- 4	♂- 0	
Campsis radicans		
Lapsana communis		
Lasioglossum ephialtum Gibbs		No
♀- 1	♂- 0	
Hypericum prolificum		

Table 2. Continued.

		Krombein 1985
Lasioglossum fuscipenne (Smith) ♀- 3 ♂- 0 *Asclepias syriaca* *Erysimum cheiranthoides* *Lapsana communis*		Yes
Lasioglossum hitchensi Gibbs ♀- 1 ♂- 0 *Hypericum prolificum*		Yes-*Dialictus atlanticus* (Mitchell)
Lasioglossum imitatum (Smith) ♀- 9 ♂- 0 *Cephalanthus occidentalis* *Hibiscus laevis*		No
Lasioglossum macoupinense (Robertson) ♀- 3 ♂- 1 *Oxalis stricta* *Oxalis stricta* *Scrophularia marilandica*		Yes-*Evylaeus macoupinensis* (Robertson)
Lasioglossum oblongum (Lovell) ♀- 1 ♂- 0 *Lapsana communis*		Yes-*Dialictus oblungus*
Lasioglossum obscurum (Robertson) ♀- 13 ♂- 0 *Cephalanthus occidentalis* *Conium maculatum* *Eupatorium purpureum* *Lindernia dubia* *Oxalis stricta* *Scrophularia marilandica*		Yes-*Dialictus obscurus* (Robertson)
Lasioglossum sp. ♀- 2 ♂- 1 *Conium maculatum* *Apocynum cannabinum* *Lindernia dubia*		NA
Lasioglossum subviridatum (Cockerell) ♀- 1 ♂- 0 *Lapsana communis*		No
Lasioglossum tegulare (Robertson) ♀- 2 ♂- 1 *Lindernia dubia* *Aster lanceolatus*		Yes-*Dialictus tegularis* (Robertson)
Lasioglossum quebecense (Crawford) ♀- 1 ♂- 0 *Rudbeckia laciniata*		Yes-*Evylaeus quebecensis* (Crawford)

Table 2. Continued.

		Krombein 1985
Lasioglossum weemsi (Mitchell)		No
♀- 2	♂- 0	
Cephalanthus occidentalis		
Lycopus rubellus		
Megachilidae		
Coelioxys sayi Robertson	Parasitic	Yes
♀- 3	♂- 2	
Apocynum cannabinum	*Apocynum cannabinum*	
Verbena urticifolia	*Verbena hastata*	
Megachile mendica Cresson		Yes
♀- 2	♂- 11	
Erysimum cheiranthoides	*Asclepias syriaca*	
Rudbeckia laciniata	*Cephalanthus occidentalis*	
	Eupatorium coelestinum	
	Eupatorium purpureum	
	Stachys tenuifolia	
	Aster lanceolatus	
	Verbena hastata	
	V. urticifolia	

other species in the network (Fig. 1). The lack of a trend towards generalization or specialization ($H'_2 = 0.5$) is curious. This is likely because certain strong generalists in this network, such as *C. maculatum* and *A. syriaca*, also were characterized by high levels of specialization (large d' values). This phenomenon could have increased the specialization value, even if the network was characterized by generalist interactions.

Strength and Specialization

Sampling bias can significantly affect network structure by altering network skew (nestedness) and inaccurately estimate the degree of specialization and generalization (Blüthgen et al. 2008). The number of hours spent at each plant positively correlated with the degree and strength for each plant species. The extent to which this affected network topography can be assessed by examining Bluthgen's specialization index (d') for particular species, which was not significantly affected by the number of sampling hours per plant. However, while d' is unaffected by sampling effort, it is affected by sampling completeness, as the maximum values for the theoretical distributions of Bluthgen's index, to which the empirical values are compared to generate d', are set by the number of interactions recorded (Blüthgen et al. 2006) (i.e., The value of d' can bypass limitations set by partner abundances *collected* by accounting for partner interaction frequency, but it cannot bypass limitations set by missed interactions). While this sounds obvious—that missing data provides limitations to analysis—it is necessary to discuss because interactions are likely missing from many studies of plant-pollinator interactions, regardless of variable sampling effort between plant species (Chacoff et al. 2012, Rivera-Hutinel et al. 2012). Moreover, d' and other network
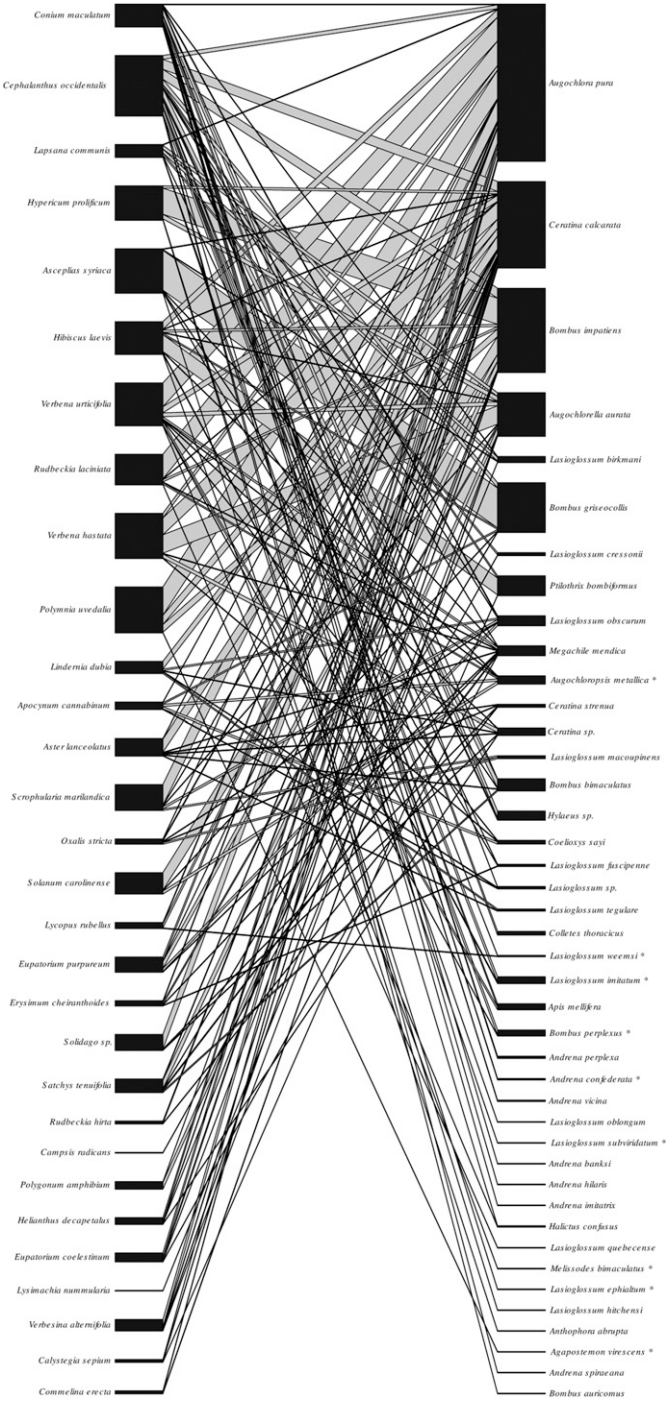
Fig. 1. Bipartite bee-plant visitation web. Plant and bee species are organized by species strength from top to bottom. Plants are depicted on the left and bees on the right. The width of boxes is proportional to species abundance while the width of lines indicates interaction frequency. Asterisks by the names of bees indicate that these species were not present in a historical checklist.
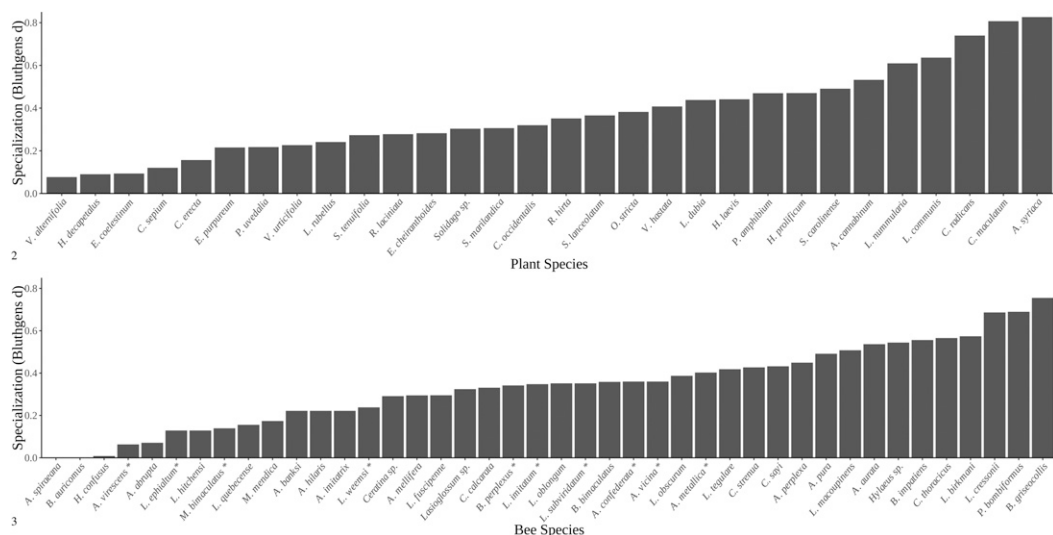
Figs. 2, 3.   Specialization index (d') values. 2, Plants. 3, Bees. A larger d' value indicates a greater reliance on fewer partners. Only one known pollen specialist was collected in this study: *Ptilothrix bombiformus*, which had the second largest d' value. The most 'specialized' bee species was the social generalist *Bombus griseocollis* that formed a strong relationship with *Asclepias syriaca*, the plant with the largest d' value.

metrics can display weekly variation throughout a season (CaraDonna and Waser 2020) and metrics alone may not accurately predict species interactions without biologically relevant information (Olito and Fox 2015). Below, we discuss notable species from our dataset according to network metrics, in relation to relevant information, such as phenological overlap and documented foraging preferences.

The plant with the highest strength and largest d' score (Figs. 1 and 2) was *C. maculatum*, which flowered in early June in both years. However, bees were only collected from the plant in 2013 (n hours = 2 hours in 2012 vs. 4.5 hours in 2013). *Conium maculatum* was a host for a suite of early season bees such as members of the genus *Andrena* and species in the family Colletidae. Notably, five females of *Colletes thoracicus* Smith were collected from *C. maculatum* on June 5, 2013 representing the

only time *C. thoracicus* was collected in the study. The high diversity of these 'rare' species collected on *C. maculatum* in early summer likely led to its classification as both a strong and specialist plant. *Conium maculatum*'s strength comes from it connecting a subset of 'rare' species which otherwise have no connections to the network, while its high level of specialization is likely related to its phenology and sampling effort. Because d' reflects the potential that two species could interact, and *C. maculatum* was observed in bloom for a relatively short period of time in early summer, the high d' values suggest that this was a potentially important plant for early season bees specifically. Further sampling of *C. maculatum*, along with knowledge of the relative abundances of these 'rare' bee species, are required to understand the true importance of *C. maculatum* to the bee diversity of Plummers Island.

The plant with the second highest strength, *C. occidentalis*, also had the highest number of individual visits (abundance = 79) and highest number of bee species visitors (k = 16, Table 1). *Cephalanthus occidentalis* is a native shrub with large white spherical inflorescences and was in bloom from early June through mid-July in a sunny location near the east end of the island. It attracted a wide variety of bees, both rare and abundant, and had a d' value in the lower 2nd quartile. The plant with the third highest strength, *L. communis*, had the fifth largest d' value. *Lapsana communis* was not collected on the island in 2012, so all interactions were observed in 2013 (n hours = 4.25). Again, the strength and specialization of *L. communis* may come from its attractiveness to 'rare' species such as members of the genus *Lasioglossum* which represented 5 of the 7 species which visited *L. communis*. Three of these bees (*Lasioglossum fuscipenne* Smith, *Lasioglossum oblongum* (Lovell), and *Lasioglossum subviridatum* (Cockerell) were collected only once in two years and only from *L. communis*.

Asclepias syriaca, which had the highest specialization value among the 30 plant species, stores its pollen in pollinia that is inaccessible to pollinators. Therefore, any visits to *A. syriaca* were definitively for nectar. Ninety percent (52/58) of total visits to *A. syriaca* were made by *B. griseocollis*, the bee species with the highest specialization value. Those 52 visits represented 80% (52/65) of the total visits recorded for *B. griseocollis*. Half of these visits (26/52) were made by male *B. griseocollis*. While the importance of bumblebees for *Asclepias* reproduction is well documented (Betz et al. 1994, Ivey et al. 2004, Stoepler et al. 2012), the importance of *Asclepias* for bumblebee re-

production is not. The strong interaction between *A. syriaca* and *B. griseocollis* during a phase of the bumblebee reproductive period suggests this plant to be an important nectar resource for mating bees. It is noteworthy that *A. syriaca* was in bloom in June of both years (never past July 1), and while this seems early for bumblebees to be undergoing their second brood period (the reproductive phase), it is not undocumented to find male *B. griseocollis* out as early as June in North America (Williams et al. 2014).

The bee with the highest strength, *A. pura*, was also the most abundant bee represented by 205 collected individuals (compared to 113 *Ceratina calcarata* collected, the next most abundant bee). Of the *A. pura* collected, 73% (149/205) were males. Male bees do not forage for pollen, they visit flowers for nectar only. The actual strength and importance for specific plants may differ if males and females are pollinating plants with varying effectiveness.

Invasive plants

Non-native plants can significantly alter plant-pollinator interaction network metrics by altering foraging patterns of native bees (Seitz et al. 2020). Two of the three strongest plants examined are non-native to North America. *Lapsana communis* is native to Eurasia and North Africa and is considered a weedy species that can compete with crops in agricultural areas (O'Kennon et al. 1999, Francis et al. 2011). *Conium maculatum* is native to Eurasia and is regarded as a highly invasive plant that can actively compete with native plants via allelopathy (Hillman 1997, Vetter 2004); its position as the plant with the highest strength metric in the network is notable. Invasive plants can act as 'super-generalists' and can attract as many or more visitors compared to native plants (Aizen

and Morales 2006, Aizen et al. 2008), but their presence can also result in less generalized networks (lower overall network specialization and lower specialization among individual plants) (Kaiser-Bunbury et al. 2017), potentially leading to loss of rare species from the network.

Conium maculatum may be supporting early native bee communities, as invasive plants have been shown to provide additional resources for native pollinators (Bjerknes et al. 2007, Tepedino et al. 2008). However, invasive plants have the potential to reduce native plant fitness by drawing pollinators away from native plants and/or by increasing the rate of hetero-specific pollen transfer between plants (Brown amd Mitchell 2001, Chittka and Schurkens 2001). It is unknown what plants *C. maculatum* may be displacing, or if those same bees would be present regardless of the presence of *C. maculatum*. Future sampling of plant-pollinator relationships on Plummers Island can assess the extent to which invasive and non-native plants are affecting native plant and bee communities.

Literature Cited

Aizen, Marcelo A., and C. L. Morales. 2006. Invasive Mutualisms and the Structure of Plant-Pollinator Interactions in the Temperate Forests of North-West Patagonia, Argentina. Journal of Ecology 94 (1): 171–80. https://doi.org/10.1111/j.1365-2745.2005.01069.x.

Aizen, Marcelo A., C. L. Morales, and J. M. Morales. 2008. Invasive Mutualists Erode Native Pollination Webs. PLoS Biology 6 (2): 0396–0403. https://doi.org/10.1371/journal.pbio.0060031.

Bascompte, Jordi, P. Jordano, and J. M. Olesen. 2006. Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. Science 312: 431–33. https://doi.org/10.1126/science.1123412.

Bascompte, Jordi, P. Jordano, C. J. Melian, and J. M. Olesen. 2003. The Nested Assembly of Plant – Animal Mutualistic Networks. PNAS 100 (16): 9383–87.

Bjerknes, Anne L., Ø. Totland, S. J. Hegland, and A. Nielsen. 2007. Do Alien Plant Invasions Really Affect Pollination Success in Native Plant Species? Biological Conservation 138 (1–2): 1–12. https://doi.org/10.1016/j.biocon.2007.04.015.

Blüthgen, Nico, J. Fründ, D. P. Vázquez, and F. Menzel. 2008. What Do Interaction Network Metrics Tell Us About Specialization and Biological Traits. Ecology 89 (12): 3387–99. https://doi.org/10.1890/07-2121.1.

Blüthgen, Nico, F. Menzel, and N. Blüthgen. 2006. Measuring Specialization in Species Interaction Networks. BMC Ecology 6 (9): 1–12. https://doi.org/10.1186/1472-6785-6-9.

Brandenburg, David M. 2010. Field Guide to Wildflowers of North America. Sterling Publishing Co. 673 pp.

Brosi, Berry J, K. Niezgoda, and H. M. Briggs. 2017. Experimental Species Removals Impact the Architecture of Pollination Networks. Biology Letters. 13: 20170243. https://doi.org/10.1098/rsbl.2017.0243.

Brown, J. W. 2005. Long-Term Data Show Declines in Insect Composition on Plummers Island, Chesapeake and Ohio Canal National Historic Park. Natural Resource Year In Review-2004: 69.

Brown, Beverly J., and R. J. Mitchell. 2001. Competition for Pollination: Effects of Pollen of an Invasive Plant on Seed Set of a Native Congener. Oecologia 129 (1): 43–49. https://doi.org/10.1007/s004420100700.

Burkle, Laura A., J. C. Marlin, and T. M. Knight. 2013. Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and

Function. Science 339 (6127): 1611–1615. https://doi.org/10.1126/science.1232728.

Chacoff, Natacha P., D. P. Vázquez, S. B. Lomáscolo, E. L. Stevani, J. Dorado, and B. Padrón. 2012. Evaluating Sampling Completeness in a Desert Plant-Pollinator Network. Journal of Animal Ecology 81 (1): 190–200. https://doi.org/10.1111/j.1365-2656.2011.01883.x.

CaraDonna, Paul J. and N. M. Waser. 2020. Temporal Flexibility in the Structure of Plant–Pollinator Interaction Networks. Oikos. 129: 1369–1380. https://doi.org/10.1111/oik.07526.

Chittka, L., and S. Schurkens. 2001. Successful Invasion of a Floral Market. Nature 411 (6838): 653.

Danforth, B. N., S. C. Cardinal, C. Praz, E. A. B. Almeida, and D. Michez. 2013. The Impact of Molecular Data on Our Understanding of Bee Phylogeny and Evolution. The Annual Review of Entomology 58: 57–78. https://doi.org/10.1146/annurev-ento-120811-15633.

Dormann, C.F., Gruber B. & Fruend, J. (2008). Introducing the bipartite Package: Analysing Ecological Networks. R news 8 (2): 8–11.

Dormann, Carsten F. 2011. How to Be a Specialist? Quantifying Specialisation in Pollination Networks. Network Biology 1 (1): 1–20.

Dormann, Carsten F, J. Fruend, and H. M. Schaefer. 2017. Identifying Causes of Patterns in Ecological Networks: Opportunities and Limitations. Annual Review of Ecology, Evolution, and Systematics 48: 559–584. https://doi.org/10.1146/annurev-ecolsys-110316-022928.

Forup, Mikael Lytzau, K. S. E. Henson, P. G. Craze, and J. Memmott. 2008. The Restoration of Ecological Interactions: Plant-Pollinator Networks on Ancient and Restored Heathlands. Journal of Applied Ecology 45 (3): 742–52. https://doi.org/10.1111/j.1365-2664.2007.01390.x.

Francis, Ardath, S. Darbyshire, D. Clements, and A. DiTommaso. 2011. The Biology of Canadian Weeds. 146. *Lapsana Communis* L. Canadian Journal of Plant Science 91 (3): 553–69. https://doi.org/10.4141/cjps10169.

Hillman, Janell M. 1997. Potentially Allelopathic Effects of Poison Hemlock (Conium Maculatum) on Native Plant Revegetation at Wilder Ranch State Park. California Exotic Pest Plant Council: Symposium Proceesings. 1–6.

Jordano, Pedro, J. Bascompte, and M. J. Olesen. 2003. Invariant Properties in Coevolutionary Networks of Plant – Animal Interactions. Ecology Letters 6: 69–81. https://doi.org/10.1046/j.1461-0248.2003.00403.x.

Kaiser-Bunbury, Christopher N., J. Mougal, A. E. Whittington, T. Valentin, R. Gabriel, J. M. Olesen, and N. Blüthgen. 2017. Ecosystem Restoration Strengthens Pollination Network Resilience and Function. Nature 542 (7640): 223–27. https://doi.org/10.1038/nature21071.

Kremen, Claire. 2008. Crop Pollination Services from Wild Bees, pp. 10–26. *In* R. James and T. L. Pitts-Singer, eds. Bee Pollination in Agricultural Ecosystems, Oxford University Press. 232 pp. https://doi.org/10.1093/acprof.

Krombein, K.V. 1985. Preliminary Checklist of Plummers Island Bees Including Notes on Floral Associations.

Memmot, Jane. 1999. The Structure of a Plant-Pollinator Food Web. Ecology Letters 2: 276–80.

Memmott, Jane, N. M. Waser, and M. V. Price. 2004. Tolerance of Pollination Networks to Species Extinctions. Proceedings of the Royal Society B: Biological Sciences 271 (1557): 2605–11. https://doi.org/10.1098/rspb.2004.2909.

Michener, Charles D. 2007. The Bees of the World. Second Edition. The John Hopkins University Press, Baltimore, MD. 913 pp.

Nielsen, Anders and J. Bascompte. 2007. Ecological Networks, Nestedness and Sampling Effort. Journal of Ecology 95 (5): 1134–41. https://doi.org/10.1111/j.1365-2745.2007.01271.x.

O'Kennon, Robert J., T. M. Barkley, G. M. Diggs Jr, and B. Lipscomb. 1999. *Lapsana Communis* (Asteraceae) New for Texas and Notes on Invasive Exotics. *SIDA,* Contributions to Botany 18 (4): 1277–83.

Olito, Colin and J. W. Fox. Species Traits and Abundances Predict Metrics of Plant – Pollinator Network Structure, but Not Pairwise Interactions. 2015. Oikos. 124: 428-436. https://doi: 10.1111/oik.01439.

Petanidou, Theodora, A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardelis, and J. D. Pantis. 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 (6): 564–75. https://doi.org/10.1111/j.1461-0248.2008.01170.x.

RStudio Team (2020). RStudio: Integrated Development Environment for R. RStudio,

PBC, Boston, MA URL http://www.rstudio.com.

Radford, Albert E., H. E. Ahles, and C. R. Bell. 1964. Manual of the Vascular Flora of the Carolinas. The University of North Carolina Press. 1245 pp.

Rivera-Hutinel, A., R. O. Bustamente, V. H. Marin, and R. Medel. 2012. Effects of Sampling Completeness on the Structure of Plant–Pollinator Networks. Ecology 93 (7): 1593–1603.

Rodríguez-Gironés, M. A., and L. Santamaría. 2006. A New Algorithm to Calculate the Nestedness Temperature of Presence-Absence Matrices. Journal of Biogeography 33 (5): 924–35. https://doi.org/10.1111/j.1365-2699.2006.01444.x.

Saavedra, Serguei, D. B. Stouffer, B. Uzzi, and J. Bascompte. 2011. Strong Contributors to Network Persistence Are the Most Vulnerable to Extinction. Nature 478 (7368): 233–35. https://doi.org/10.1038/nature10433.

Sajjad, Asif, S. Saeed, M. Ali, F. Z. A. Khan, Y. J. Kwon, and M. Devoto. 2017. Effect of Temporal Data Aggregation on the Perceived Structure of a Quantitative Plant–Floral Visitor Network. Entomological Research 47: 380–87. https://doi.org/10.1111/1748-5967.

Sann, Manuela, O. Niehuis, R. S. Peters, C. Mayer, A. Kozlov, L. Podsiadlowski, S. Bank, K. Meusemann, B. Misof, C. Bleidorn, and M. Ohl. 2018. Phylogenomic Analysis of Apoidea Sheds New Light on the Sister Group of Bees. BMC Evolutionary Biology 18 (71): 1–15. https://doi.org/10.1186/s12862-018-1155-8.

Sazatornil, Federico D., M. Moré, S. Benitez-Vieyra, A. A. Cocucci, I. J. Kitching, B. O. Schlumpberger, P. E. Oliveira, M. Sazima, and F. W. Amorim. 2016. Beyond Neutral and Forbidden Links: Morphological Matches and the Assembly of Mutualistic Hawkmoth-Plant Networks. Journal of Animal Ecology 85 (6): 1586–94. https://doi.org/10.1111/1365-2656.12509.

Seitz, Nicola, D. vanEngelsdorp, and S. D. Leonhardt. 2020. Are Native and Non-Native Pollinator Friendly Plants Equally Valuable for Native Wild Bee Communities? Ecology and Evolution. 10 (23): 12838–12850. https://doi.org/10.1002/ece3.6826.

Shetler, Stanwyn G., S. S. Orli, E. F. Wells, and M. Beyersdorfer. 2006. Checklist of the Vascular Plants of Plummers Island, Maryland (Contribution XXIX to the Natural History of Plummers Island, Maryland). Bulletin of the Biological Society of Washington 14 (1): 1–57.

Staines, C. L. 2004. Changes in the Chrysomelid (Coleoptera) Community Over a 95-Year Period on a Maryland River Island (USA), pp. 613–622. *In* Jolivet, P., J. A. Santiago-Blay, and M. Schmitt, eds., New Developments in the Biology of Chrysomelidae. Academic Publishing, The Hague. 803 pp.

Tepedino, V. J., B. A. Bradley, and T. L. Griswold. 2008. Might Flowers of Invasive Plants Increase Native Bee Carrying Capacity? Intimations From Capitol Reef National Park, Utah. Natural Areas Journal 28 (1): 44–50. https://doi.org/10.3375/0885-8608(2008)28[44:mfoipi]2.0.co;2.

Vazquez, Diego P., and M. A. Aizen. 2004. Asymmetric Specialization: A Pervasive Feature of Plant-Pollinator Interactions. Ecology 85 (5): 1251–57.

Vázquez, Diego P., N. Bluthgen, L. Cagnolo, and N. P. Chacoff. 2009. Uniting Pattern and Process in Plant-Animal Mutualistic Networks: A Review. Annals of Botany 103 (9): 1445–57. https://doi.org/10.1093/aob/mcp057.

Vetter, J. 2004. Poison Hemlock (*Conium Maculatum* L.). Food and Chemical Toxicology 42 (9): 1373–82. https://doi.org/10.1016/j.fct.2004.04.009.

Williams, Paul, R. Thorp, L. Richardson, and S. Colla. 2014. Bumblebees of North America: An Identification Guide. Princeton University Press, Princeton, NJ. 208 pp.