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RARE PLANT’S NEED FOR NATIVE POLLINATORS THREATENED BY INVASIVE PLANT-POLLINATOR RELATIONSHIP

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Abstract—Many flowering plants rely on pollination for their reproductive success, but the introduction of non-native plants can impact these essential plant-pollinator relationships. *Chloropyron maritimum* ssp. *maritimum* is a rare salt marsh plant that has been known to benefit from insect pollination, and its habitat is being encroached on by the non-native *Limonium duriusculum*. We use plant-pollinator observation, network analysis, and small-scale experimental removal of *L. duriusculum* to understand which insects are visiting *C. maritimum maritimum*, and the impact, if any, of *L. durisiculum* on *C. maritimum maritimum* pollination and the plant-pollinator network. We documented infrequent visitation to *C. maritimum maritimum* at the Carpinteria Salt Marsh, California, USA, with native bees being the only observed *C. maritimum maritimum* visitors. We found that the pollinator composition of *C. maritimum maritimum* and *L. duriusculum* were significantly different. The vast majority (96%) of *L. duriusculum* visitors were two non-native insect species (Hymenoptera: *Apis mellifera* and Diptera: *Eristalinus aeneus*), neither of which entered *C. maritimum maritimum* flowers. The experimental removal of *L. duriusculum* had no effect on *C. maritimum maritimum* visitation. However, the plant-pollinator network was more nested, more connected and had higher specialization when *L. duriusculum* was removed. Future studies should implement larger-scale removal to further investigate these findings. Additionally, subsequent work should investigate if there is adequate nesting habitat for *C. maritimum maritimum* pollinators in surrounding areas, to ensure the survival of the few plant-pollinator interactions this rare plant currently maintains.

Keywords—*Chloropyron maritimum* ssp. *maritimum*, non-native plants, non-native pollinators, plant-pollinator networks, rare plant pollination

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INTRODUCTION

Pollination is a critical process for the reproductive success of many flowering plants, contributing to enhanced genetic diversity and ecosystem stability (Albrecht et al. 2012; Ollerton, 2017). The quantity and quality of pollination services to a plant species can be impacted by the plant population size, population density, and the context of the vegetation community that surrounds that population (Thomson 1981; Kearns et al. 1998).

The introduction of non-native flowering plants can significantly impact the structure and stability of plant–pollinator interactions within a community. Non-native plants can have a wide range of impacts on the quantity of pollination services, competing for pollinators to decrease native plant visitation (Fiedler et al. 2011; Baskett et al. 2011; Goodell & Parker 2017), having no impact on native plant visitation (Kaiser-Bunbury et al. 2011), or even facilitating native plant visitation (McKinney & Goodell 2010; Etter et al. 2021). All these pollinator quantity impacts can also exist in the same community; Ferrero et al. (2013) found that non-native plant removal resulted in higher, lower, and negligible differences in pollinator visitation to different flowering plants within the same community. Additionally, the pollinator community composition may be changed, and the abundance of distinct pollinators or pollinator groups may be impacted differently (Etter et al. 2021). Beyond the impact on pollinator abundance and composition, the presence of non-native plants may also impact the quality of pollination services provided by altering pollen transfer, resulting in heterozygous pollen deposition on native plants (Etter et al. 2021), which could negatively impact native plant reproduction (Arceo-Gómez & Ashman 2016). Alternatively, the presence of a non-native plant has been observed to have negligible or possibly positive impacts on fruit set (Ferrero et al. 2013). Because of this lack of consistency in the impact of non-native plants on native plant pollination, it is essential that studies of plant invasion be repeated across a wide variety of target communities (Charlebois & Sargent 2017).

The analysis of plant-pollinator networks can serve as a valuable tool for understanding complex interactions between plants and their pollinators within a community context (Ings et al. 2009; Elle et al. 2012). Plant-pollinator networks can also provide insight into how non-native plant species integrate into communities when they arrive. Connectance is a common metric in network analyses and describes the number of observed interactions divided by the number of possible interactions. Generally, higher connectance in a network is considered a positive reflection of that network's structure and stability. A study by Aizen et al. (2008) found that the presence of non-native species did not change the overall connectance of networks, but that highly invaded networks had less connectance between native plant and pollinator species than less invaded networks. However, the impact of non-native plant integration into networks is variable and understudied, especially at the community level (Parra-Tabla & Arceo-Gómez 2021). Overall, plant-pollinator networks can help us understand the impact of plant invasion on a community as a whole, especially when networks with and without the non-native plant can be compared (Lopezaraiza–Mikel et al. 2007).

Considering that non-native plants can have such a profound impact on ecosystems, the removal of non-native plant species is an often-used management practice in restoration and conservation contexts. After non-native plant removal, native plant cover often increases, but it may take many years to reflect a pre-invasion plant community (Copeland et al. 2019), if this happens at all. Impacts on pollinator services can be observed on a shorter-time scale, and differences in pollinator services can often be observed just weeks after non-native plant removal (Baskett et al. 2011; Fiedler et al. 2011; Ferrero et al. 2013; Etter et al. 2021). Because non-native plant removal can vary widely in its effect on pollinators, it's important to understand the impact of non-native plant removal on pollinators and the pollination service they provide prior to large-scale intervention, especially when vulnerable rare plants occur within that system.

Chloropyron maritimum ssp. *maritimum* (Fig. 1A) is a United States federal and California state listed endangered plant species restricted to coastal salt marshes in Southern California, USA and Baja California, Mexico. Within the salt marsh, *C. maritimum maritimum* tends to be found in higher elevation areas above sea level that are not as regularly inundated by salt water brought by changing tides. *C. maritimum maritimum* is also a hemiparasitic plant that can extract water and nutrients from neighboring plants. The plant has been found to parasitize a variety of salt marsh plants including: *Distichlis spicata*, *Salicornia virginica*, *Jaumea carnosa*, *Limonium californicum*, *Cressa truxillensis*, and *Frankenia salina* (Vanderwier & Newman 1984).

Chloropyron maritimum ssp. *maritimum* populations are currently threatened by a range of factors including climate change, sea level rise, the loss of surrounding areas for future population migration, the loss of pollinator's nesting sites due to urbanization, and the introduction of non-native invasive plant species (Fellows & Zedler 2005; Garner et al. 2015; U.S. Fish and Wildlife 2020). One of the invasive plants threatening *C. maritimum maritimum* and its native parasitic host plants is *Limonium duriusculum* Fig. 1B, which has a moderate Cal-IPC (California Invasive Plant Council) ranking due to its impact on the plant community and its ability to quickly spread locally. Native to southwestern Europe, *L. duriusculum* produces large inflorescences of easily accessible flowers available to pollinators most of the year, and it is now widespread across Californian salt marshes. *Limonium duriusculum* not only physically competes with *C. maritimum maritimum* for space within higher elevation areas, forming dense mats across the salt marsh (Archbald & Boyer 2014; personal obs), but may also alter the community of pollinators (*i.e.*,

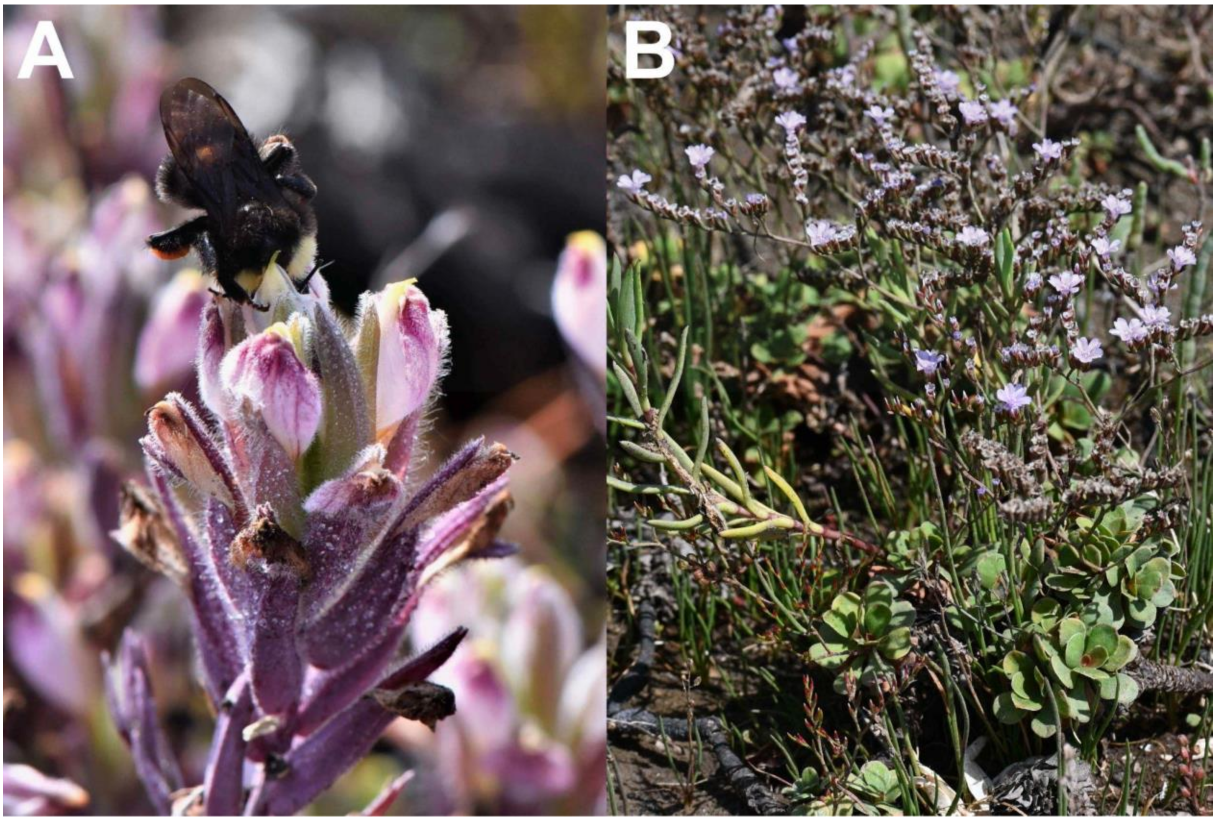

Figure 1. A) ***Chloropyron maritimum*** **ssp.** ***maritimum*** **in bloom being visited by** ***Bombus californicus*** **and B)** ***Limonium duriusculum*** **in bloom at the Carpinteria Salt Marsh, California, USA. Photos: Kylie Etter**

pollinator abundance, pollinator diversity, and/or pollinator foraging behaviour) that *C. maritimum maritimum* depends upon for reproduction.

While *C. maritimum maritimum* is self-compatible, it has been shown to have significantly higher seed set in flowers with open pollination or hand pollination than in bagged, pollinator-inaccessible flowers (Lincoln 1985). The keel-shaped flower requires pollinators to push apart the lips of the corolla to access nectar and pollen. Previously recorded pollinators of *C. maritimum maritimum* were mainly bees (*Anthidium edwardsii, Anthidium palliventre, Bombus californicus*, *Bombus crotchii*, *Bombus sonorus*, *Melissodes tepidus* ssp. *timberlakei*, *Colletes* sp., halictine bees (like *Lasioglossum*), *Ceratina* sp., *Hylaeus* sp.), but also flies in family Bombyliidae (Lincoln 1985; Parsons & Zedler 1997; Knapp et al. 2024). However, pollinators may be unequally effective. Past studies have noted that large-bodied bees may touch the reproductive parts of *C. maritimum maritimum* more often and be more important for reproductive success than smaller halictine bees (Lincoln 1985; Parsons & Zedler 1997).

One of the largest remaining populations of *C. maritimum maritimum* is located at the Carpinteria Salt Marsh in Carpinteria, California, USA. Despite the population size, relatively little is known about the *C. maritimum maritimum* pollinator abundance and composition at this particular salt marsh or what impact the invasive *L. duriusculum* plant is having on *C. maritimum maritimum*'s pollinator visitation and reproductive success. To address this, we investigate the following questions:

1. Which insects are visiting *C. maritimum maritimum* flowers at Carpinteria Salt Marsh, and how frequently?
2. Do the *L. duriusculum* and *C. maritimum maritimum* pollinator compositions overlap?
3. How does the connectance, nestedness, and specialization of the realized network compare to randomly generated null model networks? What role do *L. duriusculum* and *C. maritimum maritimum* and their pollinators play in the shared network?

4. How does the removal of flowering *L. duriusculum* from 2 x 2m plots influence visitation to *C. maritimum maritimum* and the entire plant-pollinator network?

MATERIALS AND METHODS

SITE DESCRIPTION

To evaluate the composition and dynamics of pollinator communities visiting *C. maritimum maritimum* and neighboring plants, we conducted our study at the Carpinteria Salt Marsh Reserve in the years 2017, 2019, 2021, 2022, and 2023. The Carpinteria Salt Marsh Reserve is managed by the University of California, Santa Barbara as part of the UC Natural Reserve System and contains 50 hectares of salt marsh in Carpinteria, California, USA (34.4020, -119.5374). The Carpinteria Salt Marsh is entirely bordered by development, enclosed by the Union Pacific Railroad and U.S. 101 highway along the northern border, and residential development along the other edges (Fig. 2). The marsh is 1m below to 3 m above mean sea level and receives an average of 38 cm of rain per year (Carpinteria Salt Marsh Reserve). The salt marsh is important habitat for both flora and fauna, being used as a resource by migratory birds and acting as a nursery for fishes (Carpinteria Salt Marsh Reserve). Our experiment was conducted in the northwest population of *C. maritimum maritimum* along Sand Point Road. The northwest population, as of 2024, covered about 3,200 square meters. A smaller population of *C. maritimum maritimum* exists in the southeast part of the marsh but was not used in our experiment (Fig. 2).

PLOT ESTABLISHMENT

In August 2017, we established 29 2 x 2 m plots within the northwest population of *C. maritimum maritimum* (Fig. 3) while only a single plot could be established in the smaller southeastern population (Plot 25, not pictured in Fig. 3). We determined plot location using a random stratified sampling

Figure 2. Northwest and Southeast populations of *Chloropyron maritimum* ssp. *maritimum* at the Carpinteria Salt Marsh, California, USA. We established experimental plots in the Northwest population.

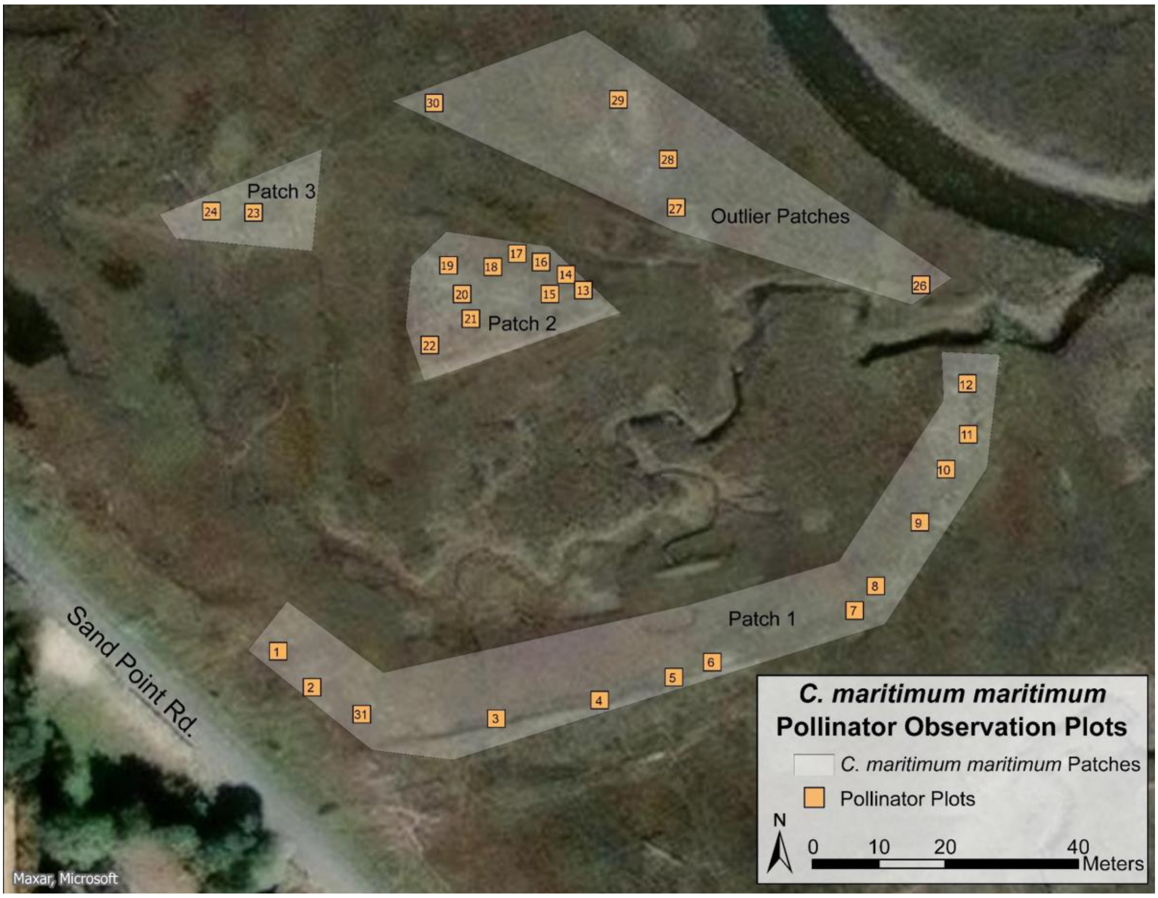

Figure 3. Map showing the four primary *Chloropyron maritimum* ssp. *maritimum* patches and 30 2 x 2 m pollinator observation plots within the Northwest population. Orange squares depict pollinator observation plots and grey polygons depict population subsets of *C. maritimum maritimum* separated by lower elevation areas of marsh.

method among subsets of the existing northwest *C. maritimum maritimum* population. Population subsets were defined as four patches of *C. maritimum maritimum* separated by lower elevation areas of marsh (Figure 3: 'Patch 1', 'Patch 2', 'Patch 3', and 'Outlier Patches'), and the patches were 10 to 40 meters away from adjacent patches. In 2017, all plots contained naturally occurring *C. maritimum maritimum*, but because the plant is an annual species, not all plots contained *C. maritimum maritimum* in subsequent years. We recorded the coordinates for the northwest corner of each plot and marked the corner with a piece of rebar and a PVC pipe. All plots were similar in elevation, ranging from 15 cm-1 m above sea level, and occupied similar microhabitats. The single plot in the southeast population (Plot 25) was abandoned after 2017, due to its long distance from other plots and inaccessibility from Sand Point Road. In 2019, we established Plot 31 within the Northwest population to establish a total of 30 plots sampled each year between 2019-2023. Plot observation was not conducted in 2018 due to limited funding and time, and in 2020, while data was collected, it was unfortunately lost. Here, we present all of the data we were able to collect and maintain over the seven-year period.

Vegetation Monitoring & Experimental Invasive Removal

During the first survey of each year, we conducted vegetation monitoring in all plots. The first survey was executed in mid to late June in 2019-2023. In 2017, however, vegetation monitoring was conducted in August when the plots were first established. We recorded the number of *C. maritimum maritimum* flowers, percent *C. maritimum maritimum* vegetation cover, percent *L. duriusculum* vegetation cover, and percent total vegetation cover for each plot. Two observers independently estimated each plot's percent cover, then combined estimates to determine a single measure of percent cover within plots. We also recorded the number of *C.*

maritimum maritimum flowers available to pollinators during each subsequent survey (Fig. A1).

In March 2020, all *L. duriusculum* was hand removed from half of the plots (even-numbered plots). In Spring 2021, 2022, and 2023, we continued to remove reemerging *L. duriusculum* from those plots. During every pollinator observation survey in 2021-2023, we recorded the number of flowers on other flowering plants (*Cuscuta* sp., *Frankenia salina, Jaumea carnosa,* and *Cressa truxillensis*) and the percentage of flower coverage over the plot for densely flowering plants (*Limonium duriusculum* and *Limonium californicum*) in each plot, to better understand resources available to foraging pollinators at the time of the survey.

POLLINATOR OBSERVATION

During pollinator observations, floral visitors that successfully entered the *C. maritimum maritimum* flower (and thus could contact the anthers) were recorded as "pollinators" (regardless of if they touched the exserted stigma). For all other flowering plants, floral visitors that touched any floral reproductive parts and thus could potentially contribute to pollination were recorded as "pollinators". To the best of our ability, we recorded individual pollinators rather than the total number of visits. As such, if the same insect visited multiple flowers of one plant species within a plot, it was recorded as a single pollinator visiting that plant. All flowering plants within a plot were observed over three, five-minute periods in 2017 and 2019, and three, 10-minute periods in 2021, 2022, and 2023. We observed plots during three different time periods in an observational round to capture daily temporal differences in pollinator abundance and diversity. We used the discrete time periods established by Lincoln (1985) as a template: morning (9:00AM-11:30AM), midday (11:30AM-2:00PM) and afternoon (2:00PM-5:00PM). The number of observational rounds and timing of rounds varied from year to year and is summarized in Table 1. To avoid biased sampling due to abiotic conditions, we only conducted pollinator observations on sunny or bright overcast days with minimal wind. Observational rounds were timed to encompass peak *C. maritimum maritimum* bloom between June-September. While all plots established in 2017 had *C. maritimum maritimum* present, the plant was absent from some plots in the following years. Plots lacking *C. maritimum maritimum* were still observed as long as flowers of at least one other plant species were available to pollinators. Plots without open flowers of any kind were not observed. Other flowering plants observed within our plots included: *Limonium duriusculum*, *Cuscuta* sp., *Frankenia salina*, *Jaumea carnosa*, *Limonium californicum* and *Cressa truxillensis*.

During pollinator observation, we caught representative pollinators, dispatched them with ethyl acetate, and later identified them to the lowest taxonomic rank possible, usually to genus. Images of pollinators and plants that were taken in the field or lab were uploaded to iNaturalist to document interactions and identify unknown taxa (https://www.inaturalist.org/projects/salt-marsh-bird-s-beak-pollination-study).

DATA ANALYSES

All analyses were performed in R v4.3.1 (R Core Team 2023). To address our first question and determine which insects are entering *C. maritimum*

Table 1. Synopsis of the number of observation rounds, dates, and minutes per survey conducted on the plots each year.

Year:	2017	2019	2021	2022	2023
# of Observation Rounds:	1	2	2	3	3
Dates:	Aug 9	June 10-11 July 8, 11, 16	June 24-25 July 22-23	June 28-29 July 26-28 Aug 30, Sept 1	June 28-29 July 25-26 Aug 20-23
Survey Time per plot x3	5 min	5 min	10 min	10 min	10 min
= Plot Round Time:	15 min	15 min	30 min	30 min	30 min
Total observation time (min/year):	430 min	875 min	1680 min	2640 min	2700 min
Observation Time on plots with flowering *C. maritimum maritimum*	415 min	710 min	900 min	2070 min	2700 min

maritimum flowers and how often, we list the interactions recorded and qualitatively compared the rate of pollinator visitation (average number of pollinators per 10-minute period of observation) to *C. maritimum maritimum* between years.

To address our second question and compare pollinator composition between *C. maritimum maritimum* and *L. duriusculum*, we used non-metric multidimensional scaling (NMDS), specifically using the "metaMDS" function in the 'vegan' package (Oksanen et al. 2022). To evaluate differences in pollinator composition, we performed 1,000 repetitions of permutational multivariate analysis of variances (PERMANOVAs) with the "adonis" function in the 'vegan' package. Pollinators were grouped to the lowest consistent field identification. For example, some bombyliid flies were identified to genus, but because others were only identified to familial level, all are grouped under the family Bombyliidae as their "pollinator group" for analysis. The pollinator groups used for analyses were: *Apis mellifera*, Araneae, *Bembix*, *Bombus*, Bombyliidae, Diptera (other than Bombyliidae and Syrphidae), *Eristalinus aeneus*, Formicidae, green sweat bee (*Agapostemon* or *Augochlorella*), *Halictus*, Hesperiidae, *Lasioglossum* (*Dialictus*), *Melissodes*, *Polydontomyia curvipes*, Pompilidae, *Pontia protodice*, and Syrphidae. Bombyliidae and Syrphidae are both Diptera families that are easy to identify and common floral visitors, so they were split out as their own pollinator groups and not included in the Diptera pollinator group. *Eristalinus aeneus* is a syrphid fly that was easy to identify and one of the most common visitors, so it was recorded as its own pollinator group as well. Only pollinator observations on plots that were not manipulated (*i.e., L. duriusculum* was not removed) and had flowering *C. maritimum maritimum* were used to make the community matrices for each plant. Matrices were made for each unique pollinator observational round in 2017-2023, for a total of 11 unique matrices (Table 1).

To address our third question, and understand how the observed plant-pollinator network compared to null networks and determine what role *C. maritimum maritimum* and *L. duriusculum* play within the larger community, a single plant-pollinator network was created using pollinator observations from all plots that were not manipulated to remove *L. duriusculum* and had flowering *C. maritimum maritimum* (4,185 minutes of observation, 11 observational rounds, Table 1). Once assembled, we calculated the metrics of 'nestedness', 'connectance', and 'specialization' of the network with the "networklevel" function in the 'bipartite' package (Dormann et al. 2009). As in Ealy et al. (2023), we generated 1000 iterations of three different null model methods ('r2d', 'swap.web', and 'vaznull') with the "nullmodel" function in the 'bipartite' package and calculated 'nestedness', 'connectance', and 'specialization' for each null model. 'R2d' maintains the observed network marginal totals only, 'swap.web' maintains the observed network marginal totals and the number of links (connectance), and 'vaznull' maintains the number of links but not the marginal totals (Vázquez et al. 2007). To determine if our networks differed significantly from the randomly assembled null networks, we compared z-scores and p-values for the network level indices: 'nestedness', 'connectance', and 'specialization' between the observed and null model networks. Additionally, to understand the role of individual plant species and pollinator groups, we used the "specieslevel" function in 'bipartite' to calculate 'weighted betweenness', 'weighted closeness', and the 'specialization' of plants and pollinator groups (Blüthgen et al. 2006; Dormann 2011).

To address our fourth question and understand the impact of experimental removal of *L. duriusculum* on *C. maritimum maritimum* visitation, we compared the visitation on control and *L. duriusculum* removal plots using a Wilcoxon rank-sum test. We were unable to create an NDMS ordination because there were too few data points. We only used post-removal observational rounds for this analysis (2021-2023) and we summed pollinator visitation to *C. maritimum maritimum* across all plots of a single plot type ('control' or '*L. duriusculum* removal') within an observational round. If no pollinators were observed entering *C. maritimum maritimum* flowers within a plot type during an observational round, that observational round for that plot type was not included in this analysis (control $N = 7$; *L. duriusculum* removal $N = 5$). Additionally, we visualized plant-pollinator networks for control plots and *L. duriusculum* removal plots and calculated network level metrics: 'nestedness', 'connectance', and 'specialization'.

RESULTS

The average amount of C. *maritimum maritimum* vegetation cover in plots per year varied from under 3% in 2019 to 15% in 2023 (Fig. 4A). *L. duriusculum* vegetation covered an average of 26.3% to 43.5% of plots per year in plots where it was not removed (Fig. 4B). We removed approximately 22 kg (~50 pounds) of *L. duriusculum* from removal plots between 2020 and 2023. In the three years following initial *L. duriusculum* removal, the average bare ground cover in removal plots (45%) was significantly higher than in control plots (20%) (Fig. 4C, t-test, *P* < 0.001). Additionally, in the three years following removal the average cover of plants other than *C. maritimum maritimum* and *L. duriusculum* in removal plots was significantly higher than in control plots; comparatively the cover of these other plants has been decreasing in control plots over time (Fig. 4D, t-test, *P* = 0.001).

We conducted over 8,340 minutes of pollinator observation on plots with and without blooming *C. maritimum maritimum*, observing 2,513 plant-pollinator interactions within the plots over the five years of observation.

WHICH INSECTS ARE VISITING C. MARITIMUM MARITIMUM FLOWERS AT CARPINTERIA SALT MARSH, AND HOW FREQUENTLY?

Addressing our first question, determining which insects are entering *C. maritimum maritimum* flowers and how often, we conducted 6,765 minutes of observation on plots with blooming *C. maritimum maritimum*. We observed 75 individual pollinators entering *C. maritimum maritimum* flowers (Table 2; Fig. 5A-D). Bees (Anthophila) from two different families (Apidae and Halictidae) made up all of the *C. maritimum maritimum* pollinators. The majority of the visits were made by *Melissodes* in the family Apidae (47%), followed by *Lasioglossum* (*Dialictus*) in the

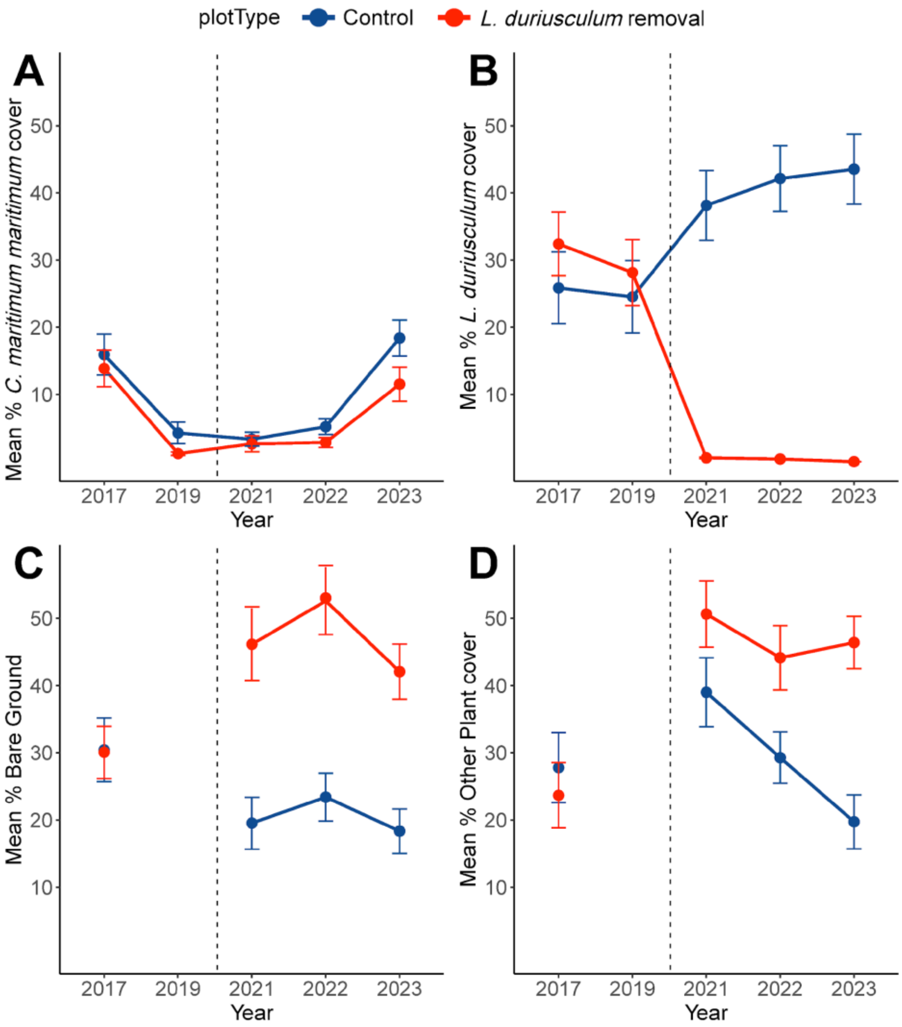

Figure 4. A) Mean percent *Chloropyron maritimum* ssp. *maritimum* cover, B) percent *Limonium duriusculum* cover, C) bare ground, and D) other plant cover in control (blue) and *L. duriusculum* removal (red) plots per year. Dashed lines represent when *L. duriusculum* removal began. Error bars represent mean +/- standard error. The percent bare ground equals 100% minus the total plant plot cover recorded. In 2019 the total plant plot cover and other plant cover was not recorded.

Table 2. The number of *Chloropyron maritimum* ssp. *maritimum* pollinators, and rate of visitation (average number of pollinators per 10 minutes of observations) per year. Rate is in parenthesis after the number.

C. maritimum maritimum pollinator	2017	2019	2021	2022	2023
Bombus californicus	0 (0)	0 (0)	5 (0.056)	0 (0)	2 (0.007)
Bombus crotchii	0 (0)	1 (0.014)	0 (0)	0 (0)	3 (0.011)
unrecorded *Bombus* sp.	-	-	-	-	1 (0.004)
Green Sweat Bee	1 (0.024)	0 (0)	0 (0)	0 (0)	0 (0)
Melissodes	7 (0.169)	0 (0)	0 (0)	0 (0)	28 (0.104)
Lasioglossum (*Dialictus*)	4 (0.096)	0 (0)	0 (0)	22 (0.106)	1 (0.004)
Total	12 (0.289)	1 (0.014)	5 (0.056)	22 (0.106)	35 (0.130)

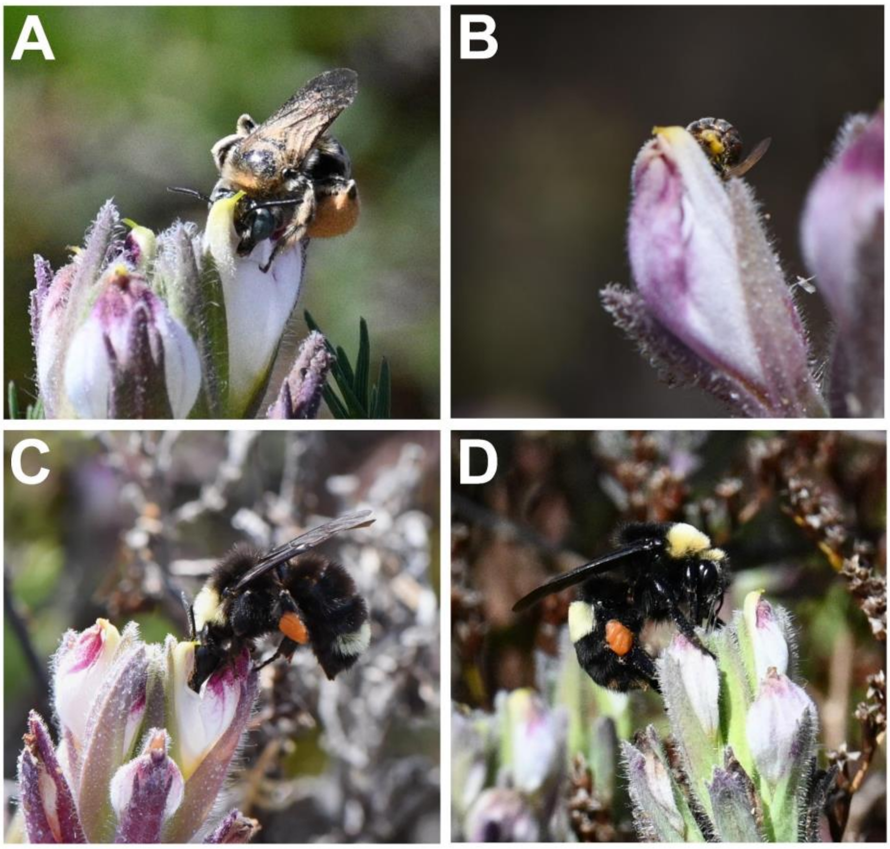

Figure 5. Photos of four *Chloropyron maritimum* ssp. *maritimum* pollinators found at the Carpinteria Salt Marsh: A) *Melissodes* sp., B) *Lasioglossum* (*Dialictus*) sp., C) *Bombus californicus* and D) *Bombus crotchii.* Photos: Kylie Etter

family Halictidae (36%), and *Bombus* in the family Apidae (16%). The identity and rate of pollinators varied year to year, and no pollinator group was recorded entering *C. maritimum maritimum* flowers every year in our plots (Table 2). *Melissodes*, the most commonly observed *C. maritimum maritimum* pollinator, was only recorded visiting in 2017 and 2023, although it was observed visiting nearby plants outside our plots in 2022. The annual pollination rate generally follows the trends of the abundance of *C. maritimum maritimum* flowers, and the rate was higher in years with more floral abundance (Table 2; Fig. A1).

DO THE *L. DURIUSCULUM* AND *C. MARITIMUM MARITIMUM* POLLINATOR COMPOSITIONS OVERLAP?

To address our second question, comparing pollinator composition between *C. maritimum maritimum* and *L. duriusculum*, our NMDS ordination revealed that the pollinator assemblages of *C. maritimum maritimum* and *L. duriusculum* were significantly different (Fig. 6; PERMANOVA $F_{1,18} = 12.33$, $P < 0.001$). There were two observational rounds, July 2019 and June 2021, that had zero *C. maritimum maritimum* pollinators and thus were not included in the visualization or

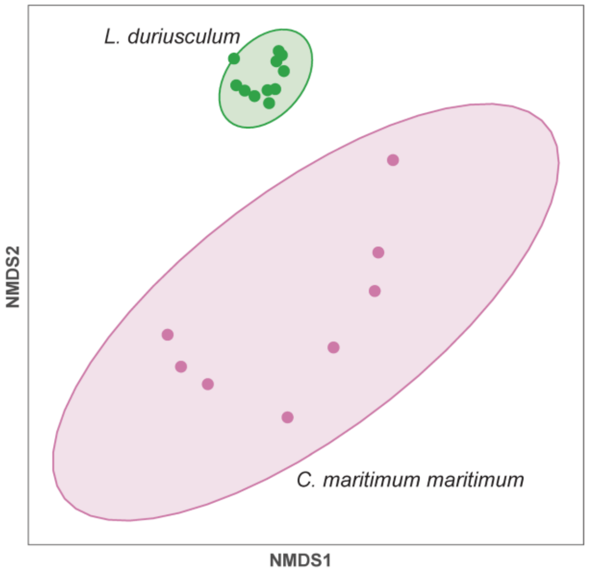

Figure 6. Ordination of pollinator assemblages to *Chloropyron maritimum* ssp. *maritimum* and *Limonium duriusculum*. We only considered plots that contained both *C. maritimum maritimum* and *L. duriusculum* for analysis. We calculated the metric of 'pollinators per minute' for each pollinator group over a single observational round for both plants (*L. duriusculum*, N = 11 observational rounds, *C. maritimum maritimum* N = 9 observation rounds, represented by a point). There were two observational rounds, July 2019 and June 2021, that had zero *C. maritimum maritimum* pollinators and thus are not visualized. Pollinators of *C. maritimum maritimum* and *L. duriusculum* occupy significantly different ordination space (PERMANOVA $F_{1,18}$= 12.33, *P* < 0.001).

PERMANOVA. *L. duriusculum* was most commonly visited by the non-native *Apis mellifera* (Apidae) and non-native *Eristalinus aeneus* (Syrphidae), neither of which ever entered *C. maritimum maritimum* flowers (Fig. 7).

How does the realized network compare to randomly generated null model networks? What role do *L. duriusculum* and *C. maritimum maritimum* and their pollinators play in the shared network?

Investigating network level statistics, we found that 'connectance' in the observed network was not significantly different than the 'r2d' or 'swap.web' null model (Table 3). The observed network had significantly higher 'nestedness' than the 'r2d' and 'vaznull' models (r2d: $Z = 2.29$, $P = 0.02$; vaznull: $Z = 2.85$, $P = 0.004$), but not the 'swap.web' model ($Z = -0.24$, $P = 0.81$). 'Specialization' was significantly higher in the observed network than any of the three models (r2d: $Z = 64.73$, $P < 0.001$; swap.web: $Z = 4.99$, $P < 0.001$; vaznull: $Z = 54.04$, $P < 0.001$, Table 3).

Investigating species level statistics for plants involved in the observed network, we found that *L. duriusculum* is a connector in the network (BC > 0) and is visited by pollinators that visited few or no other plant species (Fig. 8). *C. maritimum maritimum* and *L. duriusculum* have a similar weighted closeness (0.042 and 0.047, respectively) and were visited by proportionally the most pollinator groups in the network. *C. maritimum maritimum* had the most specialized visitation in the network (d = 0.86), compared to *L. duriusculum* which had more generalized visitation (d = 0.27).

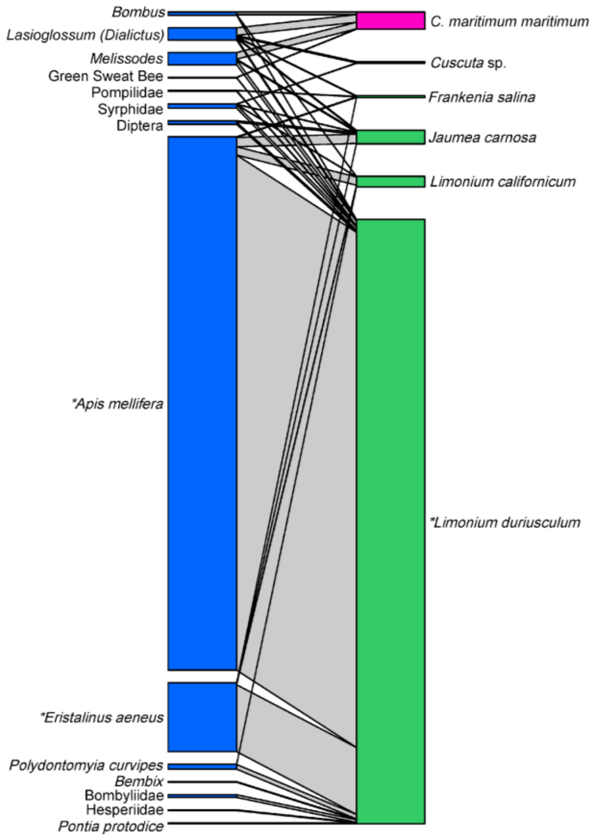

Figure 7. Diagram of the plant-pollinator network including all plots with both *Chloropyron maritimum* ssp. *maritimum* and *Limonium duriusculum* present between 2017-2023. The network documents a total of 1,971 interactions. Insect pollinators are depicted in blue and shown on the left. Floral species are depicted in green and shown on the right. Our focal plant, *C. maritimum maritimum*, is highlighted in magenta. Interactions documented between plants and pollinators are grey and weighted by frequency. Thus, thicker lines indicate interactions that occurred more frequently. *Denotes non-native species.

Metric	Observed network	Null Model	Z	P
Nestedness	14.37	r2d	2.29	0.02
		swap.web	-0.24	0.81
		vaznull	2.85	0.004
Connectance	0.42	r2d	1.85	0.06
		swap.web	-0.20	0.84
		vaznull	NA	NA
Specialization (H2)	0.36	r2d	64.73	<0.001
		swap.web	4.99	<0.001
		vaznull	54.04	<0.001

Table 3. Comparison between the observed network metrics (nestedness, connectance and specialization) and the three different null model types.

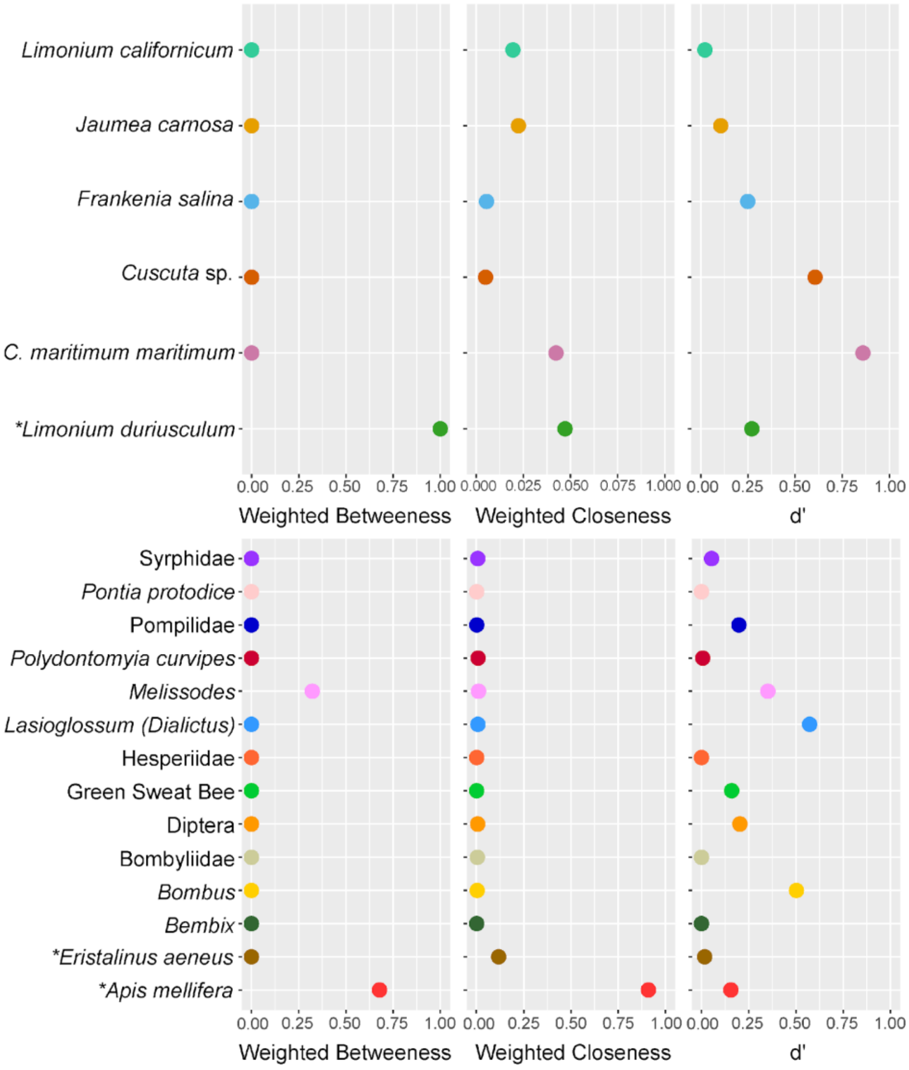

Figure 8. Diagram showing species level network indices ('weighted betweenness', 'weighted closeness', and 'specialization (d')') for the plant species (top) and pollinator groups (bottom) in the network that includes all plots with both *Chloropyron maritimum* ssp. *maritimum* and *Limonium duriusculum* present between 2017-2023. *Denotes non-native species.

Investigating species level statistics for pollinators involved in the observed network, we found that *Apis mellifera* and *Melissodes* acted as connectors (BC > 0), visiting plants that otherwise would have had few or no pollinators (Fig. 8). *Apis mellifera* had the highest weighted closeness (0.91). *Lasioglossum* (*Dialictus*) (d = 0.57) is the most specialized pollinator in our network, followed by *Bombus* (d=0.50) and *Melissodes* (d = 0.35). *Apis mellifera* and *Eristalinus aeneus*, the two most abundant pollinators to *L. duriusculum*, had more generalized visitation (d = 0.16 and d = 0.02, respectively, Fig. 8).

HOW DOES THE REMOVAL OF FLOWERING *L. DURIUSCULUM* INFLUENCE VISITATION TO *C. MARITIMUM MARITIMUM* AND THE ENTIRE PLANT-POLLINATOR NETWORK?

To address our fourth question and understand the impact of experimental removal of *L. duriusculum* on *C. maritimum maritimum* visitation, we found that the experimental removal of *L. duriusculum* did not impact the rate of pollinators entering *C. maritimum maritimum* flowers. The pollinator abundance of *C. maritimum maritimum* in control and *L. duriusculum* removal plots was not significantly different (Fig. 9; Wilcoxon, *P* = 0.53). There was one observational round (June 2019) that had available *C. maritimum maritimum* flowers, but zero *C. maritimum maritimum* pollinators in either control or *L. duriusculum* removal plots. Additionally, two observational rounds, August 2022 and July 2023, had *C. maritimum maritimum* flowers, but zero *C. maritimum maritimum* pollinators in *L. duriusculum* removal plots.

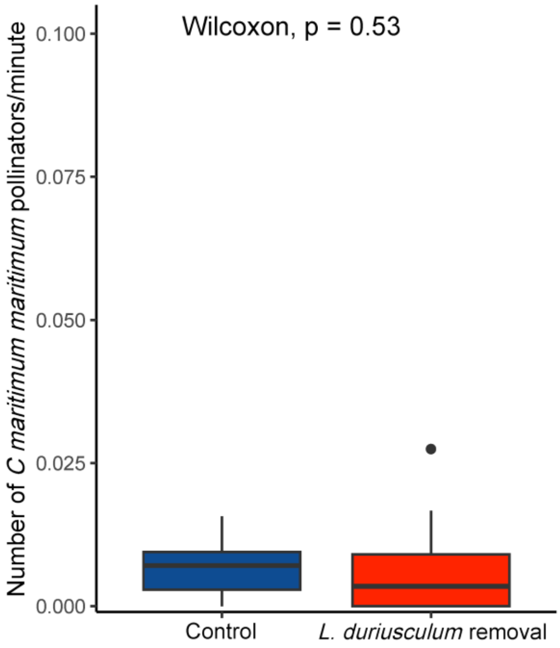

Figure 9. Boxplot of the visitation rate (pollinators per minute) to *Chloropyron maritimum* ssp. *maritimum* in control (blue) and *Limonium duriusculum* removal (red) plots during the three years after *L. duriusculum* removal. There was one observational round, June 2019, that had zero *C. maritimum maritimum* pollinators in control and *L. duriusculum* removal plots. Additionally, two observational rounds, August 2022 and July 2023, had zero *C. maritimum maritimum* pollinators *in L. duriusculum* removal plots. We calculated the metric of 'pollinators per minute' over a single observational round (control plots, *N* = 7 observational rounds, *L. duriusculum* removal *N* = 5 observation rounds).

In comparing network statistics between the control plot network and *L. duriusculum* removal plot network we found that the control plot network was more nested, more connected and had higher specialization (Table 4; Fig. 10). The *L. duriusculum* removal plots network had 6.9 times less visitation than the control plots (265 visits and 1,829 visits respectively). *Limonium duriusculum* remained abundant in the marsh, even around plots where it was experimentally removed. In a few cases, *L. duriusculum* inflorescences from individuals growing outside of the plot hung into removal plots, accidentally becoming incorporated into networks where they had been experimentally removed. While not ideal, we feel that the accidental incorporation of *L. duriusculum* had minimal effects on network structure. On average there was only 0.32% *L. duriusculum* cover in removal plots during the 2021-2023 surveys (Fig. 4). *L. duriusculum* in removal plots received 25 pollinator visits compared to 1,710 pollinators in control plots (Fig. 10).

DISCUSSION

We observed relatively low visitation (1 visit per 100 minutes) to *C. maritimum maritimum* over the five years of pollinator observation at the Carpinteria Salt Marsh. Bees were the only taxon observed to visit *C. maritimum maritimum* flowers. *Chloropyron maritimum* ssp. *maritimum* and *L. duriusculum* had significantly different pollinator compositions, not overlapping in ordination space, and *L. duriusculum* visitation was dominated by two non-native insect species, *Apis mellifera* and *Eristalinus aeneus*, neither of which entered *C. maritimum maritimum* flowers. The observed network was significantly more specialized than all three of the null networks and *C. maritimum maritimum* was the most specialized plant in the network. The experimental removal of *L. duriusculum* in half of our plots had no detectable effect on visitation to *C. maritimum maritimum*, but did impact network structure.

We observed 75 individuals from five different taxa enter *C. maritimum maritimum* flowers over the course of our study: *Bombus californicus*, *Bombus*

Table 4. Control and *Limonium duriusculum* removal plot network level statistics after *L. duriusculum* removal (2021-2023).

Network	Nestedness	Connectance	Specialization (H2)
Control plots	15.45	0.37	0.35
L. duriusculum removal plots	28.95	0.41	0.36

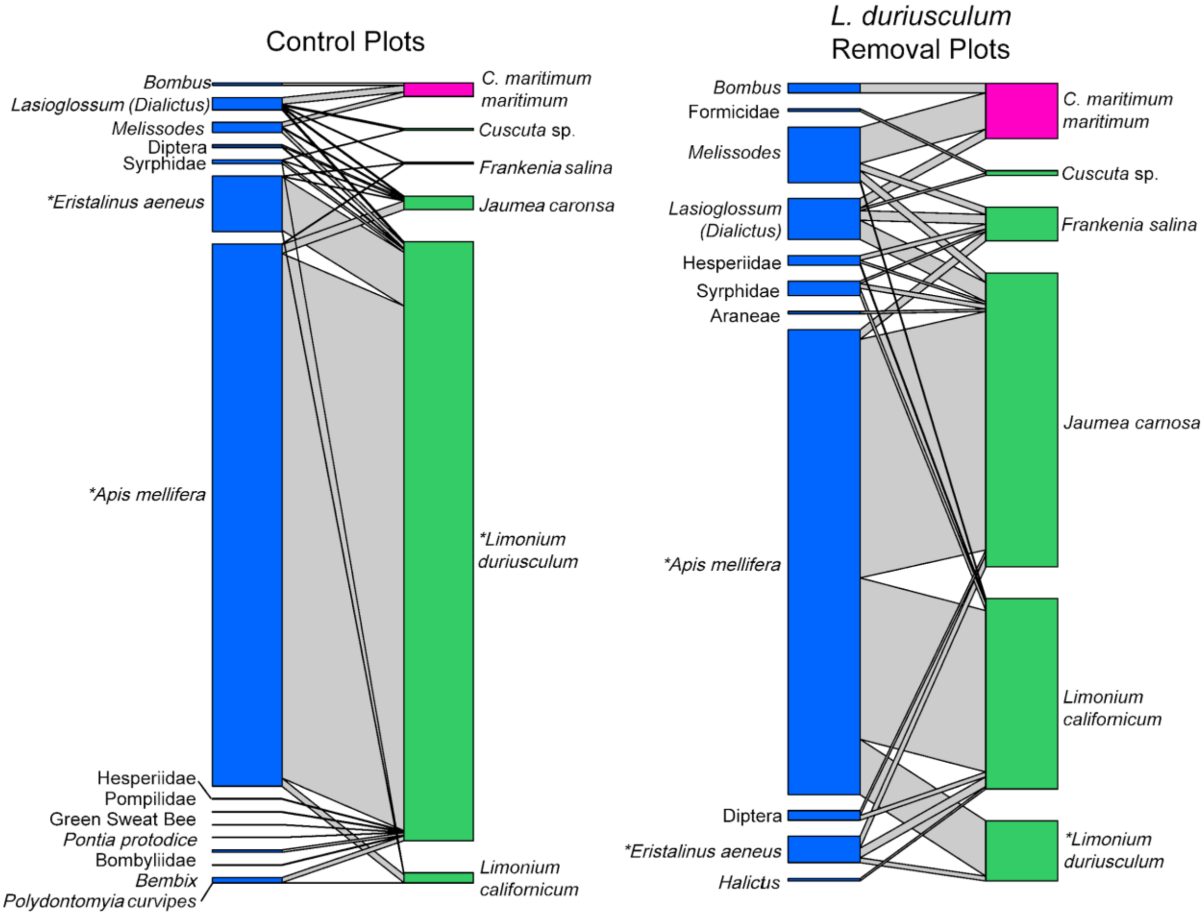

Figure 10. Control plots (left) and *Limonium duriusculum* removal plots (right) plant-pollinator networks after *L. duriusculum* removal (2021-2023). Control plots had 1,829 visits in the network and removal plots had 265 visits in the network. Pollinators are depicted in blue and shown on the left. Floral species are depicted in green and shown on the right. *Chloropyron maritimum* ssp. *maritimum* is highlighted in magenta. Interactions documented between plants and pollinators are grey and weighted by frequency. Thus, thicker lines indicate interactions that occurred more frequently. *L. duriusculum* is still present in the removal network because it was still very locally abundant outside of the removal plots, and a few inflorescences hung into the plots during observations. *Denotes non-native species.

crotchii, *Melissodes*, *Lasioglossum* (*Dialictus*), and a green sweat bee (*Agapostemon* or *Augochlorella*). *Bombus crotchii,* a rare red listed bumblebee, was observed visiting *C. maritimum maritimum* in both 2019 and 2023. We only observed a single green sweat bee enter *C. maritimum maritimum* flowers once in 2017, and another green sweat bee individual visited *L. duriusculum* once in 2021. Large-bodied bees (*Bombus* and *Melissodes*) made up 62% of the observed visitors to *C. maritimum maritimum* and smaller halictine bees (*Lasioglossum* (*Dialictus*)) made up another 37% of its pollinators.

We found that only a few taxa were visiting *C. maritimum maritimum* at Carpinteria Salt Marsh. The taxa we observed are similar to those seen by Knapp et al. (2024), which repeated a 1985 study of *C. maritimum maritimum* pollinators at Naval Base Ventura County, California, USA conducted by Lincoln. They found *C. maritimum maritimum* visitation to be dominated by *Melissodes* and

Lasioglossum and lacked *Anthidium* pollinators, which differed from Lincoln's 1985 findings, but were similar to our observations at the Carpinteria Salt Marsh (Knapp et al. 2024). Rare plants may be more susceptible to losing pollinator interactions. A study comparing past and current insect collections from northern New England found that 13 plant-pollinator associations involving six rare plants were lost over a 125-year period, and none of these rare plants have had a recorded visitor since 1990 (Mathiasson & Rehan 2020). Certain pollinator partners may also be more at risk of disappearing from a system. A study conducted by Burkle et al. 2013, evaluated historic and current plant-pollinator networks in the same locality and found a loss of over 50% of the historic bee species, and that specialist and cavity-nesting pollinators were disproportionally absent. *Anthidium* are cavity-nesting bees that are often specialists, and the last public records of them at the Carpinteria Salt Marsh were in the 1930s (GBIF; University of California, Riverside, Entomology Research Museum 2019). It would be interesting to see if the absence of specialized cavity nesters found in our study and in Knapp *et al. (*2024) is consistent across the range of *C. maritimum maritimum*.

The composition and foraging behaviour of pollinators is directly related to the quality of service provided to the rare plant. Lincoln (1985) observed that large-bodied bees, including *Bombus sonorus* and *Melissodes tepidus* ssp. *timberlakei*, touched the exserted stigma of *C. maritimum maritimum* more often while visiting flowers than small halictine bees and bombyliid flies. Parsons & Zedler (1997) found that when the large-bodied bees (*Bombus* or *Melissodes*) and halictine bees were present at sites, seed set of *C. maritimum maritimum* was significantly higher than when compared to sites where only small halictine bees were present. During our observations, we did observe *Lasioglossum* (*Dialictus*) entering the keeled flower through the side of the flower, as opposed to entering through the top near the exerted stigma like *Bombus* and *Melissodes*. (Fig. 5; video: https://www.youtube.com/watch?v=poYwmJK6c0U&t=3s). As such, even when *Lasioglossum* (*Dialictus*) were collecting *C. maritimum maritimum* pollen from within the flower, they probably spent less time touching the stigma than large-bodied bees and may be less effective pollinators.

In addition to the size of the bee, the foraging consistency of the insect can also be important for pollinator efficiency. Lincoln (1985) determined that *Anthidum edwardsii* was probably the most effective pollinator at Naval Base Ventura County due to high foraging flight constancy and pollen loads consisting of just *C. maritimum maritimum* pollen. Again, we did not observe any *Anthidium* during our study. Comparatively, Lincoln (1985) found that *Melissodes* and *Lasioglossum* had mixed pollen loads and were observed visiting multiple plant species within and among foraging bouts. These were the two most abundant *C. maritimum maritimum* pollinators in our study, and although we did not specifically record foraging path during our surveys or investigate pollen loads, we did observe both pollinators visiting multiple flowering plants in a single foraging bout. *Chloropyron maritimum* ssp. *maritimum* reproductive success is reliant on the presence of pollinators, and some pollinators, *i.e.*, large-bodied specialist bees, seem to be more effective than others.

Overall, we found that visitation to *C. maritimum maritimum* at the Carpinteria Salt Marsh is low (1 visit per 100 minutes). Two past studies examining *C. maritimum maritimum* visitation at another salt marsh, Pt. Mugu, recorded higher visitation rates: 31 visits per 100 minutes (Lincoln 1985) and 55 visits per 100 minutes (Knapp et al. 2024). In her study, Lincoln (1985) compared the visitation rate, stigmatic pollen and seed set for three different sites, and found that the site with the lowest visitation rate (2 visitors per 100 minutes) had a significantly lower mean seed set. An important next step will be to understand if the changes we see in pollinator community composition impact the plants' reproductive success, and if *C. maritimum maritimum* populations are pollinator limited. It would be interesting to understand if *C. maritimum maritimum* is as pollinator dependent now as it was in the 1980s, and if the lower visitation results in lower seed set (Lincoln 1985).

The pollinator communities visiting *C. maritimum maritimum* and *L. duriusculum* were significantly different. This difference was primarily driven by the abundance of the two most common insects visiting *L. duriusculum*: the non-native *Apis mellifera* and non-native *Eristalinus* *aeneus*. Collectively, they made up 96% of all *L. duriusculum* visitors. Additionally, both insects were the two most numerically dominant pollinators observed in the network, with *A. mellifera* representing 82% of all pollinators in the network, and *E. aeneus* representing another 11%. Neither insect was ever recorded entering *C. maritimum maritimum* flowers. Conversely, native bees observed entering *C. maritimum maritimum* flowers, including *Melissodes*, *Lasioglossum* (*Dialictus*), and *Bombus crotchii*, visited *L. duriusculum*, and their visits to *L. duriusculum* accounted for 16-38% of their total visitation in the network. Future studies should investigate the amount of pollen transfer happening in the system, and if *L. duriusculum* pollen deposition on *C. maritimum maritimum* stigmas has negative effects on reproduction. As such, even though *C. maritimum maritimum* and *L. duriusculum* pollinator compositions were significantly different, *L. duriusculum*'s attractiveness to *C. maritimum maritimum* pollinators paired with its visitation being dominated by insects that do not visit *C. maritimum maritimum* may be concerning.

We never observed *A. mellifera* visiting *C. maritimum maritimum,* which is consistent with other research that shows that *A. mellifera* visits geographic-range restricted plants, such as rare plants, less often than widespread species (Nordfolk 2018). However, *A. mellifera* did overlap with *C. maritimum maritimum* visitors in the other plants they visited (*L. duriusculum*, *L. californicum*, *J. carnosa*, and *F. salina*). *Apis mellifera* are super-generalists that visit a wide array of flowering plants that tend to visit the most abundantly blooming plants regardless of their native or non-native status (Morandin & Kremen 2013; Hung et al. 2019) and their preferences can result in reshaping communities over time. *A. mellifera* can quickly become numerically dominant in a community and can competitively exclude native pollinators from shared flowering species, causing native pollinators to alter their foraging behaviour (Goulson 2003; Thompson 2016; Lindström et al. 2016). Thompson (2016) observed that increases in *A. mellifera* were strongly correlated with *Bombus* population declines. Additionally, *A. mellifera* could be transmitting disease or parasites via flowers to native bees (Grozinger & Flenniken 2019). Valido et al. (2019) found that the introduction of *A. mellifera* into an uninvaded ecosystem resulted in lower pollinator diversity and a loss of links in the plant-pollinator network. If native bee numbers diminish due to the abundance of *A. mellifera* in the area, *A. mellifera* will not fill the *C. maritimum maritimum* pollinator gap created.

Our plant-pollinator network analyses revealed that the observed network was more nested than two of the three null models and had higher specialization than any of the three null models. *L. duriusculum* acts as a connector within the network and was visited by a few individuals from some insect groups that visited no other plant species, including *Bembix*, Bombyliidae, Hesperiidae, and *Pontia protodice*. *C. maritimum maritimum* was the plant with the most specialized visitation in the network, and only four of the 17 pollinator groups in the network entered its flowers. Even though *Lasioglossum* (*Dialictus*), *Melissodes*, and *Bombus* all visited other plants, including *L. duriusculum*, during our observations, they were the three pollinators with the most specialized visitation. *Apis mellifera* and *Eristalinus aeneus*, the two most abundant pollinators to *L. duriusculum*, had comparatively more generalized visitation. Overall, *L. duriusculum* and its main visitors were more generalized, whereas *C. maritimum maritimum* and its visitors were more specialized.

Following experimental *L. duriusculum* removal, we detected no difference in floral visitation to *C. maritimum maritimum* between the control and removal plots. Other studies (Baskett et al. 2011; Etter et al. 2021) found that the pollinator abundance and diversity that visited a focal plant changed within the same year as non-native plant removal, but we saw no change over three years following the removal of non-native plants from the salt marsh. Our findings indicate that the removal of *L. duriusculum* on this scale (2 x 2 m plots) neither positively nor negatively altered visitation to *C. maritimum maritimum*. However, we did find that the structure of the plant-pollinator network within removal plots without *L. duriusculum* were more nested, connected, and specialized than the control plots with *L. duriusculum*. Mutualistic networks that are more nested and connected are known to have higher network stability (Thébault & Fontaine 2010). As such, the removal of *L. duriusculum* may be beneficial to network structure even if it did not increase pollinator visitation in the short term at this scale.

Our study does have certain limitations. While we removed *L. duriusculum* on a small scale (2 x 2 m plots), there continues to exist a lot of *L. duriusculum* just outside of removal plots. Because pollinators in this system are relatively large and highly mobile, they likely perceive the landscape at a coarser scale, making foraging decisions at a patch rather than plot level (*i.e.*, tens of meters, rather than 2 x 2 m plots). Our failure to detect any measurable changes in pollinator activity or visitation may be due to the small scale of our change with increased scale (Hegland 2014), and future experimentation should increase the scale of removal inside and around these plots.

Understanding if the *C. maritimum maritimum* pollinators have their requirements for survival (like adequate nesting areas) at the Carpinteria Salt Marsh would also be an important next step. *Bombus* typically nest in old animal burrows, and *Melissodes* and *Lasioglossum* (*Dialictus*) build nests in the ground. As such, they are only able to nest in areas of the marsh that are higher in elevation and not regularly inundated by salt water. There may have previously been more adjacent high elevation ground for nesting on the edges of the marsh that has since been developed with housing and transportation. Additionally, the absent *Anthidium* are above-ground cavity nesters that nest in the stalks of old plants. Considering how developed the surrounding area is, more effort should be put into understanding if the current pollinators have adequate adjacent nesting areas within flight range of *C. maritimum maritimum* and how these nesting areas can be protected.

Chloropyron maritimum ssp. *maritimum* had few pollinators visit it at the Carpinteria Salt Marsh, and at low numbers. To protect its pollination and assumed reproductive success, management of this rare plant should include protecting or restoring essential ground and cavity nesting habitat for bees. In addition to protecting nesting habitat, expanding *L. duriusculum* removal could be beneficial because even though we saw a negligible effect of removal on *C. maritimum mairitimum* visitation on this scale, *C. maritimum maritimum* pollinators visited *L. duriusculum* and it is unknown how *L. duriusculum*'s most abundant visitor (*A. mellifera*) may be impacting *C. maritimum maritimum* pollinators foraging behaviour. Overall, holistic community-wide approaches to management are essential for protecting this rare plant now and into the future.

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AUTHOR CONTRIBUTION

Kylie Etter: Data curation (lead); formal analysis (lead); investigation (equal); project administration (lead); visualization (lead); writing - original draft preparation (lead); writing - review and editing (equal). **Sarah Cusser**: Formal analysis (supporting); investigation (equal); writing - original draft preparation (supporting); writing-review & editing (equal). **Denise Knapp:** Conceptualization (lead), methodology (lead), investigation (supporting), writing - review & editing (supporting).

DISCLOSURE STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data and code is openly available on FigShare (https://doi.org/10.6084/m9.figshare.28054232.v1)

APPENDICES

Additional supporting information may be found in the online version of this article:

Figure A1. The number of *Chloropyron maritimum* ssp. *maritimum* inflorescences available for pollinators in observed plots by month and year.

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