Short Communication

ENDEMIC *CASTILLEJA GRISEA* SUPPORT DIVERSE FLORAL-VISITOR ASSEMBLAGES WITH IMPLICATIONS FOR PROMOTING LOCAL PLANT COMMUNITIES

J.A. Saldivar[1,2], C. Sheena Sidhu[3,4], Erin E. Wilson-Rankin[3]*

[1]*Department of Botany and Plant Sciences, University of California Riverside, Riverside, CA 92521.*
[2] *Current address: Department of Entomology and Nematology, University of California, Davis, Davis, CA 95616.*
[3]*Department of Entomology, University of California Riverside, Riverside, CA 92521.*
[4]*Current address: Jasper Ridge Biological Preserve, Stanford University, Stanford, CA 94305.*

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*Corresponding author:
e.wilson.rankin@gmail.com

Abstract—*Castilleja grisea*, the San Clemente Island paintbrush, is endemic to San Clemente Island (Los Angeles County, California). This bushy hemiparasitic perennial was once threatened by livestock and feral herbivore grazing, but occurrences have increased since island-wide non-native herbivore removal. Recently declassified as a federally endangered species, *C. grisea* remains state listed (California Rare Plant Rank: 1B.3), and a subset of the population is surveyed annually as part of its post-delisting monitoring plan. We investigated the flower-insect interactions of *C. grisea* and its neighboring plant community at six locations during early, mid, and late in the flowering season. A total of 23 insect taxa were observed visiting 12 species of plants, with 74% of the floral-visitor taxa observed actively visiting *C. grisea* flowers. Moreover, plots with blooming *C. grisea* boasted nearly 50% higher insect species richness than areas where the paintbrush was absent or not flowering. Plant-floral-visitor networks changed over time, becoming significantly less connected and exhibiting lower interaction evenness. Our findings suggest that *C. grisea* supports a diversity of floral visitors and may be an indicator of habitat health and high plant community diversity. As a potential keystone species, conservation planning and management strategies promoting *C. grisea* may have far reaching benefits for this island ecosystem.

Keywords—California Channel Islands, endemic, plant-floral visitor networks, pollination

INTRODUCTION

The Channel Islands of California, an eight-island archipelago, harbor exceptional biodiversity and serve as a hotspot for endemic species, including more than 100 plant species that are considered rare and/or found nowhere else (Junak et al. 1995; Moody 2000). Among the islands, the southernmost, San Clemente Island (SCI), stands out for its particularly rich native flora, which includes numerous rare and specialized plant communities adapted to the island's distinct soils, climate, and disturbance regimes (Raven 1963; Ross et al. 1997; Moody 2000; Sullivan & Kershner 2005; Tierra Data 2011; Wilson Rankin & Sidhu 2016). Despite this remarkable diversity, the ecology and species interactions of many island taxa remain poorly understood, limiting our understanding of the processes that sustain these communities and how they may respond to ongoing environmental change.

Previous studies on SCI have investigated aspects of bee ecology (Sidhu & Wilson Rankin 2018) and pollinator interactions with select rare plants, revealing patterns of visitation, floral preferences, and seasonal dynamics (Sidhu et al. 2022; Hazlehurst et al. 2023). While these studies have shed light on the contributions of individual pollinator taxa to plant reproduction, they also underscore the need for comprehensive data on the diversity, composition, and structure of plant-floral visitor communities across SCI and the broader Channel Islands. Understanding these interactions at a community-wide scale is critical for elucidating the ecological networks that sustain endemic plants, identifying potential vulnerabilities in pollination systems, and informing targeted conservation strategies aimed at maintaining both plant reproductive success and broader ecosystem integrity.

San Clemente Island paintbrush (*Castilleja grisea*: Orobanchaceae) is one of the 47 plants endemic to the Channel Islands and occurs only on SCI (Junak et al. 1995). This hemiparasitic perennial subshrub has pale yellow flowers, typically grows one to two feet tall and exhibits enhanced growth and reproductive success when parasitic (Heckard 1962). In 1977, the U.S. Fish & Wildlife Service listed *C. grisea* as endangered due to overgrazing by livestock and herbivorous mammals and competition from non-native plant species (Helenurm et al. 2005). After the removal of non-native herbivores, *C. grisea* populations have expanded (Helenurm et al. 2005), prompting a 2023 recommendation to reclassify the species from federally endangered to threatened. Despite this, the species has maintained its California Native Plant Society Rare Plant Rank of 1B.3 (rare, threatened, or endangered in California and elsewhere) since 1974 (Slakey et al. 2013). To ensure its continued recovery, ongoing monitoring tracks population trends, emerging stressors, and supports restoration efforts (U.S. Fish and Wildlife Service 2023).

Although non-native herbivore removal increased *C. grisea* populations, the species remains threatened by erosion, fire, non-native plants, and land-use change (US Fish and Wildlife Service 2012). These pressures can cascade across trophic levels and contribute to insect declines (Sanchez-Bayo & Wyckhuys 2019; Wagner et al. 2021), potentially impacting even the most effective pollinators of *C. grisea.* Given that the identities of key pollinators are not well understood, characterizing plant-insect networks provides the necessary foundation for subsequent research aimed at identifying the most effective pollinators, which can then inform targeted conservation efforts. To our knowledge, this study provides the first description of the *C. grisea* floral visitor network.

MATERIALS AND METHODS

To assess the floral visitors to *C. grisea*, we established three 5 x 5 m sampling plots at six sites on San Clemente Island (Los Angeles County, California) and identified all plants within each plot (Appendix S1). Sites were selected based on known populations of *C. grisea* and spanned a cline of plant diversity: three sites on the east side of the island (Tota, Twin Dams, Burns Canyon trail) and three sites on the west side of the island (Hoppel, Waynuck Canyon, Tank trail opposite Horton Rd).

Floral visitors were collected at each sampling plot by hand-netting insects off of flowers. Surveys were conducted during the *C. grisea* bloom period (February, early March, and late March/early April 2015). This time frame encompasses early, peak and late bloom for *C. grisea; Castilleja* was present in all sites at each visit, although the number of blooms per plot increased up to peak bloom and then decreased during the late bloom period. At each visit, all insects actively visiting flowers were collected during 20-minute sampling periods. For each individual floral visitor, the plant species from which it was captured was recorded. To supplement active sampling, vane traps were placed at the center of each plot for 24 hours prior to collecting insects present at the site but not observed during timed collections.

Hummingbird observations were exclusively visual. All floral-visiting insects collected from plots were processed, pinned, and identified to the lowest taxonomic level possible based on the condition of the specimens. Only putative pollinator taxa are included in analyses, and from here on, we will refer to these floral visitors as "potential pollinators" as we currently lack verification of pollinator efficiency. Identities were confirmed by Dr. Douglas Yanega, University of California, Riverside Entomology Research Museum.

STATISTICAL ANALYSES

All analyses were conducted in R 4.4.3 (R Core Team 2025). For potential pollinators hand-netted from all species of flowering plant, we assessed whether those species had previously been observed in San Clemente Island. We collated the number of different potential pollinator taxa observed visiting each flowering species, and whether that plant species was previously reported as an associated plant of *Castilleja grisea*. Then we compiled a comprehensive list of *C. grisea* floral visitors to assess the relative efficacy of each sampling technique. We compared the proportion of known floral visitors detected by vane traps and hand-netting using the *prop.test* function in the *stats* package (R Core Team 2025). To examine temporal variation in floral visitor diversity, we fitted linear mixed models (LMMs) with floral-visitor species richness as the response variable. Fixed effects included season (early, mid, or late) and plant species richness per plot, while plot identity nested within site as the random effect.

To assess whether *C. grisea* presence influenced patterns in floral-visitor diversity, we constructed a second LMM with the same response variable (floral-visitor species richness), including season and the presence of blooming *C. grisea* in the plot (0/1) as fixed effects, and plot identity nested within site as a random effect. Post-hoc comparisons of significant categorical predictors were performed using the *emmeans* package (Lenth 2019), with false discovery rate correction for multiple comparisons. Collinearity among predictors was assessed using the *vif* function in the *car* package (Fox & Weisberg 2019).

From the visitation data, we constructed weighted bipartite interaction networks, with interaction strength determined by the frequency of observed visits. The *bipartite* package (Dormann et al. 2009) was used to calculate qualitative and quantitative network metrics at the network, trophic, and species levels to describe plant-floral-visitor interactions within the community. We generated one aggregate (pooled) network and compared networks across time (early, mid, and late season) and space (east versus west). To evaluate whether observed network metrics differed significantly from random expectation, we generated 1,000 null networks for each seasonal network (early, mid, and late) using the *generate_null_net* function in package *econullnetr* (Vaughan et al. 2018).

Metrics of interest included (1) weighted connectance, representing the proportion of potential plant-floral visitor interactions that were realized; (2) interaction evenness, which ranges from 0 (uneven) to 1 (uniform), describing the distribution and uniformity of interactions among species (Kaiser-Bunbury et al. 2011); (3) H2', representing the degree of specialization or interaction partitioning among plants and floral visitors across the entire network; and (4) partner diversity, defined as the average Shannon diversity of partners per insect or plant species.

RESULTS

Overall, we observed 318 floral visits by 23 taxa of likely pollinators actively visiting 12 species of plants (Tables 1 and 2). Hand-netting and vane traps differed in their detection of these visitors to San Clemente Island paintbrush ($X^2_1 = 9.67$, $P = 0.0019$). Of the 17 species observed visiting *C. grisea* flowers, only 47% of these taxa were detected in vane trap samples (8 species), highlighting the importance of hand-netting to determine a plant's insect associations. At the plot level, pollinator species richness increased with increasing plant species richness ($\varrho = 1.07$; $F_{1,35} = 8.17$, $P = 0.0072$) and as the season progressed ($F_{2,24} = 21.59$, $P < 0.0001$). We observed more insect taxa in late *C. grisea* bloom than in either early ($t_{25} = 5.67$, $P < 0.001$) or mid-bloom ($t_{23} = 5.30$, $P < 0.001$) (Fig. 1). Moreover, we found that floral-visitor richness was 49.5% higher in the presence of blooming *C. grisea* than if it was absent ($F_{1,7} = 6.63$, $P = 0.03525$).

Plant species varied in the diversity of floral visitors they attracted. Five species accounted for the majority of visitation events: *Eriophyllum confertiflorum, Senecio lyonii, C. grisea, Pseudognaphalium stramineum,* and *Achillea millefolium* (Table 2, Fig. 1). High visitation rates by *Copestylum* flies largely drove patterns for *E. confertiflorum, S. lyonii,* and *A. millefolium*. Seventeen floral-visitor taxa (61% of all visitors detected) were recorded actively visiting *C. grisea* flowers, with *Anthophora edwardsii* and *Habropoda depressa* as the most common bee visitors and *Copestylum avidum* the most frequent syrphid fly. *Calystegia macrostegia* also received notable visitation from *Agapostemon subtilior, Diadasia* sp., and *Eucera actuosa*. Across sites, plants shared a substantial proportion of floral visitors (vulnerability = 5.26), suggesting that efforts to promote *C. grisea* and its floral visitors may indirectly benefit a broad suite of co-flowering plant species.

Table 1. Floral visitors observed on San Clemente Island and the frequency of their detection on flowers in the current study and whether they were previously reported in 1985.

Order	Family	Floral visitor	Instances observed	Previously reported for SCI (Rust et al. 1985)
Hymenoptera	Apidae	*Anthophora edwardsii*	28	Genus
		Diadasia bituberculata	1	Species
		Diadasia sp.	2	Genus
		Eucera actuosa	2	Species
		Habropoda depressa	72	Genus
	Halictidae	*Agapostemon subtilior* *	5	Species
		Lasioglossum sp.	12	Genus
	Megachilidae	*Anthidium* sp.	1	Genus
	Pompilidae	Pompilidae sp.	2	NA
	Vespidae	*Ancistrocerus* sp.	3	New record
Diptera	Bombyliidae	*Bombylius lancifer/facialis*	24	NA
		Bombylius major	9	NA
		Bombylius sp.	9	NA
	Calliphoridae	*Lucilia sericata*	5	NA
	Muscidae	Muscidae sp.	3	NA
	Syrphidae	*Copestylum avidum*	41	NA
		Copestylum lentum	8	NA
		Copestylum marginatum	20	NA
		Copestylum mexicanum	10	NA
		Copestylum sp.	64	NA
		Nausigaster unimaculata	5	NA
Lepidoptera	Sphingidae	*Hyles lineata*	1	NA
Apodiformes	Trochilidae	*Selasphorus sasin*	1	NA

* Specimens from San Clemente Island: *Agapostemon texanus* in California have been revised to *Agapostemon subtilior* (Portman et al. 2024). [†]This table was prepared using images from www.flaticon.com: wasp, moth, and hummingbird icons by Freepik and fly icon by juicy fish. Bee icon CC BY NC by Jose Luis Ordóñez and Ignasi Bartomeus.

NETWORKS OVER TIME: EARLY, MID AND LATE *CASTILLEJA* BLOOM

Plant-floral-visitor networks during each bloom period were less connected and exhibited lower interaction evenness than expected under null networks (Appendix S2), indicating a higher degree of specialization. Network specialization (H2') was significantly greater than null expectations across all time periods (early bloom: SES = 6.46; mid bloom: SES = 10.85; late bloom: SES = 14.55). Despite this elevated specialization, both connectance and interaction evenness increased slightly over the course of the bloom. Partner diversity also increased over time but remained always lower than in the corresponding null networks for both plants and floral visitors (Appendix S2). Throughout its flowering period, *C. grisea* supported an average of 10-11 active floral-visitor taxa. By the late bloom period, additional plant species, including *Achillea millefolium, Eriophyllum confertiflorum,* and *Senecio lyonia*, received more frequent visits.

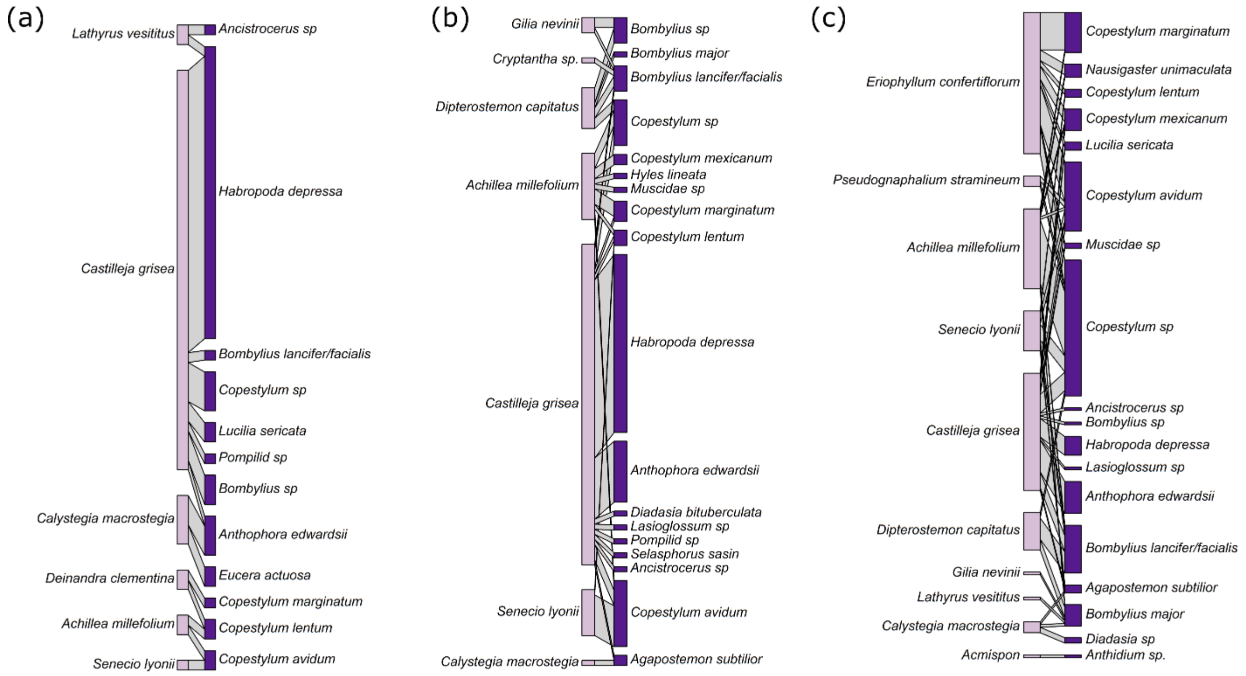

Figure 1. Plant-floral-visitor network for all observations in (a) early, (b) mid, and (c) late *Castilleja grisea* bloom. Plant species are depicted in light purple and floral visitor species are depicted in dark purple.

NETWORKS ACROSS THE ISLAND: EAST VERSUS WEST

Total plant species richness was slightly higher in plots on the island's western side compared to eastern plots; however, floral-visitor diversity was similar between the two regions. Consequently, networks from western plots were slightly larger than those from the east (21 vs. 23 species). Overall, network metrics differed little between east and west plots (Appendix S2). Compared to null networks, western networks exhibited significantly lower interaction evenness (IE) and connectance (SES = –5.68 and –6.92, respectively; Appendix S2). Eastern networks also had lower than expected connectance (SES = –4.14) but did not differ from null expectations for IE (SES = –0.99). Consistent with temporal patterns, network specialization (H2′) was significantly

Table 2. Plant species and the number of different potential pollinator taxa observed visiting each species, and whether each plant species was previously reported as an associated plant of *Castilleja grisea*.

Plant family	Plant species	N pollinator taxa visiting flowers	Previously reported as associated with *C. grisea* (Vanderplank et al. 2019)
Asteraceae	*Achillea millefolium*	10	Species
	Deinandra clementina	2	Species
	Eriophyllum confertiflorum	8	Species
	Pseudognaphalium stramineum	2	New record
	Senecio lyonii	5	Species
Fabaceae	*Acmispon argophyllus*	1	Species
	Lathyrus vesititus	3	Species
Convolvulaceae	*Calystegia macrostegia*	5	Species
Orobanchaceae	*Castilleja grisea*	17	--
Boraginaceae	*Cryptantha* sp.	1	New record
Themidaceae	*Dipterostemon capitatus*	4	Species
Polemoniaceae	*Gilia nevinii*	3	New record

higher than null expectations for both east and west networks (east: SES = 4.90; west: SES = 10.94). Partner diversity was lower than null models on both sides of the island, corroborating the H2′ results and indicating greater specialization than predicted by null networks.

DISCUSSION

Following the eradication of non-native herbivores and subsequent habitat restoration efforts, *C. grisea* has shown significant recovery across SCI. The number of documented occurrences increased from 19 at the time of its listing under the Endangered Species Act in 1977 to over 336 occurrences and 31,694 individuals by 2011–2012 (Vanderplank et al. 2019), prompting the species to be reclassified from endangered to threatened. In this study, we provided one of the first detailed characterizations of the *C. grisea* floral-visitor community network on SCI, an island with high endemism. We identified a diversity of arthropods visiting *C. grisea* and neighboring plants at different locations and throughout the spring *Castilleja* bloom. We found *C. grisea* to be the most generalist plant in the networks identified in terms of floral-visitor taxa. *Castilleja grisea* had the highest degree (17), highest species strength (9.43), highest partner diversity (1.82) and number of effective partners (6.2) in the pooled network. When examining plant composition, pollinator diversity was highest when *C. grisea* was present (6.08 ± 0.63 versus 4.07 ± 0.51). These findings indicate that conserving *C. grisea* could have broader ecological benefits, potentially supporting not just the species itself but also the wider plant-insect communities.

This study underscores the importance of accounting for temporal and spatial variation, as we observed the system to be highly dynamic. Both plant and floral-visitor richness increased throughout the spring season, with *C. grisea* emerging as the most frequently visited plant species (Table 2). Notably, we recorded three plant species previously unreported in association with *C. grisea* (Vanderplank et al. 2019). These results suggest that *C. grisea* may play a pivotal role in supporting floral visitors, particularly during the early flowering period. Furthermore, the high number of floral visits to *C. grisea* by a diverse assemblage of bees, flies, and wasps aligns with findings from Hersch and Roy (2007) indicating that the absence of vivid inflorescences does not substantially limit visitor attraction.

Further analysis of seasonal dynamics revealed that *Habropoda depressa* accounted for nearly all *C. grisea* floral visits during the early season and dominated visitation through mid-season. In contrast, late-season visitation was primarily driven by *Anthophora edwardsii* and *Copestylum* spp., which emerged as the most frequent visitors (Fig. 1). Targeted studies during early bloom stages could further clarify the ecological significance of *C. grisea* for floral-visitor communities, especially regarding floral constancy; for instance, three species (*Anthopoda edwardsii*, *Hebropoda depressa*, and *Pompilid* sp.) showed nearly exclusive visitation to this host (Fig. 1). Although this study did not directly quantify pollination, our findings provide a valuable framework for identifying floral visitors that may function as effective pollinators of *C. grisea*. Identifying the primary pollinating taxa and their temporal dynamics could inform conservation and management strategies aimed at enhancing populations of the most influential pollinators, thereby contributing to the long-term persistence of *C. grisea*.

Additional factors influencing *C. grisea* that may shape its population and community dynamics, as well as plant-floral-visitor networks, are linked to its hemiparasitic life history strategy. As a hemiparasite, *C. grisea* relies partly on host plants for water and nutrients while maintaining photosynthetic capacity, introducing a complex set of ecological interactions. Floral visitation and subsequent seed production may depend on host nutrient status, as nutrient-rich hosts can enhance parasite vigor and floral display, thereby increasing attractiveness to visitors (Adler 2003). Likewise, the uptake of secondary compounds from hosts may improve parasite defense and reduce herbivory (Adler & Wink 2001), with potential indirect effects on floral visitor composition. Investigating host identity and network structure could therefore provide critical insight into the ecological mechanisms regulating *C. grisea* population dynamics and its role within plant-floral-visitor and plant-herbivore networks.

Our findings indicate that *C. grisea* plays a central role in its ecological community. The species attracts a diverse array of arthropod floral visitors and is frequently the most generalist plant, supporting the highest insect diversity and number of effective partners. This suggests that management strategies focused on promoting and conserving *C. grisea* are likely to have broader ecological benefits, extending beyond the species itself to the wider plant-insect communities of SCI. Understanding these dynamics will be critical for informing restoration efforts and predicting long-term population trajectories.

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AUTHOR CONTRIBUTION

EWR and CSS conceived the study, CSS conducted fieldwork, JAS and EWR conducted final statistical analyses, JAS and EWR wrote the manuscript with feedback from all authors.

DISCLOSURE STATEMENT

The authors report no conflict of interest.

GENERATIVE AI DISCLOSURE STATEMENT

No AI tools were used in the writing of this manuscript.

DATA AVAILABILITY STATEMENT

Data are provided in Appendix S3 as part of the online supplemental materials.

APPENDICES

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

Appendix S1: Locations of the six sampling sites on San Clemente Island.

Appendix S2. Results of null network analyses for pooled, seasonal and location networks.

Appendix S3. Potential pollinator data from vane trap sampling and floral visitation collections.

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