The Restoration of Serpentine Plant-Pollinator Mutualisms

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Abstract

Plant-pollinator mutualisms contribute to biodiversity and ecosystem function. Invasive species, however, can alter the structure and function of plant-pollinator mutualisms. Illuminating how restoration affects plant-pollinator mutualisms can provide insights into how mutualistic communities assemble and can inform management. We investigated how removing invasive barbed goatgrass (*Aegilops triuncialis*) influenced the diversity, abundance, and structure of plant-pollinator interactions in a California serpentine meadow. Goatgrass removal treatments resulted in decreased goatgrass cover and increased native forb cover compared to the control treatment. Restored plots had increased pollinator morphospecies richness, Shannon diversity, and pollinator abundance across all years. The restored network had a less nested structure than the control network. Plant-pollinator networks for the restored treatments had higher mean numbers of shared plant partners among pollinators and higher pollinator niche overlap relative to the control. The native forb goldfields (*Lasthenia californica*) acted as a generalist hub for pollinators within the networks, contributing more strongly to network nestedness in the restored treatment relative to the control. Overall, we found that removing invasive goatgrass increased pollinator diversity and abundance, resulting in higher niche overlap among pollinators visiting a generalist wildflower species. Network-based approaches can inform the restoration of plant-pollinator mutualisms, while providing insights into how mutualistic communities respond to invasive species.

Introduction

Plant-pollinator mutualisms contribute to biodiversity and ecosystem function with an estimated 87.5% of flowering plant species relying on animals for pollination (Potts et al., 2010; Ollerton et al. 2011). Globally, populations of pollinators and pollinator-dependent plants are declining rapidly due to anthropogenic stressors, with invasive species as a cause for concern (Biesmeijer et al. 2006; Traveset & Richardson, 2006; Potts et al. 2010; Dirzo et al. 2014; Vanbergen & Initiative 2013). Many restoration efforts, however, lack data on how pollinator communities and plant-pollinator interactions respond to restoration treatments (Williams 2011; Menz et al. 2011; MacPhail et al. 2018; Genes & Dirzo 2022). Restoration efforts often prioritize conserving plant communities under the assumption that restoring the plant community will consequently restore the pollinator community (Palmer et al. 1997). Such restoration efforts include removing invasive species, planting target native species or some combination thereof (Palmer et al. 1997). Incorporating pollinators and their interactions with plants into restoration efforts can enhance ecosystem function and services and provide a benchmark for monitoring success (Kremen et al. 2004; Menz et al. 2010).

In addition to its practical value for conservation and enhancement of biodiversity and function, restoration can provide an empirical means by which to examine core concepts in community assembly (Wainwright et al. 2018) and investigate which mechanisms explain changes in community structure and niche space following the removal of invasive species for restoration purposes (Young et al. 2005; Perring et al. 2015; Doerfler et al. 2020; Derhé et al. 2016). Mutualistic niche theory can explain why mutualisms are stable (Valdovinos et al. 2016; Peay, 2016; Valdovinos 2019; Valdovinos & Marsland, 2021), yet most

restoration studies have examined niche theory in the context of antagonistic interactions (Young et al. 2005; Wainwright et al. 2018). Niche-based approaches to mutualism can inform understandings of how community structure and assembly change in response to restoration (Valdovinos & Marsland 2021; Genes & Dirzo 2022). Following restoration efforts that removed invasive species, mutualistic interactions can have increased niche overlap, increased niche complementarity or both of these aspects (Kaiser-Bunbury et al. 2017). Removing invasive plant species increased functional redundancy, niche complementarity, and the degree of generalism for rocky outcrop plant-pollinator networks in the Seychelles (Kaiser-Bunbury et al. 2017). A gap remains as to how generalizable these findings about invasive species removal are to plant-pollinator mutualistic community assembly across a broader range of ecosystems.

Removing invasive plants can increase the diversity of plant-pollinator interactions, increase pollinator abundance and increase floral visitation and fruit set (Kaiser-Bunbury et al. 2017, 2009), or produce species losses in cases where the invasive plant has become heavily used by pollinators (Valdovinos et al. 2009). Moreover, restoration practices, such as planting native plant species, can result in plant-pollinator communities that are similar in function to intact communities (Forup & Memmott 2005; Forup et al. 2007, but see Williams 2011). Species interaction networks offer one approach to investigating how removing invasive species affect the structure of plant-pollinator interactions. These networks relate interaction structure to stability and ecological function (Schleuning et al. 2015; Moreira et al. 2015), help to predict how anthropogenic changes will affect species interactions (Tylianakis & Morris 2017; Tylianakis et al., 2010), and can inform management (Tylianakis et al. 2010; Kaiser-Bunbury et al. 2017).

Nestedness, a common property of mutualistic networks, is the extent to which interactions in a network are subsetted within generalist plants and pollinators (Bascompte & Jordano 2007). A highly nested network thus has core hubs of generalist species that interact with both generalist and specialist partners (Bascompte & Jordano 2007). The network's structural stability decreases with increased nestedness if core generalist species are removed (Landi et al. 2018; Stouffer & Bascompte 2011; Delmas et al. 2019), but nestedness can increase stability if core generalist species are retained during perturbations (Morrison et al. 2020). Core generalist plants or pollinator species may therefore contribute disproportionately to network nestedness by acting as a critical hub for interaction partners within the network. Niche overlap increases with increasing nestedness (Valdovinos et al. 2016). However, when pollinators adaptively forage in response to changing floral resource availability, niche partitioning decreases niche overlap in nested networks (Valdovinos et al. 2016).

Few studies, however, have empirically tested the effects of removing invasive plants on plant-pollinator network structure (Kaiser-Bunbury et al. 2017, 2009; Russo et al. 2019). Moreover, past studies removed invasive plant species with large showy flowers that are very attractive to pollinators (Russo et al. 2019; Bartomeus et al. 2008), rather than wind-pollinated invasive grasses which are a less preferred resource for pollinators (Arathi & Hardin 2021). A knowledge gap persists regarding how invasive grasses may indirectly affect plant-pollinator interactions. Removing invasive grasses may have more indirect effects on pollinators through increasing the abundance of native forbs preferred by pollinators (Arathi & Hardin

2021). Fast-growing invasive grasses can decrease native forb diversity and abundance (Davies 2011), so removing invasive grasses can create shifts toward forb-dominated systems that may benefit pollinators (Arathi & Hardin 2021). Likewise, some pollinators prefer nesting on bare patches of soil (Anderson & Harmon-Threatt 2016), so removing dense invasive grass cover may increase the quality of pollinator nesting habitat.

The California Floristic Province has high plant and pollinator biodiversity with over 5,000 native plant species, of which 37% are endemic (Burge et al. 2016; Harrison 2013), and at least 1,600 documented native bee species (Frankie et al. 2009). Invasive species have decreased plant diversity in California grasslands, displacing diverse communities of native forbs sometimes preferred by pollinators (Seabloom et al. 2003). Serpentine soils provide a refugium for native California grassland plant communities (Harrison et al. 2006). Most invasive plant species cannot establish on serpentine soils due to the high magnesium to calcium ratio, lack of essential nutrients, and high concentrations of heavy metals (Aigner & Woerly 2011).

Aegilops triuncialis (barbed goatgrass), however, is an invasive annual grass that can tolerate serpentine soils and even performs better on serpentine soils than non-serpentine soils (Lyons et al. 2010; Meimberg et al. 2010). After its introduction to the United States from Eurasia in 1914, *A. triuncialis* spread rapidly across California grasslands during the second half of the twentieth century (Peters et al. 1996; Lyons et al. 2010). In serpentine meadows, *A. triuncialis* forms dense, monotypic stands, displacing the diverse community of native wildflower species (Aigner & Woerly 2011). Aigner and Woerly (2011) found that hand-pulling, grass-specific herbicides, and mowing restoration treatments effectively decreased *A. triuncialis* abundance relative to control treatments. *A. triuncialis* removal treatments increased the abundance of native forbs including the most abundant forb species at our site *Lasthenia californica* (goldfields) (Aigner & Woerly 2011).

Higher floral abundance can increase pollinator visitation (Fowler et al. 2016). The most abundant forb at our site *Lasthenia californica* offers a generalist floral resource for pollinators. *L. californica* is an, annual, spring-blooming forb that grows in serpentine grasslands (O'Dell & Rajakaruna 2011). *L. californica* is self-incompatible at the stigma and relies on insect pollination (Ornduff 1966; Hendrickson et al. 2018). Its small, composite flower shape provides accessible floral rewards to a diversity of pollinator types, particularly short-tongued bees and flies (Thorp & Leong 1998).

We investigated how *Aegilops triuncialis* removal affects the diversity, abundance, and structure of plant-pollinator interactions in a California serpentine meadow. We hypothesized that removing *A. triuncialis* would (1) increase wildflower abundance and (2) consequently increase pollinator abundance and diversity. We further hypothesized (3) that *A. triuncialis* removal would increase the nestedness and increase niche overlap of plant-pollinator networks, and that (4) *Lasthenia californica*, the most abundant native forb species, would act as a hub for pollinators, more strongly influencing the structure of the restored network than the control network.

Methods

Study System

The study took place at the University of California, Donald & Sylvia McLaughlin Reserve in California's inner North Coast Range. The study site consisted of serpentine grasslands, located in Morgan Valley (Lake County, CA 38.861°N, 122.408°W). Prior to the experimental treatments, the site was heavily invaded *Aegilops triuncialis* but had few additional non-native species (Aigner & Woerly 2011).

Study Design: The study was carried out within the context of a larger *Aegilops triuncialis* removal experiment (see Aigner & Woerly 2011). Focal 2m x 2m plots were arranged within 10 experimental blocks based on *A. triuncialis* density and randomly positioned within each block (Fig. 1). The experiment included five treatments: control, hand-pulling of *A. triuncialis*, mowing, fluazifop applied mid-season, and clethodim applied mid-season. Experimental treatments were carried out during the spring of 2008–2010. In 2011, after three years of treatment, *A. triuncialis* density was very low with a mean of 4.50% cover following restoration (Aigner & Woerly 2011) in the 40 pollinator plots with a consistent reduction in *A. triuncialis* for each of the *A. triuncialis* removal methods. For pollinator data, we pooled all *A. triuncialis* removal treatments together and compared them to the control.

Aigner and Woerly (2011) previously found that hand-pulling, grass-specific herbicides, and mowing restoration treatments relative to control treatments effectively decreased *Aegilops triuncialis* abundance as well as decreased the abundance of other species of non-native annual grasses that were present in small amounts. *A. triuncialis* removal treatments increased the frequency of native grasses and forbs (Aigner & Woerly 2011).

All plant cover data were obtained in 2011 and 2012 based on visual estimates using a 1 m x 1 m frame placed in the center of each plot. We estimated cover using square pieces of cardboard representing 0.1%, 1%, 5%, 10%, and 25% cover as references (see Aigner & Woerly 2011). Cover was estimated by two trained observers per plot in 2011 and one trained observer per plot in 2012. Within each treatment, we divided plots evenly between observers.

Floral Visitor Observations: For the pollinator observations, we used 50 plots with ten plots for the control treatment and 40 plots for the restoration treatments. Trained observers visited each plot and recorded plant-floral visitor interactions and floral visitor abundance for a gi ven time period. All observations were done during morning and afternoon on sunny days when pollinators were active. Each plot was visited for one-minute observation periods in 2011 and for two-minute observation periods in 2012 & 2013. We recorded all flower visits by flying insects during the observation period, recording the taxon of the floral visitor and the flower. Pollinators were collected as voucher specimens and later identified outside the observation period by Prof. Robbin Thorp. We identified pollinators to the level of morphospecies. We further classified floral visitors into the following functional groups based on existing literature: butterflies/moths, syrphids, bombyliids, non-bee mimic flies, short-tongued bees, medium to long-tongued bees, and kleptoparasitic bees. We conducted 17 observation sessions over a three-year period. In 2011,

observation dates were April 16, 22, 27, and June 30. In 2012, observation dates were April 21, 22, May 2, and September 7, 8, and 11. In 2013, observation dates were April 12, May 22, 24, 31, and August 14, 15, and 28. This made for a total of 25 observer hours. A floral visit was recorded if an insect made contact with the reproductive parts of a flower. If a plot had no flowering plants present, pollinator visitation data were not collected.

Statistical Analysis

For all linear and generalized linear models, we scaled the variable year using the scale() function in R that centers a numeric matrix for each of the years, and we calculated plant and pollinator community variables at the plot level for each year. To determine whether *Aegilops triuncialis* removal would affect wildflower cover, we used linear models to examine if *A. triuncialis* cover, total cover for all annual grass species present, *Lasthenia californica* cover, and total cover for all native forb species visited by pollinators varied by treatment, year, and their interaction (e.g. Cover ~ Treatment*Year). For the wildflower cover analysis, we used all native forb species whose flowers were visited by pollinators (Table 1). We found no significant differences in pollinator community response between *A. triuncialis* removal treatments, so we pooled all *A. triuncialis* removal treatments together in our analyses.

Table 1
Native forb species observed being visited by pollinators. Taxonomic names follow Baldwin et al. (2012). Abbreviation used network diagram noted in second column. *Navarretia pubescens* does not appear in network diagram, as plant was visited by an unidentified bee, whose morphospecies could not be determined.

Species Name	Abbreviation	Family	Naming Authority
Acmispon wrangelianus	LOWR	Fabaceae	(Fisch. & C.A. Mey.) D.D. Sokoloff
Agoseris heterophylla	AGHE	Asteraceae	(Nutt.) Greene
Calycadenia pauciflora	CAPA	Asteraceae	A. Gray
Delphinium variegatum	DEVA	Ranunculaceae	Torr. & A. Gray
Dichelostemma capitatum	DICA	Themidaceae	(Benth.) Alph. Wood
Eriogonum nudum	ERGU	Polygonaceae	Benth.
Gilia tricolor	GITR	Polemoniaceae	Benth.
Grindelia camporum	GRCA	Asteraceae	Greene
Hemizonia congesta	HECO	Asteraceae	D.C.
Holocarpha virgate	HOVI	Asteraceae	A. Gray
Lasthenia californica	LACA	Asteraceae	Lindl.
Leptosiphon bicolor	LIBI	Polemoniaceae	Nutt.
Lomatium hooveri	LOHO	Apiaceae	(Mathias & Constance) Constance & Ertter
Microseris douglasii	MIDO	Asteraceae	(D.C.) Sch. Bip.
Navarretia jepsonii	NAJE	Polemoniaceae	Jeps.
Navarretia pubescens	NAPU	Polemoniaceae	Benth. (Hook & Arn.)
Ranunculus californicus	RACA	Ranunculaceae	Benth.
Trifolium albopurpureum	TRAL	Fabaceae	Torr. & A. Gray
Trifolium fucatum	TRFU	Fabaceae	Lindl.
Viola douglasii	VIDO	Violaceae	Steud.

To test whether *Aegilops triuncialis* removal would affect pollinator diversity and abundance, we used a linear model to further examine if Shannon diversity for pollinators varied by treatment, year, and their interaction. After testing for overdispersion, we used a generalized linear model with a Poisson distribution to test whether pollinator morphospecies richness varied by treatment, year, and their interaction. To examine whether removing *A. triuncialis* improved habitat for ground-nesting bees, we

used a generalized linear model with a negative binomial distribution to test whether ground-nesting bee abundance varied by treatment, year, and their interaction. We further tested whether the proportion of ground nested bees (ground nested bee abundance/total abundance) varied by treatment, year and their interaction using a generalized linear model with a gaussian distribution. We classified bees as ground-nesters based on information obtained from existing literature (LeBuhn 2013). We used a generalized linear model with a negative binomial distribution to test whether total pollinator abundance across all morphospecies varied by treatment and year, and their interaction.

To test whether changes in floral cover had an additional effect on pollinator diversity within restored plots, we used generalized linear models with Poisson distributions to test whether pollinator morphospecies diversity varied by preferred forb diversity, total preferred forb cover and *Lasthenia californica* cover respectively. Within restored plots, we further used generalized linear models with negative binomial distributions to test whether pollinator abundance varied by preferred forb diversity, total preferred forb cover and *L. californica* cover. All models were run using the 'lme4' package in R (Bates et al. 2015).

We used the adonis2 function in the 'vegan' package in R to compare pollinator community composition between the restored and control treatments using a permanova with a Bray-Curtis dissimilarity index with 999 permutations (Dixon 2003). To test for differences in community dispersion, we used the betadisper(_) function followed by permutest to run beta dispersion tests.

To test whether *Aegilops triuncialis* removal would affect plant-pollinator network structure, we calculated the observed NODF (nestedness) of the networks using the bipartite package (Dormann et al. 2009). To address the sensitivity of NODF to network size, we calculated a measure of NODF normalized to network size (NODFc) using the maxnodf package (Hoeppke & Simmons 2021). However, the small size of the control network warrants caution in interpreting these values for normalized nestedness as the number of links in the control network was below the minimum threshold.

To account for size and sampling effects, we further used Bayesian inference on a model that accounts for the relative abundance of species in the network, the effect of observation error, and the probability a true interaction exists (Young, Valdovinos & Newman 2021). This model included all interactions across the restored and control treatments since experimental plots were located in the same meadow and were therefore populated by species of the same community. We sampled the model 10000 times. For each sample we calculated two NODFc values for the interaction matrix among species observed in the control plots and the restored plots, respectively. Together, this procedure accounts for both size and sampling effects to more accurately compare nestedness between the control and restored treatments.

We then compared observed network niche properties to the 'swap web' null model to test for whether plant-pollinator network structure differed between restoration treatments using the 'bipartite' package in R (Dormann et al. 2009). The 'swap web' null model generates marginal totals identical to those observed and the same connectance as observed. We compared mean number of shared partners for both plants and pollinators, and niche overlap, as calculated by the Morisita-Horn Index, for both pollinators between

observed and null models using z-scores. The Morisita-Horn Index calculates dissimilarity in plant species visited for pollinators and dissimilarity in pollinator visitors for plant species (Horn 1966). To account for temporal turnover in plant-pollinator interactions, we then repeated these analyses for data subsetted to include only the spring plant community (plant-pollinator interactions recorded in April and May) (see Supplementary Methods for further detail).

To test our fourth hypothesis that the most abundant forb species would strongly influence network structure, we further assessed individual contribution of each plant species to nestedness using the nestednesscontribution() function in the R bipartite package (Dormann et al., 2009). This function estimates the degree to which the interactions of each plant species increase or decrease community nestedness by comparing to a random null model that is designed to control for the effect of differences in degree. Networks included plant-pollinator interaction data from both spring and summer across three years. To account for differences in network size, we compared networks to null models via z-scores. To account for potential interaction turnover, we then repeated these analyses for only the spring plant-pollinator interactions of species temporally co-occurring with the abundant, generalist forb *Lasthenia californica*. For each network type across all seasons, we then tested whether mean plant species cover, as collected independently of the network data, explained plant species' individual contribution to nestedness using a generalized linear model with a gaussian distribution.

Results

We observed a total of 522 individual pollinators across all three years. We documented a total of 21 plant species and 50 pollinator morphospecies across all treatments and years, comprising 134 unique pairwise interactions. Common pollinators included halictid bees, andrenid bees, and syrphid flies with moths and butterflies less frequently observed.

We found evidence to support Hypothesis 1: the *Aegilops triuncialis* removal treatments were effective and increased native wildflower abundance compared to the control. Removal treatments had significantly lower *A. triuncialis* cover than the controls (t=-8.503, p = 2.43 $x10^{-13}$; Fig. 2A; restored 4.5% +/- 5.43, control 28.11% +/- 22.82). Likewise, the removal treatments had significantly lower total annual grass cover than the controls (t= -7.210, p = 1.28 $x10^{-10}$; Fig. 2B). *A. triuncialis* cover and total annual grass cover did not significantly differ by year or by an interaction of year and treatment. Removal treatments had significantly higher *L. californica* cover than controls (t = 3.034, P = 0.003; Fig. 2C; restored 2.32% +/- 2.74, control 0.44%+/- 0.98). *L. californica* cover did not differ by year, and there was no treatment-by-year interaction. Removal treatments had significantly higher cover of pollinator-preferred forbs than the controls (t = 5.050, p = 2.10 $x10^{-6}$; Fig. 2D; restored 27.59% +/- 12.90, control 11.78% +/- 12.34) (Fig. 2C). Total cover of preferred forbs did not differ by year and there was no treatment-by-year interaction.

We also found evidence to support Hypothesis 2: pollinator communities in the *Aegilops triuncalis* removal treatments had increased diversity, increased abundance, and higher Shannon diversity than the

controls. The removal treatments had significantly higher pollinator morphospecies richness than the controls ($z = 3.881$, $p = 1.04 \times 10^{-4}$; Fig. 3A). The removal treatments had significantly higher total pollinator abundance than the controls ($z = 5.009$, $p = 5.47 \times 10^{-7}$; Fig. 3B). Likewise, the removal treatments had significantly higher pollinator morphospecies Shannon diversity than the controls ($t = 4.434$, $p = 1.96 \times 10^{-5}$; Fig. 3C). Pollinator morphospecies richness, Shannon diversity index, and total abundance did not significantly differ by year or an interaction of year and treatment. Short-tongued bees, medium to long tongued bees, syrphid flies, and other non-bee mimic flies visited flowers in both treatment types. Butterflies/moths and bombyliid flies only visited flowers in restored plots, although these functional groups were low in abundance. Bombyliids made fewer than 2% of all visits to flowers in restored plots, and butterflies/moths made fewer than 3% of all visits to flowers in restored plots. The removal treatments had a significantly higher abundance of ground-nesting bee morphospecies than the control treatments ($z = 3.882$, 1.04×10^{-4}; Fig. 3D). The removal treatments had a non-significantly higher proportion of ground-nesting bees relative to all pollinators observed ($t = 1.737$, $p = 0.085$).

Within the restored plots, pollinator morphospecies richness significantly increased with *Lasthenia californica* cover ($z = 2.201$, $p = 0.0277$) but not with total pollinator preferred forb diversity and cover ($z = 0.160$, $p = 0.872528$ diversity; $z = 1.040$, $p = 0.299$ cover). Within restored plots, pollinator morphospecies abundance significantly decreased with increased cover of total preferred forbs ($z=-2.737$, $p = 0.00619$), but not with *L. californica* cover and preferred forb diversity ($z = 0.309$, $p = 0.758$ diversity; $z=-0.332$, $p = 0.74$ for *L. californica* cover).

Control and restored pollinator communities differed in community composition. However, differences were in 2011 and 2012, and not in 2013. For all years combined, pollinator composition significantly differed by treatment (Permanova $F = 4.274$, $p = 0.001$) with significant differences in community dispersion ($F = 23.422$, $p = 0.001$). For the years 2011 and 2012, pollinator community composition significantly differed between treatments ($F = 2.94$, $p = 0.007$ 2011; $F = 2.8028$, $p = 0.004$ 2012) with significant dispersion for 2011 only ($F = 5.752$, $p = 0.014$ 2011; $F = 1.083$, $p = 0.283$ 2012). For 2013, pollinator community composition did not significantly differ by treatment ($F = 0.9802$, $p = 0.44$) nor did dispersion ($F = 1.025$, $p = 0.322$). Since plots were located within the same meadow, these changes likely reflect differences in pollinator preference among species rather than differences in relative abundance of component populations within the community.

Contrary to hypothesis 3, the restored network was less nested in structure than the control network (Fig. 4). The restored network was significantly less nested than the control network when accounting for network size and sampling effects (Bayesian inference, mean posterior NODFc 0.00205 control, 0.000338 restored network, Fig. 5). The restored network had less variance in NODFc than the control network (Fig. 5). Without accounting for differences in network size, the restored network appeared more nested than the control due to its higher plant and pollinator diversity. Without accounting for sampling effects through Bayesian inference, the raw nestedness (NODF) of the restored network was 35.42, while the NODF of the control network was 10.99. On the other hand, size-normalized nestedness (NODFc) of the restored and control network were 2.21 and 2.57 respectively without Bayesian inference. This result

shows how sensitive NODF is to network size. When further accounting for sampling effects using Bayesian inference, the size-normalized nestedness (NODFc) decreased for both networks for the following reasons. Nestedness requires a high proportion of specialist species that interact with generalists within the network (Bascompte & Jordano 2007). Sampling effects, however, often overestimate how specialized rare species are (Young, Valdovinos & Newman 2021). Consequently, observed networks can assume rare generalist species are specialists. The restored network contained more rare pollinator species and was more sensitive to these sampling effects than the control network.

We found evidence to partially support hypothesis 3: pollinator niche overlap increased with restoration. For pollinator niche overlap, the restored network had significantly higher Morisita-Horn Index of niche overlap than expected by the null model ($z = 6.371$, 1.88×10^{-10}), while the control network did not significantly differ from null expectations ($z=-1.121$, $p = 0.262$). Likewise, pollinators in the restored network shared a higher number of plant partners than pollinators in the control network. The restored network had a significantly higher mean number of shared partners for pollinators than the null model ($z = 4.497$, $p = 6.88 \times 10^{-6}$), while the control did not significantly differ ($z=-1.117$, $p = 0.264$). Plant niche overlap did not significantly differ between the restored and control networks (restored $z= -1.507$, $p = 0.132$; control $z=-0.295$, $p = 0.768$). The restored network had a significantly higher number of shared partners for plants than the null model ($z = 3.261$, $p = 0.0011$), while the control did not significantly differ ($z=-0.085$, $p = 0.932$). When using only the spring plant-pollinator community to account for temporal turnover in interactions, we similarly found that the restored network had higher pollinator nice overlap but not plant niche overlap than the control network (see Supplemental Results).

In support of hypothesis 4, the most abundant forb species, *Lasthenia californica*, had the highest individual contribution to nestedness. For both the restored and control network, *L. californica* contributed the most to nestedness among plant species. For the restored network, *L. californica* had an individual contribution to nestedness significantly higher than null expectations ($z = 5.443$, $p = 5.23 \times 10^{-8}$), while the control network had a non-significantly higher nestedness contributions than null expectations ($z = 1.404$, $p > 0.05$). When using only the spring plant community of species temporally co-occurring with *L. californica*, we likewise found that *L. californica* contributed the most to nestedness for both the control and restored network, and this contribution was significantly higher than null expectations for the restored network ($z = 5.93$, $p = 3.03 \times 10^{-9}$) but not the control network ($z = 0.886$, $p = 0.376$). For the full growing season, mean plant species cover (mean percent cover measured independently of the network) was non-significantly positively correlated with increased individual contribution to nestedness for the restored treatment ($t = 2.099$, $p = 0.125$) and control ($t = 0.304$, $p = 0.769$).

Discussion

Restoration treatments decreased invasive grass cover and increased native forb cover compared to the invaded controls. Across all years, restored plots had higher pollinator morphospecies richness, higher Shannon diversity, and greater pollinator abundance. The restored network had lower nestedness than the control network. Restored plant-pollinator interaction networks showed higher pollinator niche overlap

than the control network, with *Lasthenia californica* individually contributing more to nestedness in the restored network. Compared to invaded controls, the restored treatments had higher mean numbers of shared plant partners among pollinators.

The observed decrease in *Aegilops triuncialis* cover in restored plots relative to the invaded control suggests that restoration treatments created a plant community that was more suitable to pollinators. Invasive *A. triuncialis* can outcompete native forbs (Aigner & Woerly, 2011), so removing *A. triuncialis* can open up niche space for native forbs to become a more dominant component of the plant community. Restored plots with decreased *A. triuncialis* cover had increased native wildflower cover, particularly for the generalist forb species *L. californica*. No pollinators in the network acted as generalist hubs for plants for either the restored or control plots. Plants may thus receive a higher quality and quantity of pollinator visits in restored areas, which can potentially increase plant fecundity and fitness (Valdovinos et al. 2016; Kaiser-Bunbury et al. 2017; Valdovinos & Marsland 2021).

Restored plots had increased pollinator diversity and abundance relative to the invaded controls, likely in response to increased floral rewards from an increased diversity and abundance of native wildflowers. Pollinators prefer to forage in areas with a higher quality and quantity of floral rewards (Fuccillo Battle et al. 2021; Sih & Baltus 1987). This result is consistent with past studies that found increased native plant abundance, increased pollinator species richness, and increased pollinator abundance in response to invasive plant removal in restored plant communities compared to control sites (Kaiser-Bunbury et al. 2009).

The restored network had significantly lower nestedness (NODFc) than the invaded control network when accounting for network size and sampling effects. When not accounting for network size and sampling effects, the restored network appeared to be more nested due to increased pollinator diversity and an increased number of rare pollinator species overestimated as specialists. This finding contrasts with previous work that suggests more diverse plant-pollinator networks are more nested (Bascompte & Jordano 2007). This result may challenge classic assumptions that higher nestedness arises from more biodiverse mutualistic networks and warrants further research exploring the relationship between biodiversity and nestedness.

Restored networks had higher pollinator niche overlap relative to the control, suggesting that restored plots may have a pollinator community with more functional redundancy. Increased functional redundancy of pollinators is often associated with increased stability (Memmott et al. 2004; Williams 2011), suggesting that the restoration networks may have greater functional group stability than the control network. Likewise, the removal of invasive plants in an island plant community increased the generalization of plant-pollinator networks relative to the control, suggesting that restored networks had higher functional redundancy (Kaiser-Bunbury et al. 2017). This increase in pollinator niche overlap was driven by an increased diversity of pollinators in the restored network visiting the same plant species, particularly the abundant generalist forb *Lasthenia caliofrnica*.

Lasthenia californica had the most pollinator visits and contributed the most among the plant species to network nestedness, suggesting that *L. californica* acts as a generalist hub for a diversity of pollinator species. Moreover, *L. californica* had a stronger contribution to nestedness in the restored than the control plots, perhaps due to its increased abundance in restored plots relative to controls. *L. californica* also had a much higher percent cover, independent of the network, than other native forbs. In total, 30 pollinator morphospecies visited *L. californica* across both treatment types and all years. However only eight of these 30 visited *L. californica* in the control network, whereas all 30 morphospecies visited it in restored plots. Within restored plots, pollinator diversity significantly increased with increasing *L. californica* cover. Furthermore *L. californica* hosted all functional groups observed in the study: butterflies/moths, syrphids, bombyliids, non-bee mimic flies, short-tongued bees, medium to long-tongued bees, and kleptoparasitic bees. As such, it appears to play a core role in increasing pollinator diversity in restored plots relative to controls. Similar important influence of dominant flowering species on the structure and stability of plant-pollinator communities has been shown in other studies (Kaiser-Bunbury et al., 2009). Indeed, invasive flowering plants themselves may have a similar effect (Russo et al. 2019; Bartomeus et al. 2008).

More abundant plant species had non-significantly higher individual contributions to nestedness for the restored network and the control. The lack of a significant trend for the control was likely driven by *Aegilops triuncialis*. *A. triuncialis* had high percent cover but a very low contribution to nestedness. As a wind-pollinated grass, *A. triuncialis* offered an inferior reward to pollinators relative to native forbs and received very few visits in the control network. Indeed, it is unclear whether the pollinator species that visited *A. triuncialis* received any floral reward from landing on it.

Time since restoration treatment may dampen compositional differences between control and restored plots, but otherwise did not significantly affect pollinator diversity and abundance between years. Given that annual serpentine grasslands experience high year to year variability in rainfall (Harrison et al. 2020), and that climatic differences can contribute to variation in serpentine plant community composition (Harrison et al. 2000), future research could examine serpentine plant-pollinator interactions over longer time scales. Future research could aim to sample plant-pollinator interactions across a broader range of time to better understand how phenological turnover in flowering species and their visitors may influence the restoration of plant-pollinator mutualisms (Arroyo-Correa et al. 2020). Additional research should aim to measure plant and pollinator fecundity to elucidate whether restoration efforts increase plant and pollinator fitness.

We found that the restored plots had significantly lower total cover for all annual grass species than the control, a trend primarily driven by the removal of invasive *Aegilops triuncialis* from the system. Removing *A. triuncialis*, which often occurs in tall, dense patches, may open up more patches of bare ground for pollinators to nest. Ground-nesting bee species visited flowers in the study, including several andrenid morphospecies, several halictid morphospecies, two *Anthophora* species, and *Eucera actuosa*. The restored plots had significantly higher total abundances of ground-nesting bees than the controls, but the proportion of ground-nesting bees relative to the whole community non-significantly increased with restoration. The restored plots had a non-significantly higher abundance of ground-nesting bees caught

in emergence traps compared to the control (Paul Aigner, *unpublished data*). Within restored plots, pollinator abundance significantly decreased with increasing preferred forb cover, suggesting that the increase in pollinator abundance in restored plots may be due to increased bare ground rather than increased floral abundance. Future research should seek to elucidate how removing invasive species may affect pollinator nesting habits through changes in ground cover and soil conditions and whether tradeoffs exist between increased ground cover of forbs and increased bare ground.

This study offers several insights into the restoration of plant-pollinator mutualisms. By removing invasive *Aegilops triuncialis*, restoration treatments resulted in increased pollinator abundance and diversity relative to the control. Furthermore, we demonstrate that a network approach can elucidate how invasive grass removal affects plant-pollinator mutualisms. The network analysis suggested that *Lasthenia californica* acts as a generalist hub for a diversity of pollinator species. Restoration efforts should prioritize well-connected, abundant native species like *L. californica* to maximize the restoration of plant-pollinator interaction structure. Ongoing removal of *A. triuncialis* in serpentine meadows can effectively restore pollinator diversity and function. From a management perspective, all *A. triuncialis* removal methods had similar outcomes in increased pollinator diversity and abundance, suggesting that managers have flexibility in which approaches they can use for restoration.

Declarations

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Fernanda Valdovinos, Paul Aigner; Writing - original draft; Rebecca Nelson; Writing - review & editing. Rebecca Nelson, Sabine Dritz, Fernanda Valdovinos, Paul Aigner.

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Figures

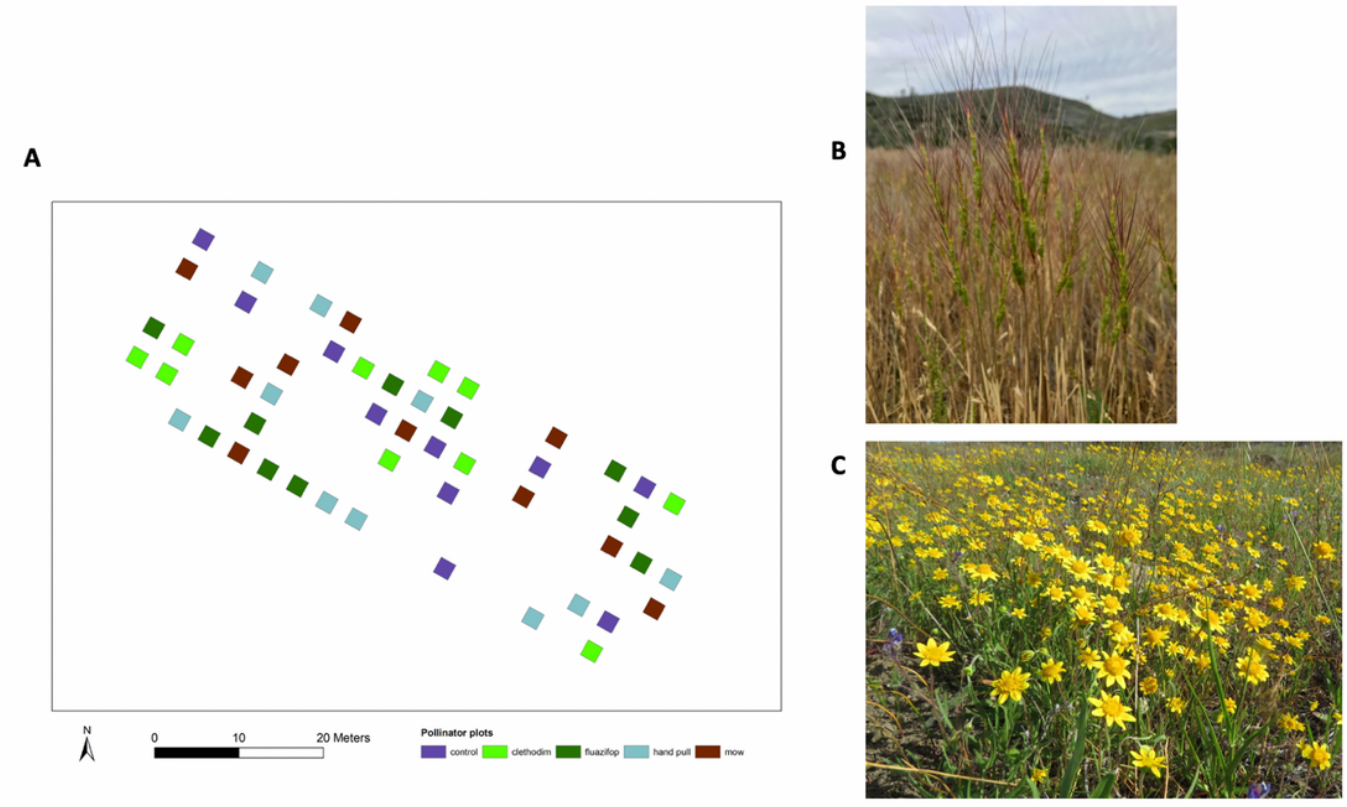

Figure 1

Study design. (A) Map of study site and experimental design. Each square represents a study plot from Aigner and Woerly 2011. Highlighted plots were surveyed for pollinators. (B) A serpentine plant community invaded by *Aegilops triuncialis* (barbed goatgrass). Image credit: Paul Aigner. (C) A typical

native serpentine meadow plant community. The main forb shown in the picture is *Lasthenia californica* (goldfields). Image credit: Rebecca Nelson

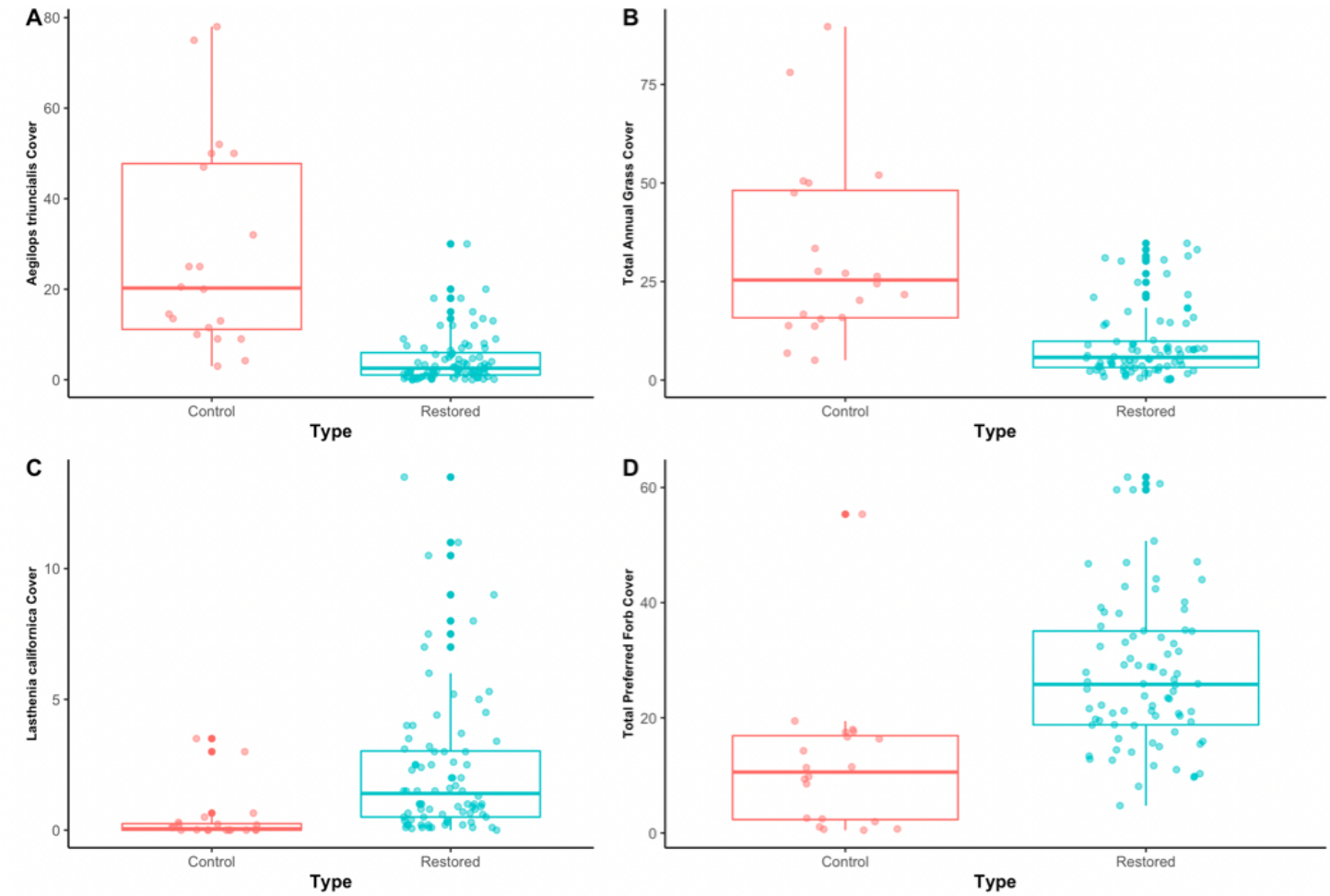

Figure 2

Plant Community metrics by treatment type for (a) *Aegilops triuncalis*cover (b) total annual grass cover (c) *Lasthenia californica* cover and (d) total native forb cover for species visited by pollinators. Control refers to the control treatment and restored refers to all *A. triuncialis* removal treatments combined. Asterisks denote significant differences between the restored and control treatments for an alpha level of 0.05.

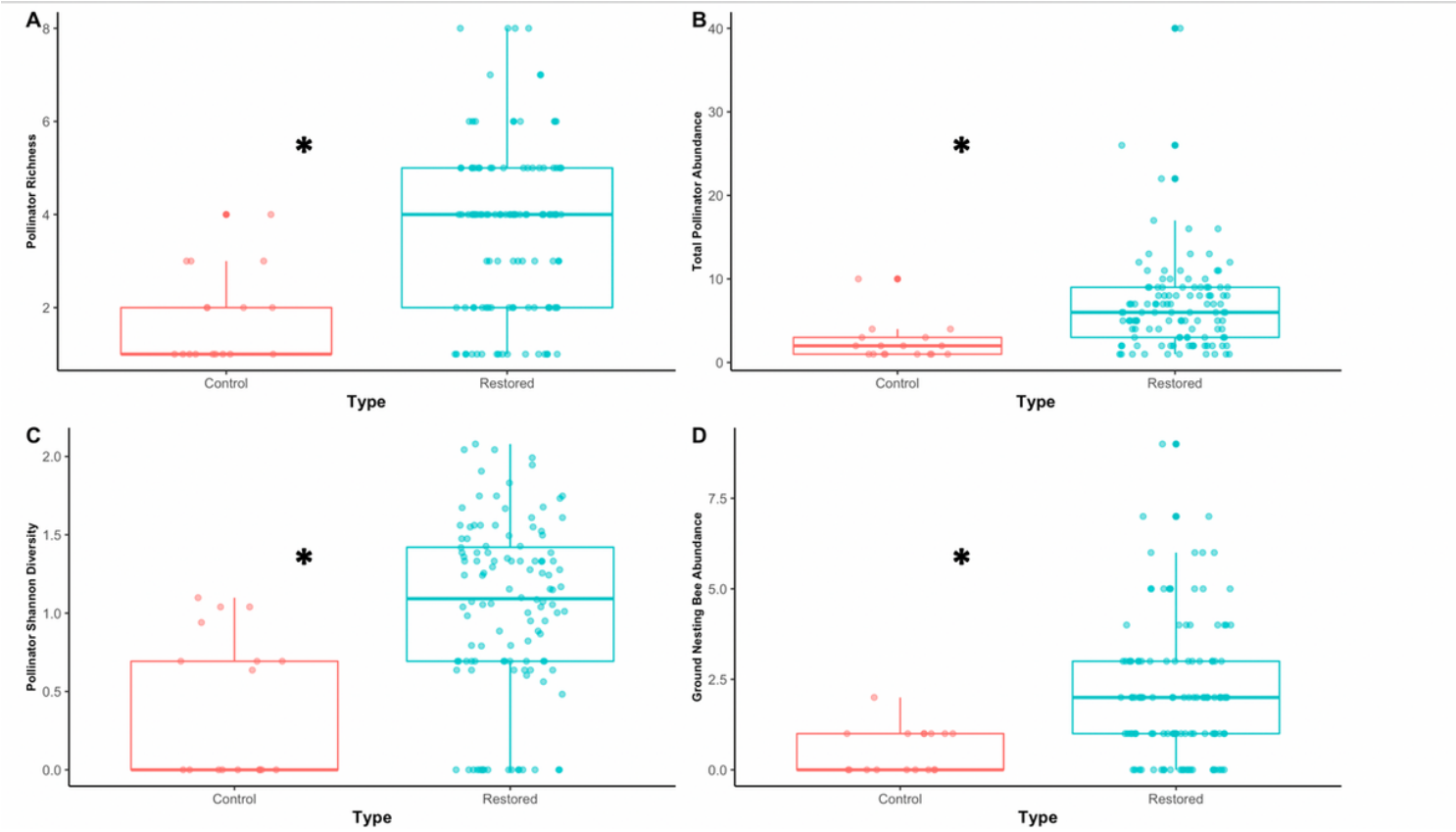

Figure 3

Pollinator Community Metrics by Treatment Type for (a) pollinator morphospecies richness, (b) total pollinator abundance, (c) pollinator Shannon diversity, and (d) total abundance of ground-nesting bee species. Control refers to the control treatment and restored refers to the *A. triuncialis* removal treatments. Asterisks denote significance for an alpha level of 0.05

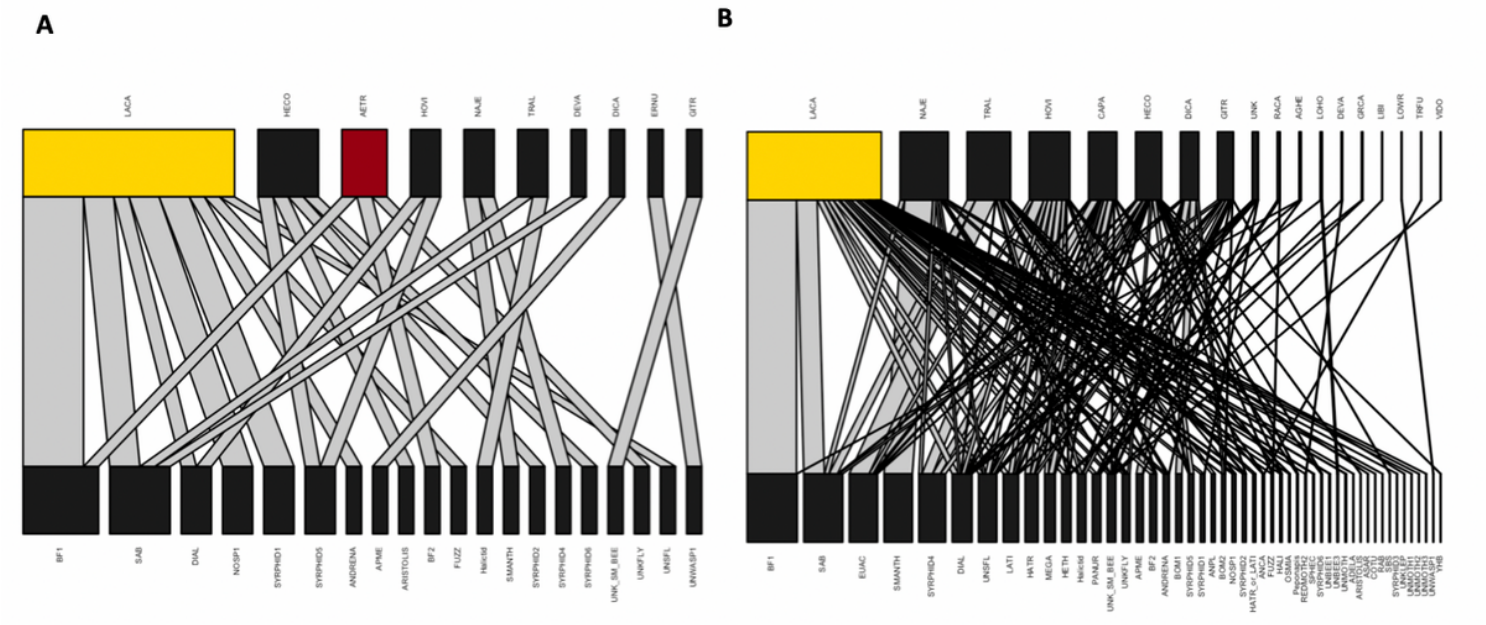

Figure 4

Plant-Pollinator Networks by *Aegilops triuncialis* Removal Treatment. Bipartite plant-pollinator networks across all three years of data collection for (A) the control treatment (B) the restored treatments. Each rectangle in the top row represents a plant species, abbreviated by a four-letter species code. *Lasthenia californica* (labeled LACA) is shaded in yellow. *Aegileops triuncialis* (labeled AETR) is shaded in dark red. Each rectangle in the bottom represents a pollinator morphospecies with its abbreviated species code. Gray lines between rectangles represent interactions between plants and pollinators. The thickness of lines as well as the size of each rectangle is proportional to the frequency of a given interaction, plant, or pollinator respectively in the network data. See Table 1 for full list of native forb abbreviations. UNK refers to an unidentified forb. See Supplementary Table 1 for a full list of pollinator morphospecies and their abbreviations

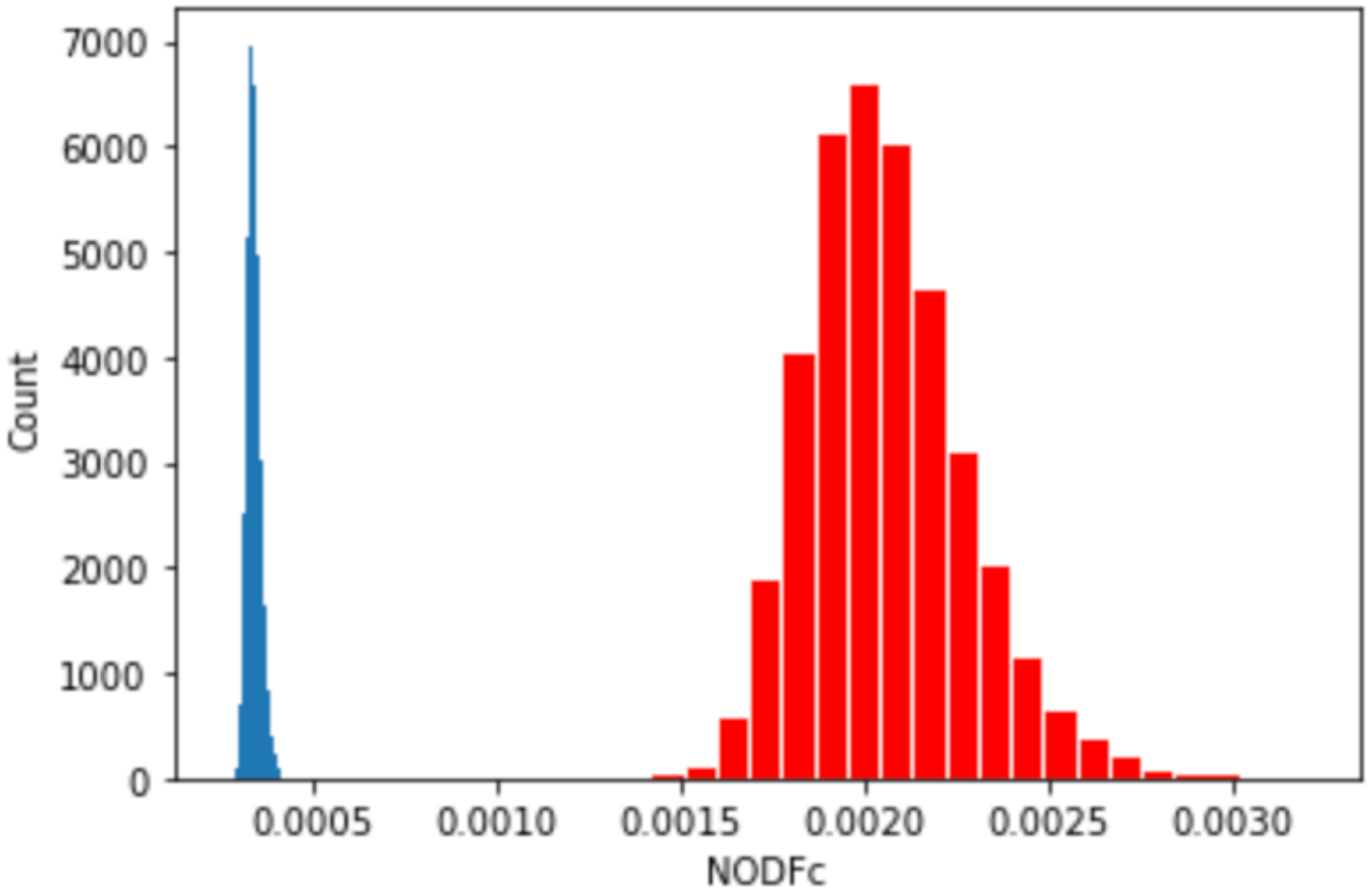

Figure 5

NODFc (relative nestedness) posterior probability distribution from Bayesian inference for restored and control networks. The restored network is depicted in blue, and the control network is depicted in red. The maximum posterior NODFc is .00334 for the control and 0.000479 for the restored network. The mean posterior NODFc is 0.00205 for the control network and 0.000338 for the restored network

Supplementary Files

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