

Plant–flower visitor networks in a serpentine metacommunity: assessing traits associated with keystone plant species

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Abstract Consistent topology of plant–pollinator networks across space may be due to substitutability of the plant species most important for community function (keystone species). It is unclear, however, whether keystone species identity varies within a community type and what traits underlie this variation. Using a network biology approach, we assess whether keystone plant species vary across a metacommunity of five serpentine seeps in California and determine the features that predict their identity. We define keystone species as those with high strength, low node specialization index (NSI), and/or low d' and determine whether these parameters are predicted by floral traits (flower biomass, number of open flowers per plant,

symmetry, or stamen number) and/or ecological features (variation in local floral abundance, endemism) within seeps and across the metacommunity. Keystone species identity varied among seeps and was associated with local flower abundance: mean floral abundance correlated positively with strength but negatively with NSI within most seeps as well as across the metacommunity. For the metacommunity, flower biomass correlated negatively with NSI while variation in flower abundance correlated negatively with strength. Across the metacommunity, the d' metric was associated with flower biomass, whereby plants with smaller flowers interacted with the most abundant pollinators across the metacommunity. Results suggest that connectance and interaction evenness may not be greatly influenced by community composition turnover due to substitution of keystone plant species across space. Keystone species can be predicted by functional traits but which trait (flower abundance or size) depended on the metric used and the level observed.

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Introduction

Understanding factors that contribute to stability or variation among plant–pollinator networks is crucial for predicting and preventing consequences of habitat loss, global change and species extinction (Memmott et al. 2007; Hegland et al. 2009; Burkle and Alarcón 2011). The drivers of variation in pollination networks are just beginning to be understood (e.g., Dicks et al. 2002; Dupont et al. 2009; Burkle and Irwin 2009; Kaiser-Bunbury et al. 2014). For

example, large-scale variation among habitats (Forup et al. 2008; Lopezaraiza-Mikel et al. 2007) or along ecological gradients (Olesen and Jordano 2002; Devoto et al. 2005; Geslin et al. 2013; Nielsen and Totland 2014) can be pronounced, but less is known about the extent or consequences of spatial variation within a community type, i.e., at the level of the metacommunity (sensu, Leibold et al. 2004) because observations are usually conducted at a single site, or are pooled across similar sites to create networks (Burkle and Alarcón 2011). Little variation in the overall structure of plant–pollinator networks at a fine spatial scale has been documented (Burkle and Irwin 2009) and may result from the substitutability of taxa that contribute strongly to network interaction diversity (i.e., ecological redundancy; Dupont et al. 2009; Nielsen and Totland 2014). A metacommunity, where species composition in a given community is determined by local extinction and colonization dynamics, offers an ideal system in which to address ecological redundancy in plant–pollinator networks.

In pollination networks, some species contribute more to the maintenance of diversity than others by having more interaction partners (network asymmetry; Jordano et al. 2003; Bascompte and Jordano 2007) and/or by maintaining a highly interconnected network of interactions within which more specialized species are linked (nestedness; Bascompte et al. 2003; Vázquez and Aizen 2004). Identifying these species may be a first step toward understanding why network functionality remains constant across communities despite species turnover. Species-specific network parameters that describe a species' ecological role in the network can help identify the taxa that contribute strongly to network stability. For example, plants with high 'strength' are those upon which one or many flower visitors depend (sum of pollinator dependencies on plants; Bascompte et al. 2006). Strength is a quantitative measure that takes into account both a species' number of interaction partners and the frequency of interactions. A low 'node specialization index' (NSI) for a plant species indicates that it may be important for network diversity as well—species with low NSI interact with many flower visitors that co-flowering plants also utilize (Dormann 2011). Finally, a high degree of generalization may be important for maintaining floral visitor diversity, or hosting more common pollinators that may visit other co-flowering taxa. The d' -index measures the degree of a plant's specialization on flower-visiting taxa, with a lower value representing an 'opportunistic', or, a plant that is visited by the most common flower visitor(s) in a community (Blüthgen et al. 2006; Dormann 2011). Thus, high strength, low NSI, or low d' indicate plants that are important to the maintenance of flower visitor, plant, and/or interaction diversity.

Keystone species are those that have exceptionally large effects on communities and ecosystems through processes such as trophic interactions, habitat modification, and mutualism (de Visser et al. 2013). The keystone species concept has been strongly related to food web theory and ecological networks (e.g., Vasas and Jordán 2006), as models have shown that the loss of species that engage in many ecological interactions can lead to secondary extinctions that threaten ecosystem stability (Solé and Montoya 2001; Christianou and Ebenman 2005). While keystone species can be defined as those that contribute to community function disproportionately relative to their abundance (e.g., a species with high strength but low proportional abundance; Power et al. 1996), distinguishing between important species with high abundance ('dominant' species sensu Power et al. 1996) and lower abundance may be arbitrary from a community importance standpoint (Power et al. 1996; Davic 2003; Cottee-Jones and Whittaker 2012). Despite contention surrounding the definition and application of the term 'keystone species' (Mills et al. 1993; Power et al. 1996; Cottee-Jones and Whittaker 2012), the term has been proposed for use in plant–pollinator networks (Memmott 1999; Jordano et al. 2003; Dupont and Oleson 2009) to define any species with an important role in network functioning. Therefore, we apply the keystone concept to taxa with high strength, low NSI, and/or low d' and determine specifically how these parameters vary with abundance.

Beyond identifying keystone species, pinpointing traits associated with them is a goal of both community ecology and conservation biology (McGill et al. 2006). Recently, authors have stressed the importance of this approach for understanding keystone plant species in pollination networks (Dupont et al. 2009). Spatial replication of networks in particular allows for an assessment of whether certain traits are consistently associated with keystone species. One well-studied trait, flower abundance, is known to influence aggregate pollination network metrics (reviewed by Vázquez et al. 2009) and can be predictive of the number of pollinator species that a plant hosts (Stang et al. 2006, 2007; Jędrzejewska-Szmek and Zych 2013; however see Lopezaraiza-Mikel et al. 2007). Abundance may also be used to identify species that contribute greatly toward network stability (i.e., highly linked species; Winfree et al. 2014). But, other plant functional traits (e.g., morphology, life history; McGill et al. 2006) may also be important determinants of keystone species. Floral traits that attract flower visitors and/or represent plentiful or easily accessed rewards (e.g., abundant and/or large floral displays, high pollen availability, radially symmetric corolla shape; Willmer 2011; Hegland and Totland 2005) can increase visitation intensity and/or the breadth of visiting functional groups (Fenster et al. 2004; Geslin et al. 2013). Thus,

incorporation of these features into plant–pollinator network studies can shed light on which traits are most important for mediating a plant’s importance to pollinators in a community (e.g., Stang et al. 2006; 2007; Junker et al. 2013; Kaiser-Bunbury et al. 2014). In addition to traits, ecological characteristics of range extent and resource reliability could be predictive of a plant’s role in the network in a metacommunity context. For example, plant taxa with large geographic ranges can have a large number of interaction partners (Bascompte and Jordano 2007). As an extension of this concept, species with restricted ranges (endemic) are expected to have fewer partners than a cosmopolitan species. Moreover, if pollinators prefer reliably abundant resources across space (e.g., Sih and Baltus 1987), then species with consistent floral abundances across a metacommunity may be more likely to be keystone. Thus, a more complete understanding of the features that characterize a keystone species can be achieved by the analysis of ecological and functional traits in the context of spatially replicated networks.

Flower visitors are often categorized into functional groups based on morphological, physiological and behavioral traits that make them ecologically similar. Flower visitors of a given functional group are expected to be more similar to each other as pollinators than members from other functional groups (Zamora 2000; Fenster et al. 2004; Ollerton et al. 2007; Rosas-Guerrero et al. 2014). Evidence that increased functional diversity of flower visitors can enhance plant fitness supports this prediction (Hoehn et al. 2008; Albrecht et al. 2012; Fründ et al. 2013). At the level of community-wide interactions, functional diversity of pollinators has also been observed to increase plant diversity (Fontaine et al. 2006). Thus, plant–flower visitor networks based on insect functional groups inform network structure from the perspective of function rather than species identity (e.g., Fang and Huang 2012; Fontaine et al. 2006) and thereby can reveal patterns in the functionality and sustainability of complex plant–pollinator communities when studied across gradients or replicates (e.g., Fontaine et al. 2006; Geslin et al. 2013). Spatial variation in flower visitor importance for individual plant species has been examined for a number of systems (Price et al. 2005; Moeller 2005; Gómez et al. 2008); however, less is known about flower visitor variation among networks (but see Dupont et al. 2009) though it may have implications for plant fitness and community composition.

We addressed whether substitutability of keystone plant species could underlie similarly structured plant–flower visitor communities of serpentine seeps in northern California. These unique plant communities are separated from one another by a matrix of grassland and chaparral (Freestone and Harrison 2006) and form a metacommunity (Harrison et al. 2000), making them ideal for spatial

replication of pollination networks. We first determined whether networks were similarly structured and then identified functional traits that predicted a plant species’ importance in the network. Specifically, we assessed the association of plant features with species-specific network parameters (strength, NSI, and d'), specific values of which we defined as hallmarks of keystone species. We addressed the following hypotheses: (1) within a community, keystone plant species are those that have abundant flowers or have permissive or widely preferred functional features (i.e., large, radially symmetric flowers, many open flowers per plant, and many stamens), and (2) at the metacommunity level, keystone plant species will be those with broader ranges and low variation in floral abundance across space.

Materials and methods

Study system

We observed plant–flower visitor interactions in serpentine seep communities at the McLaughlin Natural Reserve in northern California, USA (38°51'29.45"N 122°24'33.49"W). Serpentine seeps are ecologically similar in that they share unique soil chemistry, experience moisture late in the season (Freestone and Harrison 2006), and host a plant community characterized by high levels of endemism (Freestone and Inouye 2006; Safford et al. 2005). In addition, local colonization/extinction dynamics underlie the seep plant community composition making aggregates of seeps a metacommunity (Harrison et al. 2000). We identified five seeps that were separated by 0.3–5 km linear distance (Fig. 1; see also Alonso et al. 2013). Fifty co-flowering, animal-pollinated plant species occurred within the whole metacommunity. Thirty-four of these were observed to be visited by insects (Online Resource 1) and thus were included in our network analyses. Of the 34 species, 20 were visited by insects at more than one seep (Online Resource 1).

Plant–flower visitor interactions

To characterize plant–flower visitor interactions in an unbiased manner, we established 20–30 permanent 1 × 2 m plots every 5 m along linear transects at each seep. This spatially explicit sampling scheme reduces biases toward any particular plant or insect species in the community (Sørensen et al. 2012) and sufficiently captures overall plant species diversity at these sites (Alonso et al. in review). We conducted observations on sunny, non-rainy days between 0800 and 1600 h over the entire flowering season (June and July 2010). We conducted 5-min

Fig. 1 Spatial distribution of serpentine seep communities (TPW, TP8, RHA, RHB, BS) at McLaughlin Natural Reserve in Lake County California, USA. Gray areas represent bodies of water



Table 1 Total seep-specific sampling effort for plant–flower visitor interaction webs in serpentine seeps of northern California (A), first-order network metrics for each seep (B), and second-order network metrics for each seep (C)

Seep	(A) Sampling effort		(B) First-order metrics					(C) Second-order metrics			
	Interactions observed	Hours observed	Plant spp.	Plant spp. not visited	Pollinator functional groups	Observed links	Percent asymptotic richness	Connectance		Interaction evenness	
								Random	Observed	Random	Observed
RHA	1,492	87.5	34	14	14	82	84	0.51	0.29***	0.81	0.78***
RHB	925	52	28	10	10	49	88	0.48	0.27***	0.76	0.72***
BS	445	53	27	11	12	47	80	0.36	0.20***	0.82	0.80***
TPW	1,997	37.5	26	13	14	43	86	0.45	0.24***	0.50	0.43***
TP8	394	22.5	11	3	13	32	98	0.61	0.31***	0.78	0.60***

For descriptions of first and second-order metrics, robustness values, and determination of their significance, see “Materials and methods” section

spp. = species

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$

observations at each plot twice per week (once in the morning and once in the afternoon) for a total of 252.5 h of observation across all five seeps (Table 1). We recorded the total number of insect visits to flowers of each animal-pollinated plant species within each plot. We categorized insect visitors into 15 functional groups according to their body size, energetic requirements, foraging/feeding behavior, and pollen placement on body (Fenster et al. 2004; Moretti et al. 2009). These are as follows: large social bees, extra large social bees, small solitary bees, medium solitary bees, large solitary bees (carry pollen on legs), large solitary bees (carry pollen on body), bee flies,

small syrphid flies, large syrphid flies, other flies, butterflies, beetles, wasps, ants, and other (full descriptions in Online Resource 2). Similar functional groupings have been used in other plant–flower visitor networks (Fontaine et al. 2006; Fang and Huang 2012).

To evaluate the sampling completeness of plant–flower visitor interactions at each site, we estimated the percent asymptotic interaction richness detected by dividing the observed number of interactions at each site by the estimated number of interactions (Chacoff et al. 2012). We computed plant–flower visitor interaction accumulation curves and an estimator of asymptotic richness (Chao 1)

using the program EstimateS (Version 9, Colwell 2005). We chose Chao 1 as a richness estimator because it is appropriate for abundance-based rarefaction and is valid when the number of singletons (i.e., interactions only observed once) represents less than 50 % of the total observed interactions (Gotelli and Colwell 2008; Colwell 2005), both of which apply to our data set. Abundance-based rarefaction curves of interaction diversity were constructed using the cumulative number of plots observed per day at each site as the unit of sampling effort.

Plant traits

For each plant species in the metacommunity, we measured floral traits known to influence flower visitation: flower biomass, number of simultaneously open flowers, stamen number, and floral symmetry. We collected and dried ten flowers per species at 60 °C for 24 h and weighed them to the nearest 0.1 mg on a digital scale (Mettler AE2000, Mettler-Toledo, Columbus, OH, USA). We calculated the per-flower biomass and used it as a proxy for individual flower size. We enumerated the number of open flowers on ten haphazardly chosen plants per species and used the average in analyses. We determined the average stamen number per flower from ten haphazardly collected flowers for all species except *Streptanthus breweri* where we used the Brassicaceae characteristic of six stamens. Floral symmetry was scored as bilaterally symmetrical (zygomorphic) or radially symmetrical (actinomorphic) for each species. For each species, we quantified mean daily flower abundance within each seep as the number of open flowers in established plots (see “Plant–flower visitor interactions” section) divided by the number of days of observation. We calculated the coefficient of variation (CV) of flower abundance across seeps for species that occurred at two or more seeps. We also designated each species as range-restricted (endemic) or not (non-endemic). Endemics were based on Safford et al. (2005) definition of ‘strict endemic’, i.e., ≥ 95 % of occurrences on serpentine soil. This is a good indicator of range size since serpentine endemics are known to have small geographic ranges (Alexander 2007).

Network characterization

We constructed and parameterized plant–flower visitor networks at each seep using the bipartite package in R (Dormann et al. 2008; R Development Core Team 2012). To describe networks, we calculated three first-order network metrics (the number of plant species, number of insect functional groups and number of links [unique interactions]), and three second-order metrics commonly used to define topology of plant–pollinator networks (connectance and interaction evenness) (Bascompte and

Jordano 2007; Burgos et al. 2007; Almeida-Neto et al. 2008). Connectance is the fraction of realized links relative to total possible links, while interaction evenness estimates the degree to which pollinator functional groups are uniformly distributed across all plant species (Alatalo 1981). The significance of connectance and interaction evenness for each seep was tested against a null model obtained by constructing 1,000 random networks using the ‘r2dtable’ method in the bipartite package (Dormann et al. 2008; R Development Core Team 2012).

Identifying keystone species

To determine each plant species’ ecological function and identify keystone species, we generated strength, NSI, and d' for each species in each seep and then calculated the mean and standard deviation of strength, NSI and d' for each species across the metacommunity. If a species occurred in only one seep, we used the values from that seep. To control for variation related to seep-specific plant diversity and insect visitation, we relativized the mean strength and d' of each species across seeps (e.g., relative strength = $\text{strength}_{\text{species } x} / \text{sum of strength across species}$). For example, because strength is calculated as the sum of dependencies (Bascompte et al. 2006; Dormann 2011), an increase in the number of interaction partners at a particular site will inflate the value of strength for a particular species relative to sites with smaller networks. Therefore, by calculating the relative strength and d' of each species, we achieved standardized values that could be compared across seeps that differed in the number or abundance of interaction partners. NSI was not relativized because this metric is not dependent upon the NSI of other species in the seep network. Plant species that were never observed to be visited by any insect functional group at a given seep, and thus could not be used to estimate node specialization or d' within networks, were removed from the dataset when estimating these parameters at that seep. We identified the two species with the highest strength, lowest NSI, and lowest d' in each seep to determine keystone species. More than two species were identified if there were ties. We identified pollinator functional groups with highest strength and lowest NSI and d' in each seep as well to evaluate whether keystone functional groups varied spatially (Online Resource 3).

Functional traits associated with keystone plant species

To determine which traits were most associated with keystone species we assessed the relationship of plant species-level metrics (strength, NSI, d') with plant functional traits and ecological factors within each seep and across all seeps (five seeps pooled). Within seeps, sample sizes were small,

so we evaluated the relationship of species-specific network metrics with each continuous plant trait (flower biomass, number of simultaneously open flowers per plant, stamen number, flower abundance) individually using linear regressions. Continuous traits were \ln or $\ln + 1$ transformed to ensure normality of residuals. We used Mann–Whitney U tests for traits coded as discrete (range restriction and floral symmetry). The sample size for each test depended upon the number of plant species in the network at each seep and availability of trait information ($N = 8$ – 20). For two plant species, data were missing for number of open flowers per plant and flower biomass (*Lessingia micradenia* and *Linanthus* sp., respectively), so these were not included in analyses involving those traits.

For the evaluation across all seeps, we used multiple linear regression to model relativized strength, d' (averaged across all seeps), and NSI as functions of range restriction, floral symmetry, number of stamens per flower, flower biomass, number of open flowers per plant, mean abundance of flowers per plot, and the coefficient of variation for flower abundance across seeps. We Z -transformed flower biomass, stamen number, and number of flowers to relativize trait values across seeps and to ensure normality of the residuals we used a $\ln + 1$ transformation for stamen number, biomass, and number of open flowers, and a \ln transformation for mean flower abundance, the CV of flower abundance, strength and NSI. Range restriction (0 = non-endemic; 1 = endemic) and floral symmetry (0 = actinomorphic; 1 = zygomorphic) were coded as binary traits in the regression model.

Results

The plant–pollination networks in the five serpentine seeps studied were similarly structured. Over all seeps, 5,253 visits were recorded and our sampling effort captured 80–98 % of estimated interaction richness at each seep (Table 1A; Online Resource 4) indicating that our sampling effort sufficiently characterized these plant species–pollinator functional group networks. Within seeps, 11–34 insect-pollinated plant species and 10–14 functional groups of flower visitors were observed (Table 1B). Although the number of pair-wise interactions varied (range 32–82; Fig. 2), the levels of connectance and interaction evenness showed little variation among the seeps (Table 1C), and all were significantly lower than null expectations ($P < 0.05$).

Species-specific network metrics and keystone identity

Absolute species strength ranged from 0.006 to 2.930, and *Mimulus guttatus*, *Plagiobothrys stipitatus*, *Triteleia peduncularis*, and *Zigadenus venenosus* had the highest

strengths (in descending order). Relative strength also varied several orders of magnitude from 0.0005 to 0.23 and the same four species had the highest mean values across seeps, although the order was slightly different (Fig. 3a). These means, however, belie the variation in relative strength for a given species among seeps (Fig. 3b). For example, relative strength for *M. guttatus* varied nearly an order of magnitude (from 0.065 at RHA to 0.58 at TPW) across seeps. NSI values also varied widely, from 1.000 to 1.833 (Fig. 3c). *M. guttatus* and *T. peduncularis* had the lowest NSI, whereas *Anagallis arvensis* had the highest (Fig. 3c). Absolute d' ranged from 0.12 to 0.93. Across seeps, species with the lowest d' were *Castilleja rubicundula*, *Lessingia micradenia*, *Streptanthus breweri*, and *Trichostema laxum*, while *Z. venenosus* and *A. arvensis* had the highest d' values (Fig. 3e). Relative d' ranged from 0.02 to 0.19, and the highest and lowest species were similar as for absolute d' (Fig. 3f).

The identity of keystone species as determined by high strength varied greatly across seeps (Fig. 2). However, both *T. peduncularis* and *M. guttatus* had highest strength in two of the five seeps in which they occurred. Variation in keystone species as determined by NSI also showed variation but less so. For example, *T. peduncularis* had lowest NSI in four sites and *M. guttatus* had lowest NSI in all sites (Fig. 2). Keystone species also varied among seeps as determined by d' , but *L. micradenia* had lowest d' within all three seeps in which it occurred.

Keystone flower visitor functional groups also varied with metric and seep identity. However, the small solitary bee group had high strength, and low NSI in all five seeps, while the medium solitary bee group had high strength in three seeps and low NSI in four (Online Resource 3). Variation in the functional group defined as keystone with respect to d' was extensive (Online Resource 3).

Functional trait associations of keystone plants within seeps and across the metacommunity

Within each seep, species-specific strength increased with flower abundance ($\beta = 0.70$ – 2.86 ; RHA, RHB, BS, TPW, all $P < 0.05$; TP8, $P < 0.07$; Table 2A). On the other hand, NSI decreased with flower abundance in three of the five seeps ($\beta = -0.05$ to -0.30 ; RHA, RHB, TPW; $P < 0.05$; Table 2A). None of the other plant traits or ecological features measured were significantly associated with strength or NSI within the seeps (Table 2A, B). Interestingly, d' was not associated with flower abundance in any seep, nor with flower biomass, the number of open flowers, or stamen number (Table 2A). However, in one seep (TPW) species with bilaterally symmetric flowers and endemic species had lower d' (Table 2B).

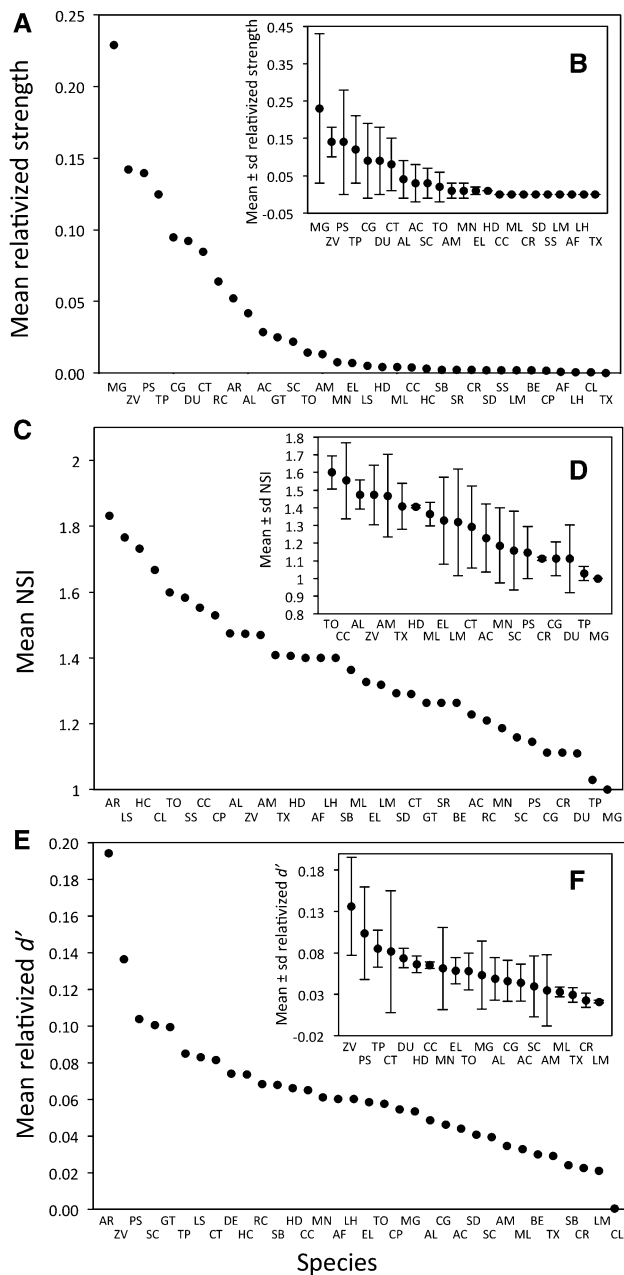


Fig. 3 Distribution of **a** mean relative strength, **c** NSI, and **e** mean relative d' for all plants visited in at least one of the five serpentine seep communities. *Inset graphs* show mean and one standard deviation of **b** relative strength, **d** NSI and **f** relative d' for all plant species for which insect visits were recorded in two or more seeps. For two-letter species codes, see Online Resource 1

At the metacommunity level (i.e., across all five seeps), all floral traits and ecological features scored explained about 70 % of the variation in species-level relative strength ($P < 0.0001$). Strength increased with mean flower abundance ($\beta = 0.02$; $P < 0.0001$; Table 2C) but

decreased marginally with the CV of flower abundance ($\beta = -0.04$; $P < 0.07$; Table 2C). Floral traits and ecological features accounted for 48 % of the variation in NSI ($P < 0.02$) across seeps. NSI decreased with flower abundance ($\beta = -0.05$; $P < 0.01$; Table 2C) and flower biomass ($\beta = -0.08$; $P < 0.05$). None of the other plant traits measured were significantly associated with strength or NSI at the metacommunity level (all $P \geq 0.1$; Table 2C). All plant features scored explained 43 % of the variation in d' across the metacommunity, and only flower biomass was associated with d' —plants with lower flower biomass had lower d' ($\beta = -0.55$; $P < 0.05$; Table 2C).

Discussion

Network structure

Serpentine seep communities displayed variation in the number of plant species, flower visitor functional groups, and interactions at a small spatial scale (some seeps were as close as 0.3 km), corroborating other studies that document spatial variation in the number of links for the same community type (Dicks et al. 2002; Burkle and Irwin 2009; Burkle and Knight 2012). Variability in the presence of plants, insects and links, may derive from differences in physical habitat size, abiotic conditions and/or microclimates of the seeps (Freestone and Harrison 2006). For instance, the seeps varied in length, which could have influenced diversity at both trophic levels, and indeed, the longest seep (RHA) had the highest number of observed interactions. Burkle and Knight (2012) similarly showed that interaction richness increased with habitat size in Ozark glade communities.

Despite the turnover in species composition among seeps, network structure remained rather constant. In particular, connectance and interaction evenness remained constant among seeps (Table 2), suggesting that the interaction webs were structured similarly regardless of the number and identity of species or interactions observed. These results corroborate other studies that have found little variation in network structure across space and/or time despite turnover of the composition of plant and pollinator taxa (Burkle and Irwin 2009; Dupont et al. 2009). Therefore, plant–flower visitor networks in serpentine seeps, regardless of the number of interacting species, could be able to withstand perturbations that may influence the presence and absence of certain species or functional groups (Nielsen and Totland 2014) if these metrics are a realistic measure of community functioning.

Table 2 Regression coefficients from univariate regression of plant species-specific strength, node specialization index (NSI), and *d'* on quantitative plant traits (stamen number, flower biomass, open flowers per plant, mean flower abundance) within each seep (A), Mann-Whitney's *U* statistic for association discrete features (floral symmetry, endemism) with strength, NSI and *d'* (B), and partial regression coefficients for multiple linear regression of strength, NSI and *d'* across the metacommunity (C)

Plant trait	Seep															
	RHA			RHB			BS			TPW			TP8			
	Strength	NSI	<i>d'</i>	Strength	NSI	<i>d'</i>	Strength	NSI	<i>d'</i>	Strength	NSI	<i>d'</i>	Strength	NSI	<i>d'</i>	
(A)																
Stamen number	0.88	-0.01	0.09	0.21	-0.07	0.04	0.51	0.09	0.03	0.05	0.07	0.12	0.62	0.12	0.17	
Flw. biomass	-0.1	-0.01	-0.01	0.04	-0.02	0.02	0.69	-0.11	0.01	-0.67	-0.01	-0.08	0.04	-0.08	-0.12	
Open flws. per plant	-0.19	0.01	0.01	0.56	-0.08	0.05	1.32	0.1	0.01	-0.72	0.04	-0.00	0.24	-0.00	-0.06	
Flw. abundance	0.70**	-0.05**	0.04	2.01***	-0.19*	0	1.65*	-0.07	-0.04	2.86*	-0.08	0.03	1.25	0.03	0.17	
Flw. abundance CV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
(B)																
Flw. symmetry	60	35	58	38	54	51	20.5	33.5	38.5	28	24.5	37*	11	8	11	
Endemism	49	50.5	44	16	38	27	30	21.5	27.5	18	19.5	27*	12	8	8	
(C) Metacommunity																
Strength																
Stamen number																NSI
Flw. biomass																-0.02
Open flws. per plant																-0.08*
Flw. abundance																0.09
Flw. abundance CV																-0.05
Flw. symmetry																-0.06
Endemism																0.01
Strength																
Stamen number																0.39
Flw. biomass																-0.55*
Open flws. per plant																-0.003
Flw. abundance																0.14
Flw. abundance CV																-0.27
Flw. symmetry																-0.65
Endemism																-0.18

The CV of flower abundance was only scored for the metacommunity

“-” = not tested

Significant coefficients bold, underlined $P < 0.08$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Variation in keystone species across space and association with functional traits

Variation in the identity of keystone species was pronounced among seeps, but also depended upon the species-specific network metric. For example, *M. guttatus* and *Centaureum trichanthum*, while present at all seeps, had highest strength in only two and one seep, respectively. This supports that the plant species upon which pollinators were most dependent changed spatially across the metacommunity. The identity of the keystone species defined by low NSI varied, but some taxa were consistently keystone under this definition. For example, abundant *M. guttatus* had one of the lowest NSI values in every seep, and large-flowered *T. peduncularis* had low NSI in four of five, suggesting that these species are consistently important for hosting a wide diversity of insect functional groups that are also shared by other co-flowering plants. Conversely, while present in four of the seeps, *Antirrhinum cornutum* had low NSI in only one. Nielsen and Totland (2014) report similar findings that a given plant species varies in its functional role in plant–pollinator networks across space and Burkle and Irwin (2009) found variation in the identity of core plant and pollinator taxa across sites with different nitrogen supplementation. Conversely, Dupont et al. (2009) found that ‘hub plant species’, i.e., those connected to many pollinators, were nearly identical across three networks in heathland fragments. Thus, while the majority of studies (including the present one) suggest that keystone plant species are substitutable across space, this notion may be system specific and requires further datasets to draw more general conclusions.

The identity of keystone plant species based on strength and NSI both within seeps, and across the metacommunity, was most strongly associated with flower abundance. Other studies confirm that abundance alone predicts functionally important species in plant–pollinator networks. Winfree et al. (2014) found abundance to be a key trait for predicting highly linked pollinator species, without which networks are more likely to collapse (Dunne et al. 2002; Memmott et al. 2004; Kaiser-Bunbury et al. 2010). Our work adds to a growing body of network literature that highlights the functional importance of abundant plant and pollinator species (Stang et al. 2006, 2007; Burkle and Irwin 2009; Jędrzejewska-Szmek and Zych 2013; Winfree et al. 2014). We show that flower abundance is also correlated with two important species-level measures, strength and NSI, and thus is important for predicting the identity of keystone species (Table 2). Plants with abundant flowers were visited more often and hosted a wider variety of insect functional groups shared by co-flowering plants with scarcer flowers.

Interestingly, the d' metric, which evaluates how ‘opportunistic’ or ‘specialized’ a plant species is on flower visitors by taking into account flower visitor proportional availability (Blüthgen et al. 2006; Dormann 2011), was not associated with flower abundance. Taken together with the results of strength and NSI, this suggests that, while interacting frequently with common flower visitor groups, plants with abundant flowers tended to interact with rarer functional groups as well, elevating their d' values. However, the plants with lowest d' in each seep (more opportunistic or generalist) tended to be those that interacted with both small and medium solitary bees at low frequency, but not with other functional groups (Fig. 2). These flower visitor groups, being the most common, were also frequent visitors to many other plant taxa. These results perhaps indicate that d' may not be the best indicator of a keystone plant species (that acts as a facilitator or a common host of flower visitor functional groups), when networks are based on flower visitor functional groups.

Species with larger flowers (i.e., higher biomass) had lower values of NSI across the entire metacommunity. This suggests that both large-flowered species and those with more abundant flowers engage frequently in plant–plant interactions via shared pollinators and may be instrumental in maintaining network structure. Plants with low variation in local abundance tended to be keystone species across the entire metacommunity as defined by high strength (Table 2), supporting that consistently abundant resources (flowers) across space are important for maintaining insect visitor diversity. However, floral symmetry, endemism and stamen number were less important than flower abundance for determining which plant species are keystone as measured by NSI and strength within these pollination networks (Table 2). While the effect of floral abundance on plant strength and NSI outweighed that of other traits measured in this study, traits not measured here (e.g., nectar-holder depth, Stang et al. 2006, 2007 or ‘floral complexity’, Kaiser-Bunbury et al. in press) could be important for mediating a species’ importance in pollination networks. Across the metacommunity, plants with smaller flowers (less biomass) had lower d' , that is, they were visited by the most common functional groups in the serpentine seep communities, small and medium solitary bees. Size constraints can be similarly important for determining species degree in other networks (Stang et al. 2006) and may reflect handling constraints set by flower size. We must caution that sampling bias, whereby rarer plants received less observation time, could influence all species-specific and overall network metrics evaluated in this study (Blüthgen et al. 2008; Dormann 2011). For example, strength may be underestimated, and d' overestimated for rarer species that were not common in our

observation plots (Dormann 2011). The d' metric should be robust to this sampling bias (Blüthgen et al. 2006, 2008); however, the issue of many taxa comprising flower visitor functional groups, and lack of abundance data on functional groups may still be limiting factors.

The importance of flower visitor functional groups showed little spatial variation when evaluated by strength and NSI. Small and medium solitary bees tended to be the keystone functional groups based on the definitions herein. However, this should be evaluated with caution as these groups could comprise more taxa than other groups. Similar to the patterns found for plant species, the identity of keystone flower visitor functional groups when characterized by low d' were different from those when strength and NSI were used to define them. Here, they were the groups that interacted with the most common or abundant flowering plant species.

Conclusions

Our results indicate that changes in plant composition across a serpentine metacommunity resulted in little fluctuation in plant–flower visitor network structure. This constancy in network structure may be due in part to the substitutability of keystone plant species that maintain structure. We extend findings of similar studies by determining that plants with high local flower abundance were keystone plant species as determined by the species-specific network metrics, strength and node specialization index. Determination of keystone species using d' , however, revealed that abundance was less important, while small flower size was more important for hosting the most abundant flower visitor functional groups in serpentine seeps—small and medium solitary bees. Our findings yield a positive outlook since common, abundant plant species may buffer plant–flower visitor communities against possible ill effects of environmental change, but also caution that conclusions can be metric specific so care needs to be taken when interpreting these relationships within communities.

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