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Bee Ecology of Serpentine Grasslands: Community, Functional Trait, and Network Perspectives

By

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DISSERTATION

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Abstract

Soil transitions underly many terrestrial landscapes and are well-established drivers of plant community structure. Yet, edaphic characteristics are frequently excluded from hypotheses of how environmental features structure ecological communities for higher trophic levels. In this dissertation, I test whether a particular type of soil, serpentine, structures bee communities and the flowers they depend on. Building on a foundation of classic ecological studies, I establish where and why flowers and bees distribute themselves across the mosaic landscapes of California serpentine soils by using both community and functional ecology tools. Functional trait ecology plays a key role in revealing what mechanisms filter local bee communities. And finally, I categorize how these bee and flower communities produce emergent patterns of interaction using network approaches. This dissertation demonstrates that soil, and perhaps many other underlying environmental conditions, not only filter and structure plant communities, but also the wild bee communities that visit them.

Chapter One documents and categorizes wild bee and flower communities across serpentine and non-serpentine meadows in California's coastal mountain ranges. Soil characteristics are well-established environmental drivers of local plant community diversity and composition, but their effects on mobile organisms in higher trophic levels are less well understood. We analyzed whether pollinator (mostly wild bee) and floral communities—distributed across a discrete serpentine soil boundary in California's coast ranges—differed according to the underlying soil type (serpentine or non-serpentine). We found that wild bee richness and abundance were significantly lower in non-serpentine meadows, but the taxonomic composition of bee communities did not differ between soil types. Spring floral richness, abundance, and composition were also lower in non-serpentine meadows, but floral communities

had different compositions on the two soil types. In both bee and floral communities, there were strong phenological effects on abundance, richness, and composition over the course of the spring season that were parallel. Both bees and flowers were markedly more diverse and abundant in serpentine meadows, particularly in the late spring when non-serpentine meadows stopped flowering.

Chapter Two utilizes a functional trait framework to test whether soil characteristics affect the functional diversity of wild bee communities, either directly or indirectly via changes to vegetation-related nesting and foraging habitat quality. We demonstrate that soil type affects the functional diversity of bee communities, with those on serpentine soils being more functionally rich. Rather than direct soil-bee impacts, soil type appears to indirectly filter bee communities via interactions between vegetation-based habitat quality and bee nesting and foraging traits. We use a fourth-corner analysis to show that nesting and foraging habitat quality correlates with particular bee functional traits. Specifically, above-ground nesting bees are filtered out of serpentine meadows, and late-flying bees are filtered out of non-serpentine meadows. Despite a growing literature on landscape drivers affecting bee community functional richness, the indirect pathways filtering bees are rarely quantified. In contrast to the strong direct filters that infertile soils exert on plant communities via functional response traits, the indirect effects on pollinators are more complex. Soil fertility's indirect effects of "cascading up" to structure the functional diversity of other higher trophic communities may be a broader pattern, but evidence is scant.

Chapter Three takes a network perspective to understand how interactions (and not only species) turn over across serpentine and non-serpentine grasslands. Ecologists have long sought to understand and dissect interaction networks among co-occurring species and to understand if

these interactions assemble into networks with common emergent properties like nestedness, modularity, and specialization. In addition, how interactions turn over—and consequently affect network structure and resilience to perturbations—across other environmental gradients is a field of important, and current, focus. We analyzed how soil type affected the network structure and interaction turnover of plant-pollinator communities. We demonstrate that plant-pollinator network structure differed significantly between serpentine and non-serpentine meadows. We also utilized a parallel analysis of network microstructure, where we focused on the turnover of interactions between networks. The difference in overall network structure appears to be driven by interaction turnover; serpentine networks exhibited lower interaction turnover between themselves than non-serpentine networks, and interaction rewiring—when shared species switch interaction partners—contributed to turnover between serpentine networks more frequently. Interaction rewiring contributed very little to interaction turnover in general, and only ~20% of interaction turnover between sites was among shared species. And when compared to a regional pooled meta-web, serpentine networks were more unique than non-serpentine networks. Although serpentine meadows are more unique in a regional context, the more frequent rewiring and lower interaction turnover between serpentine meadows drives less specialized, more resilient plant-pollinator networks in these low-resource environments.

Acknowledgements

Working toward a PhD is often portrayed as an intensely solitary pursuit and much of it is, but I have benefitted a great deal from my broad and supportive community during my time as a graduate student. So much of what I have learned during graduate school—well beyond what is in this dissertation—I owe to casual conversation and long wandering travels with my close friends, attentive mentors, and Davis' broader community both at the university and far beyond.

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As I mentioned, I did not begin graduate school imagining I would study the bee and flower communities of California's serpentine grasslands. Cathy Koehler and Paul Aigner provided immeasurable insight into serpentine natural history, field site identification, etc., and are wonderful friends and hosts at McLaughlin Reserve. Susan Harrison has also offered lots of help understanding the serpentine world via generous data sharing, manuscript reading, and more. And thank you to Terry Griswold and Skyler Burrows at the USDA Bee Lab for helping me identify thousands of bees; my dissertation would have been impossible without their hard work.

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Chapter 1: Soil type and floral phenology interact to structure wild bee communities in California serpentine grasslands

Ross M. Brennan, Terry Griswold, & Neal M. Williams

Introduction:

Abiotic environmental conditions structure local ecological communities and biotic interactions within them. Notably, these abiotic microhabitat drivers operate at finer scales than the geographic patterns of climate, geology, etc. that determine regional species pools (Mittelbach and Schemske 2015, Cornell and Harrison 2014). For plants, the local-scale mechanisms are often straightforward: aspect, slope, and soil type (among many other factors) filter the regional species pool to determine local-scale diversity and abundance (Kraft and Ackerly 2014, Luzuriaga et al. 2012, Menezes et al. 2020). For higher trophic levels, abiotic factors may structure communities directly, for example, thermal habitat suitability for fishes in a river, or indirectly via vegetation-based trophic regulation or by altering the outcome of biotic interactions with lower trophic levels (Welsh Jr. et al. 2001, Mee et al. 2018). The contexts in which plant biomass and diversity determine higher trophic level structure link central concepts in food web ecology with key questions in community assembly for herbivores and their predators (Hairston et al. 1960, Trivellone et al. 2017, Perović et al. 2018). It is clear that abiotic drivers affect the interactors and outcomes of antagonistic interactions, but how strongly abiotic drivers structure mutualistic communities, such as those between plants and their pollinators, is less understood (Levine and HilleRisLambers 2009, HilleRisLambers et al. 2012, LaManna et al. 2021).

Among abiotic factors, edaphic characteristics are a central aspect of local habitat that is likely to drive patterns of local biodiversity. Most research documenting the effects of soil type on the diversity and composition of biological communities focuses on plants (or soil microbial communities). Chalk (i.e. calcareous), alkaline, and serpentine soils all harbor unique—and often distinct—plant communities (Kruckeberg 1969, Steffan-Dewenter and Tscharntke 1999, Karlík and Poschlod 2009). Much of this research on plant community diversity has been conducted in serpentine grasslands. The famous "C-S-R" paradigm emerged from serpentine grasslands, and extensive work over five decades has shown that there is high beta-diversity among plant communities distributed across patches of serpentine soil (Grime 1977, Harrison and Inouye 2002, Harrison and Rajakaruna 2011). In addition to filtering regional species pools into invasion-resistant local communities, the physical structuring and chemical stresses serpentine soils exert on plants drive selection that yields locally adapted endemic plants, resulting in distinct communities compared to those on surrounding non-serpentine soils (Harrison et al. 2006). Although there is strong evidence for soil type structuring the composition of plant and microbial communities, there is far less evidence for whether these effects extend to higher trophic levels via second order interactions (Cahill et al. 2008, Buckles and Harmon-Threatt 2019).

Notably, serpentine soils can affect organisms at higher trophic levels, and there is some evidence that these effects ultimately contribute to the composition of local herbivore communities. Serpentine soils, in particular, structure insect herbivore and florivore communities on several common chaparral plants, but these studies focused on individual plant species and many of the herbivores were relatively immobile (i.e., caterpillars and florivorous beetles; Meindl et al. 2013, Robinson and Strauss 2018). Organisms whose foraging stages are highly mobile (e.g., bees, birds; Gregory and Baillie 1998, Heath et al. 2017), in contrast, may be less affected by soil type—particularly in heterogeneous landscapes—because they can traverse different soil types, leading to a greater similarity of these communities between differing soil types (Wolf and Thorp 2011).

Insect pollinators, and bees specifically, provide a useful system for testing hypotheses of how soil type may structure higher trophic communities. Flowering plants depend on animal pollinators, of which bees are the most common and most effective, for successful reproduction (Kearns et al. 1998). Bees are also restricted to floral nectar and pollen as their food source and exhibit various degrees of trophic specialization ranging from generalized among plant families to specialization on a single plant genus (Cane and Sipes 2006). Bees are also diverse, mobile at relatively small scales surrounding an anchored nest location, and have divergent nesting habits (Michener 2007, Greenleaf et al. 2007). Therefore, bee species are differentially affected by their surrounding nesting and floral resource mosaics, which could drive differences in local bee community composition and abundance. Finally, research on wild bee communities has focused on the effects of both broad-scale biodiversity drivers, as well as local habitat characteristics (Kremen et al. 2007, Rollin et al. 2015, Palma et al. 2017). However, there is scant work linking the effects of soil type on bee community composition or habitat use (Harmon-Threatt 2020). Determining whether such a fundamental abiotic property structures bee communities is a critical knowledge gap given bees' foundational role in wild plant communities and working landscapes. Their described sensitivity to biotic environmental drivers such as floral diversity, abundance, and phenology also provides the opportunity to untangle whether edaphic characteristics might indirectly drive bee community composition.

We sought to test the hypothesis that edaphic differences structure the richness, abundance, diversity, and composition of higher trophic communities, using bee communities across serpentine and non-serpentine grasslands as a study system. If edaphic characteristics are important, we would expect that bee communities in serpentine and non-serpentine grasslands differ in richness, abundance, and/or composition. We also consider interconnected mechanisms for whether potential differences in community structuring of bee communities are due to indirect effects of edaphic characteristics by changes to bee and floral phenology or floral community characteristics at the meadow scale. Following a wealth of research on serpentine plant communities (Kruckeberg 1969, Harrison and Rajakaruna 2011), we expected the floral community to differ significantly in abundance, richness, composition, and perhaps phenology between serpentine and non-serpentine grasslands. If edaphically driven floral community characteristics in turn drive differences among bee communities across soil types, we would expect patterns of community composition in flowers and bees to be correlated.

Materials & Methods:

Study design & field sites

A total of twelve sites from the inner Coast Ranges of northern California were selected to represent serpentine and non-serpentine soil types. An original eight sites were selected and sampled during the 2017 field season, and an additional four were added in 2018. We selected sites in pairs to include adjacent non-serpentine and serpentine soils. We identified potential sites using existing maps of underlying serpentinite geology, land ownership, etc. We then selected sites after field scouting in March 2017 and 2018. Each site was located an average 1.6 km from its paired site, and pairs of sites were separated from one another by an average of 31.5 km. Our sites were located on public lands administered by the Bureau of Land Management, and on private lands managed by the McLaughlin Reserve (University of California) and the Land Trust of Napa County. Serpentine soils are distributed throughout the Coast Ranges of California and are readily identifiable. Sampling sites were in grasslands located within a surrounding matrix of chaparral dominated by chamise (*Adenostoma fasciculatum*) and *Ceanothus* species, interspersed with oak (*Quercus* spp.) savannah and gray pine (*Pinus sabiniana*). Non-serpentine grasslands are dominated by invasive Eurasian grasses and have a noticeable flowering peak during May when the dominant, invasive *Vicia villosa* flowers in extensive mats. In contrast, serpentine grasslands harbor a broad community of California native forbs, including many serpentine endemics, that maintain a more consistent community floral abundance across the flowering season. The floral community turns over rapidly across time.

Field sampling protocols

To compare floral and wild bee communities across soil types, we delineated sampling units within grasslands at each site. Sampling areas varied from the entire meadow area—where meadows were small—to a portion of larger meadows; we limited the size of the sampling area to minimize the effect of sampling area on our results. Nonetheless, the area of sites did vary.

We sampled field sites during the spring flowering period—early April through late June—in both 2017 and 2018, re-visiting each site every 10 to 14 days. On average, each site was visited 6 times within each year. We collected bees that were actively visiting flowers in each site; each bee was collected using an insect net (all by R. Brennan). Bees were netted in two 45-minute collecting sessions, one in the morning (8 AM to 12 PM) and one in the afternoon (1 PM to 5 PM). We focused on areas within a site that had high floral abundance. These areas changed—spatially—between visits, so we used a dynamic sampling design that allowed us to follow high densities of flowers. As such, we carefully traced the wandering transect (2 m in width) we followed to collect bees and calculated its area along with the floral richness and abundance. This allowed us to control for differences in floral abundance or sampling area across different sites and visits. Bees were only collected when weather conditions permitted – when temperatures were above 15 °C and wind speeds were less than 5 m/s.

During each visit, we sampled the floral community using two different methods. First, we identified all plant species that were in flower at each site—those species that did not have flowers providing pollen or nectar accessible to wild bees were excluded from our analyses—and estimated the floral abundance ($\log_{10}$(abundance)) of each species across the entire site. This metric served as an estimate of the floral community available to bees during each sampling visit within the local grassland. We also sampled the floral community off which bees were collected (see above). This estimate was a true count of open flowers of all species within the bee sampling transect (density; abundance / m^2). We also calculated the area sampled within this transect. All flower species that could not be identified in the field were collected and later identified in the lab.

Bees are curated and currently housed at the University of California, Davis. We (R. Brennan and T. Griswold) identified species according to published taxonomic revisions. Many specimens (from a variety of taxa) were identified by T. Griswold, and bees in the genus *Andrena* were identified by H. Ikerd (USDA ARS Pollinating Insect Laboratory, Logan, UT). We identified all specimens to species, except for two poorly resolved species groups (*Panurginus* and *Dialictus*) where we identified them to morphospecies.

Statistical analysis

Abundance and richness

We used a generalized linear mixed model framework to test the effect of soil type on plant communities, bee communities and the interactions between them, using the R package *glmmTMB* (Brooks et al. 2017). Because all three likely respond strongly to season, we included season and its interaction with soil-type as fixed effects in the model. We analyzed abundance and richness at the sample-round level, as a function of soil type (varying across sites), season (as day of year, DOY, varying across samples within sites), and the interaction of these two predictors. A significant effect of soil type would indicate that soil types differ in the abundance or richness of community samples across the growing season. We analyzed floral richness, two different estimates of abundance, and our dataset of bee richness and abundance using the same model structure: Abundance (or Richness) ~ soil type + DOY + DOY^2 + Soil Type:DOY + Soil Type : DOY^2 + year + (1|site). We used AICc for model comparison and selection between biologically relevant simpler models for each response. We only compared sub-models that represented ecologically plausible hypotheses. Once we determined which model structure was most parsimonious (the model with the lowest AICc value by at least 4 points), we used a log-likelihood comparison to evaluate whether the selected model performed significantly better than a null model that only included random effects. All analyses were performed in R 3.5.3 (R Core Team 2019).

We also tested the hypothesis that the richness or abundance of netted wild bees was predicted by the local floral richness or abundance and soil type. We developed a full model of the form: Bee Abundance (or Richness) ~ Floral Abundance (or Richness) + Soil Type + Floral Abundance : Soil Type + year + (1|site) + (1|sample round). We conducted the same analysis as for the models of bee and floral abundance in which each sample was a replicate, and sample round was a random effect. For this analysis, we used zero-inflated models, and the model of bee abundance had a negative binomial variance structure.

Community composition, alpha diversity, and beta-diversity

We summarized the floral and bee community composition according to the most frequent (among site-years) and numerically dominant (within each site-year) taxa. For floral communities, we summarized the most frequent flowering species within each soil type as well as the dominant flower species for each site-year. We also calculated mean and SE for the proportional abundance of each species within each soil type based upon the cumulative $\log_{10}$(abundance) for each species. For bee communities we summarized at the genus rather than species level using true abundance of netted bees, because individual species were often rare and were distributed unpredictably.

We used PerMANOVA to assess whether floral or bee community composition differed between sites or soil type. For these analyses, we pooled our data in two different ways: at the site level (pooled across sample rounds) and at the sample round level. The site-level pooled data elucidate whether floral and bee community composition of sites differed significantly based upon soil type; the sample round level data allowed us to examine whether sites' floral and bee composition differed across time, soil type, or an interaction of the two. We used the Morisita-Horn index to assess pairwise differences among samples because it weights pairwise community distances by species abundances, and it is sensitive to both turnover and richness differences. We tested for potential multivariate heterogeneity among samples using beta dispersion tests; all tests were non-significant.

To visualize the distances between sites (or samples within sites) as well as their dependence on soil type and sample round, we conducted a principal coordinates analysis

(PCoA) with a Cailliez correction for negative eigenvalues. PCoA uses an untransformed distance matrix to ordinate sites, rather than their rank-order distances, meaning it more accurately depicts our multivariate dataset than other non-metric approaches. Community composition, alpha, and beta-diversity were all analyzed using the *phyloseq* and *vegan* packages for R (McMurdie and Holmes 2013, Oksanen et al. 2018).

Results:

Floral abundance and richness

Serpentine sites harbored more species of flowers than non-serpentine sites and richness decreased across the spring flowering season (Figure 1.1A). At non-serpentine sites, however, there was a notable peak in floral richness between DOY 115 and 122 (late April), which was 22 to 29 days after flowering began. Floral abundance showed a similar pattern to flower richness (Figure 1.1C). Flowers were more abundant at serpentine sites and floral abundance decreased across the season. Flowering abundance at non-serpentine sites peaked a couple of weeks after flowering began.

The full model was most parsimonious for both richness and $\log_{10}$(floral abundance) (Table 1.1). A slightly simpler model, excluding year was most parsimonious for floral density. For each of the three response variables, the most parsimonious model was significantly better than a null model that only included random effects (log-likelihood comparison). All included predictor variable coefficients were highly significant in each of the three models (Table 1.1).

Bee abundance and richness

Netted bee richness was also higher in serpentine sites—only marginally so—and decreased linearly across the spring season (Figure 1.1B). Netted bee richness in non-serpentine sites was nonlinear, increasing to a peak near DOY 120 (April 30), and decreasing thereafter (Figure

1.1B). The abundance model predicted that regardless of the day of year, netted bee abundance was higher in serpentine sites. At serpentine sites, netted bee abundance was non-linear over the season, with a minimum in the middle of the sampling period (~ May 20, Figure 1.1D); in contrast, the abundance of netted bees at non-serpentine sites decreased across the sampling season. For bees, the full model was most parsimonious for abundance. The same simpler model as for floral density (without year) proved most parsimonious for netted bee richness. Both models were significantly different from a null model (Table 1.1).

Bee richness and abundance as a function of floral richness and abundance

At low floral richness and density, bees were less speciose and abundant at non-serpentine meadows compared to serpentine meadows. However, as floral richness or density increased, the predicted bee richness and abundance at non-serpentine meadows surpassed that in serpentine meadows (Figure S1.1A and S1.1B). Full zero-inflated models of both netted bee richness and abundance as a function of soil type and floral richness or density (abundance per square meter) were the most parsimonious.

Floral community composition

The most frequent and dominant flower species present differed between soil types. In non-serpentine meadows, *Vicia villosa* was the most frequent (occurring at 8 of 10 site-years, Table 1.2) and was also the dominant flower at 7 of the 8 site-years where it occurred. *Ranunculus occidentalis* was dominant at 2 site-years and *Brodiaea elegans* was the dominant flower at the final site-year. Serpentine sites also lacked any flower species that occurred at all 10 site-years. *Sidalcea diploscypha* was the most frequent floral species, occurring at 9 site-years. In contrast to non-serpentine meadows, the dominant floral species was more variable across serpentine meadows, with *Lasthenia californica* dominant at 4 site-years, and other species dominating the remaining site-years (Table 1.2). On average, the proportional abundance of the dominant floral species was lower in serpentine meadows, suggesting that serpentine floral communities were generally more even.

Floral communities at sites differed marginally based on soil type ($F_{1,18} = 2.156$, p-value = 0.0624; Figure 1.2A). Our sample-round analysis did not show difference between soil types; however, it revealed that composition changed significantly across the sample rounds ($F_{1,89} = 8.592$, p-value $< 2 \times 10^{-5}$; Figure 1.3A), and this change itself did not depend on soil type (soil type x DOY, $F_{1,89} = 0.7344$, p-value = 0.696).

Bee community composition

Bee communities, like floral communities, varied in which genera and species were most frequent or dominant across soil types. At the genus level, several genera were frequent on both serpentine and non-serpentine soils; notably, *Osmia*, *Andrena*, and *Bombus* were present at almost all (if not all) site-years, regardless of soil type (Table 1.3). These same genera were dominant at 9 of the 10 non-serpentine site-years (pooled across the season). At serpentine sites, the most frequent genera were dominant at relatively few site-years; however, bees in the genus *Diadasia* were dominant at 6 of 10 site years (Table 1.3). Similar to floral communities, dominant bee genera represented a lower average proportional abundance on serpentine soils, suggesting they were less numerically dominated by a small number of genera than non-serpentine meadows.

Site-level bee community composition did not significantly differ between serpentine and non-serpentine soil types (soil type, $F_{1,18} = 1.021$, p-value = 0.409; Figure 1.2B); although, visual examination of PCoA plots suggests clustering of sites into separate groups based upon soil type. When we considered sample round-level bee community data, samples differed significantly across time, but again were not different between soil types (sample round, $F_{1,79} = 5.547$, $p < 2x10^{-5}$; Figure 1.3B).

Discussion:

Soil transitions are ubiquitous characteristics of ecosystems and are often documented as driving differences between ecological communities, particularly plants. Here, we corroborate long-standing evidence that plant communities are strongly structured by underlying edaphic differences (Kazakou et al. 2008). In addition, we show that edaphic effects on plant communities indirectly affect wild bee community composition both spatially and phenologically. Bees forage across broad habitat mosaics (Williams and Kremen 2007), and our research suggests that underlying edaphic transitions can structure local bee communities by affecting the local richness and abundance of floral resources. In agro-ecological systems, there is evidence that bee communities are structured both spatially and temporally by differences in floral community composition and phenology—particularly due to different historical land management regimes (Mandelik et al. 2012). We show that natural underlying soil transitions may drive patterns in bee communities, mediated by changes to local floral communities. In our system, it appears that local bee abundance and community composition track the abundance of flowers across the landscape. Serpentine grasslands may harbor richer, more abundant bee communities than non-serpentine communities because floral abundance is more consistent across the season, and the flowering season is extended, coinciding with the phenological turnover of the bee community (Mallinger et al. 2016). As a result, serpentine meadow "islands" buffer floral resource scarcity in the broader landscape, concentrating bees in the early and late spring, when non-serpentine sites have less reliable floral resources.

Wild bee abundance and species richness were significantly lower in grasslands on non-serpentine soils. However, somewhat surprisingly, the composition of bee communities visiting floral resources in the two soil types did not differ between them, but rather only across the growing season. Similar to bee communities, floral richness and abundance were both lower in non-serpentine grasslands when compared to serpentine. These results suggest that the core floral assemblages in the two different soil types are similar, but their abundances differ between soil types. The higher floral abundance in serpentine sites supports this hypothesis. Overall, serpentine soils directly affected both bees and flowers by increasing richness and abundance, although more detailed patterns appear structured by phenology.

Phenology is known to strongly structure both floral and bee communities (CaraDonna et al. 2014, Harrison et al. 2018) and our results support this general trend. When we analyzed data across sampling rounds floral community composition only changed across time, *not* between soil types, suggesting that patterns of floral composition across soil type are more complex and perhaps mediated by the seasonal phenology of individual plant species. Although not statistically significant, our ordination analyses suggest that floral communities may cluster into three rough groups based on both soil type and date: early-season serpentine, late-season serpentine, and non-serpentine. However, there also appears to be a core group of common bee species that are shared across both soil types (e.g. *Andrena*, *Bombus*, and *Osmia* spp.; Table 1.3), regardless of floral community and phenology. This core group of shared bees may drive the lack of a difference in bee community composition between soil types.

Previous work characterizing the drivers of local pollinator abundance and richness frequently show the importance of floral abundance and species richness (Potts et al. 2003, Grundel et al. 2010). We found similar trends in our research; there were more bee species and individuals collected where and when floral richness and abundance were greater. Both bee and flower abundances peaked near DOY 120 (April 30). In our case bee richness and abundance started at higher values early in the season and decreased as the growing season progressed, regardless of soil type.

In addition to patterns in the abundance and richness of flowers and bees, community composition also changed across time. Floral community composition changed over time but was not different between soil types, and likewise the bee community changed across time but not between soil types. We hypothesize that most wide-ranging bees traverse foraging ranges that are much larger than a single meadow, and opportunistically forage wherever flowers are in greater abundance (Williams and Kremen 2007, Martins et al. 2018). As the growing season progresses, however, floral resources in non-serpentine grasslands precipitously decrease, while flowers continue to be relatively abundant in serpentine meadows. During the same time, bees continue to cross both soil types, but forage more in serpentine meadows where there are still abundant flowers (bees cannot be collected if no flowers are in bloom). The extended floral phenology of serpentine meadows isolates them as resource islands early and late in the growing season, and they support a group of late-spring bee species that forage there and not in non-serpentine meadows.

There are two important limitations to our data set that we should note. First, the power to detect changes in bee communities among soil types is constrained by a “zero value problem”. We cannot compare a sample with the composition of zero flowers (or bees) to samples with non-zero abundances because there are no values in the community matrix to compare. Therefore, sampling dates and sites that had no flowers also had no net-collected bees and these samples were omitted from the community composition analyses. The majority of these samples were from non-serpentine sites late in the flowering season. Second, we sampled the bee community by netting individuals from flowers, which may bias our data towards bees that were actively foraging in each site, rather than traversing across it. Although additional sampling methods may have sampled pollinator species not observed in our data set, we were most interested in bees actively foraging in each site, and hence focused on net sampling at as many sites, and as often, as possible.

Much of the recent examination of bee communities and the plants they use has focused on the role of anthropogenic drivers: e.g., agriculture, forest management, wildfire, etc. (Kennedy et al. 2013, Galbraith et al. 2019a, 2019b, LeBuhn and Vargas Luna 2021). Very few studies address whether underlying environmental factors contribute to expected community variation at local to landscape scales. Yet, clearer understanding of such factors will be increasingly important as more focus and effort is paid to pollination communities. For example, will efforts to mitigate anthropogenic drivers of land use change also mitigate effects on bee communities, or do underlying environmental factors prevent such mitigation? And what environmental factors should be considered when planning restoration, conservation, or enhancement actions for wild bee communities? Here we show that due to their higher floral richness, abundance, and phenological consistency, serpentine meadows are valuable habitats for regional bee conservation and restoration efforts. Expanding our understanding of how other soil types besides serpentine may indirectly structure bee communities could help with conservation planning in other mosaic habitats.

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Author Contributions:

RMB and NMW designed the study, RMB conducted field work and data analysis, RMB and TG conducted lab work. RMB and NMW wrote the manuscript, and TG edited later versions of it.

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Figures:

Figure 1.1 Floral and bee species richness and abundance as a function of day of year and soil type. In all panels, lines are generalized linear mixed model predictions and error bars represent 95% full-model bootstrapped confidence intervals. Brown circles are observations from non-serpentine sites, and turquoise diamonds are from serpentine sites. Panels A and B show how floral and netted bee richness vary across the spring growing season. Panels C and D show how $\log_{10}$(floral abundance) and netted bee abundance vary across the growing season.

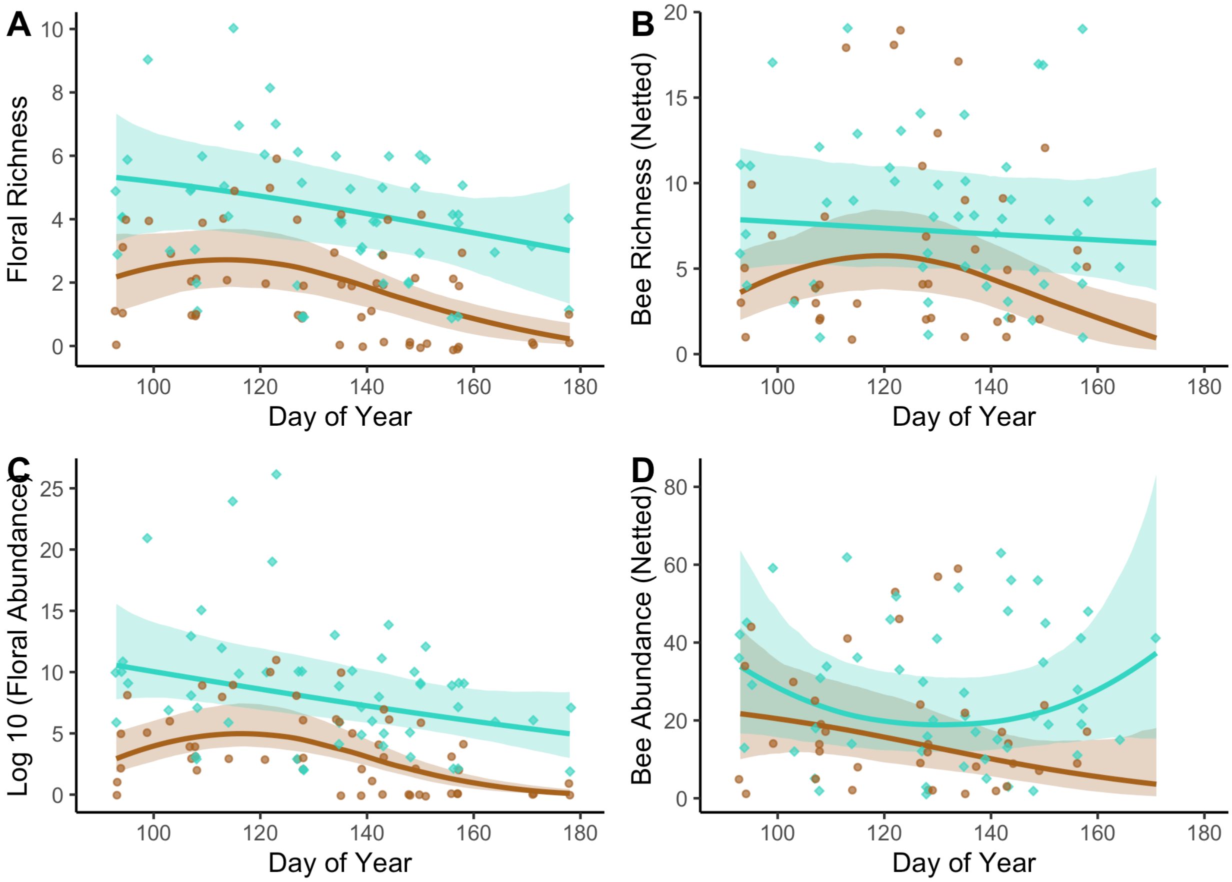


Figure 1.2 Principal coordinates analysis (PCoA) of abundance-weighted (A) floral and (B) wild bee communities at each sampling site. Each point represents each unique site*year combination, aggregated across all sampling visits. Brown circles are observations from non-serpentine sites, and turquoise diamonds are from serpentine sites. Percentages for each axis represent the amount of variation in the distance matrix explained by that axis. Site to site distances were calculated using a Horn-Morisita index, which incorporates both the identity and abundance of communities at each site ($\log_{10}$(floral abundance) and total bees netted).

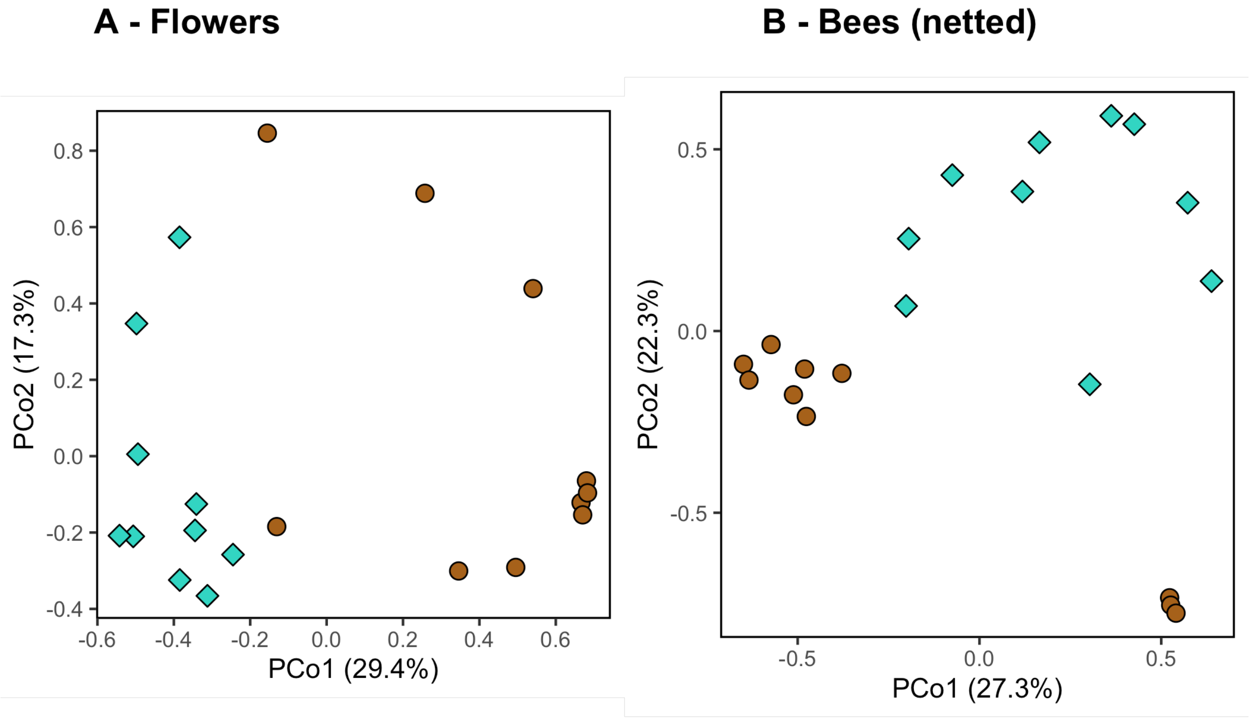
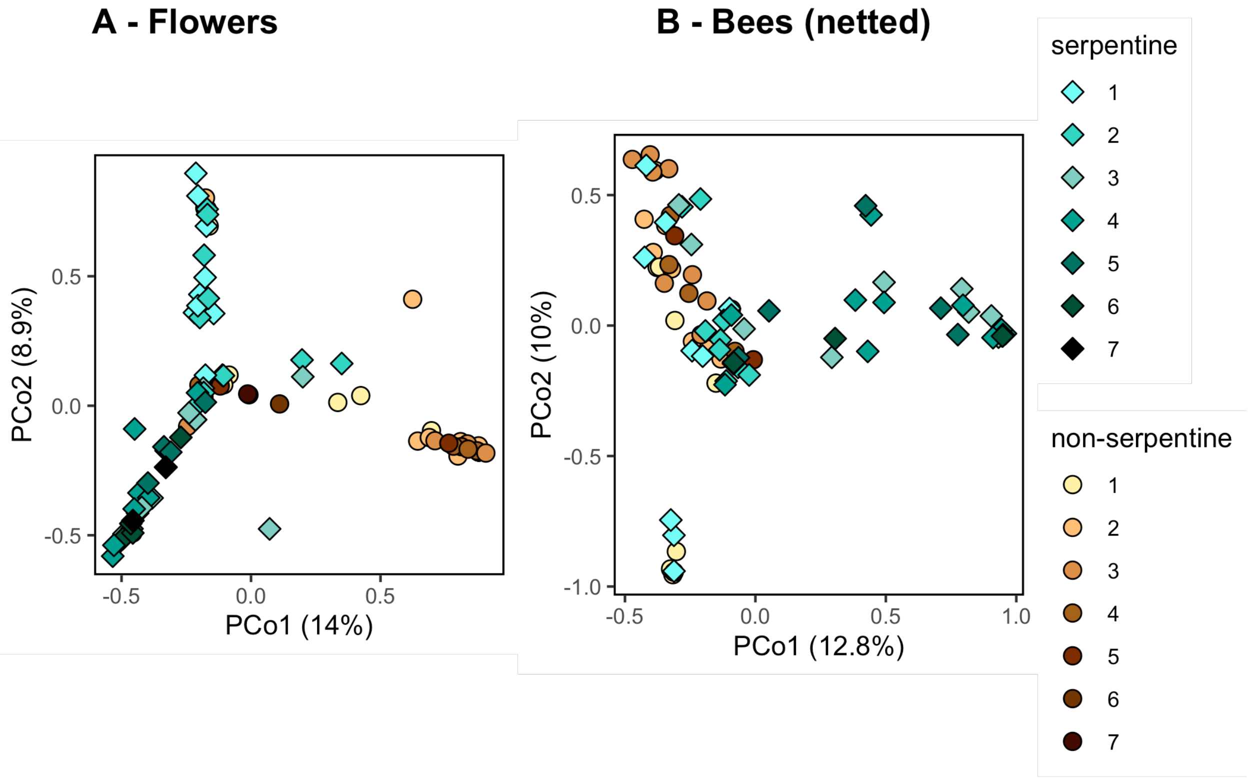


Figure 1.3 Principal coordinates analysis (PCoA) of abundance-weighted (A) floral and (B) wild bee communities for each site*sampling date combination. Each point represents each unique site*sample round combination. Lighter colors are earlier sample rounds (starting ~ April 1st) and dark colors are later sample rounds (ending ~ June 25th). Percentages for each axis represent the amount of variation in the distance matrix explained by that axis. Community distances were calculated using a Horn-Morisita index, which incorporates both the identity and abundance of species at each site ($\log_{10}$(floral abundance) and total bees netted).



Tables:

Table 1.1 Coefficients (and SE) from generalized linear mixed models testing if serpentine and non-serpentine meadows differ in abundance and richness changes throughout the growing season.

	Dependent variable:				
	Floral Richness (1)	Floral Abundance/m^2 (2)	log$_{10}$(Floral Abundance) (3)	Bee Richness (4)	Bee Abundance (5)
Soil Type	0.929***	0.924**	1.116***	0.525*	0.597*
	(0.177)	(0.380)	(0.200)	(0.272)	(0.317)
DOY	-4.761***	-14.364***	-6.562***	-1.720**	-3.869***
	(1.386)	(2.788)	(1.172)	(0.809)	(1.478)
DOY^2	-3.212**	-12.926***	-5.358***	-2.466***	-0.833
	(1.442)	(2.636)	(1.214)	(0.878)	(1.347)
Year	-0.416***		-0.406***		-0.282*
	(0.123)		(0.087)		(0.158)
Soil Type: DOY	3.264**	10.012***	4.520***	1.260	3.244*
	(1.569)	(2.976)	(1.281)	(0.926)	(1.711)
Soil Type: DOY^2	2.978*	14.893***	5.226***	2.461**	2.464
	(1.631)	(2.845)	(1.327)	(0.980)	(1.607)
Intercept	0.719***	-0.144	1.201***	1.453***	2.699***
	(0.167)	(0.302)	(0.165)	(0.202)	(0.264)
Observations	107	107	107	89	89

Note: Soil Type was coded as a factor, with "serpentine" as 1 and "non-serpentine" as 0.

$^{*}p<0.1$; $^{**}p<0.05$; $^{***}p<0.01$

Table 1.2 Most frequent and dominant flower species (and abundance) according to soil type

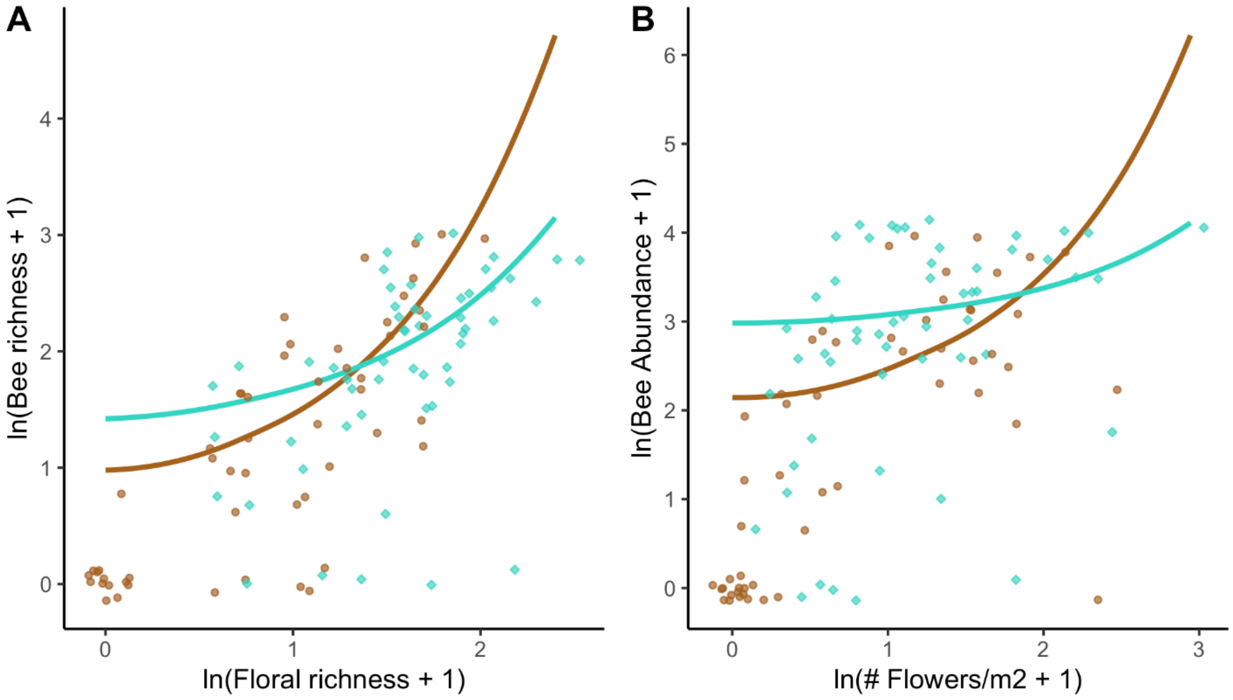
Soil Type	Flower Species	# Sites Present	# Sites Dominant	Mean Proportional Abundance	$\log_{10}$(Abundance) - Mean ± SD
Non-serpentine	*Vicia villosa*	8	7	40.5%	8.13 ± 3.91
	Ranunculus occidentalis	4	2	43.6%	3.75 ± 1.26
	Brodiaea elegans	3	1	14.5%	2.67 ± 2.89
Serpentine	*Eriophyllum lanatum*	4	2	8.2%	3.50 ± 3.32
	Lasthenia californica	7	4	12.8%	6.7 ± 3.45
	Phacelia corymbosa	4	1	11.1%	5.25 ± 2.22
	Astragalus rattanii	3	1	8.6%	4.00 ± 3.46
	Sidalcea diploscypha	9	1	10%	4.89 ± 2.93
	Hemizonia congesta	2	1	11.9%	4.00 ± 0.00

Table 1.3 Most frequent and dominant bee genera according to soil type

Soil Type	**Genus**	**# of Sites Present**	**# of Sites Dominant**	**Mean Proportional Abundance**
Non-serpentine	*Osmia*	9	3	20%
	Andrena	8	3	33%
	Bombus	8	3	32%
	Eucera	8	1	16%
Serpentine	*Diadasia*	10	6	26%
	Osmia	10	1	9%
	Halictus	10	1	5%
	Andrena	9	1	15%
	Bombus	9	2	9%

Appendix S1.1 Effects of floral abundance on bee abundance in each soil type

Figure S1.1 (A) Netted bee richness and (B) abundance as a function of soil type and floral abundance per square meter (on a log-log scale). Lines are zero-inflated generalized linear mixed model predictions. Brown circles are observations from non-serpentine sites, and turquoise diamonds are from serpentine sites. Axes, points, and predictions were transformed to the natural log(x +1) scale simply for graphical presentation purposes.



Chapter 2: Soil type indirectly structures bee community functional composition by altering vegetation-based nesting and foraging habitat quality

Ross M. Brennan & Neal M. Williams

Introduction:

Local ecological communities are assembled from the regional species pool based on traits that determine individual species' responses to local environmental conditions and their access to key resources such as food and nesting sites (Lavorel et al. 1997, Lavorel and Garnier 2002, Williams et al. 2010). The role of such functional traits in species response means that although taxonomic analyses of communities are useful for assessing biodiversity and quantifying species turnover across space and time (Anderson et al. 2011), they are less effective in identifying general mechanisms that structure communities and could guide actions to promote and conserve biodiversity (Mouillot et al. 2013).

Research identifying and quantifying which environmental factors filter ecological communities—and according to which functional response traits—has been heavily pursued in recent years (Cornwell and Ackerly 2009, Pavoine et al. 2011). And although the functional ecology of arthropods has also received considerable attention, many studies of arthropod communities focus on broad-scale environmental drivers such as agriculture, land use intensification, and climate that alter multiple aspects of local habitats and indirectly filter higher trophic levels (Hoiss et al. 2012, Rader et al. 2014, Forrest et al. 2015). Integrating the influences on community structure of both local habitat *and* broad-scale drivers—for higher trophic levels—is far less understood, but critical for quantifying the contribution of lower trophic levels to trait filtering in higher trophic levels (Sydenham et al. 2015, Thakur and Wright 2017).

Soil characteristics naturally vary across space, with wide-ranging effects on local plant communities (Kruckeberg 1969, Reynolds et al. 2003, Ordoñez et al. 2009). Soil characteristics could also affect local habitat quality for higher trophic levels—such as by altering food availability/quality (Proctor and Whitten 1971)—but such effects have rarely been quantified (Johnson et al. 1968). For these higher trophic levels soil characteristics could directly determine the habitat for species whose nesting or other life stages interact with it (Kruckeberg 1969, Harmon-Threatt 2020, Blundell et al. 2020). Soil characteristics may also indirectly impact higher trophic levels through their effects on plants (Proctor and Whitten 1971, Robinson and Strauss 2018). Such added complexity of responses for higher trophic levels has been proposed as a framework to understand pests and their natural enemies in agricultural systems (Perović et al. 2018) but the framework has not been more broadly applied. Northern California's serpentine outcrops offer an opportunity to test both soil characteristics' direct and indirect filtering pathways on higher trophic levels according to functional response traits due to their digitated spatial distribution, distinct soil transitions, and strong effects on local plant communities (Kruckeberg 1954, Proctor and Woodell 1975, Harrison et al. 2006).

Serpentine plant communities have many endemic and serpentine-tolerating species, comprising communities that converge on several functional traits correlated with low-fertility soils—shorter stature, smaller specific leaf area index values (SLA), and lower leaf water content (Spasojevic et al. 2014). These traits are generally associated with higher water use efficiency and slower growth rates (Harrison et al. 2015). Although low-fertility soils filter plant communities toward particular suites of functional traits and are generally less productive

(Eskelinen and Harrison 2015), they also support more diverse forb species, many of which are endemic and have evolved to thrive in harsh serpentine environments more than on adjacent non-serpentine sites (Brady et al. 2005). Yet, whether these strong effects of soil-fertility on plant traits "cascade up" to affect the diversity of higher trophic levels has rarely been studied (Robinson and Strauss 2018).

Insect pollinators, and bees specifically, are a useful organismal group for testing hypotheses of how soil type may structure higher trophic communities and for partitioning direct versus indirect effects on higher trophic levels (Williams et al. 2010, Wong et al. 2019). Bees require two major resource types: nesting resources and floral trophic resources. Soil type could alter the availability and quality of both resources; in turn, nesting and floral resources interact with multiple bee functional response traits. Bees vary in nest location from those that nest in the soil, to those that nest in wood or other plant-based substrates (e.g. hollow stems), and species vary in the nesting materials they gather (e.g. mud, leaves, sand, etc.; Danforth et al. 2019). Trophic specialization varies from polylectic species that feed on pollen and nectar from many plant families to oligoleges that collect pollens from plant species in a single family (or even genus; Cane and Sipes 2006, Danforth et al. 2019). In addition, bees forage for floral resources from a central nest, and foraging range varies with body size, which itself varies widely among bee taxa (Greenleaf et al. 2007). Bee also exhibit a range of social organization, which can structure their interactions with the environment (Michener 2007). And finally, bees have divergent phenologies that temporally limit their interaction with floral resources (Vázquez et al. 2009).

We quantified the functional response trait diversity of bees across serpentine and non-serpentine grasslands and tested a series of hypotheses for how this edaphic characteristic could filter bee communities through nesting and foraging trait pathways. We expected bees to respond differently to changes in each habitat axis. (1) We hypothesized that serpentine soils would have lower quality above-ground nesting habitat, i.e. cavities in dead wood and other plant-based substrates, due to the lower primary productivity on low-nutrient serpentine soils (Brady et al. 2005). As such, we expected a lower proportion of above-ground nesting bees on serpentine soils. Soil type might also directly affect bee communities by altering the chemical or physical quality of below-ground nesting substrate (Harmon-Threatt 2020, Antoine and Forrest 2021), i.e. serpentine soils could be acutely toxic or physically unsuitable for the larvae of ground-nesting bees due to their high chemical contents (Mg, Fe, Ni, Cr; Brooks 1987), although we found no previous evidence showing adverse effects of soil chemistry. (2) We expected differences in local floral communities to affect bee communities, but less strongly than nesting habitat effects. We hypothesized that floral communities would be different and more diverse in serpentine grasslands—compared to adjacent non-serpentine—because serpentine soils often support distinct, more diverse plant assemblages compared to adjacent non-serpentine grasslands (Fernandez-Going et al. 2012). Local floral composition could differentially affect specialist versus generalist bees if flowering plant communities on one soil type were dominated by host plants of specialist bees.

(3) We hypothesized local floral composition could also interact with bee body size; non-serpentine meadows may be more likely to support larger-bodied bees that can forage across broad, resource-scarce landscapes. (4) Finally, floral phenology could directly interact with bee flight phenology; moreover, serpentine soils often support more diverse flowering plants with later flowering phenology than sister taxa on non-serpentine soils (Sianta and Kay 2021).

Therefore, we hypothesized that flowering phenology would be later on serpentine soils, and these later flowering plant communities would support later-flying bee communities.

Materials & Methods:

Study design & field sites

We selected twelve paired sites from the inner Coast Ranges of northern California representing serpentine and non-serpentine soil types. An original eight sites (four pairs) were selected and sampled during the 2017 field season, and an additional four (two pairs) were added in 2018. Sites within a pair were located an average of 1.6 km apart, and site pairs were separated from one another by an average of 31.5 km. Sites were located on public lands administered by the Bureau of Land Management and on private lands managed by the McLaughlin Reserve (University of California) and the Land Trust of Napa County. All sites were in grasslands located within a surrounding matrix of chaparral dominated by chamise (*Adenostoma fasciculatum*) and *Ceanothus* species, interspersed with oak (*Quercus* spp.) savannah and gray pine (*Pinus sabiniana*). Chaparral communities differ in species composition between serpentine and non-serpentine soils, but they were not the focus of this study. Non-serpentine grasslands are dominated by invasive Eurasian grasses and have a noticeable flowering peak during May when the abundant invasive forb *Vicia villosa* flowers in extensive mats. In contrast, serpentine grasslands harbor a diverse community of California native forbs, including many serpentine endemics, that maintain a more consistent community-wide floral abundance until late June (Kruckeberg 1954, Walker 1954, Harrison and Rajakaruna 2011). The floral communities at both habitats turn over rapidly across time.

Field sampling protocols

We sampled field sites during the spring flowering period—early April through late June—in 2017 and 2018, re-visiting each site every 10 to 14 days. On average, each site was visited 6 times within each year. We netted bees that were actively visiting flowers in each site (all by R. Brennan). Bees were netted in two 45-minute collecting sessions, one in the morning (8 AM to 12 PM) and one in the afternoon (1 PM to 5 PM). We focused on areas within each site that had high floral abundance, so that exact locations within the sites changed spatially between visits. To account for potential differences in sample area we carefully traced the walk transect followed on each date to collect bees and calculated its area along with the floral richness and abundance. Bees were only collected when weather conditions permitted—when temperatures were above 15 °C and wind speeds were less than 5 m/s. Bees are curated and currently housed at the University of California, Davis. We identified all specimens to species, except for two poorly resolved species groups (*Panurginus* and *Dialictus*) some of which were identified to morphospecies.

During each visit, we sampled the floral community and its abundance. We identified all plant species that had open inflorescences and estimated the floral abundance of each species—recorded as $\log_{10}$ bins—within 70 m of site center (Williams et al. 2012). This metric served as an estimate of the floral community available to bees during each sampling visit within the local grassland. All flower species that could not be identified in the field were collected and later identified in the lab (Baldwin et al. 2012).

Environmental habitat variables

We collected site-specific environmental data to estimate the availability of various bee nesting habitat resources using three 100 m transects and five 1 m^2 quadrats at each site. Transects were parallel and spaced approximately 20 m apart. Along each transect, we counted the number of trees that were greater than 10 cm diameter at breast height (DBH), the number of shrubs with a volume >1 m^3, and the number of pieces of dead wood (tree limbs or larger). We used these data to construct a summary metric of above-ground nesting resources that equally weighted each of the three components and varied continuously between 0 and 1. No pithy stems were encountered, so we excluded them from analysis. Within each quadrat we also estimated the % bare ground that would be available to ground-nesting bee species, calculating a mean value for each site (Forrest et al. 2015). Habitat data were collected during spring 2020. These broad habitat traits are not expected to vary widely across years.

We also used the values from the first axis of a floral community principal coordinates analysis ("floral PCo 1"; Appendix S2.1: Table S2.1.1) as an environmental variable. This axis summarizes the floral community composition of each site-year and describes the greatest amount of variation in the taxonomic composition and abundance of floral communities. We used it as a proxy for floral community composition because we hypothesized that the floral community composition could filter bees according to their flight phenology, diet breadth, or body size.

The same flower count data were used to calculate a metric of floral phenology for each site: median flowering day. This was calculated as the day of year (DOY) when 50% of cumulative floral abundance ($\log_{10}$ bins) was observed at each site. This metric summarizes how quickly flowers accumulate for the community and how extended the flowering season is at a site compared to other sites.

Independent collection of bee species traits

We collected data for five species traits describing nesting habit, diet breadth, body size, flight phenology, and sociality for bees in our study collection. These five traits summarize key axes of life history and are common in analyses of bee community response to environmental drivers (Williams et al. 2010). The nesting habit traits were nesting in the ground versus above-ground (in cavities, stems, or wood), and social versus solitary. We scored bees' diet breadth according to binary criteria: bees were considered oligolectic if females are known to collect pollen within a single plant family (or more restrictive taxonomic grouping; Cane and Sipes 2006). All other bees were scored as polylectic. Categorical traits (nesting habit, sociality, and diet breadth) were scored using well-established resources to assign a trait state for each bee species (Krombein 1967, Krombein et al. 1979, Michener 2007). We estimated bee body size by measuring the intertegular distance (ITD), the distance across the thorax between the base of a bee's wings, for between 1 and 5 specimens for each species. We interpolated the median flight day (DOY) for each bee species based on our collections. Median flight day was the DOY on which a cumulative 50% of all individuals of each bee species were collected across all sites (Forrest et al. 2015).

Our database of bee species traits was based on one compiled for a previous study in our region (Forrest et al. 2015); we then added entries for species not already available from the previous study. ITD and median flight day for every species in our dataset were estimated from specimens collected for this study.

Statistical analysis

Soil type, environmental drivers, & multivariate functional diversity

We conducted all statistical analyses in R Statistical Programming Language version 3.6.3 (R Core Team 2020). We tested whether there was a relationship between soil type and each of our environmental variables using generalized linear mixed models (GLMM's, R package *glmmTMB*; Brooks et al. 2017). We used a beta family error distribution for above-ground nesting quality and a normal error distribution for floral PCo1 and median flowering day. Each site-year combination was a replicate (n = 20). We used Akaike's Information Criterion (AICc, corrected for small sample sizes) to select the most parsimonious candidate model for each response variable.

We analyzed bee species traits using two different approaches. First, we analyzed the multivariate functional diversity of each bee community and computed two trait diversity indices (trait richness and trait dispersion) using the 'FD' package, weighted by distance with the Cailliez correction for non-Euclidean distances (Villéger et al. 2008, Laliberté and Legendre 2010). We calculated trait richness (FRic), which is a measure of how much functional space is occupied by a community—a measure of multivariate trait complementarity (Cornwell et al. 2006, Villéger et al. 2008, Mouchet et al. 2010). We also calculated trait dispersion (FDis), which summarizes the average multivariate distance in trait space of each species to its abundance-weighted community centroid (Laliberté and Legendre 2010). Because we were interested in how (or if) the functional diversity of bee communities differed between soil types, we used GLMM's to analyze differences in FRic or FDis as a response to soil type, year, above-ground habitat quality, and floral community composition. Our full model was of the form FRic (or FDis) ~ soil type + floral PC1 + soil type : floral PC1 + above-ground habitat quality + year. All analysis and model selection protocols were the same as for environmental variables. We used a beta family error distribution for both response variables.

Fourth-corner tests

In contrast to multi-variate measures of functional diversity, which described the multidimensional functional composition of bee communities on each soil type, fourth-corner tests allowed us to test explicit hypotheses about which environmental factors interacted or filtered which bee response traits. We tested different single trait compositions across our environmental variables (soil type, above-ground nesting habitat, floral community composition, and floral phenology) using these fourth-corner tests (R package *ade4*; Dray and Dufour 2007). Fourth-corner tests calculate the correlation between species' traits and the average environmental conditions of sites—unique site-year combinations, in this case—occupied by each species, weighting by species' abundances (Dray and Legendre 2008). We then tested the significance of the trait-environmental variable correlations by randomizing the environmental variable across sites. This null model is effective in identifying whether trait compositions vary across environmental variables—including soil type. However, randomly assigned null traits (i.e., not driven by environment) may produce similar trait-environment correlations that reflect other differences between sites including differences in species richness, abundance, or beta-diversity. We used a second null model—randomizing trait states across species—to test whether the patterns of trait-environment correlations we observed were indeed support for ecological links between traits and our environmental variables more independently of species. To control for autocorrelation of trait states among closely related species, we constrained trait state randomizations across species so that trait values were more likely to be swapped between more closely related species. Although such phylogenetic controls have been proposed for fourth-corner analyses, we are aware of only one study that has implemented them (ter Braak et al. 2017, Harrison et al. 2018). We adapted the analysis pipeline outlined in Harrison et al. (2018) to our own study design and used the same set of criteria to interpret the outputs of our fourth-corner tests, i.e. correlations between traits and environmental variables needed to be significant in both null models to be interpretable.

To visualize differences in trait values across environmental variables, we calculated the community weighted mean (CWM) for each of our four traits across species within each site-year combination. CWM is the relative abundance-weighted mean of trait values across all the species in a community.

Results:

Soil type and habitat quality

Above-ground nesting habitat quality, floral PCo1, and median flowering date all differed significantly between soil types. The simplest model, in which habitat quality is only a function of soil type, proved most parsimonious for all habitat metrics. Non-serpentine sites had marginally higher quality above-ground nesting-habitat (Z-score = -1.933, p-value = 0.0533; Figure 2.1A). Floral PCo1 values were much lower for serpentine sites (Z-score = -7.976, p-value < 0.001; Figure 2.1B); the sign of floral PCo1 does not matter, but rather the difference signifies that floral PCo1 differentiates serpentine and non-serpentine floral communities in terms of abundance and composition. Finally, median flowering day was significantly later in serpentine sites (Z-score = 2.089, p-value = 0.0367; Figure 2.1C)

Multivariate functional diversity, soil type, and habitat quality

We used 111 species (1743 specimens, Appendix S2.2: Table S2.2.1, 2.2.2) in the complete dataset to analyze the multivariate functional diversity of the bee community at each site-year combination. Functional trait richness (FRic) was significantly higher at serpentine sites and was a function only of soil type—to the exclusion of other habitat quality metrics (Z-score = 2.473, p-value = 0.0134; Figure 2.2A). In contrast, functional trait dispersion (FDis), was not significantly different between soil types (Figure 2.2B). None of the more complex models that included floral community or nesting habitat quality (above-ground habitat quality and % bare ground) metrics as predictors proved more predictive of bee functional richness or dispersion (FRic and FDis).

Fourth-corner tests

We used a dataset of up to 111 species (1743 specimens; some species lacked trait values for at least one of the traits, Appendix S2.2: Table S2.2.2) to analyze environment-trait relationships for nesting habit, diet breadth, flight phenology, body size, and sociality. Of five soil-by-trait comparisons, soil type X bee flight phenology (median flight day) was the only significant soil type-trait interaction; serpentine was correlated with later flying bee species (Pearson's chi-squared = 211.6416, p-value = 0.0012). In addition, three habitat characteristics significantly correlated with bee traits. Above-ground nesting quality was positively correlated with the proportion of above-ground (cavity, wood) nesting bees (Pearson's r = 0.2045, p-value = 0.0523; Figure 2.3A). Floral composition (floral PCo 1) was correlated with bee flight phenology (median flight day), with a higher proportion of late-flying bees associated with more negative values of floral PCo 1 (Pearson's r = -0.2370, p-value = 0.0325; Figure 2.3C). Floral phenology (median flowering day) was also correlated with bee flight phenology (median flight day), with later-flying bees associating with later-flowering plant communities (Pearson's r = 0.2716, p-value = 0.002; Figure 2.3B). Other environment-trait interactions proved non-significant (Appendix S2.3: Table S2.3.1). Oligoleges made up a greater proportion of specimens in serpentine communities than non-serpentine and social species were more prevalent at non-serpentine sites (Appendix S2.3: Figure S2.3.1), but neither pattern was significant.

Discussion:

Although multiple studies show the direct impacts of soil on plant communities, we demonstrate that soil type can also affect the community structure of higher trophic levels. Rather than direct effects, impacts to pollinators were through soil-type effects on vegetation characteristics that define resource quality and influence bloom timing in California serpentine grasslands. Soil type correlated directly with only one bee functional response trait (flight phenology) within bee communities. In contrast, soil type strongly correlated with bee habitat quality metrics arising from vegetation. All three habitat quality metrics(above-ground nesting habitat quality, floral composition, and floral phenology) correlated with two separate bee functional traits (nesting guild and flight phenology). Three often-considered additional functional traits (sociality, oligolecty, and body size; Moretti et al. 2009, Williams et al. 2010) did not correlate with habitat quality. Our work concurs with one study, from a different system, showing that environmental drivers can indirectly structure bee communities based upon changes to nesting habitat and floral phenology, which interact with bee functional traits (Wray and Elle 2015).

Bee functional richness was higher in serpentine sites but was not related to the habitat quality metrics. The higher bee functional richness at serpentine sites indicates that serpentine bee communities occupy more functional niche space than communities from non-serpentine meadows, but similar functional dispersion values between soil types indicate that the bee communities across soil types had similar relative abundances of different trait combinations (Laliberté and Legendre 2010) . Thus, although serpentine bee communities represent more unique trait combinations, the extreme trait combinations are represented by relatively rare species. Our results show similar patterns as other recent environmental contrasts, particularly those that compared bee functional diversity across agricultural land use gradients (Rader et al. 2014, Forrest et al. 2015) and disturbance regimes (Moretti et al. 2009).

Serpentine soils could have affected bee communities directly through deleterious chemical and physical effects on ground-nesting bees or their offspring, but our analysis suggests this is not the case. Soil texture, moisture, and pH can be important aspects of nesting-habitat suitability for ground-nesting bees and chemicals in soils may affect ground-nesting bee survival and reproduction (Cane 1991, Harmon-Threatt 2020, Antoine and Forrest 2021). Serpentine origins of soils affect their pH, soil chemistry, texture, heavy metal accumulation, and these soil characteristics support strongly divergent plant communities (Walker 1954, Proctor 1971). Thus, the lack of direct soil type effects on ground-nesting bees was unexpected.

Instead of strong direct effects on bee functional response traits, soil type affected bee functional trait distribution indirectly through its impact on plant communities and the nesting and floral resources these provided to bees. All three habitat characteristics differed between soil types. Serpentine sites generally had lower quality above-ground nesting habitat and a different, later-flowering community compared with non-serpentine sites. In some regards this result is largely confirmatory, as serpentine soils support fewer, smaller-stature woody species than their non-serpentine counterparts due to their low nutrient characteristics, resulting in less woody debris and other persistent above-ground structural vegetation (Kruckeberg 1967). Instead, serpentine soils are dominated by diverse forb communities and a community of serpentine-endemic forbs (Brady et al. 2005, Kay et al. 2011). These forb communities extend their flowering season because of the greater number of locally-adapted species and later flowering taxa on serpentine soils (Williamson and Harrison 2002, Thomson et al. 2011).

Bees sorted between soil types across the landscape according to interactions between vegetation-based habitat and both nesting and foraging functional response traits. Above-ground nesting bees were filtered out of serpentine sites that supported lower quality above-ground nesting habitat, while late-flying bees were filtered out of non-serpentine sites where there were not flowers present into the spring-summer season. Thus, non-serpentine sites could better support both nesting guilds, but these bees were generally early-flying species. In contrast, serpentine sites could support a broader range of flight phenologies (early to late-flying species), but they were more likely to be ground-nesting species.

Our results are consistent with research along agricultural land use gradients in multiple bioregions. Serpentine sites constrained nesting traits similarly to agricultural sites, where less woody material was available for above-ground nesting bee species (Forrest et al. 2015, Harrison et al. 2018). Phenological constraints based on temporal floral availability parallel those found among habitats in agricultural-natural mosaic landscapes in different regions. The earlier flight season of bees on non-serpentine is similar to an earlier flight phenology of bees found on organic farms relative to those on natural habitats in central California oak woodland (Forrest et al. 2015). In the mid-Atlantic US, forested remnants had fewer late-flying bees than adjacent agricultural or urban sites because spring canopy closure of forests brings an end to understory floral resources (Harrison et al. 2018).

Although flight phenology significantly correlated with both floral community composition and floral phenology, we hypothesize that the main habitat-trait interaction is between floral phenology and bee flight phenology. Our metric of flowering phenology—median flowering day—incorporated no data on floral composition, only describing the accumulation of flowers over time. Flowering phenology proved more strongly correlated with bee flight phenology and offered a more parsimonious explanation than floral composition of how bee flight phenology interacts with local floral resources. The broader generality among ecosystems appears to be that sites that accumulate flowers (of any species) later in the flowering season are correlated with bee species that have later median flight days.

The lack of an interaction between soil type, floral composition, and oligolecty was unsurprising. Like in previous studies, oligoleges were distributed across sites and floral communities, based upon where their host plants were located (Minckley et al. 1999, 2013). This result makes sense, as we had no reason to expect that oligolege-hosting plant species would be more common on one soil type than the other. Sites also had similar size distributions of bees, regardless of soil type or floral resources, which indicates that bees were not traveling farther distances to visit floral resources in particular soil types or with particular community compositions. And finally, sociality was uncorrelated with any local habitat metric or with soil type, indicating that there are not deeper evolutionary relationships between sociality and local landscape structure (Danforth et al. 2019).

The decoupling of nesting and trophic filters across soil types could have important impacts for bees' use of nesting and floral resources in these landscapes. Because bees have specific nesting requirements, they are anchored to places that provide necessary substrates and materials. Thus, places where there were more above-ground nesting species (in our study at non-serpentine sites) are most likely to have spatially discrete, locally-nesting bee communities—hence the correlation between above-ground nesting quality and above-ground nesting bees. Trophic resources, in contrast, can be distributed within a foraging radius of a bee's nest, and bees will cross different habitats in search of highly abundant or high-quality trophic resources (Mandelik et al. 2012). Consequently, bees integrate resources across a variable trophic landscape surrounding their nests, and in a naturally fragmented landscape like our study area, bees could forage across adjacent serpentine and non-serpentine meadows.

Generally, low-fertility serpentine soils affected bee functional diversity in predictable ways, based upon how low-fertility soils affect the functional and taxonomic diversity of plant communities. In contrast to plant communities, however, bee functional response traits had different responses to low-fertility soils based on whether nesting or foraging traits were considered. This is important because it shows that low-fertility serpentine soils expand rather than constrain the functional richness of bee communities. Whether other low-fertility soil types filter bee communities—directly or indirectly through plant-based habitat effects—remains untested. Illuminating which indirect trait filtering pathways are the most important is a key future research direction.

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Figures:

Figure 2.1 (A) Above-ground nesting quality was significantly higher in non-serpentine sites, and (B) floral community PC1 significantly differed between sites on different soil types. (C) Median flowering day was significantly later (10 days) in serpentine sites. Large points represent mean ± 95% confidence intervals, and jittered points represent values for individual sites within each soil type.

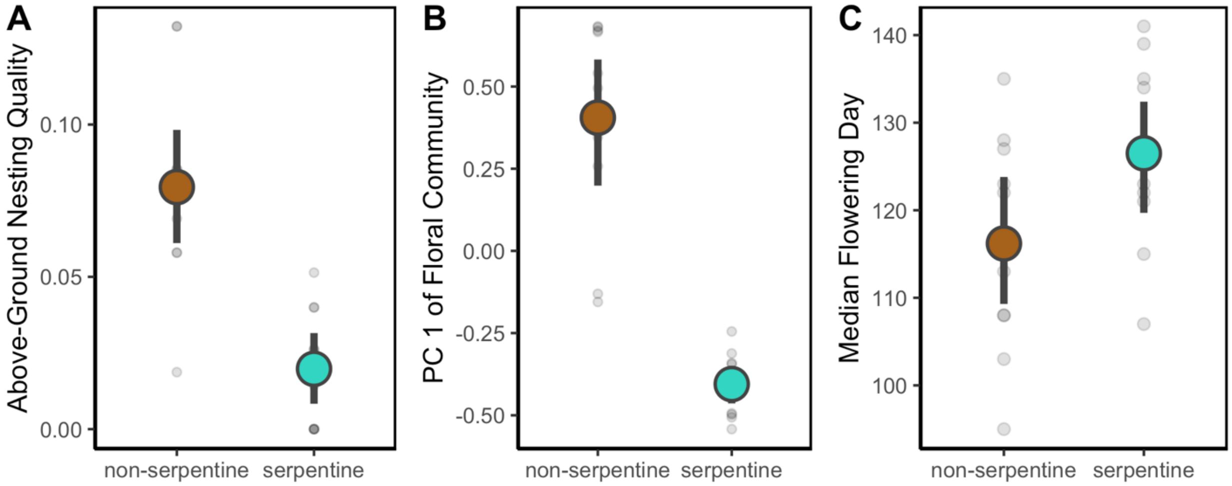


Figure 2.2 (A) Serpentine sites harbored bee communities with greater functional richness but (B) did not differ in functional dispersion. Plot attributes as in Figure 2.1.

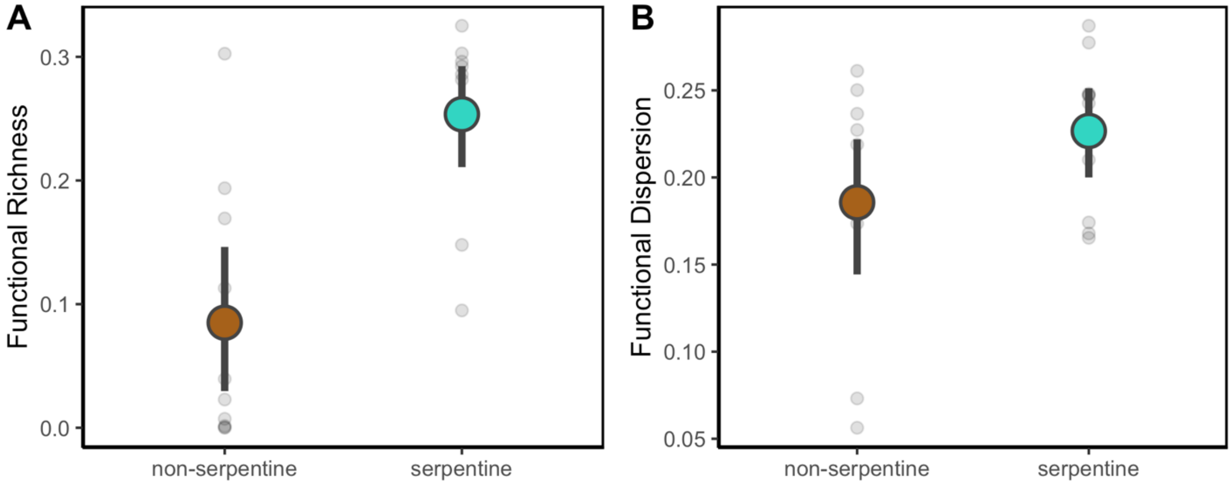
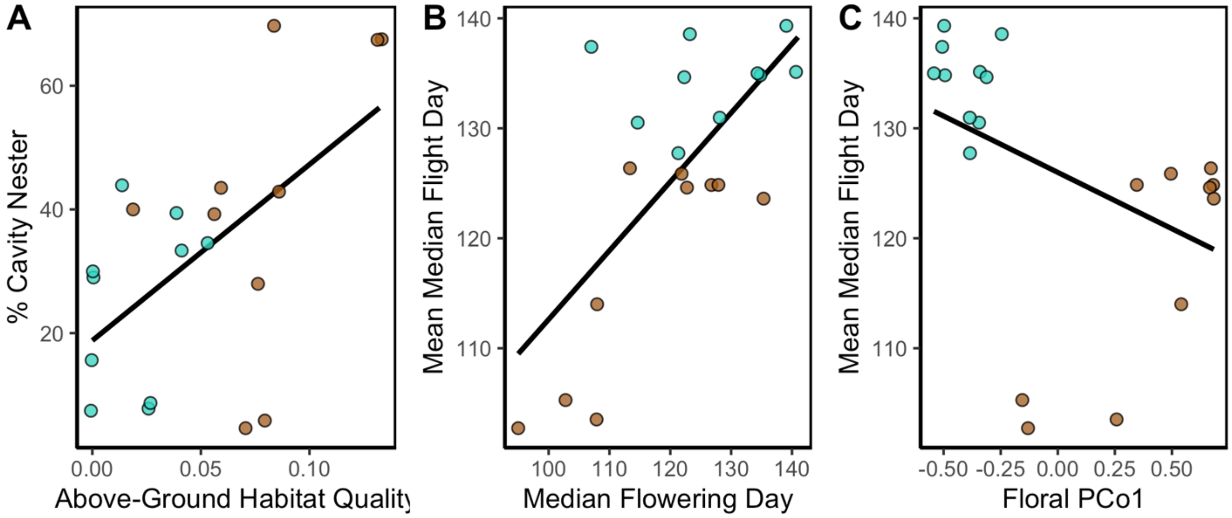


Figure 2.3 Relationships between bee functional traits and local environmental variables. (A) Sites with higher above-ground habitat quality harbored a greater proportion of cavity nesting bees. (B) Sites with a later median flowering day (day 50% of flowers were counted) harbored communities with a greater proportion of late-flying bee species. (C) Sites with more negative Floral PCo1 values harbored communities with a greater proportion of late-flying bee species. Each point represents a unique site-year combination (n = 20), and points are colored corresponding to soil type (turquoise = serpentine, brown = non-serpentine). The black trendline is included for graphical representation only but is *not* related to fourth-corner metrics. Fourth-corner tests for each environment-by-trait interaction proved statistically significant.



Supporting Information

Appendix S2.1 Habitat Quality Metrics

Table S2.1.1 Soil type and habitat variable values for each sampling site and year.

Site Name	**Year**	**Soil Type**	**Floral PCo1**	**Floral PCo2**	**Mean % Bare Ground**	**Cavity Availability**	**Median Flowering Day**
Black Diamond NS	2017	non-serpentine	-0.131	-0.185	33	7.78	95
Black Diamond NS	2018	non-serpentine	-0.155	0.846	33	7.78	103
Black Diamond S	2017	serpentine	-0.384	-0.324	51.8	4.00	121
Black Diamond S	2018	serpentine	-0.341	-0.125	51.8	4.00	141
Cathy and Paul Meadow S	2017	serpentine	-0.245	-0.258	39.6	0.00	123
Cathy and Paul Meadow S	2018	serpentine	-0.494	0.005	39.6	0.00	135
Davis Creek Road NS	2018	non-serpentine	0.680	-0.065	21	1.87	127
Delphinium Hollow S	2018	serpentine	-0.506	-0.210	24.8	1.43	107
Guard Shack NS	2017	non-serpentine	0.666	-0.122	7.6	13.22	123
Guard Shack NS	2018	non-serpentine	0.683	-0.096	7.6	13.22	135
Judge Davis NS	2018	non-serpentine	0.257	0.688	9.6	6.91	108
Lake County Line NS	2017	non-serpentine	0.346	-0.301	13.4	8.54	128
Lake County Line NS	2018	non-serpentine	0.540	0.439	13.4	8.54	108
Lynch Canyon S	2017	serpentine	-0.345	-0.194	33.8	2.62	115
Lynch Canyon S	2018	serpentine	-0.385	0.573	33.8	2.62	128
Snell Valley NS	2017	non-serpentine	0.495	-0.291	13	5.79	122
Snell Valley NS	2018	non-serpentine	0.670	-0.154	13	5.79	113
Snell Valley S	2017	serpentine	-0.312	-0.366	37.4	0.00	122
Snell Valley S	2018	serpentine	-0.542	-0.208	37.4	0.00	134
Walker Ridge S	2018	serpentine	-0.498	0.347	43.2	5.14	139

Appendix S2.2 Bee Community Diversity Summary

Table S2.2.1 Bee Community Taxonomic Richness & Functional Diversity for each site-year combination.

Site Name	Year	Soil Type	Bee Species Richness	FRic	FDis
Black Diamond NS	2017	non-serpentine	8	0.08560378	0.169374
Black Diamond NS	2018	non-serpentine	4	3.34E-04	0.07363059
Black Diamond S	2017	serpentine	25	0.62876509	0.28950472
Black Diamond S	2018	serpentine	22	0.771266	0.28971203
Cathy and Paul Meadow S	2017	serpentine	25	0.78023911	0.24805324
Cathy and Paul Meadow S	2018	serpentine	28	0.62276104	0.23974571
Davis Creek Road NS	2018	non-serpentine	6	0.02859883	0.21888063
Delphinium Hollow S	2018	serpentine	15	0.36280066	0.2483313
Guard Shack NS	2017	non-serpentine	22	0.45748453	0.17667556
Guard Shack NS	2018	non-serpentine	18	0.39575436	0.22725516
Judge Davis NS	2018	non-serpentine	5	0.00447476	0.03964224
Lynch Canyon S	2017	serpentine	17	0.3242698	0.1737839
Lynch Canyon S	2018	serpentine	15	0.78440561	0.1656132
Lake County Line NS	2017	non-serpentine	7	0.29203763	0.25015266
Lake County Line NS	2018	non-serpentine	6	0.24667398	0.17801255
Snell Valley NS	2017	non-serpentine	25	0.74556317	0.24117554
Snell Valley NS	2018	non-serpentine	28	0.56933787	0.26183169
Snell Valley S	2017	serpentine	27	0.59469244	0.16534228
Snell Valley S	2018	serpentine	33	0.70977078	0.24769177
Walker Ridge S	2018	serpentine	21	0.71496535	0.21814125

Table S2.2.2 Functional Trait summary for all species & traits

Species	Nesting Location	Lecty	Sociality / Parasitic	Mean Inter-tegular Distance (mm)	Median Flight Day (DOY)
Agapostemon texanus	below-ground	polylectic	solitary	2.06	129
Andrena angustitarsata	below-ground	polylectic	solitary	1.84	93
Andrena baeriae	above-ground	oligolectic	solitary	1.46	122
Andrena caerulea	above-ground	oligolectic	solitary	1.69	94
Andrena chalybioides	below-ground	oligolectic	solitary	1.82	99
Andrena chlorogaster	below-ground	polylectic	solitary	1.20	108
Andrena cuneilabris	below-ground	oligolectic	solitary	2.08	103
Andrena hallii	above-ground	oligolectic	solitary	2.57	115
Andrena lativentris	above-ground	UNK	solitary	1.68	110.5
Andrena lewisorum	above-ground	oligolectic	solitary	1.93	137
Andrena microchlora	above-ground	polylectic	solitary	1.24	108
Andrena orthocarpi	below-ground	polylectic	solitary	1.45	113
Andrena pallidifovea	below-ground	oligolectic	solitary	2.00	122
Andrena pallidiscopa	above-ground	UNK	solitary	2.13	115
Andrena pensilis	below-ground	oligolectic	solitary	1.94	123
Andrena plana	above-ground	oligolectic	solitary	1.87	127.5
Andrena suavis	below-ground	oligolectic	solitary	1.57	103
Andrena subchalybea	below-ground	oligolectic	solitary	1.80	99
Andrena submoesta	above-ground	oligolectic	solitary	1.47	122
Anthidium collectum	above-ground	polylectic	solitary	2.70	127
Anthidium edwardsii	above-ground	polylectic	solitary	2.40	157
Anthidium illustre	above-ground	polylectic	solitary	3.45	127
Anthidium utahense	above-ground	polylectic	solitary	UNK	157
Anthophora urbana	below-ground	polylectic	solitary	UNK	151
Anthophorula nitens	above-ground	UNK	solitary	1.28	150.5
Anthophorula torticornis	above-ground	oligolectic	solitary	1.45	171
Apis mellifera	above-ground	polylectic	social	2.95	109
Ashmeadiella cactorum	above-ground	polylectic	solitary	UNK	157
Ashmeadiella californica	above-ground	polylectic	solitary	1.57	157

Ashmeadiella cubiceps clypeata	above-ground	polylectic	solitary	1.35	140
Ashmeadiella timberlakei	above-ground	polylectic	solitary	1.19	150
Bombus californicus	above-ground	polylectic	social	3.55	142
Bombus melanopygus	above-ground	polylectic	social	1.82	108
Bombus vosnesenskii	below-ground	polylectic	social	4.22	128
Calliopsis anthidius anthidius	above-ground	oligolectic	solitary	2.25	157
Calliopsis boharti	above-ground	oligolectic	solitary	UNK	121
Calliopsis cincta hurdi	above-ground	oligolectic	solitary	2.30	143
Chelostoma californica	above-ground	oligolectic	solitary	1.43	95
Diadasia angusticeps	above-ground	oligolectic	solitary	2.02	150
Diadasia bituberculata	below-ground	oligolectic	solitary	3.22	137
Diadasia laticauda	above-ground	oligolectic	solitary	2.45	150
Diadasia nigrifrons	above-ground	oligolectic	solitary	2.40	144
Diadasia nitidifrons	above-ground	oligolectic	solitary	2.33	149
Dianthidium dubium dubium	above-ground	polylectic	solitary	2.03	150
Dufourea calientensis	above-ground	UNK	solitary	1.03	103
Eucera actuosa	below-ground	polylectic	solitary	2.57	139
Eucera frater albopilosa	above-ground	polylectic	solitary	3.71	129
Eucera lunata	below-ground	polylectic	solitary	3.17	107
Eucera monozona	above-ground	polylectic	solitary	3.36	128
Eucera primiveris	above-ground	polylectic	solitary	3.33	128
Eucera virgata	below-ground	polylectic	solitary	3.05	148
Habropoda sp. 1	above-ground	UNK	solitary	3.82	130
Habropoda sp. 2	above-ground	UNK	solitary	3.72	126
Habropoda sp. 3	above-ground	UNK	solitary	3.90	123
Habropoda sp. 4	above-ground	UNK	solitary	3.65	107
Halictus farinosus	below-ground	polylectic	social	2.34	149
Halictus ligatus	below-ground	polylectic	social	1.77	135
Halictus tripartitus	below-ground	polylectic	social	1.20	149
Hesperapis regularis	above-ground	oligolectic	solitary	2.03	138
Hoplitis albifrons maura	above-ground	polylectic	solitary	2.54	135
Hoplitis fulgida platyura	above-ground	polylectic	solitary	1.72	96

Hoplitis hypocrita	above-ground	polylectic	solitary	2.80	110.5
Hoplitis producta gracilis	above-ground	polylectic	solitary	1.27	142.5
Hoplitis sambuci	above-ground	polylectic	solitary	2.36	134
Lasioglossum incompletum	below-ground	polylectic	social	0.94	135
Lasioglossum mellipes	below-ground	polylectic	solitary	2.07	118
Lasioglossum punctatum	above-ground	polylectic	social	1.05	105
Lasioglossum robusta	above-ground	polylectic	social	1.74	134
Lasioglossum sisymbrii	above-ground	polylectic	social	1.85	113
Lasioglossum sp. 16	above-ground	polylectic	social	1.61	134
Lasioglossum sp. 2	above-ground	polylectic	social	0.99	134
Lasioglossum titusi	below-ground	polylectic	solitary	2.08	135
Megachile apicalis	above-ground	oligolectic	solitary	2.51	160.5
Megachile angelarum	above-ground	polylectic	solitary	UNK	150
Megachile gentilis	above-ground	polylectic	solitary	3.00	148
Megachile gravita	above-ground	oligolectic	solitary	2.73	149.5
Megachile parallela	below-ground	polylectic	solitary	3.30	151
Megachile pascoensis	above-ground	oligolectic	solitary	2.84	139
Melissodes lupina	below-ground	oligolectic	solitary	2.15	157
Osmia aglaia	above-ground	polylectic	solitary	2.27	150
Osmia atrocyanea	above-ground	polylectic	solitary	2.90	127
Osmia brevis	above-ground	oligolectic	solitary	2.46	122
Osmia californica	above-ground	polylectic	solitary	3.04	118
Osmia cara	above-ground	UK	solitary	3.13	122.5
Osmia clarescens	above-ground	polylectic	solitary	2.70	108
Osmia coloradensis	above-ground	oligolectic	solitary	2.37	129
Osmia cyanella	above-ground	UK	solitary	2.43	113
Osmia densa	above-ground	polylectic	solitary	2.77	118
Osmia gabrielis	above-ground	polylectic	solitary	2.91	132.5
Osmia glauca	above-ground	oligolectic	solitary	1.47	108
Osmia granulosa	above-ground	UK	solitary	2.04	128
Osmia kincaidii	above-ground	polylectic	solitary	1.64	108
Osmia laeta	above-ground	polylectic	solitary	2.31	134.5
Osmia latisulcatus	above-ground	polylectic	solitary	2.80	128
Osmia lignaria	above-ground	polylectic	solitary	2.87	123
Osmia melanopleura	above-ground	UNK	solitary	2.03	113
Osmia montana quadriceps	above-ground	polylectic	solitary	2.76	95
Osmia nemoris	above-ground	polylectic	solitary	UNK	142

Osmia nigrifrons	above-ground	oligolectic	solitary	3.10	117
Osmia pusilla	above-ground	polylectic	solitary	1.96	137
Osmia regulina	above-ground	polylectic	solitary	2.02	146.5
Osmia trevori	above-ground	polylectic	solitary	2.26	142
Osmia visenda	above-ground	polylectic	solitary	2.93	123
Panurginus nigrellus	below-ground	polylectic	solitary	UNK	99
Panurginus nigrihirta	above-ground	polylectic	solitary	UNK	93.5
Protosmia rubifloris	above-ground	polylectic	solitary	1.58	127
Stelis montana	above-ground	UNK	parasite	2.10	135
Stelis pavonina	above-ground	UNK	parasite	2.38	117
Triepeolus sp. 1	below-ground	UNK	parasite	UNK	157
Xylocopa californica	above-ground	polylectic	solitary	6.30	127
Xylocopa tabaniformis	above-ground	polylectic	solitary	5.70	127

Appendix S2.3 Fourth Corner Analyses

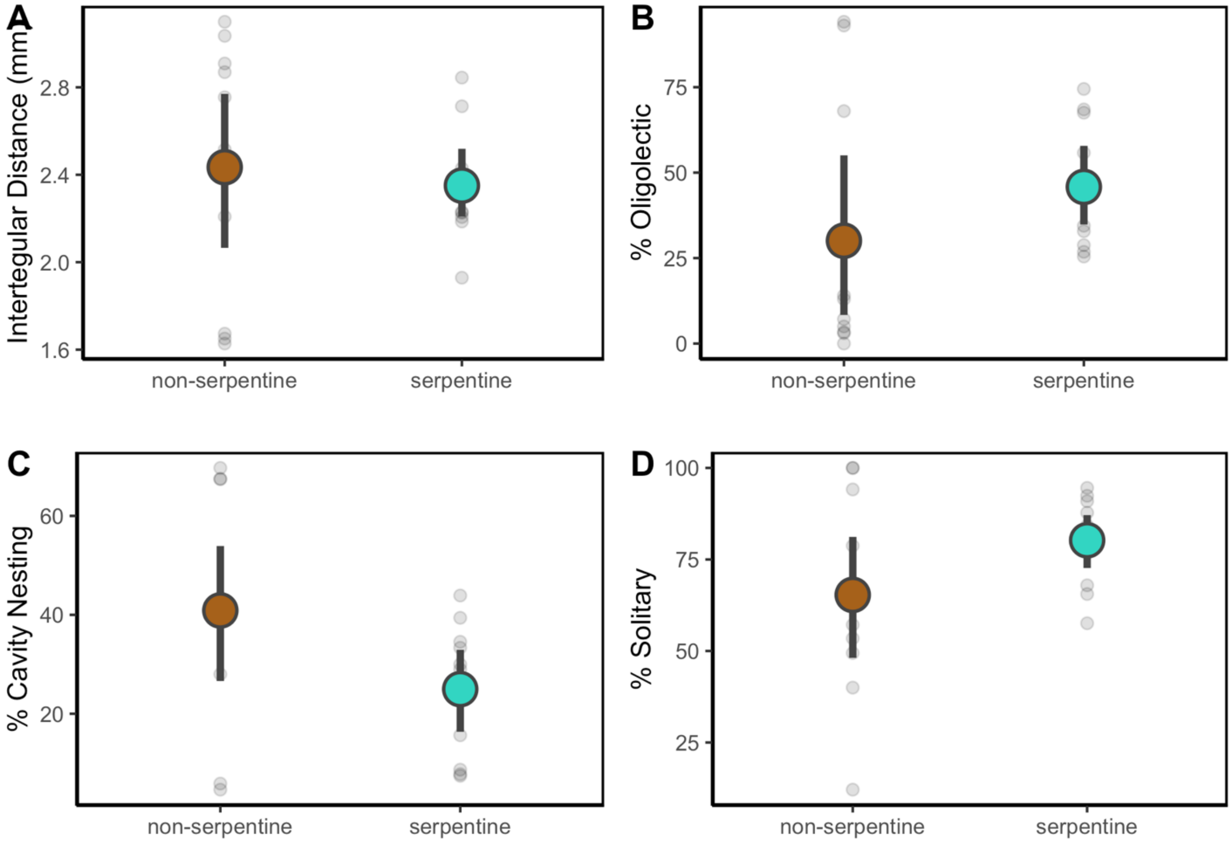


Figure S2.3.1 Community-weighted mean values for bee functional traits contrasted by soil type. (A) Intertegular Distance (ITD), (B) % of individuals that were oligolectic, (C) % of individuals that nested in cavities, etc., and (D) % of individuals that were solitary. Fourth-corner analyses show that there were no significant correlations between soil type and any of the functional traits shown here. Large points represent mean ± 95% confidence intervals, and jittered points represent values for individual sites within each soil type.

Table S2.3.1 Fourth-Corner Analysis Summary for all Habitat by Trait Combinations

Habitat Variable	Trait	Test Statistic	Test Value	p-value (species permutations)	p-value (site permutations)	Number of Species	Number of Specimens
Soil Type	Lecty	Pearson's Chi-Squared	12.8470	0.4863	0.5176	101	1697
Soil Type	Inter-tegular Distance	Pearson's Chi-Squared	6.6707	0.6294	0.5714	103	1681
Soil Type	Sociality	Pearson's Chi-Squared	0.2853	0.8897	0.8881	111	1743
Soil Type	Nesting Habit	Pearson's Chi-Squared	18.0287	0.4526	0.3506	106	1724
Soil Type	Median Flight Day	Pearson's Chi-Squared	211.6416	0.0008	**0.0023** **	111	1743
Above-ground Nesting Habitat	Nesting Habit	Pearson's r	0.2002	0.0665	**0.0555 †**	106	1724
Floral PCo1	Lecty	Pearson's r	-0.1582	0.1238	0.2291	101	1697
Floral PCo1	Inter-tegular Distance	Pearson's r	0.1526	0.2429	0.1490	103	1681
Floral PCo1	Median Flight Day	Pearson's r	-0.2370	0.0140	**0.0274** *	111	1743
Median Flowering Day	Median Flight Day	Pearson's r	0.2716	0.0018	**0.0087** **	111	1743

Chapter 3: Plant-pollinator networks are marginally less specialized and more unique in serpentine habitats, driven by lower interaction turnover and higher frequency pollinator rewiring

Ross M. Brennan & Neal M. Williams

Introduction:

Species diversity and community similarity are the focus of considerable attention in community ecology, particularly with regards to biodiversity gradients (Hillebrand 2004), anthropogenic biodiversity loss, and global and local biodiversity hotspots (Orme et al. 2005). In addition to local richness of species (α-diversity), the turnover of species across space and time ($\boldsymbol{\beta}$-diversity; Anderson et al. 2011), strongly structures patterns of species diversity, both along natural and anthropogenic environmental gradients (Dornelas et al. 2014, Socolar et al. 2016, Nielsen et al. 2019). Spatial and temporal $\boldsymbol{\beta}$-diversity increase with separation among sites in space and time (Nekola and White 1999).

In addition to the turnover of species, understanding the drivers that structure interactions among species is a critical field of study. Interactions among species can have wide-ranging effects on communities and ecosystem functions, including determining community sensitivity and resilience to environmental changes (Memmott et al. 2004). Species interactions can also reflect patterns in the intensity of competition within communities and the balance of niche and neutral processes in structuring ecological communities (Vázquez et al. 2009).

Network analyses are an important tool for quantifying interaction patterns at the community level and have been used to evaluate bipartite interactions between herbivores and food sources, as well as mutualistic pollination networks where pollinators visit floral resources.

Quantifying the topology of different networks can help determine if interactions deviate from neutral processes and can offer holistic summary metrics to compare networks (Dormann et al. 2009). However, these network-level metrics lack any information on the identity of species or links in the network—network "microstructure". Thus, two networks could "look" similar—show similar values for a given network metric—although they might not share any species or links. Although such network-wide properties are useful for comparing network topology across systems and identifying emergent properties (Thébault and Fontaine 2010), they obscure important information regarding shared species and links among networks (Kaiser-Bunbury et al. 2014).

The temporal and geographic turnover of species and interactions in networks has received growing attention in recent years, and species show strong temporal and spatial plasticity in linkage patterns across small and broad temporal and geographic scales (Burkle et al. 2013, Trøjelsgaard et al. 2015, Cirtwill et al. 2018). Yet, species and interaction turnover are not limited to spatiotemporal gradients, and the turnover of interactions across other environmental gradients continues to be a focus of research, generally finding that less invaded, more natural, and more restored networks are more resilient to disturbance (Noreika et al. 2019, Arroyo-Correa et al. 2020, Morrison and Dirzo 2020).

Regardless of the environmental gradient, interaction turnover among networks is due to either species turnover at one or both levels or interaction turnover among shared species (Novotny 2009, Poisot et al. 2012). Interaction turnover among shared species can be further partitioned into rewiring (shared species switch interaction partners between networks) and interaction richness (shared species expand or contract the number of interaction partners between networks) components (Figure 3.1; Noreika et al. 2019, Fründ 2021). In pollination systems, partitioning interaction $\boldsymbol{\beta}$-diversity reveals the extent to which pollinator behavioral plasticity contributes to overall link structure and network flexibility across environmental or temporal gradients (CaraDonna et al. 2017), potentially highlighting the drivers behind local biodiversity and network resilience.

There is abundant recent focus on interaction $\boldsymbol{\beta}$-diversity across spatial and temporal gradients, with several studies decomposing plant-pollinator interaction turnover into its additive components (Carstensen et al. 2014, Trøjelsgaard et al. 2015, CaraDonna et al. 2017, Bramon Mora et al. 2020). Whether interactions turn over similarly across other environmental gradients (e.g. time since restoration) is an emerging field (Noreika et al. 2019). Understanding the relative contribution of pollinator behavior and species turnover to network structure may provide insights into network resilience in different environmental contexts (Burkle and Alarcón 2011); pollinator foraging flexibility is often cited as a key network property for ensuring system resilience and stability, particularly after restoration or invasion (Albrecht et al. 2014, Ponisio et al. 2017). Thus, it is essential to accurately quantify how strongly interaction rewiring contributes to interaction turnover among local networks (Simanonok and Burkle 2014). And importantly, species and interactions may be filtered by different environmental and biotic conditions, meaning species and interactions may respond differently to natural or anthropogenic changes.

Here, we focus on plant-pollinator (i.e., bee-flower) interaction networks and their turnover across an abrupt environmental transition in soil type between serpentine and non-serpentine grasslands in northern California. Although the natural edaphic boundaries are abrupt in our system, the pollinators (mostly wild native bees) are highly mobile and potentially link interactions among flowering communities on the two soil types. Thus, we expected the potential interactions to be markedly different between soil types, where flower communities deviate, and we anticipated that the turnover of interactions could be driven via host-switching by pollinators that occurred in networks on both soil types. As such, we had four key aims. First, we quantified network topology for each local network and tested whether network topology differed between networks located on serpentine and non-serpentine soils. This would tell us whether edaphic transitions generate differences in overall network structure, regardless of the interacting species' identities. Second, we characterized interaction turnover among sites and between soil types, testing whether interaction composition among networks within the same soil type was more similar than between soil types. Here, we were interested to know whether interactions followed similar patterns to flower and bee species turnover across soil type. Third, we decomposed interaction turnover into species turnover, interaction richness differences among shared species, and rewiring to understand whether interaction turnover differences among sites or across soil types differed in the contribution of pollinator behavioral plasticity to interaction turnover. And finally, we compared local networks to a regional meta-web to evaluate each network's uniqueness compared to the regional interaction pool. This metric tells us how much local networks varied in interaction diversity compared to a pooled network of shared interactions.

Methods:

Study design & field sites

We selected twelve paired sites from the inner Coast Ranges of northern California representing serpentine and non-serpentine soil types. An original eight sites (four pairs) were sampled during the 2017 and 2018 field seasons, and an additional four (two pairs) were added in 2018. Sites within a pair were located an average of 1.6 km apart, and site pairs were separated from one another by an average of 31.5 km. Sites were located on public lands administered by the Bureau of Land Management and on private lands managed by the McLaughlin Reserve (University of California) and the Land Trust of Napa County. All sites were in grasslands located within a surrounding matrix of chaparral dominated by chamise (*Adenostoma fasciculatum*) and *Ceanothus* species, interspersed with oak (*Quercus* spp.) savannah and gray pine (*Pinus sabiniana*). Chaparral communities differ in species composition between serpentine and non-serpentine soils, but they were not the focus of this study. Non-serpentine grasslands are dominated by invasive Eurasian grasses and have a noticeable flowering peak during May when the abundant invasive forb *Vicia villosa* flowers in extensive mats. In contrast, serpentine grasslands harbor a diverse community of California native forbs, including many serpentine endemics, that maintain a more consistent community-wide floral abundance until late June (Kruckeberg 1954, Walker 1954, Harrison and Rajakaruna 2011). The floral communities at both habitats turn over rapidly across time.

Field sampling protocols

We sampled field sites during the spring flowering period—early April through late June—in 2017 and 2018, re-visiting each site every 10 to 14 days. On average, each site was visited 6 times within each year. We netted bees that were actively visiting flowers in each site (all by R. Brennan). Bees were netted in two 45-minute collecting sessions, one in the morning (8 AM to 12 PM) and one in the afternoon (1 PM to 5 PM). We focused on areas within each site that had high floral abundance, so that exact locations within the sites changed spatially between visits. To account for potential differences in sample area we carefully traced the walk transect followed on each date to collect bees and calculated its area along with the floral richness and abundance. Bees were only collected when weather conditions permitted—when temperatures were above 15 °C and wind speeds were less than 5 m/s.

We identified species according to published taxonomic revisions. Many specimens (from a variety of taxa) were identified by T. Griswold, and bees in the genus *Andrena* were identified by H. Ikerd (USDA ARS Pollinating Insect Laboratory, Logan, UT). We identified all specimens to species, except for two poorly resolved species groups (*Panurginus* and *Dialictus*) which were identified to morphospecies. Bees are curated and currently housed at the University of California, Davis.

During each visit, we also quantified floral abundance of all non-grass flowering plant species at the site. We identified all plant species that had open inflorescences and estimated the floral abundance of each species—recorded as $\log_{10}$ bins—within 70 m of site center (Williams et al. 2012). This metric served as an estimate of the floral community available to bees during each sampling visit within the local grassland. All flower species that could not be identified in the field were collected and later identified in the lab (Baldwin et al. 2012).

Data analysis

Plant-pollinator interaction network metrics

We conducted all statistical analyses in R (R Core Team 2020). Network metric calculations were calculated using the 'bipartite' package (Dormann et al. 2008). We constructed quantitative bipartite matrices of pollinator-flower interactions for each site-year and calculated the following network topology metrics: *connectance*, *network-level specialization* (H_2'), and *weighted nestedness* (*wNODF*). *Connectance* summarizes a key component of network complexity and is calculated as the proportion of possible network links that are realized. H_2' is a frequency-derived metric that measures the amount of interaction specialization in a network; it indicates the overall deviation of species' interaction patterns compared to those expected by relative frequencies (Blüthgen et al. 2006). *wNODF* is a measure of nestedness based on overlap and decreasing fill, which describes the extent to which specialized species (with relatively few links) interact with more generalized species (with many links; Almeida-Neto and Ulrich 2011).

We tested whether these network-level metrics differed by soil type using zero-inflated generalized linear mixed models (GLMMs) in the ‘glmmTMB’ package (Brooks et al. 2017). For *connectance* and H_2', which are bounded between 0 and 1, we used GLMMs with beta family error distributions; beta error distributions do not include the values 0 or 1, so for response values of 1, we subtracted a nuisance value of 0.0001 from the response. Because we were interested in whether network metrics differed between soil types—not their absolute values—subtracting a nuisance value should not influence our overall interpretation of results. For the *wNODF* GLMM, we used a tweedie family error distribution. All models had the same basic structure, with random effects for each unique site-year combination (n = 20) and fixed effects for soil type and year. Year was only included as a fixed effect because it only had two levels, so could not be included as a random effect.

In addition to testing whether there were differences in network metrics between soil types, we tested if our GLMM coefficients differed from those derived from random interaction networks using a null model approach using Patefield’s formulation, which allows connectance to vary (“r2d” in the ‘bipartite’ package). We constructed 4,999 sets of randomized local networks (n = 20 in each set) and fit our GLMM to the network metrics for each set of 20 randomized networks and stored the coefficients from each GLMM. Finally, we calculated a two-tailed p-value for our observed coefficient values compared to the distribution of coefficient values from randomized networks. We did not use null models for *wNODF* as the GLMMs often failed to converge.

We also calculated a specialization metric for each pollinator species—*d’*. This is a species-level analog to H_2', i.e. the degree to which a species' interactions deviate from a pattern expected based upon the frequency of potential interactors; it allowed us to deconstruct H_2' to understand whether species are, on average, more specialized on one soil type than the other (0 = complete generalization, 1 = complete specialization). We used the same approach as for network-level metrics, with GLMMs to test for differences in d' between soil types (but with "species identity" as a random factor). Importantly, we added a zero-inflated model component to this GLMM because d' data included zero values, which a beta error distribution will not model.

Plant-Pollinator Interaction $\boldsymbol{\beta}$-diversity Decomposition

We quantified the turnover of interactions among networks by making pairwise comparisons between all networks. We calculated interaction $\boldsymbol{\beta}$-diversity as quantitative Jaccard dissimilarity (Ružička index) in the 'bipartite' package, using function 'betalinkr' and the "common denominator" method for decomposing interaction $\boldsymbol{\beta}$-diversity (Dormann et al. 2008, Fründ 2021). We then deconstructed total interaction $\boldsymbol{\beta}$-diversity ($\boldsymbol{\beta}_{\mathrm{WN}}$) into its additive components: interaction $\boldsymbol{\beta}$-diversity among shared species ($\boldsymbol{\beta}_{\mathrm{OS}}$) and interaction $\boldsymbol{\beta}$-diversity due to species turnover ($\boldsymbol{\beta}_{\mathrm{ST}}$). Furthermore, we used a secondary decomposition of $\boldsymbol{\beta}_{\mathrm{OS}}$ to partition it into "true rewiring" ($\boldsymbol{\beta}_{\mathrm{OS.repl}}$) and shared-species $\boldsymbol{\beta}$-diversity due to differences in link richness ($\boldsymbol{\beta}_{\mathrm{OS.rich}}$, Figure 3.1; Noreika et al. 2019).

Based on the distance matrices from pairwise comparison of local networks, we tested if interaction $\boldsymbol{\beta}$-diversity differed between soil types using Permutational Analysis of Variance (PerMANOVA; function 'adonis' in the 'vegan' package, Oksanen et al. 2018). To visualize differences between soil types, and the multivariate distances among sites within and among soil types, we plotted our data using nonparametric multidimensional scaling (NMDS) also using the ‘vegan’ package. Each point in the plot corresponds to a local network, and 2-dimensional distances among them represent the relative $\boldsymbol{\beta}$-diversity between any given point and all other points.

To test whether behavioral plasticity affected interaction turnover differently in different soil types, we modeled interaction $\boldsymbol{\beta}$-diversity and its components using a zero-inflated GLMM with $\boldsymbol{\beta}_{\mathrm{WN}}$ (and its components) as the response with a predictor assigning whether the compared sites were both serpentine, both non-serpentine, or from different soil types. This allowed us to test whether interaction dissimilarity differed within soil types versus across soil types. All models included a random observation-level variable to correct for overdispersion. All models used a beta-family error distribution, and if response variables included zeroes, these were modeled using a logit-based zero-inflation model. We used a log likelihood ratio to test whether our grouping factor was a significant predictor.

Comparison to the meta-web

In addition to our pairwise analysis of interaction $\boldsymbol{\beta}$-diversity, we compared each site-level network for each year to an aggregated network across all sites and years, the “meta-web” (Poisot et al. 2012). Comparing local networks to a pooled meta-web can provide insight regarding what proportion of regional links each local network captures, i.e., to what extent local networks are unique subsets of the regional meta-web versus small replicates of it (Carstensen et al. 2014). This can be quantified by calculating the interaction $\boldsymbol{\beta}$-diversity between a local network, and the portion of the meta-web that shares species with the local network, known as $\boldsymbol{\beta}'_{\mathrm{OS}}$. When $\boldsymbol{\beta}'_{\mathrm{OS}}$ approaches 1, there is a large difference between the interactions observed in the local network and those found in the shared portion of the meta-web. If, on the other hand, a local network shares most interactions in the shared portion of the meta-web (or relative abundances are similar), then $\boldsymbol{\beta}'_{\mathrm{OS}}$ approaches zero.

We tested whether local networks were more unique on one soil type by constructing a GLMM with $\boldsymbol{\beta}'_{\mathrm{OS}}$ as the response variable. $\boldsymbol{\beta}'_{\mathrm{OS}}$ was calculated as the quantitative $\boldsymbol{\beta}'_{\mathrm{OS}}$ using the original formulation (Poisot et al. 2012). This model tested whether the interaction dissimilarity between local networks and the shared portion of the total meta-web was higher on serpentine or non-serpentine soils. The predictor for this model was the soil type for each site-year network, with random effects for each site pair and each unique network. We used a beta-family error distribution, without a zero-inflated model component or nuisance subtraction as no values were equal to zero or one.

Results:

Network-wide and species-level metrics

Both connectance and network-level specialization (H_2') were lower for networks in serpentine meadows than in non-serpentine meadows, although H_2' was only marginally so (Figure 3.2, Table 3.1). Nestedness (*wNODF*) did not differ significantly between networks on different soil types. Species-level specialization (*d'*) did not differ between networks on the two soil types, but pollinator species in non-serpentine networks were more likely to have a *d'* of zero. For all GLMMs, null models showed that model coefficients were significantly different from those calculated for randomized networks (Table 3.2).

Pairwise interaction $\boldsymbol{\beta}$-diversity

Pairwise interaction $\boldsymbol{\beta}$-diversity ($\boldsymbol{\beta}_{\mathrm{WN}}$) was high (mean = 0.94) among sites and the majority of interaction turnover was due to species turnover ($\boldsymbol{\beta}_{\mathrm{ST}}$). In all pairwise comparisons (n = 190), interaction turnover among shared species made up on average only 14% of total interaction turnover, and on average only 3.6% of interactions truly rewired. The PerMANOVA showed that interaction composition of networks on serpentine soils did not differ significantly from those on non-serpentine soils (F = 0.839, $r^2 = 0.0445$, p-value = 0.730).

When we examined pairwise interaction turnover between sites within and among soil type, we found that overall interaction turnover ($\boldsymbol{\beta}_{\mathrm{WN}}$) was significantly higher between sites from different soil types, than between sites from the same soil type. $\boldsymbol{\beta}_{\mathrm{WN}}$ also was significantly lower between serpentine sites than between non-serpentine sites (Figure 3.2). The portion of interaction turnover due to species turnover ($\boldsymbol{\beta}_{\mathrm{ST}}$) followed a similar pattern: $\boldsymbol{\beta}_{\mathrm{ST}}$ was highest between sites from different soil types, followed by $\boldsymbol{\beta}_{\mathrm{ST}}$ between non-serpentine sites, and finally the lowest $\boldsymbol{\beta}_{\mathrm{ST}}$ values were between serpentine networks. In other words, more interaction turnover was due to species turnover among sites from different soil types, and serpentine sites had the lowest interaction turnover due to species turnover.

Interaction turnover among shared species ($\boldsymbol{\beta}_{\mathrm{OS}}$) showed more complex patterns. $\boldsymbol{\beta}_{\mathrm{OS}}$ was more likely to be zero between sites on different soil types than between non-serpentine sites, and $\boldsymbol{\beta}_{\mathrm{OS}}$ was non-zero between all serpentine sites. For $\boldsymbol{\beta}_{\mathrm{OS}}$ values that were non-zero, $\boldsymbol{\beta}_{\mathrm{OS}}$ was higher between sites from different soil types, but $\boldsymbol{\beta}_{\mathrm{OS}}$ among serpentine sites was similar to $\boldsymbol{\beta}_{\mathrm{OS}}$ among non-serpentine sites (Figure 3.3). This means that species turnover contributed more to overall interaction turnover between networks on different soil types than between networks on the same soil type. True rewiring ($\boldsymbol{\beta}_{\mathrm{OS.repl}}$) followed a similar pattern: $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ was most likely to be zero between sites on different soil types and $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ among non-serpentine networks was more likely to be zero than $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ among serpentine networks (Figure 3.4; Table 3.3). For pairs where $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ was non-zero, $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ was similar between serpentine sites and non-serpentine sites and $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ between networks on different soil types was significantly lower (Figure 3.3; Table 3.3). This means that true rewiring of interactions was lowest between networks on serpentine versus non-serpentine soils, and highest between networks that were both on serpentine soils.

Dissimilarity to the meta-web

When we compared each network to the pooled meta-web, we found that $\boldsymbol{\beta}'_{OS}$ was significantly higher for serpentine meadows (serpentine = 0.643, non-serpentine = 0.495, Wald chi-squared = 5.262, p-value = 0.0218; Figure 3.5, Table 3.3). This means that each serpentine network was more distinct from its shared portion of the meta-web than each non-serpentine network was from its shared portion of the meta-web.

Discussion:

In this study, we examined variation in the structure of flower-bee networks and identified whether broad/emergent differences in network structure—as described by network topology—were driven by network microstructure due to differences in soil type. We quantified differences among networks using network-wide metrics, deconstructed these into their species-level components, and tested whether these metrics differed for networks in grasslands on different soil types. We also used newly modified interaction turnover analyses to identify whether differences in overall network structure were due primarily to changes in pollinator behavior (true re-wiring) among networks, or due to species turnover and richness differences among networks.

Bee-flower visitor networks on serpentine sites had lower *connectance* than those on non-serpentine sites and were marginally less specialized (H_2'). Higher *connectance* in non-serpentine networks was unsurprising, since it is inversely correlated with the overall size of the network (number of plant and pollinators represented; Blüthgen et al. 2008). Non-serpentine networks were substantially smaller than serpentine ones, so their higher *connectance* is most likely a result of this smaller network size. The lower specialization (H_2') in serpentine networks is more informative because it is invariant across different network sizes (Blüthgen et al. 2006). In our study system, the marginally lower specialization in serpentine networks suggests that, overall, bees at these sites visited flowers more in proportion to their relative abundances, rather than focusing on specific flower species. Two potential processes could drive such a network-level observation. First, bee species that are shared across multiple networks may change their behavior to become more specialized in non-serpentine networks than in serpentine networks, i.e., individuals foraging on different soil types visit different flower species at different frequencies. Alternatively, different species of bees and flowers could be present in serpentine and non-serpentine networks, and differences among networks may be due to species-level difference in specialization rather than behavioral changes in shared species. Network-level topology metrics effectively summarize holistic network structure but offer little insight into differences in the constituent species in compared networks.

We tested whether species-level specialization (*d'*) differed among bee species in serpentine and non-serpentine networks to evaluate whether bee species (as constituent pieces of the entire network) were less specialized in serpentine networks. When we decomposed specialization to the species level, differences between serpentine and non-serpentine networks disappeared. In other words, on average, bee species in non-serpentine networks were not more specialized than those in serpentine. H_2' was more specialized for non-serpentine networks probably because there were fewer flower species available (Chapter 1), and so interactions were heavily skewed to just a few flower species even if they were proportional to floral abundance. In contrast, *d'* did not differ between soil types because bees on each soil type were not differentially visiting flowers out of proportion to the flowers' abundance. Parallel interaction turnover analyses quantify how much the identity of interactions changes between networks, which is not captured by either *d'* or H_2*'*.

To better understand the ecological drivers of network-level and species-level topology, we analyzed the interaction $\boldsymbol{\beta}$-diversity for all networks ($\boldsymbol{\beta}_{\mathrm{WN}}$). Interaction $\boldsymbol{\beta}$-diversity was very high among sites, primarily driven by high species turnover of both bees and flowers. Decomposition of interaction $\boldsymbol{\beta}$-diversity also showed that a relatively small proportion of interaction turnover was due to changes in interactions among shared species (14%) compared to previous studies (Simanonok and Burkle 2014, CaraDonna et al. 2017, Noreika et al. 2019). The proportion of $\boldsymbol{\beta}_{\mathrm{WN}}$ due to true rewiring was also low (3.6%), but comparable to some other natural plant-pollinator systems (Simanonok and Burkle 2014). The majority of interaction turnover that occurred among shared species ($\boldsymbol{\beta}_{\mathrm{OS}}$) was due to differences in interaction richness, i.e., changes in pollinator diet breadth. This secondary decomposition of $\boldsymbol{\beta}_{\mathrm{OS}}$ into richness and replacement (true rewiring) components is crucial for elucidating whether species adapt across different ecological contexts. Across the region we sampled, it appears shared pollinators show plastic foraging patterns, primarily by expanding or contracting their diet breadth in different resource contexts—74% of $\boldsymbol{\beta}_{\mathrm{OS}}$ was due to differences in interaction richness—rather than rewiring (26% of $\boldsymbol{\beta}_{\mathrm{OS}}$) to visit different floral resources from the shared pool of plant species among the different networks. This pattern is similar to the results of the only other pollination network study we know of that has used this dissimilarity decomposition (Noreika et al. 2019).

The relative contribution of shared species' interactions and true rewiring to overall interaction turnover, $\boldsymbol{\beta}_{\mathrm{WN}}$, among networks on the same soil type varied between serpentine and non-serpentine, showing that pollinators' behavioral plasticity contributed differently to interaction turnover among sites with the same soil type. $\boldsymbol{\beta}_{\mathrm{WN}}$ was higher among non-serpentine networks than among serpentine networks, and interaction turnover among shared species, $\boldsymbol{\beta}_{\mathrm{OS}}$, was similar in each group. Moreover, according to our model, true rewiring was similar between serpentine networks and between non-serpentine networks, when rewiring occurred at all. However, rewiring was far more likely to occur between serpentine networks than between non-serpentine networks, suggesting that across geography, bees in serpentine networks more frequently changed which flowers they visited, rather than expanding or contracting their diet breadth. In addition, the higher frequency of rewiring among serpentine networks suggests that they may be more resilient compared to non-serpentine networks. Bees in serpentine meadows more frequently replaced portions of their diets, in comparison to bees in non-serpentine meadows, which more frequently expanded or contracted their diet breadths in response to changes in floral context.

Comparing each local network to the regional meta-web showed that each serpentine network represented a smaller proportion of realized links (compared to potential pooled links in the meta-web) than each non-serpentine site (Poisot et al. 2012). A greater proportion of interactions in each local non-serpentine network—and at similar relative abundances—are shared with the meta-web than is the case for each local serpentine network. We infer that each non-serpentine network is therefore a more representative sample of the sub-web it shares with the meta-web. The pairwise interaction $\boldsymbol{\beta}$-diversity comparison supports this inference: The higher frequency of rewiring between serpentine networks translates into a lower proportion of interactions realized in each local network compared to the meta-web—higher $\boldsymbol{\beta}'_{\mathrm{OS}}$. Differences in interaction richness in shared species networks ($\boldsymbol{\beta}_{\mathrm{OS.rich}}$) would drive decreases in each network's $\boldsymbol{\beta}'_{\mathrm{OS}}$ because they are more likely to be unique to each local network. Thus, the higher differentiation of each serpentine network appears to be due to the higher frequency of rewiring among serpentine networks. Although a proposed analytical method, comparing networks to a meta-web is a new analytical approach with few studies to base our interpretations on (Noreika et al. 2019, Campos-Moreno et al. 2021).

Our analysis does have some important limitations. Recent analyses of interaction turnover have highlighted the importance of phenological turnover in structuring networks (CaraDonna and Waser 2020, Schwarz et al. 2020, CaraDonna et al. 2021). We did not analyze the seasonal phenological turnover of networks and interactions in this study (but see Chapter 1). Such analyses require large amounts of data, to levels which are rarely collected in pollination community studies, and our sample-round data were too sparse to analyze within-season phenological turnover. We opted to pool our data to gain a more complete snapshot of each site's overall season-wide network. As a result, there are unrealized links within our site-level networks that are phenologically forbidden, because plants and pollinators did not overlap in phenology (Vázquez 2005). Moreover, we were most interested in how soil type affected network and interaction structure at the site-level, so we opted not to incorporate phenology into our null models or GLMM analyses. Undoubtedly, phenology structures interactions in our study system, as we know both bee and flower communities turned over quickly across the spring flowering period (Chapter 1).

Taken in sum, our results point to divergent effects of soil type on local network resilience. First, the marginally lower specialization (H_2') of serpentine networks suggests that they may prove more resilient to species loss or disturbance than non-serpentine networks. H_2' quantifies both specialization and niche complementarity, and lower values indicate higher redundancy across the network (Blüthgen and Klein 2011, Fründ et al. 2016). Higher frequency of rewiring among serpentine networks further supports this conclusion; lower specialization in serpentine networks could be driven by pollinator species more often using different hosts in communities in different serpentine meadows rather than expanding or contracting their diet breadth. This result is consistent with increased foraging flexibility. However, it is important to note that although rewiring was less frequent between non-serpentine networks, rewiring was quantitatively similar between non-serpentine networks when it did occur. In contrast, at a regional scale, each serpentine network proved more selective in its representation of the pooled meta-web. So, from a regional perspective, each serpentine network is more unique than each non-serpentine network, even though the bee communities on each soil type did not differ (Chapter 1). Again, this is consistent with the idea of greater flexibility in foraging among the serpentine meadows.

Overall, our results highlight key differences in how plant-pollinator networks vary between soil types even across small spatial scales within the same region. From interaction $\boldsymbol{\beta}$-diversity to network-wide topology, serpentine networks exhibited a greater flexibility and redundancy than non-serpentine networks. This makes sense when we consider that serpentine floral resources were more dynamic over time than non-serpentine floral resources (Chapter 1). Serpentine meadows flowered for longer, and supported a distinct, richer floral community than non-serpentine meadows. On the one hand, this greater floral richness and longer phenology supported richer bee communities in serpentine, and we might have expected bees to act more specialized in such a context. We did not observe such a pattern. Part of this could be due to most of the interaction dissimilarity being due to species turnover—community composition and context differed greatly among sites, regardless of soil type—so bees needed to be particularly flexible in their foraging choices among serpentine sites. Serpentine networks' higher selectivity compared to the metaweb supports such a conclusion. In conclusion, our results show that small-scale variation in soil type has immediate impacts on the turnover of interactions and on the emergent properties of plant-pollinator networks.

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Figures

Figure 3.1 Conceptual diagram of the additive components of interaction beta-diversity ($\boldsymbol{\beta}_{\mathrm{WN}}$). (A) A baseline bipartite network with numbers representing one level and letters representing the other. Other panels are compared to this baseline network. (B) True rewiring ($\boldsymbol{\beta}_{\mathrm{OS.repl}}$) occurs when links between shared species are replaced by new links between other shared species. (C) Turnover among shared species due to differences in interaction richness ($\boldsymbol{\beta}_{\mathrm{OS.rich}}$) occurs when links are gained or lost, but species are shared between networks. (D) Interaction turnover due to species turnover ($\boldsymbol{\beta}_{\mathrm{ST}}$) occurs when interaction turnover occurs due to species joining or exiting the network. Components of interaction turnover can simultaneously occur from one transition to the next, but are shown separately for simplicity.

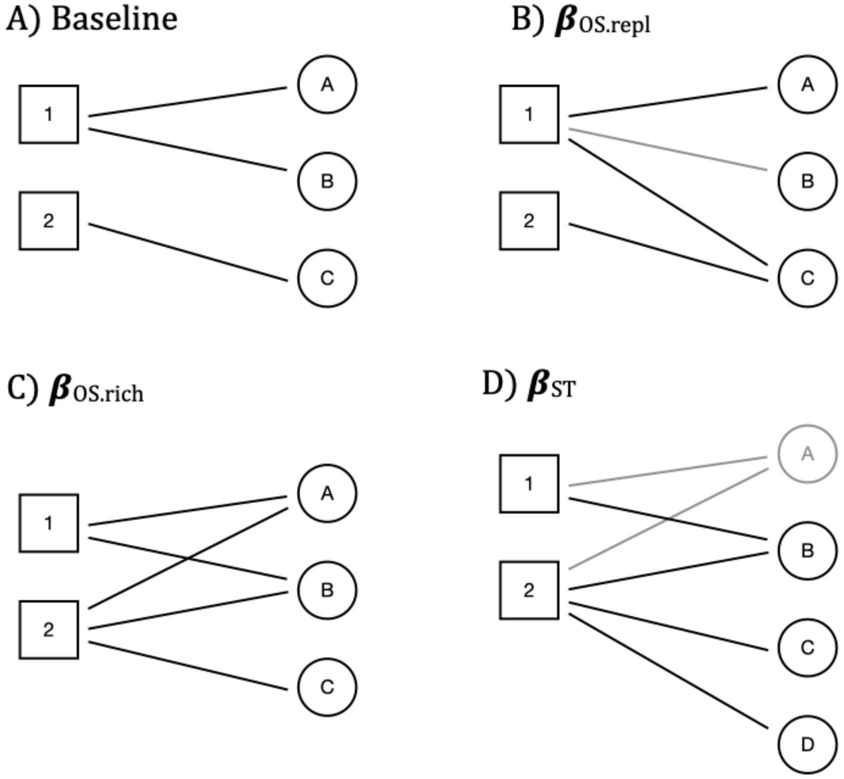


Figure 3.2 (A) *Connectance* was significantly higher in non-serpentine networks. (B) *H2'*, network-wide specialization, was marginally lower in serpentine networks. (C) *wNODF*, a measure of nestedness, did not differ between soil types.

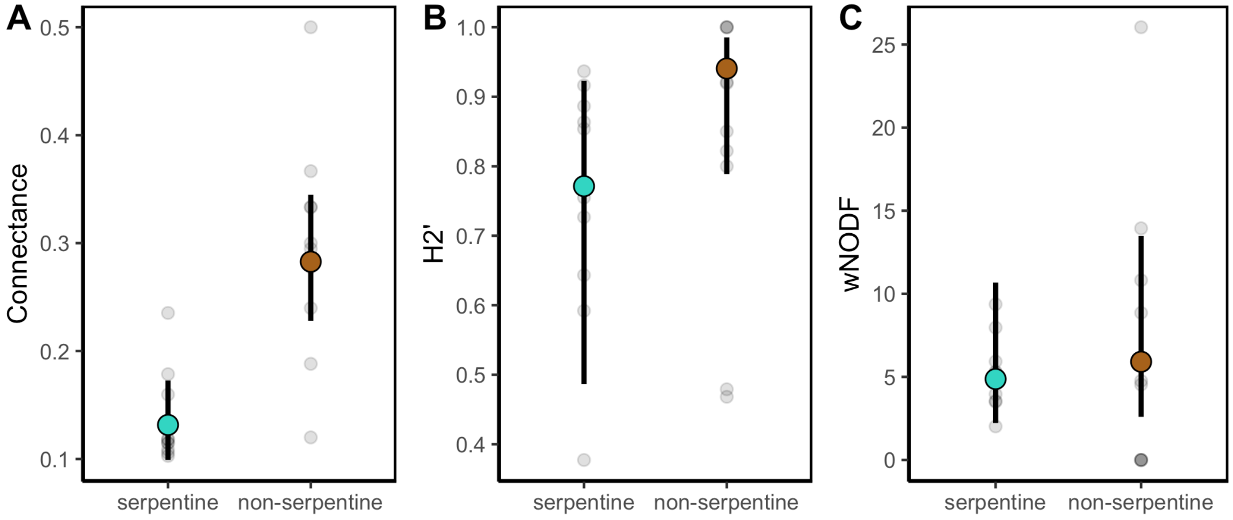


Figure 3.3 (A) $\boldsymbol{\beta}_{\mathrm{WN}}$ was high regardless of what soil type networks were on. It was highest between networks on different soil types and lowest among networks on serpentine soils. (B) $\boldsymbol{\beta}_{\mathrm{ST}}$ made up the majority of $\boldsymbol{\beta}_{\mathrm{WN}}$ and was significantly different among serpentine sites and among non-serpentine sites. It was lowest among serpentine sites. (C) $\boldsymbol{\beta}_{\mathrm{OS}}$ made up ~20% of $\boldsymbol{\beta}_{\mathrm{WN}}$, and $\boldsymbol{\beta}_{\mathrm{WOS}}$ among serpentine sites was similar to $\boldsymbol{\beta}_{\mathrm{WOS}}$ among non-serpentine sites. $\boldsymbol{\beta}_{\mathrm{WOS}}$ between sites from different soil types was significantly higher. (D) $\boldsymbol{\beta}_{\mathrm{WOS.repl}}$ (rewiring) among serpentine networks was similar to $\boldsymbol{\beta}_{\mathrm{WOS.repl}}$ among non-serpentine sites, and contributed ~10% to $\boldsymbol{\beta}_{\mathrm{WN}}$. $\boldsymbol{\beta}_{\mathrm{WOS.repl}}$ among networks on different soil types was significantly lower.

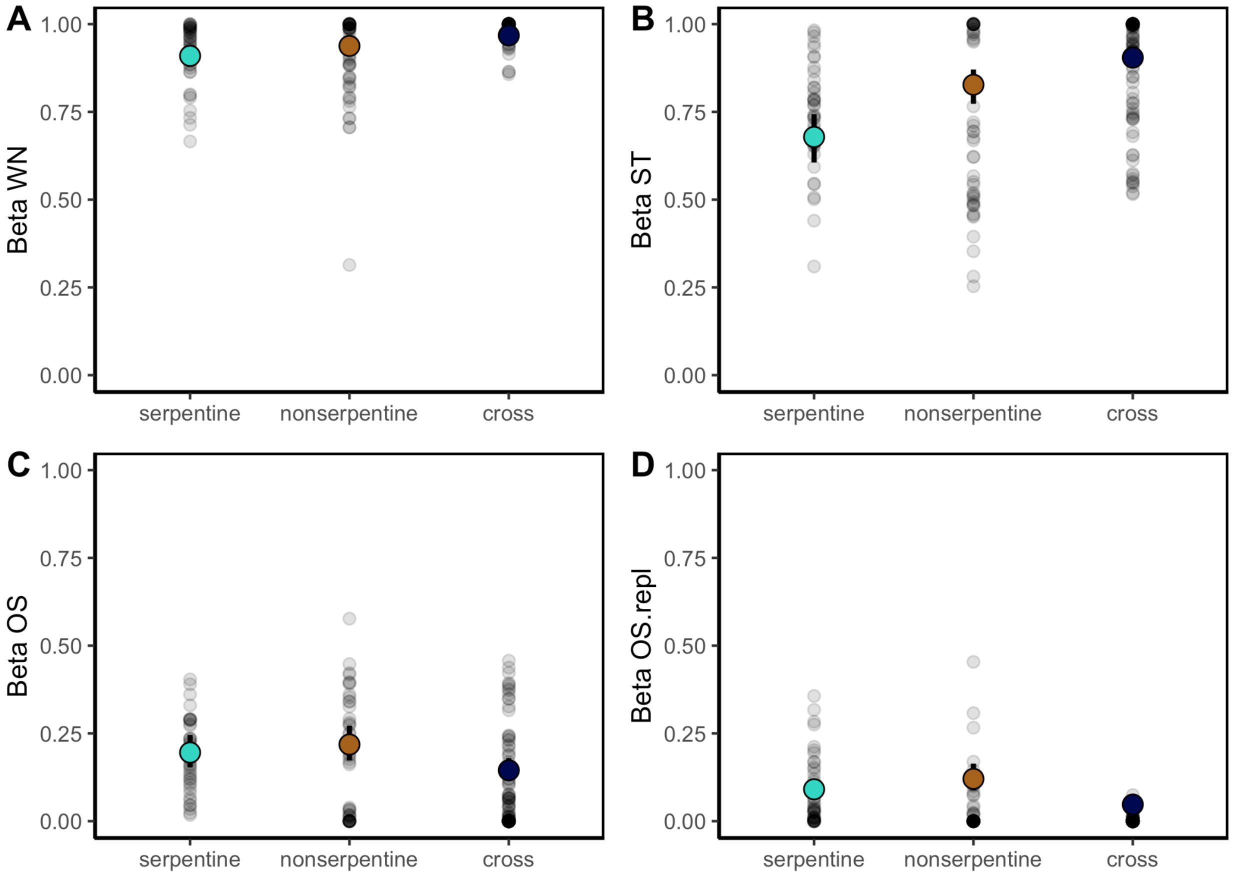


Figure 3.4 (A) $\boldsymbol{\beta}_{\mathrm{OS}}$ was significantly more likely to be zero among networks from different soil types than among networks on non-serpentine soils. $\boldsymbol{\beta}_{\mathrm{OS}}$ was never zero among serpentine sites. (B) $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ was significantly more likely to be zero among networks from different soil types than among non-serpentine sites. $\boldsymbol{\beta}_{\mathrm{OS.repl}}$ was the least likely to be zero among serpentine sites, and significantly so.

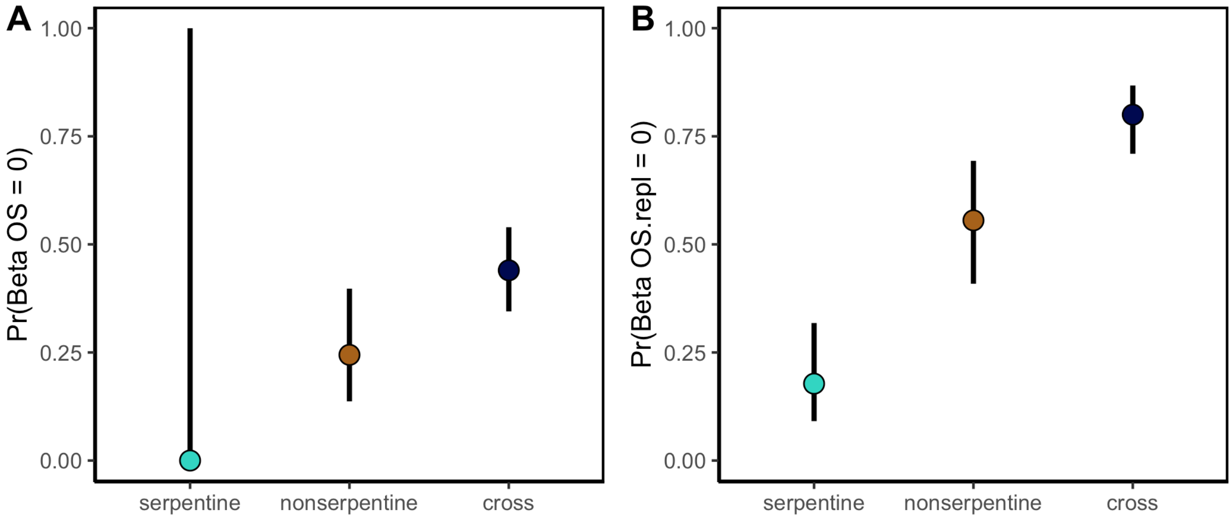
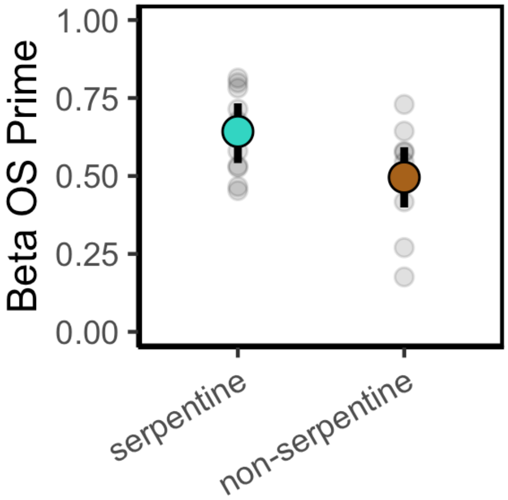


Figure 3.5 $\boldsymbol{\beta}'_{\mathrm{OS}}$ was significantly higher for serpentine networks compared to non-serpentine networks. Serpentine networks were more selective compared to the regional meta-web.



Tables:

Table 3.1 Contrast Analyses for Network Metrics

Network Metric	Contrast (soil type)	Odds Ratio	SE	DF	t Ratio	p-value
Connectance	non-serpentine/serpentine	2.6	0.519	15	4.797	0.0002
H2'	non-serpentine/serpentine	4.7	4.13	15	1.761	0.0985
wNODF	non-serpentine/serpentine	1.21	0.602	13	0.39	0.7027
d'	non-serpentine/serpentine	1.57	0.687	399	1.03	0.3038
d' – (ZI component)	non-serpentine/serpentine	5.92	2.25	399	4.677	<0.0001

Table 3.2 Null Model Results for Network Metrics

Network Metric	Model Term	Coefficient Estimate	p-value
Connectance	Intercept	-1.1104139	< 0.0002
	Serpentine	-0.9563	< 0.0002
H_2'	Intercept	2.63	< 0.0002
	Serpentine	-1.546	< 0.0002

Table 3.3 Model Significance of Soil Type Grouping for Components of Interaction $\boldsymbol{\beta}$-Diversity

Interaction $\boldsymbol{\beta}$-Diversity Component	Log-likelihood	Chi-squared	p-value
$\boldsymbol{\beta}_{WN}$	562.74	38.071	5.407×10^{-9}
$\boldsymbol{\beta}_{ST}$	326.26	51.003	8.412×10^{-12}
$\boldsymbol{\beta}_{OS}$	8.5843	89.051	5.696×10^{-10}
$\boldsymbol{\beta}_{OS.repl}$	17.450	66.884	4.556×10^{-13}
$\boldsymbol{\beta}'_{OS}$	11.0301	4.7372	0.02952