Environmental Entomology, 45(4), 2016, 909–919
doi: 10.1093/ee/nvw032
Advance Access Publication Date: 6 June 2016
Research article

Generalist Behavior Describes Pollen Foraging for Perceived Oligolectic and Polylectic Bees

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Received 24 October 2015; Accepted 12 March 2016

Abstract

Native bees provide essential pollination services to cultivated and wild plants worldwide. Despite the need to conserve pollinators, the foraging patterns of native bees are poorly understood. Classic concepts of resource use have typically categorized bee species as specialists or generalists based on floral visitation patterns. While intraspecific variation in bee foraging likely depends on local land use, sex, and phenological period, among other factors, these potential drivers of floral visitation are rarely explicitly investigated. In this study, we explore the potential for inter- and intra-specific variation in floral visitation by investigating the pollen loads of two solitary, similarly sized, ground-nesting native bee species within the Apinae, *Melissodes tepaneca* (Cresson) and *Diadasia rinconis* (Cockerell), categorized as generalist and specialist based on past floral visitation studies, respectively. Our analyses reveal generalist foraging and indicate that natural habitat availability significantly drives pollen load composition for both species. The putative specialist, *D. rinconis*, exhibited significant differences in pollen load composition between males and females, between pan and net collection methods, and between the different phenological periods. The putative generalist, *M. tepaneca*, exhibited significant differences in pollen load composition between the sexes, but only in the late season. Both species exhibited significant preference levels for multiple native plant species across the study region. Given that pollen collection is essential for native bee population persistence across natural and human-dominated habitats, our findings suggest consideration of both pollen collection and floral visitation patterns to holistically describe floral usage and develop pollinator conservation strategies.

Key words: *Diadasia*, foraging breadth, floral community, *Melissodes*, ordination

Among animal pollinators, bees constitute a species-rich (~30,000 species) and efficient group of obligate flower visitors (Kearns et al. 1998). Bees are estimated to provide pollination services for ~70% of global crop species (Klein et al. 2007), including a range of food and fiber crops; however, wild bee pollination service is dependent on the availability and proximity of local food and nesting resources (Ricketts et al. 2008). While it is established that floral resource availability is an important driver of native bee abundance (Westphal et al. 2003, Ricketts 2004, Grundel et al. 2010), specific patterns of floral usage and preference are not well-understood, especially across heterogeneous landscapes. Pollen and nectar are both essential food resources for bees, and pollen quantity and quality have been shown to impact larval growth, adult bee size, and overall survivorship (reviewed in Roulston and Cane 2000). Despite this fact, few studies have examined how patterns of floral visitation and pollen collection vary across bee species, sexes, phenological periods, and heterogeneous landscapes.

For bees, those species with specialized diets that exhibit high fidelity for particular pollen taxa are known as "oligolectic" bees, and are believed to be physiologically, temporally, and/or environmentally constrained to a narrow resource breadth (Fox and Morrow 1981, Devictor et al. 2010), while "polylectic" bees forage on a wide variety of plant species for pollen. While the most precise means of designating oligolecty versus polylecty is by examining the composition of pollen masses that female bees allocate to their brood cells (Wcislo and Cane 1996, Cane and Sipes 2006), nest provisions do not fully describe the floral interactions engaged in by the adult bee, as both males and females will visit a variety of floral hosts for nectar (Minckley and Roulston, 2006). From a pollinator conservation perspective, the process of examining pollen on the bodies of foraging bees can be a particularly effective strategy to reveal broad floral visitation patterns (Cane and Sipes 2006), unfiltered with respect to larval provisions. Thus, to determine the full spectrum of floral usage by a pollinator, observations of floral visits are ideally combined with pollen analyses from netted bees (Cane and Sipes 2006). While pollen load analyses can be an effective method to reveal past floral visitation patterns, the classification of floral usage for many native bees has largely been based on floral visitation data, not pollen collection (Roulston and Cane 2000, Bosch et al. 2009).

Furthermore, though degrees of diet specialization and floral preference have traditionally been used as species-level categorizations, recent studies have demonstrated that resource preferences may be dependent on several other factors, including the availability of local resources, phenological overlap, and the sex of the individual (Bolnick et al. 2002, Dupont et al. 2009, Ne'eman et al. 2006). "Preference" for a specific food or habitat is defined as elevated resource usage relative to availability (Beyer et al. 2010); thus, strong preference could theoretically drive intraspecific variation in pollen collection if resource availability varies within an organism's foraging range. While relatively understudied in the field, preferences may be particularly strong in native bee species, given that many small-bodied solitary species are confined to a limited foraging range of around 150–600 m from nesting sites (Gathmann and Tscharntke 2002). Similarly, preferences may change through the season depending on the phenologies of flowering plants and bee foraging activity (Dupont et al. 2009). If an individual's foraging phase does not fully overlap with the bloom of a preferred flower species, it may concentrate its foraging activity on other resources. In addition, the sex of an individual may affect resource specialization, as differences in life histories and behavior could alter resource usage between males and females of the same species (Bolnick et al. 2002, Ne'eman et al. 2006). In bees, food resource utilization has largely been documented for females, not males (Roulston et al. 2000, Thorp 2000, Müller and Kuhlmann 2008, Eckhardt et al. 2014), as females provision the offspring with pollen and nectar, whereas males forage to meet their individual metabolic needs and thus are believed to predominantly forage for nectar. Thus, it has been hypothesized that floral resource usage for male bees may be distinct and broader than usage for females of the same species (Carvell et al. 2007, Kraus et al. 2009), though this has not been rigorously investigated across landscapes.

Finally, one additional challenge to investigating pollinator floral visitation patterns is the potential biases introduced in the process of insect collection, given that collection itself can depend on a collector's netting proficiency, expectations of which plants are correct "hosts", and ability to perceive an insect (Cane and Sipes 2006, Roulston et al. 2007). Indirect methods, such as pan trapping, which are widely used to sample native bees (Leong and Thorp 1999, Cane et al. 2000, Winfree et al. 2009, Jha and Vandermeer 2010), could potentially be used in conjunction with netting to maximize sampling effort and reduce collector-mediated biases (Roulston et al. 2007); however, it is not known if such indirect methods yield similar pollen composition trends as netted collections, given the possibility of pollen loss or contamination (e.g., in the water of pan traps). Given the ubiquity of pan trapping in pollinator sampling, a study comparing the pollen carried by pan-trapped versus netted bees could provide insight into a potentially useful tool for determining insect floral visitation patterns.

In this study, we investigate the degree of specialization and difference in pollen collection between the putatively specialist and generalist native solitary bee species, *Diadasia rinconis* (Cockerell) (*Opuntia* specialist, tribe Emphorini) and *Melissodes tepaneca* (Cresson) (generalist, tribe Eucerini), across the heterogeneous Central Texas prairie system. Visual observations for *D. rinconis* indicate a strong degree of specialization, with little or no observations on non-*Opuntia* plant species (Ordway 1987, Neff and Simpson 1992), while visual observations for *M. tepaneca* suggest visitation to more than 15 plant families (Laberge 1956). We focus on native solitary bees, as this lifestyle describes the majority of bee species (Michener 2000), yet remains much less studied from a resource-usage perspective compared with honey bees and bumble bees (Kearns et al. 1998; Goulson et al. 2008; Potts et al. 2010a,b). Further, both *M. tepaneca* and *D. rinconis* are common soil-nesting species that occur throughout the American Southwest, and both are members of the subfamily Apinae within the Apidae, representing a relatively closely related pair within the Central Texas prairie region. In this study, we also examine the utility of pan trap sampling for bee foraging analyses, specifically by comparing pollen collection among netted bees with their pan-trapped counterparts. We test three sets of hypotheses and related predictions examining the relationship between specialization and floral resource preference across landscapes and between the sexes: 1) the generalist (*M. tepaneca*) visits a greater diversity of flowering plants than the specialist (*D. rinconis*) and thus pollen richness is not distinct between collection type (pan vs. net) or across phenological periods for the generalist; 2) the generalist exhibits broader diet breadth in more natural landscapes than the specialist, and thus the composition of plant species in pollen loads is more dissimilar for the generalist, is dissimilar between the sexes for the specialist, and is driven by natural land cover for the generalist; and 3) the specialist exhibits stronger preferences for a select group of plant species than the generalist.

Materials and Methods

Study Sites and Bee Collection

In total, 10 study regions were established across the Central Texas prairie system. The 10 study regions were located in seven counties (Tarrant, Dallas, Hunt, Lamar, Travis, Hays, and Burnet) and provide geographic spread of more than 500 km (SW corner: 30.1015 N, 97.9608 W, NE corner: 33.6494, 95.6987 W). Within each of the 10 study regions, pollinators were sampled at five equidistant sites on a 1.2-km linear transect (275 m apart), for a total of 50 study sites. Each site comprised a 50 × 50m square-shaped study plot (sides following the cardinal directions). All sites were classified into land use categories at local (250 m radius) scales using the land cover data from the National Land Cover Database (NLCD, http://www.mrlc.gov/ last accessed February 2, 2016) for 2011. The NLCD provides land classification data at 30 m resolution, and for the study regions, includes classification for 14 different land use types. Four land use types comprised less than 0.5% of the landscape (barren, water, cultivated crops, and woody wetlands) and were thus not included in the analysis. The remaining 10 land use types were classified into four major habitat types relevant to native bees and quantified for each site: Developed – composed of all levels of development including a mixture of constructed materials and vegetation with greater than 20% impervious surfaces; Grassland – composed of areas dominated by herbaceous vegetation, generally greater than 80% of total vegetation; Shrub – composed of areas dominated by shrubs less than 5 m tall; and Forest – composed of areas dominated by trees generally greater than 5 m tall, including deciduous, evergreen, and mixed forests (Fig. 1) .

In the summer of 2012, pollinator sampling was conducted using two methodologies, netting and pan trapping. Pan trapping and netting for all sites were conducted three times over three distinct phenological periods: early bloom (April 18 to May 15), mid-bloom (May 20 to June 16), and late bloom (June 20 to July 14). All netting surveys were conducted between the hours of 7 am and 12 pm, and in each site, netting was conducted for a total of 30 min by two researchers. In this 30-min period, all bees and butterflies within the plot were caught and the flowers visited were recorded. Netted bees were captured and killed separately in kill jars to prevent cross contamination. For pan trapping, 30 pans (6-oz plastic bowls, SOLO

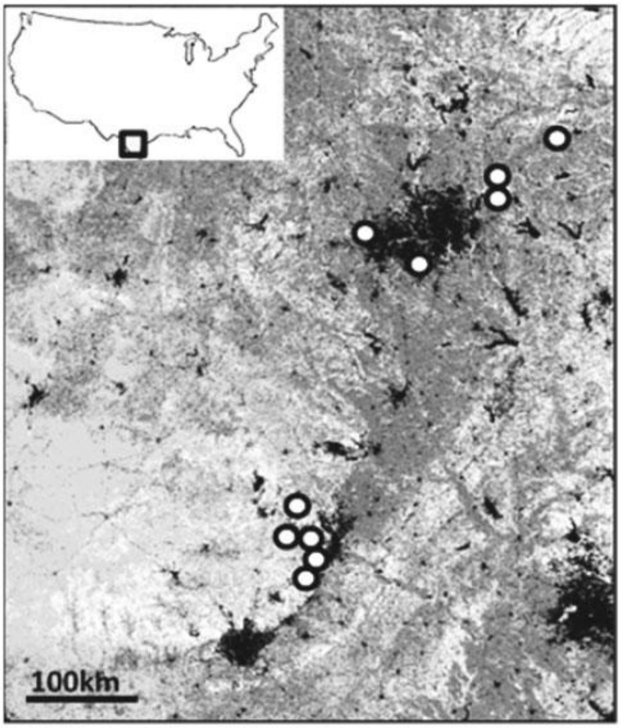

Fig. 1 Location of study system in Texas (square outline within U.S. map) and detailed land use map with the 10 study regions marked by white circles. The four major land types are Developed (black), Grassland (dark gray), Shrub (light gray), and Forest (white).

model number: PB6-0099) were painted, 10 blue, 10 yellow, and 10 white, and were laid out in an "X"-shaped transect in the center of the site (as recommended in LeBuhn et al. 2003, Jha and Vandermeer 2010). Pans were filled two-thirds full of soapy water (1 gallon water:1 tbsp Dawn dishwashing soap) and set out for 24 h, and then, insects within each pan trap were collected. Pan trapping was always conducted after netting and both were conducted only on sunny days. All totaled, we collected 68 *M. tepaneca* individuals (57 female and 11 male) and 87 *D. rinconis* individuals (48 female and 39 male).

During each of the three phenological periods, floral species richness, density, and vegetation cover were measured in thirty 1 × 1 m quadrats per site. Quadrats were positioned 4 m apart across three rows that ran North–South in each site, located at 10 m, 25 m, and 40 m from the NW corner of the site. In each quadrat, the number of flowering heads per species was counted, and then, the size of five flowering heads per species was measured and averaged to eventually quantify floral cover.

Pollen Identification

In the fall of 2013, a pollen reference collection was created from anthers (stored in ethanol) that were collected for all plant species encountered in the vegetation surveys during the field season. Pollen samples were visualized by vortexing the anther in ethanol for 2 min, extracting 20 µl of suspended pollen, and combining this with 60 µl of dilute Fuchsine dye, and then pipetting 50 µl of the Fuchsine-pollen mixture onto a slide (Kearns and Inouye 1993). Overall, 79 plant species were imaged. Pollen images were made using a Leica light microscope and each species was photographed once at 20× magnification, and three times, at three focal planes, at 63× magnification for the reference collection.

To compare bee pollen collection, all 155 specimens of *M. tepaneca* and *D. rinconis* collected in 2012 were washed for pollen load analysis by gently vortexing the entire specimen in ethanol to acquire pollen for imaging (Kearns and Inouye 1993; here after referred to as the "pollen load"). This protocol was modified and adapted to accommodate pinned insects in the specimen collection by fastening the pin of each specimen to the cap of a 25-mL falcon tube, inverting the falcon tube, and then soaking the specimen for 24 h in 5 mL of 95% ethanol. After the soaking period, the scopa were preened using fine-tip forceps and an insect pin for 30 s. Then, the preening utensils were rinsed with 0.5 mL of 95% ethanol over the falcon tube (for a total volume of 5.5 mL ethanol). This sample was vortexed for another minute and 30 s and then centrifuged for 1 min at 1,800 rpm. Finally, 5 mL of the ethanol supernatant was removed, resulting in a single final pollen sample of 500 µL per specimen.

To create the pollen slide for each individual bee, 20 µL of pollen solution plus 60 µL of Fuchsine dye were plated for each slide. Plating was repeated until the final pollen sample was depleted. For each bee, the first 300 pollen grains encountered on the slide were identified to species. When an unknown pollen grain was encountered, it was designated with a morphospecies ID and photographed at 20× and 63× magnification for future reference. Unidentified pollen grains from the family Asteraceae were treated as one group, due to nearly identical morphologies; otherwise, all unique pollen types were counted as their own species. All totaled, unknown morphologies comprised less than 5% of the total species-wide pollen grains and were included in all analyses except those examining floral preference.

Because many specimens did not have 300+ pollen grains (mean number of pollen grains counted = 112.44, ±9.57), we removed all specimens with fewer than 50 pollen grains, yielding a total of 43 *M. tepaneca* (32 females, 11 males; 18 netted, 25 pan-trapped) and 36 *D. rinconis* (16 females, 20 males; 23 netted, 13 pan-trapped) for all analyses. While this number of pollen grains is lower than some studies (Neff 2008), it is sufficient for the purposes of examining relative plant species abundance and for providing evidence of previous floral visits. Also, a number of valuable previous studies of pollinator–plant interactions have used a similar sample size (~50 grains) for pollen counts (Svensson 1985, Pettersson 1991, Bristow and Martin 1999, Larson et al. 2006). In addition, to prevent the inclusion of "incidental" pollen that is simply a result of pollen contamination in the netted or pan-trapped sample, we dropped plant species that represented <4% of the pollen load (as per Müller and Kuhlmann, 2008). All totaled, 16,240 pollen grains were counted and identified to 55 floral species present in landscape surveys. All floral species were native to the study region. Of the 55 floral species identified, 29 species were excluded from the preference analysis portion of the study due to their infrequency (<2 individual occurrences) within the landscape or pollen load data. This minimum occurrence threshold was set due to the constraints in calculating variance for compositional analysis (Calenge 2006). Thus, a total of 26 species were used in a compositional analysis of pollen use to test for floral preference within bee specimens (Supp. Table 1 and Fig. 1 [online only]).

Pollen Load Diversity

Pollen load analyses were conducted using R software ver. 3.1.0 (R Core Team 2014). Individual pollen load species richness was calculated by counting the number of observed taxa within each pollen load. We then estimated species diversity of individual bee pollen loads via the Chao1 and Shannon–Wiener indices, using the vegan package in R (Oksanen et al. 2013). The Chao1 estimator was chosen because of its effectiveness in estimating richness in data sets biased toward low-abundance classes (Chao 1984), as is the case with pollen loads (Waser and Ollerton 2006, Saifuddin and Jha 2014, Requier et al. 2015). We compared the three diversity measures, species richness, Chao1 values, and Shannon–Wiener values, between *D. rinconis* and *M. tepaneca,* and within each species, we also compared the sexes and the trap methods using *t*-tests. Chao1 values were non-integer and residuals were non-normally distributed, thus these values were log-transformed for all analyses. The three diversity measures were also compared across phenological periods for each species using two-way analysis of variance (ANOVA). We report means and standard deviations for these diversity measures.

We also ran mixed-effects model sets for each species separately to examine the relationship between six predictor variables: 1) bee sex, 2) site percent Shrub, 3) phenological period (period), 4) site plant species richness, 5) trap method (pan or net), and 6) sex × trap method interaction, for each of the three diversity measures per pollen load: 1) species richness, 2) Chao1, and 3) Shannon–Wiener values. We chose site percent Shrub as the one land use predictor value (collinearity prevents inclusion of all four) because our ordination models suggested that site percent Shrub was the most important land use factor, and in many regions, shrub land exhibits high floral diversity (Naveh and Whittaker 2015). As a random effect, we included site identity nested within region. Specifically, we used linear mixed-effects models (LMM) with a normal distribution for all predictor variables. Model selection and model averaging were conducted using the package muMIn in R (Bartoń 2013). For each pollen load group (species richness, Chao1, Shannon–Wiener for each species), model subsets were generated from the full model. For each generated list of model subsets, all models with Delta AIC <10 were averaged.

Pollen Composition Dissimilarity

For composition analyses, pollen load counts were converted to proportions to allow for comparisons across different sample sizes. Nonlinear multidimensional scaling (NMDS) was used to visualize and measure compositional dissimilarity in pollen loads across species, and between the sexes within each species. NMDS is considered the most effective and robust ordination method in community ecology, and allows for visualization of ecological distance between sampling units (Faith et al. 1987, Minchin 1987). Individual bees were separately ordinated at the species level and then within their respective species at the sex level, trap method level, and phenological period level. Ordination was conducted using the Bray–Curtis dissimilarity index (Beals 1984), and compared with a permutational multivariate analysis of variance (PERMANOVA) analysis in the vegan package in R (Oksanen et al. 2013). The method is considered a robust alternative to parametric MANOVA in describing variation (McArdle and Anderson 2001). The analysis was conducted with 999 permutations stratified by site, to account for resampling, and all analyses were tested for significance through *F*-tests. We did not stratify by region, given that all regions exhibited substantial variation and overlap in composition (Supp. Fig. 2 [online only]).

In the ordination analyses, we also examined the local (250 m radius) land-use types driving pollen load composition by fitting environmental vectors onto the pollen ordination spaces of each species using the vegan package in R. Fitting vectors to ordination diagrams is a widely used method of assessing relationships between landscape composition and variation in community composition (Williams et al. 1996, Fensham et al. 1999). For each NMDS analysis, ordination scores for each bee and the proportion of land-use types at their corresponding sites were used to calculate the four environmental vectors: proportion of 1) Developed, 2) Shrub, 3) Grassland, and 4) Forest. Each vector points to the direction of most rapid change in its corresponding environmental variable within the ordination space. The significance of these vectors was evaluated using a permutation test of environmental variables and the fit determined by calculation of the correlation coefficient squared (Pearson's r^2). The arrows depicted in the ordination are scaled by their correlation coefficient value such that weak predictors have shorter arrows than strong predictors. For each ordination diagram, only the significant environmental vectors are displayed.

Pollen Preference

Preference was assessed as per traditional habitat use methods (Johnson 1980). Classical compositional analyses of habitat use (Aebischer et al. 1993) were performed at the species level using the adehabitatHS package in R (Calenge 2006). Compositional analysis of habitat use is often utilized to describe resource preference, such as the identification of pollen species that are collected significantly more than expected relative to their landscape availability (Davis et al. 2012, Jha et al. 2013). To test if pollen species usage is significantly nonrandom relative to availability per site, we compared a matrix of floral species availability per site for phenological periods 1 and 2 (proportion of floral cover, as measured from the vegetation survey) with a second matrix of pollen species use per bee for phenological periods 1 and 2 (proportion of pollen load) using Wilks' lambda. Preference could not be assessed for the third period due to the minimal sample size needed for compositional analyses. A preference matrix was then constructed for each period, indicating the mean difference between the proportion of pollen use per bee and floral cover for each species per site. This matrix was evaluated using a randomization test (500 repetitions) where significant preference for one plant species over each other species was assessed (Aebischer et al. 1993).

Results

Pollen Load Diversity

Average species richness, Shannon–Wiener diversity, and Chao1 diversity values were significantly higher in *D. rinconis* (Richness = 3.19 ± 0.19; Shannon = 1.06 ± 0.07; Chao1 = 4.19 ± 0.19) than in *M. tepaneca* (Richness = 2.40 ± 0.19; Shannon = 0.79 ± 0.08; Chao1 = 3.40 ± 0.19; *t*-test for Richness, $t = 2.93$, df = 74.94, *P*-value = 0.005; *t*-test for Shannon–Wiener, $t = 2.33$, df = 75.94, *P*-value = 0.022; *t*-test for Chao1, $t = 3.09$, df = 75.89, *P*-value = 0.003). Further, species richness, Shannon–Wiener, and Chao1 values were significantly higher for netted bees (Richness = 3.52 ± 0.22; Shannon = 1.16 ±0.04; Chao1 = 4.52 ± 0.22) than pan-trapped bees for *D. rinconis* (Richness = 2.62 ± 0.33; Shannon = 0.97 ± 0.06; Chao1 = 3.62 ±0.33; *t*-test for Richness, $t = 2.29$, df = 22.26, *P*-value=0.032; *t*-test for Shannon–Wiener, $t = 2.75$, df = 22.93, *P*-value = 0.011; *t*-test for Chao1, $t = 2.36$, df = 18.98, *P*-value = 0.029), but did not significantly differ between netted bees (Richness = 2.11 ± 0.25; Shannon = 0.90 ± 0.05; Chao1 = 3.11 ± 0.25) and pan-trapped bees for *M. tepaneca* (Richness = 2.63 ± 0.26; Shannon = 1.03 ± 0.05; Chao1 = 3.63 ±0.26; *t*-test for Richness, $t = -1.41$, df = 39.39, *P*-value = 0.166; *t*-test for Shannon, $t = -2.00$, df = 39.31, *P*-value = 0.052; *t*-test for Chao1, $t = -1.34$, df = 37.48, *P*-value = 0.189). Species richness, Shannon–Wiener, and Chao1 values were not significantly higher for *D. rinconis* collected in phenological period 1 (Richness = 3.00 ± 0.17; Shannon = 1.02 ± 0.03; Chao1 = 4.00 ± 0.17), 2 (Richness = 3.45 ± 0.20; Shannon = 1.17 ± 0.03; Chao1 = 4.45 ± 0.20), or 3 (Richness = 2.00; Shannon = 0.69; Chao1 = 2.00; ANOVA for Richness, $F = 0.035$, df = 1, P-value = 0.852; ANOVA for Shannon, $F = 1.277$, df = 1, P-value = 0.266; ANOVA for Chao1, $F = 0.035$, df = 1, P-value = 0.852), or for *M. tepaneca* collected in phenological period 1 (Richness = 2.44 ± 0.20; Shannon = 0.98 ± 0.04; Chao1 = 3.4 ± 0.20), 2 (Richness = 2.67 ± 0.17; Shannon = 1.01 ± 0.03; Chao1 = 3.67 ± 0.17), or 3 (Richness = 1.83 ± 0.12; Shannon = 0.90 ± 0.03; Chao1 = 2.83 ± 0.12; ANOVA for Richness, $F = 0.608$, df = 1, P-value = 0.440; ANOVA for Shannon, $F = 0.253$, df = 1, P-value = 0.618; ANOVA for Chao1, $F = 0.608$, df = 1, P-value = 0.440). *Diadasia rinconis* Shannon–Wiener values were significantly predicted by percent shrub ($P < 0.05$), sex ($P < 0.05$), and sex × trap ($P < 0.05$), with pollen species diversity higher in males than in females (Table 1). *Melissodes tepaneca* Chao1 values were significantly predicted by period ($P < 0.05$). None of the remaining explanatory variables explained *D. rinconis* species richness or Chao 1values, or *M. tepaneca* species richness or Shannon–Wiener values (Table 1, Supp. Table 2 [online only]).

Pollen Composition Dissimilarity

Simultaneously examining both *D. rinconis* and *M. tepaneca* ordination revealed significant dissimilarity within the specialist *D. rinconis* pollen loads, and significant dissimilarity within the generalist *M. tepaneca* pollen loads when phenological period and sex were considered. Overall, the pollen loads of the bee species were not significantly dissimilar from one another ($F = 5.32$ $P = 0.104$; Table 2; Fig. 2a); however, pollen composition was significantly dissimilar between netted and trapped bees ($F = 2.21$, $P = 0.040$; Table 2). Closer examination revealed that males and female pollen loads were not significantly dissimilar in *M. tepaneca* ($F = 1.54$, $P = 0.263$; Table 2, Fig. 2b), but were significantly dissimilar in *D. rinconis* ($F = 25.48$, $P = 0.001$; Table 2; Fig. 2c). Pollen load composition was not significantly dissimilar between netted and pan-trapped bees of *M. tepaneca* ($F = 1.199$, $P = 0.263$; Table 2), but was significantly dissimilar between netted and pan-trapped bees for *D. rinconis* ($F = 7.47$, $P = 0.001$; Table 2). In addition, the sex × trap method interaction did not explain dissimilarity in *M. tepaneca* ($F = 1.27$, $P = 0.546$, Table 2), but significantly explained dissimilarity in *D. rinconis* ($F = 8.35$, $P = 0.001$, Table 2).

Phenological period significantly explained pollen load dissimilarity across both species ($F = 3.01$, $P = 0.040$; Table 2), as did a species × period interaction term ($F = 4.13$, $P = 0.021$; Table 2). Specifically, pollen loads across phenological periods were not significantly dissimilar in *M. tepaneca* ($F = 1.04$, $P = 0.651$; Table 2; Fig. 3a), but were significantly dissimilar in *D. rinconis* ($F = 3.10$, $P = 0.001$; Table 2, Fig. 3b). However, the sex × period interaction explained dissimilarity in *M. tepaneca* ($F = 2.81$, $P = 0.032$), but did not explain dissimilarity in *D. rinconis* ($F = 1.88$, $P = 0.158$, Table 2). For *M. tepaneca,* the percent Forest and Shrub were significant drivers of pollen load dissimilarity ($P = 0.003$, $r^2 = 0.301$; $P = 0.006$, $r^2 = 0.234$, respectively; Fig. 2b), while for *D. rinconis,* the percent Developed and Shrub were significant drivers of pollen load dissimilarity ($P = 0.001$, $r^2 = 0.380$; $P = 0.003$, $r^2 = 0.315$, respectively; Fig. 2c).

Table 1. Results of model averaging and selection of full models for (a) *D. rinconis* and (b) *M. tepaneca*

Response variable	Predictor	Estimate	SE	z value	P value
a) *D. rinconis* pollen load					
Shannon–Wiener	% Shrub	0.0050	0.0021	2.235	0.0254*
	Sex				
	Male	1.203	0.1227	9.433	<0.0001*
	Female	0.9176	0.141	7.764	<0.0001*
	Trap				
	Net	1.038	0.1445	7.005	<0.0001*
	Pan	0.0301	0.1463	0.203	0.8395
	Sex × Trap	−0.3451	0.1156	2.865	0.0042*
	Period	−0.0358	0.0801	0.428	0.6684
	Plant species richness	−0.0001	0.0050	0.014	0.9890
Chao1	% Shrub	0.0066	0.0036	1.747	0.0807
	Sex				
	Male	1.7340	0.3169	5.340	<0.0001*
	Female	1.3870	0.2214	6.088	<0.0001*
	Trap				
	Net	1.4005	0.1591	8.500	<0.0001*
	Pan	0.0641	0.4811	0.133	0.8943
	Sex × Trap	−0.0763	0.0471	1.554	0.1202
	Period	−0.2116	0.1373	1.488	0.1368
	Plant species richness	0.0017	0.0045	0.203	0.8389
Richness	% Shrub	0.0067	0.0080	0.813	0.4163
	Sex				
	Male	1.2744	0.5210	2.369	0.0178*
	Female	1.0142	0.3885	2.522	0.0117*
	Trap				
	Net	1.1600	0.3145	3.549	0.0004*
	Pan	0.8713	0.3266	2.565	0.0103*
	Sex × Trap	−0.0817	0.1107	0.708	0.4792
	Period	−0.1337	0.3329	0.390	0.6967
	Plant species richness	0.0081	0.0168	0.467	0.6408
b) *M. tepaneca* pollen load					
Shannon–Wiener	% Shrub	0.0045	0.0034	1.300	0.1934
	Sex				
	Male	1.012	0.1621	6.081	<0.0001*
	Female	1.013	0.1631	6.060	<0.0001*
	Trap				
	Net	1.0147	0.1542	6.410	<0.0001*
	Pan	0.6263	0.5135	1.218	0.2234
	Sex × Trap	−0.3422	0.2192	1.509	0.1312
	Period	−0.0769	0.0416	1.788	0.074
	Plant species richness	−0.0014	0.0075	0.185	0.8534
Chao1	% Shrub	0.0085	0.0057	1.443	0.1490
	Sex				
	Male	1.3129	0.2786	4.592	<0.0001*
	Female	1.3020	0.2689	4.720	<0.0001*
	Trap				
	Net	1.3197	0.2667	4.822	<0.0001*
	Pan	0.8084	0.6758	1.193	0.2330
	Sex × Trap	−0.5032	0.3630	1.343	0.1791
	Period	−0.1437	0.0630	2.205	0.0275*
	Plant species richness	−0.5032	0.3630	1.343	0.1791
Richness	% Shrub	0.0047	0.0097	0.471	0.6380
	Sex				
	Male	0.6871	0.4733	1.407	0.1593
	Female	0.9172	0.3561	2.491	0.0127*
	Trap				
	Net	0.7842	0.3731	2.034	0.0420*
	Pan	0.9725	0.3649	2.578	0.0099*
	Sex × Trap	−0.2523	0.2715	0.897	0.3700
	Period	−0.0852	0.1676	0.491	0.6231
	Plant species richness	0.0145	0.0219	0.647	0.5178

The model selection examined the fixed predictor variables % Shrub at each site, bee sex (male or female), the trap method (net or pan), and the interaction term sex × trap, phenological period (period), and plant species richness, and the response variables, Shannon–Wiener, Chao1, or species richness. Collection site was implemented as a random effect in all models. Averaging was conducted using all models with Delta AIC <10. Reported values include the coefficient estimate (estimate), standard error (SE), z value, and P value (where an asterisk indicates $P < 0.05$).

Pollen Preference

Preference analysis revealed significant patterns of pollen selection for *M. tepaneca* (Period 1: $\lambda = 0.344$, $P = 0.006$; Period 2:

Table 2. Results of PERMANOVA comparing Sørensen dissimilarity indices between *M. tepaneca* and *D. rinconis* (species), and pan-trapped and net trapped bees (trap)

Response variable	Source	df	*F*	*P* value
M. tepaneca and *D. rinconis*				
Sørensen index ~ species × trap				
	Species	1	5.3262	0.104
	Trap	1	2.2092	0.004*
	Species × Trap	1	2.7037	0.066
	Period	1	3.0107	0.040*
	Species × Period	1	4.1282	0.021*
	Residuals	74		
	Total	77		
D. rinconis				
Sørensen index ~ sex × trap				
	Sex	1	25.4791	0.001*
	Trap	1	7.4685	0.001*
	Sex × Trap	1	8.3518	0.001*
	Period	1	3.1064	0.001*
	Sex × Period	1	1.8842	0.158
	Residuals	32		
	Total	35		
M. tepaneca				
Sørensen index ~ sex × trap				
	Sex	1	1.5350	0.263
	Trap	1	1.1979	0.654
	Sex × Trap	1	1.2730	0.546
	Period	1	1.0448	0.654
	Sex × Period	1	2.8130	0.032*
	Residuals	37		
	Total	40		

For each species individually, comparisons were made between males and females (sex), phenological period (period), and trap method (trap). Reported values include the degrees of freedom (df), *F* value (*F*), and *P* value (where an asterisk indicates $P < 0.05$).

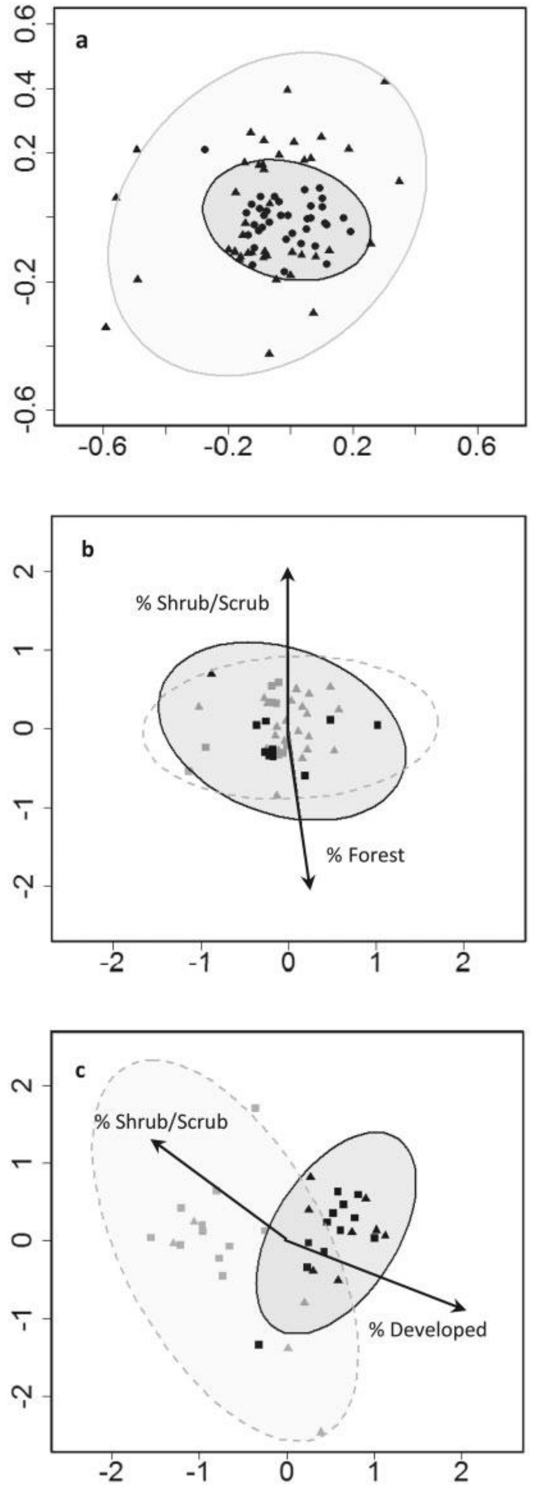

Fig. 2 NMDS (**a**) Combined species NMDS ordination diagram of *M. tepaneca* (▲) and *D. rinconis* (●) where males and females are pooled for each species, and ellipses designate the 95% confidence region for the samples within a species (gray = *M. tepaneca*, black = *D. rinconis*). Species separated NMDS ordination diagrams depicting (**b**) *M. tepaneca* and (**c**) *D. rinconis*, where males are black symbols and females are gray symbols. Squares represent the netted method, while triangles represent the pan-trapped method. Ellipses designate the 95% confidence region for the samples within the sex (gray = female, black = male). For the species separated NMDS (b and c), significant environmental drivers of pollen load community composition were fit to vectors within the ordination space ($P < 0.05$), where length of the vector describes the strength of the relationship.

$\lambda = 0.226$, $P = 0.038$), as well as *D. rinconis* (Period 1: $\lambda = 0.043$, $P = 0.002$; Period 2: $\lambda = 0.119$, $P = 0.004$; Table 3a and b). Both species exhibited a turnover in preferences over time. In *D. rinconis,* the most preferred plant species shifted from *Opuntia sp*. in Period 1 to *Cirsium texanum* (Buckley) in Period 2, while preference did not shift for the second and third most preferred plant species, *Gaillardia pulchella* (Foug) or *Mimosa nutalli* (Turner) (Table 3a and b). In *M. tepaneca,* the most preferred plant species was *G. pulchella* in both phenological periods; however, only one other species, *Monarda citriodora* (Cerv. ex Lag), remained preferred across periods 1 and 2.

Discussion

Our results illustrate that putatively generalist and specialist native solitary bee species, *M. tepaneca* and *D. rinconis,* exhibit substantial complexity in their inferred floral visitation patterns, driven by sex, landscape composition, phenological period, and collection method. Interestingly, we found that pollen load richness and diversity values (species richness, Shannon–Wiener, and Chao1) were greater in the specialist species, *D. rinconis*, compared with the generalist species, *M. tepaneca*. These results do not support our hypothesis that *M. tepaneca* visits a greater diversity of flowering plants than *D. rinconis*. Pollen load diversity was significantly higher in *D. rinconis* males than in females, but pollen load diversity did not significantly

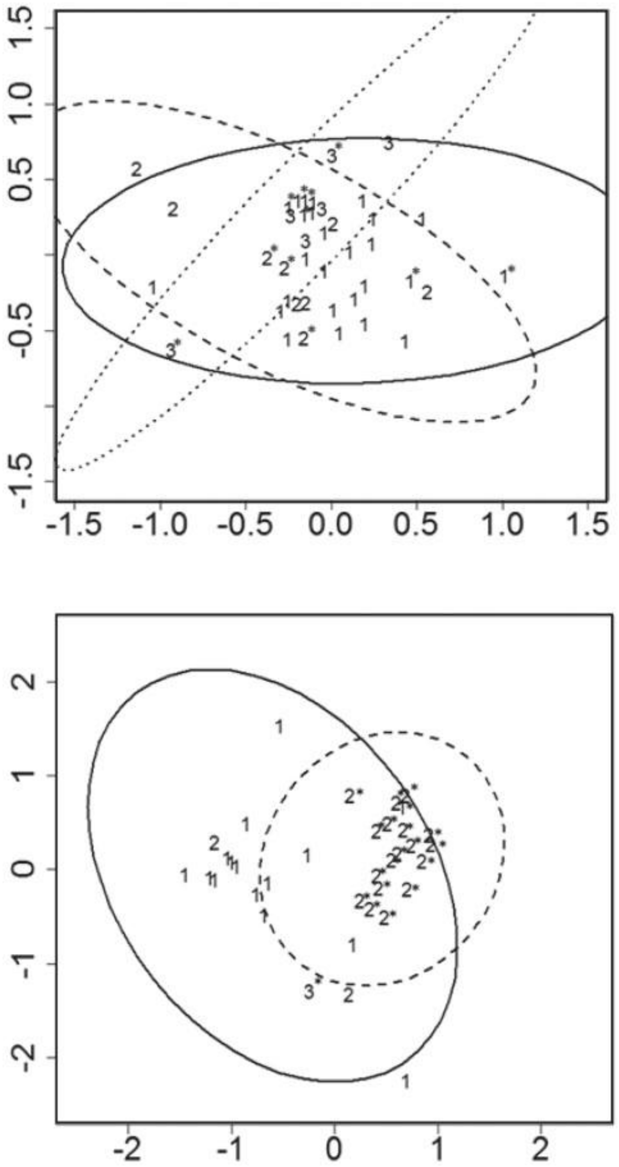

Fig. 3 NMDS ordination diagrams of *M. tepaneca* (**a**) and *D. rinconis* (**b**), where specimens are designated by their phenological period (1, 2, or 3). For both (a) and (b), males are denoted by asterisks to demonstrate sex × period interaction. In all panels, ellipses for the periods designate the 95% confidence region for the samples within each phenological period. For both (a) and (b), the solid ellipse represents Period 1, the dashed ellipse represents Period 2, and the dotted ellipse represents Period 3 (ellipse for Period 3 not depicted for *D. rinconis* given small sample size).

differ between males and females of *M. tepaneca*. We found significant dissimilarity in pollen loads between the sexes and across periods for *D. rinconis*, while *M. tepaneca* pollen loads were significantly dissimilar between the sexes only in the third sampling round. Thus, we do not find strong support for our hypothesis that pollen load composition is more dissimilar for the generalist. Likewise, we found some support for our second hypothesis that pollen load composition is driven by natural land use; however, we found this was true for both species. Our hypothesis that collection type did not affect pollen richness was also only partially supported. Netted *D. rinconis* had higher pollen load diversity than pan-trapped *D. rinconis*, but we found no significant difference in diversity between collection types in *M. tepaneca*. Similarly, pollen loads were not significantly dissimilar between the collection methods or phenological periods for *M. tepaneca*, but were significantly dissimilar between the collection types and across periods for *D. rinconis* individuals. We found that both generalists and specialists exhibited strong preferences for two pollen types, *C. texanum* and *G. pulchella*, and both exhibit shifts in preference over phenological periods, refuting our third hypothesis that *D. rinconis* exhibits stronger preferences for a select group of plant species than *M. tepaneca.*

Pollen Load Diversity

Two species of Asteraceae dominate the pollen loads of both *M. tepaneca* and *D. rinconis,* despite comprising a relatively small percentage of the landscape*: C. texanum* and *G. pulchella*. The species *C. texanum* and *G. pulchella* comprised 15.2 and 26.7% of the average *D. rinconis* pollen load, and 12.7 and 21.1% of the average *M. tepaneca* pollen load, respectively, while comprising, on average, only 0.3 and 7.2% of landscape floral cover in our study, respectively. Previous studies have revealed the important role of Asteraceae in the diets of wild bees (Tommasi et al. 2004, Fetridge et al. 2008, Müller and Kuhlmann 2008), including research conducted in Central Texas (Neff and Simpson 1991, 1997). This is possibly due to the fact that the composite inflorescences of the Asteraceae can provide high pollen and nectar rewards at a low energy expenditure cost through reduced handling and probing time (Waser and Ollerton 2006, Müller and Kuhlmann 2008). In addition, these flower species bloom from April to August (Lady Bird Johnson Wildflower Center Native Plant Database, 2016 last accessed February 2, 2016), providing a high-reward resource throughout the foraging and provisioning phases of many wild bees. Our results suggest that *C. texanum* and *G. pulchella* indeed provide native solitary bees with food resources across Central Texas prairie landscapes over long periods.

One unexpected pattern detected in our data was the high percentage of non-*Opuntia* pollen collected by *D. rinconis*. On average, *Opuntia* composed only 20.8% of the *D. rinconis* pollen load in our specimens. Examining the sexes separately, *Opuntia* content per load was lower than expected for females (51.8%) and males (<0.01%). Across phenological periods, *Opuntia* comprised 47.8% of the *D. rinconis* pollen loads in Period 1 (15 female, 1 male), 2.5% of the loads in Period 2 (2 female, 18 male), and 0% of the loads in Period 3 (1 male). These results are surprising, given that previous visitation-based studies of *D. rinconis* classify the species as a specialist (Linsley and Macswain 1958, Ordway 1987, Neff and Simpson 1992), and suggest that *Opuntia* comprises nearly 100% of pollen provisions within nests and scopal loads (Neff and Simpson 1992). While some past studies document *D. rinconis* visitation to non-*Opuntia* species, including various Asteraceae and other Cactaceae, they did not quantify pollen load content (Adlakha 1969, Ordway 1987), nor distinguish between pollen collection and nectar foraging (Mcgregor et al. 1959). One past museum-based study of pollen load composition in four *Diadasia* species found that pollen loads ranged from <1% to 27% non-*Opuntia* species. Among these four species, *D. rinconis* pollen loads had the lowest average *Opuntia* content per load (73%) and the lowest number of specimens carrying pure *Opuntia* loads (77%; Sipes and Tepedino 2005), indicating a tendency to forage more broadly than its congeners. The phenology and availability of *Opuntia* in our study region might also explain our results. *Opuntia* in our study region blooms from April to June, with few species blooming through July (LBJWC NPD 2015); our field data confirm that Opuntia comprised 0.005%

Table 3. Results of pollen preference analysis for *D. rinconis* and *M. tepaneca* in phenological period 1 (a) and phenological period 2 (b), where the top 5 preferred floral species are listed (USDA acronym in Supp. Table 1 [online only])

a) Species	Floral species	P	λ	Rank	Species	Floral species	P	λ	Rank
Diadasia		0.002*	0.04287755		*Melissodes*		0.006*	0.3443095	
	Opuntia sps			AB		*Cirsium texanum*			ABC
	Gaillardia pulchella			AB		*Gaillardia pulchella*			ABC
	Mimosa nuttallii			CD		*Thelesperma filifolium*			ABC
	Cirsium texanum			CDE		*Monarda citriodora*			ABC
	Verbena canescens			CDE		*Lygodesmia texana*			ABC

b) Species	Floral species	P	λ	Rank	Species	Floral species	P	λ	Rank
Diadasia		0.004*	0.1993234		*Melissodes*		0.038*	0.2261692	
	Cirsium texanum			A		*Cirsium texanum*			ABC
	Gaillardia pulchella			BC		*Coreopsis basalis*			ABC
	Mimosa nuttallii			BC		*Monarda citriodora*			ABCD
	Senna lindheimeriana			D		*Dracopis amplexicaulis*			CD
	Stenaria nigricans			D		*Bifora americana*			E

Rank denotes the level of preference for the particular flower species, with A being the most preferred and different letters indicating a significantly ($P < 0.05$) different level of preference. The results of the overall preference selection test (P value and Lambda) are listed for each plant species (where an asterisk indicates $P < 0.05$).

of the landscape floral cover in Period 1, but 0% of the floral cover in Period 2. Specialized bee species such as *D. rinconis* typically exhibit proximate phenological overlap with their host plants (Ordway 1987, Neff and Simpson 1992), thus we would expect fewer *D. rinconis* females foraging as the *Opuntia* bloom ends. This is supported by the observed turnover in *Opuntia* pollen and the sexes between periods in our study. Specialization, however, may still take place in terms of pollen selection for larval provision. A future exploration of this could be done by comparing body and scopal loads (Petanidou et al. 1995), though verification of specialization would require examining nest pollen provisions. From an ecological perspective, our results provide insight into overall foraging breadth and indicate that *D. rinconis* within Central Texas is a broader floral visitor than previously believed.

In contrast, we found that the generalist *M. tepaneca*'s pollen loads had lower diversity compared with the specialist *D. rinconis*, indicating a relatively low level of generalization within the study region. Potential explanations for this lower level of generalization include reduced foraging ability or duration, or increased visitation to a preferred group of flowering plant species. While foraging distance measurements have not been documented for these two species, they are approximately the same size (~2.8–3 mm intertegular distance). Because foraging distance largely correlates with body size (Greenleaf et al. 2007), we suggest that foraging ability is not the primary driver of pollen load differences. Instead, we suggest that the two species exhibit distinct levels of specialized foraging at the individual or population level (Ne'eman et al. 2006, Kleijn and Raemakers 2008, Smith et al. 2012). In this manner, increased specialization in *M. tepaneca* could be driven by floral constancy, defined as the restriction of foraging to certain plant species, despite abundance or the presence of equally rewarding species (Chittka et al. 1999, Osborne et al. 1999, Amaya-Marquez et al. 2008). *Melissodes tepaneca*'s significant preference for *C. texanum* within our study region provides further evidence that floral constancy and preference, not local floral abundance, may be driving the lower levels of generalism documented for the species in this study system.

To the authors' knowledge, this is the only study comparing pollen data from pan-trapped and netted bees. While we found no relationship between collection type and pollen diversity for M. *tepaneca*, we found that netted *D. rinconis* pollen loads had significantly greater diversity than pan-trapped *D. rinconis* specimens. Thus, we show that pollen analyses for the two different collection types could indeed yield different insights on floral visitation; interestingly, this also depends on species identity. We suggest that this pattern could be driven by differences in water-mediated pollen removal via pan trapping, which could be distinct across species due to differences in the physical pollen storage structures for each species, such as scopal structure or density, which can vary across bee species (Michener 2000). Therefore, we suggest that comparisons of pollen loads across bee species should consider collection method and ideally compare individuals using the same collection techniques. However, for both species, our results also indicate that preference trends are consistent across netted and pan-trapped bees, suggesting that collection methodology does not necessarily obscure an understanding of floral preference.

Pollen Composition Dissimilarity

We found that shrub habitat was a driver of pollen load composition for both bee species. Shrub lands in many regions exhibit high levels of flowering plant diversity (Naveh and Whittaker 2015), and thus likely provide diverse food resources for bees in our Central Texas study region. This pattern may be especially easy to detect due to the fact that both *M. tepaneca* and *D. rinconis* are small soil-nesting species reliant on primarily undisturbed substrate, potentially found abundantly within shrub habitat. Given that the foraging ranges of solitary soil-nesting bees may be largely within a 150-600 m radius of their nest site (Gathmann and Tscharntke 2002), the proximity to both nesting habitat and high floral resource diversity may explain why shrub habitat is an important driver of pollen load composition.

Our ordination analyses also reveal that pollen load composition is significantly dissimilar between the sexes in *D. rinconis*. This significant dissimilarity between males and females of *D. rinconis* is perhaps best explained through the differing life histories of the sexes: male *D. rinconis* emerge several days before females, disperse for foraging, and later patrol nest aggregations to mate with emerging females (Neff and Simpson 1992). Female *D. rinconis* bearing pollen typically ignore males, and males rarely attempt copulation at flowers (Neff and Simpson 1992). In contrast, comparatively little is known of *M. tepaneca*'s life history. Similar to *D. rinconis,* males of some *Melissodes* species with communal nesting behavior emerge before females and establish patrols around the nesting aggregate, resulting in many matings taking place in the nesting area versus on foraging bouts; although, these behaviors might not be consistent across the genus (Clement 1973, Triplett and Gittins 1988, Cameron et al. 1996).

In addition, for *D. rinconis*, we detected dissimilarity between sexes, especially for pan traps, and dissimilarity across periods, while for *M. tepaneca*, we detected dissimilarity between sexes only at specific periods. A collection method-driven pattern of dissimilarity for *D. rinconis* could be due to the fact that female bees actively forage for pollen and have various behavioral and physiological mechanisms for collection, while males only appear to collect pollen incidentally while foraging for nectar (Thorp 2000, Ne'eman et al. 2006). Because males do not actively collect and pack pollen into specialized structures, we believe that pan trapping may lead to greater pollen removal in male specimens. A consistent temporally driven pattern of dissimilarity for *D. rinconis* could be due to differences in resource requirements between males and females across phenological periods. The first phenological period roughly corresponds with peak *Opuntia* bloom, while the second period corresponds with the end of the bloom period. A decline in host plant flower availability could potentially lead to a decline in female *D. rinconis* foraging activity, explaining the observed turnover between the sexes from Period 1 to Period 2. Interestingly, for *M. tepaneca,* we only documented differences between the sexes in the third round, when floral resources are low in the landscape. One hypothesis for this pattern could be that female foraging activity shifts to accommodate the reduced availability of suitable pollen hosts in the late season, while males may forage just on the most rewarding or abundant nectar source in the late season. This contrasts with the early season, when foraging between the sexes of generalist species may be more similar, given the increased availability of highly rewarding plant species. Overall, our results indicate the importance of accounting for trapping type and within-season variation when examining plant–pollinator interactions. Future comparisons of pan trap and netted data should compare sexes across periods for other species to examine the generalizability of our findings.

Pollen Preference

We found that both *M. tepaneca* and *D. rinconis* exhibited a strong preference for native species, as all floral species collected by both species were native to the study region. The preferred floral species across phenological period comprised members of Asteraceae and Lamiaceae in *M. tepaneca*, and Asteraceae and Fabaceae in *D. rinconis*. Both bee species share two of their five most highly preferred floral species: *G. pulchella* and *C. texanum*. These preferences could be explained by the fact that both *C. texanum, G. pulchella* and several of the other preferred flower species are Asteraceae—possessive of compound inflorescences yielding high amounts of pollen and nectar, and a widely exploited nutritive resource source (Graenicher 1935, Moldenke 1979, Müller 1996). Past work in the study region also indicates that rewarding Asteraceae, such as *G. pulchella* or *C. texanum*, appear in the pollen stores of both putative polylege and oligolege bee species (Neff and Danforth 1991, Neff and Simpson 1991, 1992, 1997). *Cirsium texanum* in particular has been observed as a nectar source for Central Texas *D. rinconis* (Neff and Simpson 1992). Our results also show that floral preferences shifted across phenological period for both bees. In Period 1, *D. rinconis* preferred their host plant *Opuntia* to a similar degree as *G. pulchella*, and exhibited a lesser preference for *C. texanum*, while *M. tepaneca* preferred *G. pulchella* to a similar degree as *C. texanum*. In Period 2, the most preferred floral species shifted to *C. texanum* for both bee species. Three of the most preferred species for *D. rinconis* were collected across both periods, while only two of the most preferred species for *M. tepaneca* were collected in both periods. Future studies could compare pollen loads of generalist and specialist species within-season and across seasons to better understand how floral preference shifts overtime. The results of our preference analyses demonstrate within-season variation in plant–pollinator interactions for both generalist and specialist bees and the relative importance of highly rewarding native flowers in the diet of native bees.

Synthesis

Our findings support previous studies and reviews suggesting that categorization of pollinators as specialists or generalists can often be a result of study-framing and do not necessarily describe foraging behavior throughout a population over time and space (Waser et al. 1996, Ne'eman et al. 2006, Alarcón et al. 2008, Kleijn and Raemakers 2008, Burkle and Alarcón 2011, Smith et al. 2012). In the case of bees, oligolecty and polylecty are historically largely based upon visual observations of floral visitation or pollen collection (Linsley and Macswain 1958, Roulston and Cane 2000, Bosch et al. 2009). Our results suggest that these approaches alone may not completely describe past interactions between the plant community and bee species, and thus demonstrate the need for a multifaceted sampling approach when examining plant–pollinator interactions.

We posit that the analysis of bodily pollen provides an additional approach to understanding floral visitation patterns, and suggest that this approach could be examined across space and time. Future research could benefit from studies that investigate the relationship between specialization and floral availability through consecutive, multi-year pollinator assemblage surveys (Price et al. 2005, Dupont et al. 2009, Smith et al. 2012) followed by the analysis of nest provision for select species (as in Neff and Simpson 1992). Such surveys could elucidate the relationship between shifts in landscape floral resource composition over time with annual changes in plant–pollinator interaction networks and larval provisioning. Finally, through the inclusion of pollen preference analyses, we suggest that generalized habitat restoration may benefit both specialist and generalist pollinator species. In our study, highly rewarding floral species were visited by both putatively specialist and generalist bees. Thus, the investigation, characterization, and cultivation of such highly rewarding plant species could potentially simplify the compositional requirements of restorations, while broadly supporting native pollinator diversity in human-dominated landscapes.

Acknowledgments

Special thanks to Nathaniel Pope, and the members of the Jha Lab for their input and support. This study was funded by the University of Texas at Austin, the Army Research Office, and the National Science Foundation (SJ).

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