Title: Local nesting resources rather than floral food alter ground-nesting bee communities in grazed habitats

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Abstract

1. Understanding how the availability of both trophic and non-trophic resources impacts key ecosystem service providers is crucial for informing conservation efforts. Non-trophic resources such as space, shelter, or mates can play critical roles in ecosystem function and resilience by affecting predation and pathogen rates, reproductive success, and interspecific interactions. However, non-trophic resources are often overlooked. This holds true for insect pollinators; impacts of non-trophic resources on community dynamics and pollination remain poorly understood.
2. We investigated the importance of food (flowers) and shelter (nests) for ground-nesting bees. Because the large majority of bee species spend most of their lives underground, we explored whether nesting habitat availability is a key driver of bee abundance, diversity, and community composition. We additionally compared impacts of aboveground characteristics that describe nesting habitat with the belowground characteristics that have received significantly less attention. Habitat characteristics we considered included floral abundance; bare ground cover; vegetative biomass; and soil texture, compaction, and depth.
3. We found that belowground, but not aboveground, nesting habitat characteristics were important for ground-nesting bee assemblages. Ground-nesting bee abundance and richness was highest at sites with sandier and more compacted soils. Floral food availability also increased bee abundance. No habitat characteristics affected bee community composition.
4. *Policy implications:* Our study highlights that the availability of high-quality nesting habitat can strongly impact ground-nesting bee assemblages, and that measuring belowground characteristics of nesting habitat may be critical for understanding bee community dynamics. Thus, data-driven conservation planning should consider management-insensitive site

characteristics, such as soil texture. Because land and funding are limited, focusing on belowground site characteristics when prioritizing locations for conservation actions can facilitate conservation success.

Keywords: Apoidea; biodiversity; floral abundance; grassland; nesting habitat; pollinator; soil compaction; soil texture

Introduction

Anthropogenic change is causing dramatic resource declines for native wildlife (Gossner et al., 2016). Given these resource limitations, understanding how the availability of different resources impacts key ecosystem service providers is crucial for informing conservation efforts (Davis et al., 2023; Requier & Leonhardt, 2020). This includes insect pollinators, which provide vital pollination services and are often threatened by habitat degradation (S. G. Potts et al., 2010). The importance of trophic resources for pollinators is firmly established, with higher flower abundance and diversity generally promoting pollinators (Hyjazie & Sargent, 2022; Kral-O'Brien et al., 2021). However, the roles of non-trophic resources such as space, shelter, or mates are generally not well understood (Davis et al., 2023; Requier & Leonhardt, 2020). Non-trophic resources can impact fitness as much as, or more strongly than, trophic resources by affecting predation and pathogen rates, reproductive success, and interspecific interactions (e.g., Karban et al., 2013). Given a growing body of research that suggests non-trophic resources play critical roles in ecosystem function and resilience (Kéfi et al., 2015), there is an urgent need to understand how such resources alter pollinator communities.

Shelter, including nests and overwintering sites, is a key non-trophic resource historically overlooked in pollinator research (Harmon-Threatt, 2020; Kremen et al., 2007). Common pollinator shelter locations include underground in soil and aboveground in living or dead vegetation or leaf litter (Michener, 2007). Adults shelter for protection from heat, desiccation, and predation, and nests are crucial for offspring survival. For larvae that are largely immobile and spend significant time in nests (e.g. bees, many beetles), survival to adulthood relies heavily on appropriate nest site selection by the mother. Poor nest site choice, or limited nesting habitat, can leave offspring susceptible to predation, pathogens, floods, fires, or other natural

disturbances (C. M. Antoine & Forrest, 2021). Such threats vary with species' risk-mitigating adaptations. For example, maternal secretions can waterproof nest linings to protect larvae from floods and fungal pathogens. Additionally, species' traits such as appendages specialized for burrowing in specific substrates (soil, wood, or vegetation) can determine characteristics of ideal nesting habitat (Albans et al., 1980). Availability of habitat with suitable shelter may therefore be a key driver of insect pollinator abundance, diversity, and community composition. This is particularly important for bees, which spend all but a short period of their life cycle inside a nest.

Over 80% of bee species nest in the ground (Harmon-Threatt, 2020), yet most investigation of ground-nesting bee habitat has focused on aboveground vegetation cover and its correlate: bare ground. Female bees searching for suitable nesting habitat (and researchers) may rapidly assess such characteristics. These characteristics can influence nest access and alter the microclimate. Dense vegetation or leaf litter can protect nests from the elements and nest parasites or predators (Lucchetta et al., 2008). On the other hand, sparser cover can increase nest accessibility, and facilitate nest location via visual or odor cues when bees return from foraging (Gomez Ramirez et al., 2023; Inouye, 2000; Ostwald et al., 2019; Wuellner, 1999). Bare ground also warms up more quickly in the spring, potentially allowing bees to become active earlier in the year (J. Cane, 2021; Herb et al., 2008; Wuellner, 1999). While these mechanisms have not been explicitly tested, multiple studies have found higher bee abundance or diversity at sites with more bare ground (reviewed in Harmon-Threatt, 2020).

Belowground soil characteristics may be equally or more important for bee nesting and survival than aboveground shelter characteristics, but are rarely considered (J. H. Cane, 1991; Harmon-Threatt, 2020; Lybrand et al., 2020; Wuellner, 1999). This is in part due to challenges with locating underground nests. Habitat characteristics such as soil texture (proportions of sand, silt,

and clay particles), organic matter content, pH, and ground slope and aspect (the compass direction terrain faces) can strongly affect nest conditions. Sandier or less compacted soils tend to be easier to dig in (Brockmann, 1979; Polidori et al., 2010; S. Potts & Willmer, 1997). Nests may have more structural integrity in more compacted soils (S. Potts & Willmer, 1997), soils with more organic matter (Murphy, 2015), or in sandy soils that drain quickly and thus experience less shrinking and swelling (Jouquet et al., 2004). Rapid soil drainage (affected by texture, compaction, organic matter content, and slope) may also reduce nest susceptibility to flooding and fungal pathogens (Collis-George, 1991; Fellendorf et al., 2004; Murphy, 2015; Obayomi et al., 2019; Parr & Bertrand, 1960), or lead to brood cell desiccation (Potts and Willmer 1997). Aspect can also alter ground temperature. For instance, a southern slope may keep nests warmer in the winter or improve responsiveness to spring warming. Documented ground-nesting bee preferences for sandier soils (J. H. Cane, 1991; Fortel et al., 2016), less compacted soils (S. Potts & Willmer, 1997; Sardiñas & Kremen, 2014), and southern slopes (S. Potts & Willmer, 1997) support these hypotheses. However, these habitat characteristics can also alter plant communities and cover (Dodd et al., 2002; Pennington et al., 2017; Renne et al., 2019). Thus, it is unclear whether documented responses of bee species and assemblages to aboveground habitat characteristics (such as bare ground) indicate preferences for that characteristic itself, or for associated belowground habitat characteristics. There is a crucial need to determine impacts of belowground soil properties, in addition to aboveground vegetation, on bee communities (Harmon-Threatt, 2020).

We addressed two key questions about how floral food and shelter impact bees, focusing on several habitat characteristics that describe these resources. First, we asked whether flowers or nesting habitat more strongly determine ground-nesting bee assemblages. We hypothesized

that nesting habitat characteristics are as important as floral abundance and diversity for bee assemblages because nest site selection plays a key role in bee survival (Harmon-Threatt, 2020). Second, we determined whether above- or belowground nesting habitat characteristics are more important determinants of ground-nesting bee assemblages. We hypothesized that belowground resources are stronger drivers of ground-nesting bee assemblages because these bees spend the majority of their lives, including the vulnerable egg and larval stages, underground. To address these questions, we determined the importance of food and shelter resources for grassland bee assemblages in rangeland, a common land use type that covers 40-50% of Earth's ice-free surface with largely natural land (Sala et al., 2017) and have strong potential to support pollinator biodiversity and conservation. Because grazing may affect soil, vegetation, and ground-nesting bees, we incorporated grazing management into analyses.

Methods

Study Sites

We conducted this study on ranches in the Cross Timbers ecoregion in North Texas (Fig. S1). The Cross Timbers are characterized by tallgrass prairies interspersed with dense woodland belts, with gently rolling hills. Precipitation is highly variable, averaging 686-965 mm per year, with two wet seasons: spring and fall. Summer temperatures are hot, averaging 21-36°C, and winter temperatures are mild at -1-3°C (Griffith et al., 2007). Soils range from heavy clays to clay-loams to loams (UC Davis Soil Resource Lab et al., 2022). Ranches were managed using adaptive multi-paddock grazing with cattle and sheep kept at high densities and rotated among small paddocks every 1-3 days. We obtained grazing records to calculate grazing rest period (time since the site was last grazed by livestock) for each site prior to each sampling event.

We sampled nine open grassland sites that were sufficiently far apart relative to insect flight distances to be spatially independent (separated by at least 1.5 km; Kendall et al., 2022) and shared similar soil types based on soil maps (Fig. S1a; UC Davis Soil Resource Lab et al., 2022). Relative abundances of anticipated soil types varied across sites, creating gradients of habitat characteristics. At each site we established eight 90 m transects radiating from the site's center, one in each cardinal and intercardinal direction (Fig. S1b). Along these transects we measured floral food, aboveground nesting habitat characteristics, and bee assemblages once during the spring (April-May), summer (June), and fall (September-October) bloom periods (three times total per year) in 2021 and 2022 (six times total). We measured flowers and aboveground nesting habitat characteristics in six 1 x 1 m quadrats, located at 15 m intervals, along each transect (48 quadrats per site; Fig. S1b). Each bloom period, including summer, lasts only several weeks. Rainy and windy weather further limit suitable sampling days within each season. Thus, sampling once per season provides high-quality data that is comparable across sites. We measured aboveground vegetative biomass in December 2021 and 2022, when vegetation was largely dormant. In spring 2021 and 2022, we measured belowground nesting habitat characteristics, which do not change substantially over short time periods (Zarekia et al., 2012). We measured these characteristics at 30 and 90 m from the site center, walking 10 m to the left (30 m) or right (90 m) of the eight transects to avoid altering vegetation along transects (16 samples/site; Fig. S1b). Table S1 describes these measurements.

Floral Food

We measured each site's floral abundance and richness (Table S1) by identifying each flowering plant to species (or occasionally genus) and counting the number of flowering units

(individual flowers, umbels, or spikes depending on species, as in Lichtenberg et al., 2024) of each plant species in each 1 x 1 m quadrat. To better capture floral species richness in heterogeneous grasslands, we recorded the presence of additional flowering species found within 1 m of each cardinal and intercardinal transect. At each site, we photographed each flowering plant species and confirmed identification with experts. Plant observations are available at https://www.inaturalist.org/projects/lichtenberg-lab-rotational-grazing-study.

Aboveground Nesting Habitat Characteristics

We estimated spring, summer, and fall vegetation cover at both canopy (top of vegetation) and ground levels. Canopy cover types included live grass, live forbs, dead/senesced standing grass and forbs, wood (e.g., tree trunks), and no canopy. Ground cover types included litter, bare ground, rocks and gravel, moss, manure, green prostrate angiosperms, and stems. We quantified the portion of each quadrat's 25 squares (each 20 x 20 cm), to the nearest half square, in each category, then averaged cover proportions for each category for the site and season (as in Lichtenberg et al., 2024).

We additionally sampled aboveground vegetative biomass to estimate vegetation density. We collected all standing vegetation and litter from 0.5 x 0.5 m quadrats placed 100 m from the site's center in the four cardinal directions (Fig. S1b). We dried each sample (Soiltest Laboratory Oven, Shel Lab Force Air Oven, Thermo Scientific Precision Standard Oven, VWR Gravity Convection Oven) at 105 °C until a sample's weight was stable for at least 12 hours to determine dry grams of vegetation per square meter for each site and year.

Belowground Nesting Habitat Characteristics

We measured several belowground habitat characteristics with potential to impact ground-nesting bee nest site selection or success: soil texture, depth, organic matter content, pH, and compaction; and ground slope and aspect (Table S1). We collected 30 cm long soil cores where the soil was deep enough, and several shorter cores with a total length of at least 30 cm in shallower soils. We mixed at least three cores at each sampling location to account for small-scale soil heterogeneity (Cunningham et al., 2012). The first complete core was used to determine maximum soil depth up to 30 cm. In the lab we measured soil texture, organic matter content, and pH of each sample using standard pipette analysis, loss on ignition (LOI), and soil pH procedures, respectively (Klute, 1986; Rousk et al., 2009). We measured soil compaction by collecting soil samples of consistent volume (90.59 cm^3, using an AMS Bulk Density 2″ x 2″ SST Liner) and determining bulk density (a precise soil compaction proxy; Nawaz et al., 2013) using standard procedures (Klute, 1986). We measured ground slope and aspect using a compass and clinometer (Suunto® MC2 Pro Sighting Compass with Built-In Clinometer).

Bee Assemblages

We sampled each site's bee assemblage via passive trapping and active netting on the same day as we measured aboveground vegetation in spring, summer, and fall (Table S1). Traps included one blue vane trap at the site's center and four sets of three pan traps placed 5 m from the site's center along each cardinal direction (Fig S1b; 2 oz plastic bowls painted in colors attractive for bees: Rust-oleum Fluorescent yellow and white, Krylon bold neon blue; Kearns & Inouye, 1993; Leong & Thorp, 1999). We filled each trap with soapy water and deployed the traps for 24 hours. At each site, we netted bees on flowers along transects at 10:00 and 13:00 for 30 minutes in 2021 and 45 minutes in 2022. Bees were only netted if they touched flower

reproductive parts. We only sampled when weather allowed for normal bee activity: fully or mostly sunny, temperatures above 18 °C, and average wind speed less than 6.7 m/s with gusts less than 8.9 m/s (as in Buckles & Harmon-Threatt, 2019; Stein et al., 2020). We later identified all specimens to genus or species using morphological characteristics and available keys (e.g., Bzdyk, 2012; Dumesh & Sheffield, 2012; Gardner & Gibbs, 2023; Michener et al., 1994; Portman et al., 2022; Williams et al., 2014; complete list in Table S2) and verified identifications with taxonomic experts.

Data Analyses

We assessed the impacts of food and shelter resources on bee abundance, richness, and community composition. All analyses were conducted in R (R Core Team, 2023). First, we reviewed existing literature on bee nesting behavior to classify species as ground nesting if they nest in the ground obligately or facultatively, and nesting aboveground otherwise. When evidence of a species' nesting behavior was not available, we used documented behavior of congeners when possible (i.e., consistently below- or aboveground). Only 2.73 % of specimens (12 species) lacked nesting behavior information and were excluded from analyses. Next, we calculated ground-nesting bee abundance, richness, and Chao diversity (Chao et al., 2014) for each site and sampling season (e.g., summer 2021). Chao estimates were often very close to measured richness (Table S3), indicating that our sampling effort was sufficient to accurately capture the bee assemblages at our sites, and thus we present analyses based on measured richness.

We determined the impacts of food and shelter resources on ground-nesting bee abundance and richness using linear or generalized linear mixed models. These models included

bee abundance or richness as the response, habitat characteristics and grazing rest period as fixed effects, and sampling season (which incorporated both year and time of year) as a random effect. Models did not include site as a random effect because it was collinear with our set of fixed effects (Wooldridge, 2010). We used the identity link for richness models (lme4 package; Bates et al., 2014) but negative binomial models for bee abundance data due to overdispersion (glmmTMB package; Brooks et al., 2017). Because quantitative predictors varied in units of measurement, we standardized predictors by subtracting the mean and dividing by the standard deviation.

We selected five fixed-effect predictors that were relevant to our hypotheses and captured a range of resource-associated characteristics: floral abundance, bare ground cover, aboveground vegetative biomass, soil sand content, soil depth, and soil compaction. We confirmed that these variables were not collinear (VIF < 4; Kroll & Song, 2013). We omitted floral richness due to correlations with floral abundance and vegetative biomass (Table S4). We determined the impact of all fixed effects via model averaging (MuMIn package; Barton, 2014). Predictors were considered important for bee abundance or richness if their confidence interval in the averaged model did not overlap zero. We calculated parameter estimates and confidence intervals using the full average ("zero") method to limit the influence of parameters which rarely occurred in selected models (Burnham & Anderson, 2002).

We determined how food and shelter affected ground-nesting bee community composition. We generated a matrix of the presence or absence of each species at each site in each year, and used this to generate a Bray-Curtis (Sørensen) community distance matrix. We used presence/absence data rather than abundances to prevent potential biases from social species. We then tested impacts of the same habitat characteristics as in regressions using

PERMANOVA with marginal means, stratified by year to control for potential community differences across years (vegan; Oksanen J, Simpson G, Blanchet F, Kindt R, et al., 2022). We summarized most habitat characteristics as the yearly mean value across sampling events, and floral abundance as the total number of flowering units counted across all three seasons. Variables were binned into two groups by median.

Because we conducted this study on working ranches, it was necessary to account for potential impacts of grazing rest period on vegetation and ground-nesting bees. We determined grazing rest period impacts on food and shelter through a set of mixed models with a habitat characteristic as the response, grazing history as a fixed effect, year as a fixed effect and site as a random effect for characteristics measured yearly (vegetative biomass), and sampling season and site as random effects for characteristics measured seasonally (bare ground cover, floral abundance). We did not test impacts on soil sand content or soil depth, as severe erosion is the main force that can change these properties over relatively short time periods (Dong et al., 2022). We used logistic regression for proportional response variables (bare ground cover) with proportions weighted by the number of quadrats sampled per sampling event (48), negative binomial regression for floral abundance, and the identity link for other variables. We conducted likelihood ratio tests to measure the relative effects of grazing rest period on each habitat characteristic.

Results

Floral food and nesting habitat characteristics, and bee abundance and richness, varied considerably (Table S5). We collected 951 individual bees across 98 taxa and 29 genera. Ground nesters comprised 765 individuals (80% of all bees collected) spanning 69 taxa (70% of all taxa

collected), 20 genera, and 6 families (Table S6). The majority of ground-nesting bees were in the family Halictidae (74%), followed by Apidae (22%). *Lasioglossum* species were the most common (60% of ground-nesting bees), followed by *Melissodes* (11%), *Bombus* (9%), and *Agapostemon* (7%).

Floral food resources affected bee abundance but not richness. Sites with more flowers had more ground-nesting bees (Fig. 1; Table 1). Floral abundance did not affect ground-nesting bee community composition (Table S7).

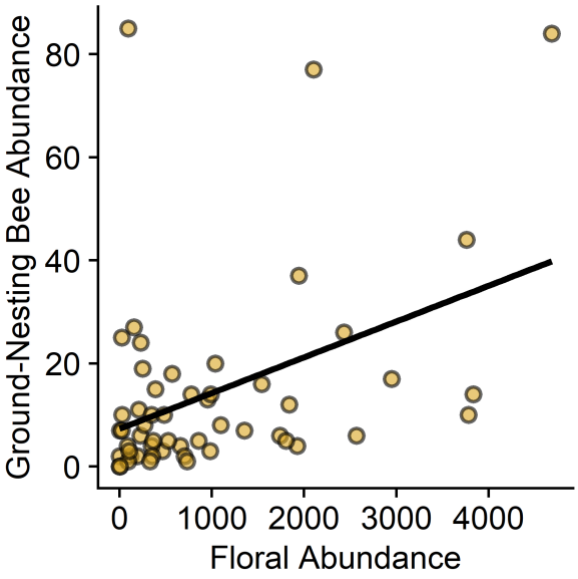

Figure 1: Sites with more flowers had more ground-nesting bees. Floral abundance indicates the total number of flowering units counted in 48 1 x 1 m quadrats at a site within a season. The line indicates best fit.

Habitat characteristic	**Coefficient**	**Lower 95% Confidence Limit**	**Upper 95% Confidence Limit**	**Importance**

(Intercept)	2.26	1.96	2.56	
Floral abundance	0.36	0.09	0.62	0.97
Bare ground cover	-0.01	-0.15	0.12	0.23
Aboveground vegetative biomass	0.25	-0.15	0.65	0.74
Soil sand content	1.09	0.71	1.46	1.00
Soil depth	-0.01	-0.15	0.13	0.21
Soil compaction	-0.67	-0.99	-0.34	1.00
Grazing rest period	0.01	-0.11	0.14	0.22

Table 1: Effects of food and shelter resources on ground-nesting bee abundance. All predictors were standardized to facilitate comparison across habitat characteristics. Coefficients, confidence intervals, and importance values (sum Akaike weights) are from the averaged model. Terms with confidence intervals that do not overlap zero are highlighted in green.

Belowground nesting habitat characteristics affected bee assemblages, while aboveground nesting habitat characteristics did not. Sandier and more compacted soils supported higher ground-nesting bee abundance and richness (Fig. 2; Tables 1,2). However, soil depth, vegetative biomass, and bare ground cover did not impact ground-nesting bee abundance or richness (Tables 1,2). No nesting habitat characteristics—including soil sand content, soil compaction, soil depth, vegetative biomass, and bare ground cover—altered ground-nesting bee community composition (Table S7).

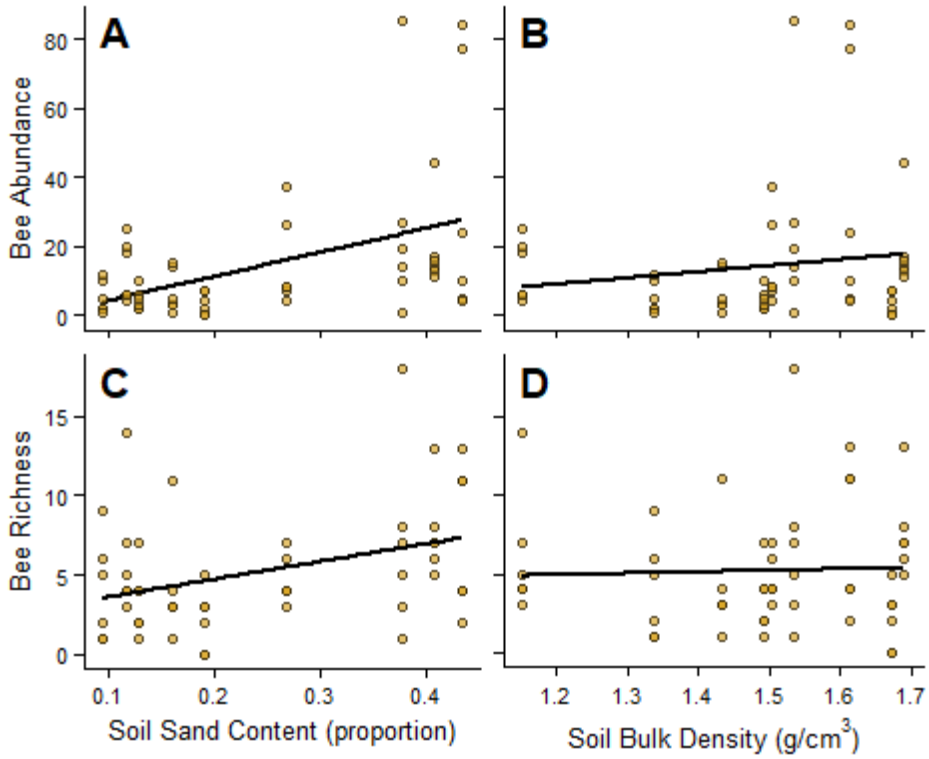

Figure 2: Ground-nesting bee (A, B) abundance and (C, D) richness was higher at sites with (A, C) sandier and (B, D) more compacted soils. Lines indicate best fit.

Habitat characteristic	**Coefficient**	**Lower 95% Confidence Limit**	**Upper 95% Confidence Limit**	**Importance**
(Intercept)	5.19	3.58	6.80	
Floral abundance	0.45	-0.56	1.45	0.57
Bare ground cover	0.11	-0.53	0.75	0.28
Aboveground vegetative biomass	0.12	-0.66	0.91	0.28
Soil sand content	2.24	0.91	3.58	0.99
Soil depth	0.06	-0.56	0.69	0.24

Soil compaction	-1.40	-2.77	-0.03	0.91
Grazing rest period	0.08	-0.45	0.61	0.25

Table 2: Effects of food and shelter resources on ground-nesting bee richness. All predictors were standardized to facilitate comparison across habitat characteristics. Coefficients, confidence intervals, and importance values (sum Akaike weights) are from the averaged model. Terms with confidence intervals that do not overlap zero are highlighted in green.

Sites with longer grazing rest periods had less aboveground vegetative biomass, more bare ground, and higher floral abundance (Fig. S3; Table S8). Despite this, grazing rest period did not directly impact bee abundance, richness, or community composition (Tables 1,2).

Discussion

Determining the impacts of trophic and non-trophic resources is critical for effective pollinator conservation. Floral food availability often promotes pollinators (S. G. Potts et al., 2003; Prendergast et al., 2022), and is sometimes assumed to be the main resource limiting bee communities. Contrary to this, but consistent with several recent studies (C. Antoine, 2023; Pardee et al., 2023; Wersebeckmann et al., 2023), we found that belowground nesting habitat characteristics were as or more important than floral food for ground-nesting bee assemblages. Ground-nesting bee abundance and richness was highest at sites with sandier and more compacted soils, while floral abundance impacted only ground-nesting bee abundance. Overall, our results demonstrate that belowground habitat characteristics may strongly influence bee nesting habitat availability and fitness.

We hypothesized that soil texture is important for ground-nesting bee assemblages because sandier soils may be easier to dig in (Potts and Willmer, 1997) and reduce nest flooding due to greater water permeability (Fellendorf et al., 2004). Ground-nesting bees were indeed more abundant and speciose in sandier soil. These findings are consistent with observational studies of bee nesting habitat (C. Antoine, 2023; J. H. Cane, 1991). However, previous experimental manipulations of soil texture found no difference in nest abundance across soils (C. Antoine, 2023; Fortel et al., 2016; Tsiolis et al., 2022). The range of soil textures available to bees in each study may explain this discrepancy, as the soils in most experiments were at least 50% sand. In contrast, our sites had relatively low sand content (10-43%, Table S5), ranging from clay-loams to heavy clays. Thus, our results suggest that predominance of an extreme soil type such as clay can restrict ground nesting niche space and limit bee nesting (Neff & Simpson, 1997; Strickler, 1979). Under such conditions, even small amounts of sand may noticeably benefit ground-nesting bees.

We also hypothesized that ground-nesting bees prefer less compacted soils, which are generally easier to dig in and have better drainage. Contrary to this, we found that ground-nesting bees were more abundant and speciose in more compacted soils. Our results are inconsistent with previous studies suggesting that higher soil compaction reduces (Sardiñas & Kremen, 2014) or does not affect (Tsiolis et al., 2022) ground-nesting bee abundance. This may reflect an underlying relationship between soil texture and compaction, and higher ground-nesting bee sensitivity to texture than compaction. Sandier soils tend to be more compacted, as they have less pore space (Singh et al., 2015). We did see a positive correlation (but not collinearity) between soil sand content and bulk density (Table S4). Experimentally manipulating soil compaction while controlling potentially confounding factors such as soil texture and floral

abundance is necessary to determine whether soil compaction directly promotes bee abundance, or is simply associated with other influential factors such as soil texture (Nawaz et al., 2013; Vaz et al., 2011).

Certain species may also prefer more compacted soils. Gregarious nesters (e.g., social *Lasioglossum* sweat bees), which were dominant at many of our sites (Table S6), may benefit from higher nest structural integrity in more compacted soils (S. Potts & Willmer, 1997; Wuellner, 1999). Additionally, the highly compacted clay soils of our study region (Table S5; median bulk density 1.51 g/cm3, dense enough to limit root growth, Harris, 1971; Morris & Lowery, 1988) potentially select for specialized digging adaptations (as in Batra & Norden, 1996; Wuellner, 1999). Studies that incorporate bee functional traits (such as Aguirre-Gutiérrez et al., 2016) will provide valuable insights into the importance of soil compaction for bee nesting.

In contrast to our results, bare ground has often been found to promote ground-nesting bees (reviewed in Harmon-Threatt, 2020). Such studies, which typically focus on community assembly or community-level responses to anthropogenic impacts, rarely measure soil texture or other belowground shelter characteristics and thus may attribute belowground drivers of community assembly to aboveground measures such as bare ground. Soil texture can strongly influence vegetative growth and thus bare ground cover (Augustine et al., 2020; Renne et al., 2019). Consistent with this, we found more bare ground and less vegetative biomass at sites with sandier soils (Table S4; habitat characteristics were not collinear). As discussed above, studies investigating the natural history or population ecology of individual ground-nesting bee species have documented preferences for soils with specific belowground properties. Our results highlight the pressing need to integrate population and community ecology approaches by

including belowground characteristics of shelter habitat when measuring resource availability for bees and other insects that shelter below ground.

Because we conducted this research on working ranches, we also investigated the impacts of grazing management (specifically grazing rest period) on bee food and nesting habitat. Sites with longer periods of no grazing had less aboveground vegetative biomass, and more bare ground and flowers. This is consistent with research showing that rotational grazing, where pastures are allowed to rest between grazing episodes, can promote plant diversity or flower availability (Harmel et al., 2021; Ravetto Enri et al., 2017). However, we found that grazing rest period did not impact bee abundance, richness, or community composition. This is probably because the habitat characteristics that most strongly affected ground-nesting bee assemblages – soil texture and compaction – did not vary with rest period. More ecological research on working lands is urgently needed to understand land management impacts on pollinator resource availability and pollinator assemblages.

Overall, our study highlights that the availability of high-quality nesting habitat impacts ground-nesting bee assemblages perhaps more strongly than floral food availability. We also found that aboveground proxies of nesting habitat such as bare ground may be inadequate. However, belowground nesting habitat characteristics such as soil texture and compaction do alter ground-nesting bee abundance and diversity. Thus, conservation planning should consider not only which actions or management types to implement, but where management-insensitive properties of systems will facilitate implementation success. Incorporating above- and belowground measures of non-trophic resources, and conducting such research across diverse soil types, is critical for determining the relative importance of diverse resources for data-driven pollinator habitat conservation and restoration.

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References

Aguirre-Gutiérrez, J., Kissling, W. D., Carvalheiro, L. G., WallisDeVries, M. F., Franzén, M., & Biesmeijer, J. C. (2016). Functional traits help to explain half-century long shifts in pollinator distributions. *Scientific Reports*, *6*(1), 24451. https://doi.org/10.1038/srep24451

Albans, K. R., Aplin, R. T., Brehcist, J., Moore, J. F., & O'toole, C. (1980). Dufour's gland and its role in secretion of nest cell lining in bees of the genus *Colletes* (Hymenoptera: Colletidae). *Journal of Chemical Ecology*, *6*(3), 549–564. https://doi.org/10.1007/BF00987667

Antoine, C. (2023). *Habitat Associations of Ground-Nesting Bees, With a Focus on Soil Characteristics* [PhD Dissertation, University of Ottawa].

Antoine, C. M., & Forrest, J. R. K. (2021). Nesting habitat of ground-nesting bees: A review. *Ecological Entomology*, *46*(2), 143-159. https://doi.org/10.1111/een.12986

Augustine, D. J., Derner, J. D., Fernández-Giménez, M. E., Porensky, L. M., Wilmer, H., & Briske, D. D. (2020). Adaptive, multipaddock rotational grazing management: A ranch-scale assessment of effects on vegetation and livestock performance in semiarid rangeland. *Rangeland Ecology & Management*, *73*(6), 796–810. https://doi.org/10.1016/j.rama.2020.07.005

Barton, K. (2014). *MuMIn: Multi-model inference.* (Version 1.10.5). http://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv:1406.5823*. http://arxiv.org/abs/1406.5823

Batra, S. W. T., & Norden, B. B. (1996). Fatty food for their brood: How *Anthophora* bees make and provision their cells (Hymenoptera: Apoidea). *Memoirs of the Entomological Society of Washington*, *17*, 36–44.

Brockmann, J. H. (1979). Nest-site selection in the great golden digger wasp, Sphex ichneumoneus L. (Sphecidae). *Ecological Entomology*, *4*(3), 211–224. https://doi.org/10.1111/j.1365-2311.1979.tb00578.x

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Buckles, B. J., & Harmon-Threatt, A. N. (2019). Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. *Journal of Applied Ecology*, *56*(11), 2443–2453. https://doi.org/10.1111/1365-2664.13479

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (2nd ed.). Springer-Verlag.

Bzdyk, E. (2012). A revision of the *Megachile* subgenus *Litomegachile* Mitchell with an illustrated key and description of a new species (Hymenoptera, Megachilidae, Megachilini). *ZooKeys*, *221*, 31–61. https://doi.org/10.3897/zookeys.221.3234

Cane, J. (2021). Global warming, advancing bloom and evidence for pollinator plasticity from long-term bee emergence monitoring. *Insects*, *12*(5). https://doi.org/10.3390/insects12050457

Cane, J. H. (1991). Soils of ground-nesting bees (Hymenoptera: Apoidea): Texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society*, *64*(4), 406-413.

Chao, A., Chiu, C.-H., & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 297–324.

Collis-George, N. (1991). Drainage and soil structure—A review. *Soil Research*, *29*(6), 923–933. https://doi.org/10.1071/sr9910923

Cunningham, S. C., Metzeling, K. J., Nally, R. M., Thomson, J. R., & Cavagnaro, T. R. (2012). Changes in soil carbon of pastures after afforestation with mixed species: Sampling, heterogeneity and surrogates. *Agriculture, Ecosystems & Environment*, *158*, 58–65. https://doi.org/10.1016/j.agee.2012.05.019

Davis, A. E., Bickel, D. J., Saunders, M. E., & Rader, R. (2023). Crop-pollinating Diptera have diverse diets and habitat needs in both larval and adult stages. *Ecological Applications*, *33*(5), e2859. https://doi.org/10.1002/eap.2859

Dodd, M. B., Lauenroth, W. K., Burke, I. C., & Chapman, P. L. (2002). Associations between vegetation patterns and soil texture in the shortgrass steppe. *Plant Ecology*, *158*(2), 127–137. https://doi.org/10.1023/A:1015525303754

Dong, L., Wang, J., Li, J., Wu, Y., Zheng, Y., Zhang, J., Li, Z., Yin, R., & Liang, C. (2022). Assessing the impact of grazing management on wind erosion risk in grasslands: A case study on how grazing affects aboveground biomass and soil particle composition in Inner Mongolia. *Global Ecology and Conservation*, *40*, e02344. https://doi.org/10.1016/j.gecco.2022.e02344

Dumesh, S., & Sheffield, C. (2012). Bees of the genus *Dufourea* Lepeletier (Hymenoptera: Halictidae: Rophitinae) of Canada. *Canadian Journal of Arthropod Identification*, *20*, 1–36. https://doi.org/10.3752/cjai.2012.20

Fellendorf, M., Mohra, C., & Paxton, R. J. (2004). Devasting effects of river flooding to the ground-nesting bee, *Andrena vaga* (Hymenoptera: Andrenidae), and its associated fauna. *Journal of Insect Conservation*, *8*(4), 311–312. https://doi.org/10.1007/s10841-004-0514-5

Fortel, L., Henry, M., Guilbaud, L., Mouret, H., & Vaissière, B. E. (2016). Use of human-made nesting structures by wild bees in an urban environment. *Journal of Insect Conservation*, *20*(2), 239–253. https://doi.org/10.1007/s10841-016-9857-y

Gardner, J., & Gibbs, J. (2023). Revision of the Nearctic species of the *Lasioglossum* (*Dialictus*) *gemmatum* species complex (Hymenoptera: Halictidae). *European Journal of Taxonomy*, *858*, 1–222. https://doi.org/10.5852/ejt.2023.858.2041

Gomez Ramirez, W. C., Thomas, N. K., Muktar, I. J., & Riabinina, O. (2023). The neuroecology of olfaction in bees. *Current Opinion in Insect Science*, *56*, 101018. https://doi.org/10.1016/j.cois.2023.101018

Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S. C., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Jorge, L. R., Jung, K., … Allan, E. (2016). Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, *540*(7632), 266–269. https://doi.org/10.1038/nature20575

Griffith, G., Bryce, S., Omernik, J., & Rogers, A. (2007). *Ecoregions of Texas*. Texas Commision on Environmental Quality.

Harmel, R. D., Smith, D. R., Haney, R. L., Angerer, J., Haile, N., Grote, L., Grote, S., Tiner, K., Goodwin, J., Teague, R., & Derner, J. (2021). Transitioning from conventional

continuous grazing to planned rest-rotation grazing: A beef cattle case study from central Texas. *Journal of Soil and Water Conservation*. https://doi.org/10.2489/jswc.2021.00159

Harmon-Threatt, A. (2020). Influence of nesting characteristics on health of wild bee communities. *Annual Review of Entomology*, *65*(1), 39–56. https://doi.org/10.1146/annurev-ento-011019-024955

Harris, WL. "The Soil Compaction Process." In *Compaction of Agricultural Soils*, edited by K. K. Barnes, W. M. Carleton, H. M. Taylor, R. I. Throckmorton, and G. E. Vanden Berg, 9–44. St. Joseph, MI: American Society of Agricultural Engineers, 1971.

Herb, W. R., Janke, B., Mohseni, O., & Stefan, H. G. (2008). Ground surface temperature simulation for different land covers. *Journal of Hydrology*, *356*(3), 327–343. https://doi.org/10.1016/j.jhydrol.2008.04.020

Hyjazie, B. F., & Sargent, R. D. (2022). Floral resources predict the local bee community: Implications for conservation. *Biological Conservation*, *273*, 109679. https://doi.org/10.1016/j.biocon.2022.109679

Inouye, B. D. (2000). Use of visual and olfactory cues for individual nest hole recognition by the solitary bee *Epicharis metatarsalis* (Apidae, Anthophorinae). *Journal of Insect Behavior*, *13*(2), 231–238. https://doi.org/10.1023/A:1007788231137

Jouquet, P., Tessier, D., & Lepage, M. (2004). The soil structural stability of termite nests: Role of clays in *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mound soils. *European Journal of Soil Biology*, *40*(1), 23–29. https://doi.org/10.1016/j.ejsobi.2004.01.006

Karban, R., Mata, T. M., Grof-Tisza, P., Crutsinger, G., & Holyoak, M. A. (2013). Non-trophic effects of litter reduce ant predation and determine caterpillar survival and distribution. *Oikos*, *122*(9), 1362–1370. https://doi.org/10.1111/j.1600-0706.2013.00297.x

Kearns, C. A., & Inouye, D. W. (1993). *Techniques for Pollination Biologists*. University Press of Colorado.

Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015). Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, *96*(1), 291–303. https://doi.org/10.1890/13-1424.1

Kendall, L. K., Mola, J. M., Portman, Z. M., Cariveau, D. P., Smith, H. G., & Bartomeus, I. (2022). The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology*, *103*(11), e3809. https://doi.org/10.1002/ecy.3809

Klute, A. (Ed.). (1986). *Methods of Soil Analysis, Part 1: Physical and Mineralogical Methods* (2nd ed.). Soil Science Society of America.

Kral-O'Brien, K. C., O'Brien, P. L., Hovick, T. J., & Harmon, J. P. (2021). Meta-analysis: Higher plant richness supports higher pollinator richness across many land use types. *Annals of the Entomological Society of America*, *114*(2), 267–275. https://doi.org/10.1093/aesa/saaa061

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., Vásquez, D. P., Winfree, R., Adams, L., Crone, E. E., Greenleaf, S. S., Keitt, T. H., Klein, A.-M., Regetz, J., & Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*, *10*(4), 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Kroll, C. N., & Song, P. (2013). Impact of multicollinearity on small sample hydrologic regression models. *Water Resources Research*, *49*(6), 3756–3769. https://doi.org/10.1002/wrcr.20315

Leong, J. M., & Thorp, R. W. (1999). Colour-coded sampling: The pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. *Ecological Entomology*, *24*(3), 329–335. https://doi.org/10.1046/j.1365-2311.1999.00196.x

Lichtenberg, E. M., Heiser, J., Baum, K. A., Neff, J. L., & Jha, S. (2024). Floral visitors differentially respond to local and landscape grassland features. bioRxiv. https://doi.org/10.1101/2024.07.01.601588

Lucchetta, P., Bernstein, C., Théry, M., Lazzari, C., & Desouhant, E. (2008). Foraging and associative learning of visual signals in a parasitic wasp. *Animal Cognition*, *11*(3), 525–533. https://doi.org/10.1007/s10071-008-0144-5

Lybrand, R. A., Fedenko, J., Tfaily, M., & Rao, S. (2020). Soil properties and biochemical composition of ground-dwelling bee nests in agricultural settings. *Soil Science Society of America Journal*, *84*(4), 1139-1152. https://doi.org/10.1002/saj2.20085

Michener, C. D. (2007). *The Bees of the World* (2nd ed.). The Johns Hopkins University Press.

Michener, C. D., McGinley, R. J., & Danforth, B. N. (1994). *The Bee Genera of North and Central America (Hymenoptera: Apoidea)*. Smithsonian Books.

Morris, L. A., & Lowery, R. F. (1988). Influence of site preparation on soil conditions affecting stand establishment and tree growth. *Southern Journal of Applied Forestry*, *12*(3), 170–178. https://doi.org/10.1093/sjaf/12.3.170

Murphy, B. W. (2015). Impact of soil organic matter on soil properties—A review with emphasis on Australian soils. *Soil Research*, *53*(6), 605–635. https://doi.org/10.1071/SR14246

Nawaz, M. F., Bourrié, G., & Trolard, F. (2013). Soil compaction impact and modelling. A review. *Agronomy for Sustainable Development*, *33*(2), 291–309. https://doi.org/10.1007/s13593-011-0071-8

Neff, J. L., & Simpson, B. B. (1997). Nesting and foraging behavior of *Andrena* (*Callandrena*) *rudbeckiae* Robertson (Hymenoptera: Apoidea: Andrenidae) in Texas. *Journal of the Kansas Entomological Society*, *70*(2), 100–113.

Obayomi, O., Bernstein, N., Edelstein, M., Vonshak, A., Ghazayarn, L., Ben-Hur, M., Tebbe, C. C., & Gillor, O. (2019). Importance of soil texture to the fate of pathogens introduced by irrigation with treated wastewater. *Science of The Total Environment*, *653*, 886–896. https://doi.org/10.1016/j.scitotenv.2018.10.378

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward, M, Bolker B, Borcard D, Carvalho G, Chirico M, De, Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti, L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith, & T, Stier A, Ter Braak C, Weedon J. (2022). *vegan: Community Ecology Package.* (Version 2.6-4).

Ostwald, M. M., Shaffer, Z., Pratt, S. C., & Fewell, J. H. (2019). Multimodal cues facilitate nest recognition in carpenter bee aggregations. *Animal Behaviour*, *155*, 45–51. https://doi.org/10.1016/j.anbehav.2019.06.023

Pardee, G. L., Ballare, K. M., Neff, J. L., Do, L. Q., Ojeda, D., Bienenstock, E. J., Brosi, B. J., Grubesic, T. H., Miller, J. A., Tong, D., & Jha, S. (2023). Local and landscape factors influence plant-pollinator networks and bee foraging behavior across an urban corridor. *Land*, *12*(2). https://doi.org/10.3390/land12020362

Parr, J. F., & Bertrand, A. R. (1960). Water infiltration into soils. *Advances in Agronomy*, *12*, 311–363. https://doi.org/10.1016/S0065-2113(08)60086-3

Pennington, V. E., Palmquist, K. A., Bradford, J. B., & Lauenroth, W. K. (2017). Climate and soil texture influence patterns of forb species richness and composition in big sagebrush plant communities across their spatial extent in the western US. *Plant Ecology*, *218*(8), 957–970. https://doi.org/10.1007/s11258-017-0743-9

Polidori, C., Rubichi, A., Barbieri, V., Trombino, L., & Donegana, M. (2010). Floral resources and nesting requirements of the ground-nesting social bee, *Lasioglossum malachurum* (Hymenoptera: Halictidae), in a Mediterranean semiagricultural landscape. *Psyche*, *2010*, 851947. https://doi.org/10.1155/2010/851947

Portman, Z. M., Arduser, M., Lane, I. G., & Cariveau, D. P. (2022). A review of the *Augochloropsis* (Hymenoptera, Halictidae) and keys to the shiny green Halictinae of the midwestern United States. *ZooKeys*, *1130*, 103–152. https://doi.org/10.3897/zookeys.1130.86413

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. (2003). Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology*, *84*(10), 2628–2642. https://doi.org/10.1890/02-0136

Potts, S., & Willmer, P. (1997). Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology*, *22*(3), 319-328. https://doi.org/10.1046/j.1365-2311.1997.00071.x

Prendergast, K. S., Dixon, K. W., & Bateman, P. W. (2022). A global review of determinants of native bee assemblages in urbanised landscapes. *Insect Conservation and Diversity*, *15*(4), 385–405. https://doi.org/10.1111/icad.12569

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ravetto Enri, S., Probo, M., Farruggia, A., Lanore, L., Blanchetete, A., & Dumont, B. (2017). A biodiversity-friendly rotational grazing system enhancing flower-visiting insect assemblages while maintaining animal and grassland productivity. *Agriculture, Ecosystems & Environment*, *241*, 1–10. https://doi.org/10.1016/j.agee.2017.02.030

Renne, R. R., Bradford, J. B., Burke, I. C., & Lauenroth, W. K. (2019). Soil texture and precipitation seasonality influence plant community structure in North American temperate shrub steppe. *Ecology*, *100*(11), e02824. https://doi.org/10.1002/ecy.2824

Requier, F., & Leonhardt, S. D. (2020). Beyond flowers: Including non-floral resources in bee conservation schemes. *Journal of Insect Conservation*, *24*(1), 5–16. https://doi.org/10.1007/s10841-019-00206-1

Rousk, J., Brookes, P. C., & Bååth, E. (2009). Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Applied and Environmental Microbiology*, *75*(6), 1589–1596.

Sala, Yahdjian, Havstad, & Aguiar. (2017). Rangeland ecosystem services: Nature's supply and humans' demand. In *Rangeland systems: Processes, management and challenges. Springer, Cham, Switzerland.* (pp. 467-489 in Briske D. D., editor.). Springer Nature.

Sardiñas, H. S., & Kremen, C. (2014). Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic and Applied Ecology*, *15*(2), 161-168. https://doi.org/10.1016/j.baae.2014.02.004

Singh, J., Salaria, A., & Kaul, A. (2015). Impact of soil compaction on soil physical properties and root growth: A review. *International Journal of Food, Agriculture and Veterinary Sciences.*, *5*, 23–32.

Stein, D. S., Debinski, D. M., Pleasants, J. M., & Toth, A. L. (2020). Evaluating native bee communities and nutrition in managed grasslands. *Environmental Entomology*, *49*(3), 717–725. https://doi.org/10.1093/ee/nvaa009

Strickler, K. (1979). Specialization and foraging efficiency of solitary bees. *Ecology*, *60*(5), 998–1009. https://doi.org/10.2307/1936868

Tsiolis, K., Potts, S., Garratt, M., Tilston, E., Burman, J., Rintoul-Hynes, N., & Fountain, M. (2022). The importance of soil and vegetation characteristics for establishing ground-nesting bee aggregations. *Journal of Pollination Ecology*, *32*, 186–200. https://doi.org/10.26786/1920-7603(2022)682

UC Davis Soil Resource Lab, UCANR, & NRCS. (2022). *SoilWeb*. https://data.nal.usda.gov/dataset/soilweb

Vaz, C. M. P., Manieri, J. M., de Maria, I. C., & Tuller, M. (2011). Modeling and correction of soil penetration resistance for varying soil water content. *Geoderma*, *166*(1), 92–101. https://doi.org/10.1016/j.geoderma.2011.07.016

Wersebeckmann, V., Warzecha, D., Entling, M. H., & Leyer, I. (2023). Contrasting effects of vineyard type, soil and landscape factors on ground- versus above-ground-nesting bees. *Journal of Applied Ecology*, *60*(4), 601–613. https://doi.org/10.1111/1365-2664.14358

Williams, P. H., Thorp, R. W., Richardson, L. L., & Colla, S. R. (2014). *Bumble Bees of North America: An Identification Guide*. Princeton University Press.

Wooldridge, J. M. (2010). *Econometric Analysis of Cross Section and Panel Data* (Second edition). The MIT Press.

Wuellner, C. T. (1999). Nest site preference and success in a gregarious, ground-nesting bee *Dieunomia triangulifera*. *Ecological Entomology*, *24*(4), 471–479. https://doi.org/10.1046/j.1365-2311.1999.00215.x

Zarekia, S., Jafari, M., Arzani, H., Javadi, S. A., & Jafari, A. A. (2012). Grazing effects on some of the physical and chemical properties of soil. *World Applied Sciences Journal*, *20*(2), 205–212.