



Impact indicators: Effects of land use management on functional trait and phylogenetic diversity of wild bees

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ABSTRACT

Changes in land use and management intensification, especially in agriculture, have led to alarming declines in bee populations and the important ecological services they provide. Little is known how wild bee communities respond to these landscape changes at the phylogenetic level. Phylogenetic diversity was found to be correlated to functional trait diversity, since the former reflects a species evolutionary history while the later reflects the traits a species has accumulated. Here we use a mix of traditional measures of biodiversity and phylogenetic methods to examine differences in wild bee assemblages at six landscapes associated with grazing pressure and different management schemes. We found that grazing pressure strongly influences bee abundance, species richness and functional trait diversity while management intensity has little effect. Interestingly, wild bee phylogenetic diversity was not highly affected by land use, management, or grazing pressure as landscapes retained high levels of phylogenetic evenness. We additionally found evidence of phylogenetic signaling of examined traits. Our findings reveal that wild bee communities can maintain functional trait diversity even with low abundance and species richness. Furthermore, our study supports the notion that trait conservation through evolutionary lineages may only occur for some traits.

1. Introduction

Worldwide, populations of wild bees are declining as a result of human mediated environmental change. The population changes observed in wild bee communities cannot be attributed to a singular cause, but rather it is the interaction of many different environmental stressors such as climate change, spread of disease and intensified land usage (Goulson et al., 2008, 2015; Vanbergen and Garratt, 2013). Of the different pressures exerted onto wild bee populations, increased land use is considered to be one of the most important drivers of change within the wild bee community (Brown et al., 2016). Intensified land use includes anthropogenic activities, such as the conversion of natural habitat to urban or agricultural landscapes, and causing the destruction of valuable bee habitat and food resources (Newbold et al., 2015; Quintero et al., 2009). Land use is also responsible in shaping how bee communities respond to environmental changes, including the loss or gain of species (Harrison et al., 2017a, 2017b; Newbold et al., 2015).

Agriculture covers an estimated 38% of the world's surface and within the US alone, an estimated 614 million acres are dedicated specifically to pasture and rangeland for cattle grazing (Harrison et al., 2017b; Kremen and M'Gonigle, 2015; Nickerson and Borchers, 2012;

Williams and Kremen, 2007). Conventional agriculture often includes applications of pesticides and other agrochemicals and converts heterogeneous landscapes to those that are dominated by monoculture, all of which negatively affect wild bee diversity (Goulson et al., 2015, 2008; Kearns et al., 1998; Mallinger et al., 2016; Quintero et al., 2009; Vanbergen and Garratt, 2013). Conversely, previous studies have shown that organic agriculture can bolster wild bee diversity. Organic farming emphasizes floral and crop diversity and reduced usage of pesticides and other agrochemicals (Tschantke et al., 2005; Winfree et al., 2007). Furthermore, increasing awareness of wild bee decline has led to a public push for the retention of semi-natural areas within or around agricultural land, as well as the establishment of restorative areas on reclaimed farmland (Billeter et al., 2008; Williams and Kremen, 2007). These conservational areas found within conventional farms include wild flower plantings, hedge rows, and even crop margins that act as significant refuges for pollinators, such as bees, and other beneficial insects (Decocq et al., 2016; Kremen and M'Gonigle, 2015; Le Féon et al., 2010; Steffan-Dewenter et al., 2002).

Ungulate grazing has been shaping environments in many areas around the globe (Noy-Meir, 1995) and can have both negative and positive impacts on environments and wild bee communities. Negative

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impacts on bee populations include the removal of nesting and food resources as well as the destruction of nests and adults (Kearns et al., 1998; Noy-Meir, 1995). Additionally, the introduction of grazing animals has shown to reduce bee diversity and abundance, especially in areas of over grazing, where the plant community has little to no recovery time (Kearns et al., 1998; Xie et al., 2008). Further problems arising from animal grazing include soil compaction which makes it difficult for soil nesting bees to excavate their nests and the direct trampling and mortality of nests and adult bees (Kearns et al., 1998; Sugden, 1985). Grazing may also have positive impacts on landscapes and previous research has shown that grazing by cattle can increase both abundance and diversity of other species, including wild bees, by keeping an environment in a constant state of moderate disturbance (Vulliamy et al., 2006). As cattle graze, they open up patches of bare soil that are suitable nesting sites for bees while additionally controlling for vegetative growth (Kimoto et al., 2012a, 2012b). Noy-Meir (1995) found that cattle grazing in Mediterranean grasslands led to higher plant species richness and diversity. Additionally in the same region, Vulliamy et al. (2006) found that the wild bee community responded favorably to the higher plant richness and diversity that resulted from grazing. Their results indicate that wild bee diversity is linked to that of their floral food source and that changes in floral diversity, like those caused by grazing, would lead to changes in wild bee communities.

Phylogenetic and functional trait diversity should inform each other, yet many studies investigating the relationship between functional trait and phylogenetic diversity have concluded the opposite (Arnan et al., 2017; Devictor et al., 2010; Losos, 2008; Webb et al., 2002). However, despite these past findings, it has been acknowledged that functional trait and phylogenetic diversity should be linked if traits are conserved (Webb et al., 2002). Moreover, for wild bees specifically, traits for nesting biology and behavior are conserved and thus their functional traits and phylogenetic diversity are thought to be linked (Grundel et al., 2010; Ricketts et al., 2008; Williams et al., 2010). Recently there has been a push to integrate the usage of phylogeny and functional traits to inform findings of community ecology (Cadotte and Davies, 2016). Phylogenetic information provides a novel tool for evaluating community structure. Recent work has determined that communities with higher phylogenetic diversity support higher ecosystem functioning due to maintaining more species diversity (Turley and Brudvig, 2016; Winfree et al., 2018). Furthermore, current research analyzing the phylogenetic diversity of different wild bee populations across landscape types indicate that many of these communities are comprised of closely related species (Harmon-Threatt and Ackerly, 2013; Hendrix et al., 2018; Hoiss et al., 2012). As such, these communities appear phylogenetically clustered. Hoiss et al. (2012) determined that the phylogenetic clustering of bee species at higher altitudes was a result of environmental filtering shaping the community, while Hendrix et al. (2018) found that a lack of flowers was the main cause of wild bee phylogenetic clustering in agricultural landscapes. Additionally, Grab et al. (2019) found that landscapes dominated by agricultural practices lose phylogenetic bee diversity in a nonrandom fashion, with some bee groups being lost more frequently and heavily, generating phylogenetically clustered communities.

Functional trait diversity and phylogenetic analyses can be used to highlight biological traits, such as nesting biology or social behavior, that make indicator species unique to specific environments. Indicator species are any species that are indicative of specific habitat and environmental conditions (Lincoln et al., 1982). In conservation and environmental management, indicator species of habitats that are of particular interest can be used to monitor and assess overall community stability and the health of specific species of interest (De Cáceres, 2013). For example, research by Kerr et al. (2000) determined that easily identified species of butterfly and skipper populations could be used to monitor and assess taxonomically challenging hymenopteran diversity at the landscape scale in endangered oak savanna habitats. Furthermore, indicator species can provide information reflecting

environmental status, impacts of environmental change, and predict the diversity of a community as these species have unique features that tie them to their chosen habitat and other species in their environment (De Cáceres, 2013). Tscharnkte et al. (1998) found that trap-nesting bees and wasps, which are ecologically constrained by their nesting biology, are good indicators of landscape change and habitat quality as changes in their populations will reflect alterations in the availability of stems and cavities in their environment. While wild bees themselves can be indicators of plant diversity in a landscape (Tscharnkte et al., 1998), certain bee guilds can be used as accurate monitors of overall bee community health. Sheffield et al. (2013) suggest that cleptoparasitic bees, which are bees that invade the nest of their host in order to lay eggs on premade pollen balls, have the potential to be bioindicators of healthy bee populations due to their parasitic nature. Parasites, including cleptoparasites, are dependent on the survival and persistence of their host and any changes in host diversity and density will first be seen in the parasites (Sheffield et al., 2013). The use of wild bees as a group and specific bee guilds as bioindicators is a valuable tool to measure how land use and environmental change affects wild bee communities.

Wild bee species respond differently to changes in habitat and floral diversity depending on certain life histories and what favors one species may not necessarily benefit another (Bartomeus et al., 2013; Tucker and Rehan, 2018; Williams et al., 2010). Both meta-analyses and comparative approaches shed light on how bees respond to environmental change by showing differences within and between different guilds over time (Bartomeus et al., 2013; Biesmeijer et al., 2006). Both Williams et al. (2010) and Bartomeus et al. (2013) found that the wild bee community response to environmental change is largely dependent on biological traits. Although their conclusions were similar, Bartomeus et al. (2013) used historic museum specimens and comparative approaches for northeastern US wild bee communities while Williams et al. (2010) used a meta-analysis approach with more recent studies conducted globally. While informative, the previous meta-analyses encompass large areas and do not consider environments and changes within wild bee communities at a regional scale. The overarching goal of this study was to investigate how land usage affects wild bee community abundance, richness, and phylogenetic composition. We combined data from three years and six land use types in New England to: i) characterize the status of wild bees across management intensity and presence of grazing, and ii) identify indicator species and discuss functional trait diversity across land use types.

2. Materials and methods

This study combines bee biomonitoring data from Strafford County, New Hampshire (43.2383 °N, 71.0236 °W). Wild bee samples were collected every two weeks from the same six landscapes over three years (2015–2017). Three of the landscapes (meadow, organic and conventional) were used for a previous comparison of management practices and yearly effects on wild bee communities (Tucker and Rehan, 2018). The remaining landscapes (clear-cut, silvopasture, pasture) are previously unpublished data presented here to investigate the effects of different forest management on wild bee communities. For our analyses, we classified the environments in two different ways: first by management intensity and second by the presence or absence of grazing (Fig. 1). For management intensity, landscapes were classified as either low (meadow, pasture), moderate (organic, silvopasture), or high (conventional, clear-cut). We followed the qualitative classifications defined in previous research for the un-grazed landscapes (Tucker and Rehan, 2018). For grazed landscapes, pastures consisted of non-pesticide use farmland with naturally occurring native and weedy plants, thus making it most similar to the un-grazed meadow landscapes. The silvopasture sites represent less disturbance and have a total of 30% canopy cover. The silvopasture and the organic landscapes are grouped together as both did not use pesticides, were located adjacent

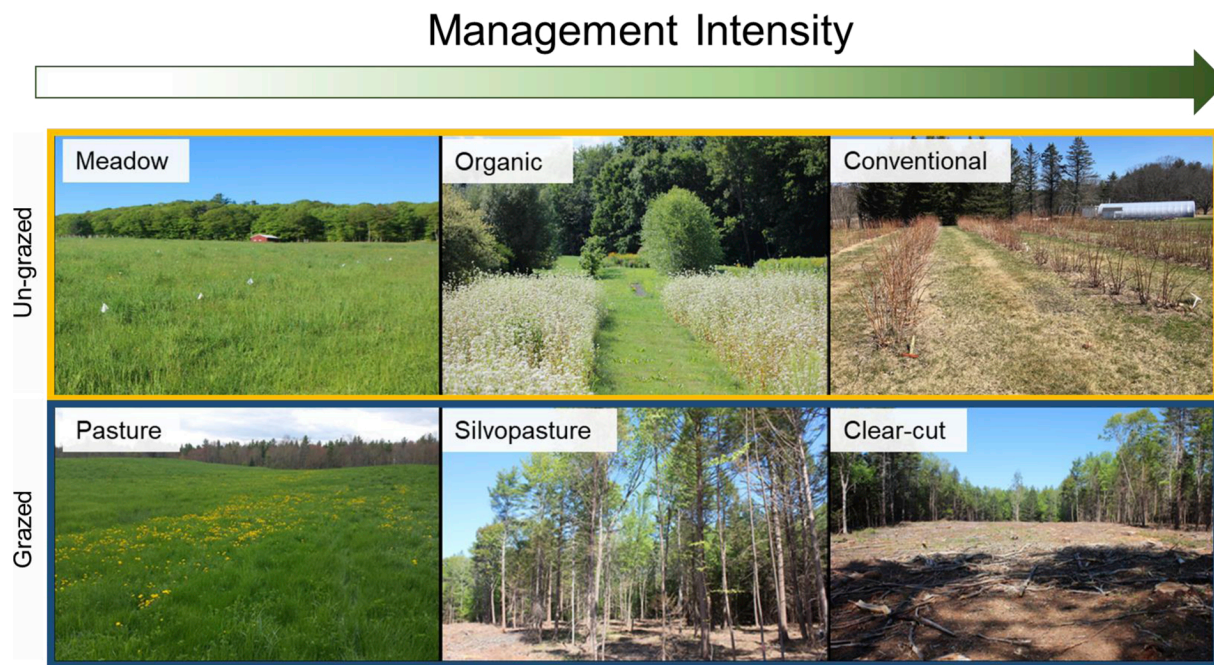


Fig. 1. The organization of landscapes by presence or absence of grazing and increasing magnitude of management intensity.

to forested areas, and had moderate landscape alteration: weekly mowing (organic) and selective tree removal (silvopasture). Lastly, of the grazed landscapes, clear-cut sites represent the most intensive management among grazed landscapes. The management intensity of canopy removal at the clear-cut sites was qualitatively similar to the intensive use of mowing and pesticide use found at conventional landscapes we surveyed. Landscapes were then either classified as un-grazed (meadow, organic, conventional) or grazed (pasture, silvopasture, clear-cut).

Bees were sampled consistently every other week starting in April through to October using a combined method of pan traps and sweep netting (Tucker and Rehan, 2018, 2017). Across all landscapes, three replicate sites were each sampled using 30 pan traps (7 cm diameter, 100 mL), colored either blue, white, or yellow, were filled with soapy water and placed along 100 m transects, alternating between the three colors and with 10 m separating each trap. All traps were set before 8AM and were collected the same day at 4 P M allowing a total of 8 h for collection. At the time of collection, contents of each trap were poured through a sieve and any specimens from that transect were placed into a vial containing 70% ethanol. Sweep netting occurred at each site where there were large areas of blooming flowers and was conducted using aerial nets between the hours of 10AM and 2 P M on the same day as the pan trapping. The timing of the sweep collection was 10 thirty second intervals (total of 5 min) with 1-minute pauses in between to allow for specimen transfer to vials filled with 70% ethanol and collection information and for bees to return to the flowers after they had been disturbed. Collected bee specimens were prepared following the protocols in Droege (2015) and then pinned and labeled with relevant location information and a QR code. Species identification was done by E. Tucker and K. Odanaka using online keys found on Discover life (<http://www.discoverlife.org/>) and previously published taxonomic keys (Gibbs, 2011; Gibbs et al., 2013; Mitchell, 1960; Rehan and Sheffield 2011; all specimens are stored in the Rehan Lab at UNH).

2.1. Statistical analyses

All statistical analyses were conducted using R (R Core Team, 2018). Negative binomial generalized linear models were used to analyze the effects of grazing presence and management intensity on both

wild bee abundance and species richness. Results from the models that were found to be significant were then analyzed further using post hoc Tukey tests. We then investigated wild bee functional trait diversity by using these models and grouping the wild bee population by three functional traits: nesting biology (ground or stem), behavior (solitary, social, or cleptoparasitic), and lecty (polylecty, oligolecty, or parasitic) (Table 1). Names of traits were used following those in Kratschmer et al. (2019). Additionally, we examined how these traits were impacted by landscape type by conducting a PCA using bee abundance and landscape, then superimposing a calculated community weighted means of each examined trait onto the PCA using the envfit function in the 'vegan' R package (Kratschmer et al., 2019). Envfit calculates the correlation between species assemblages and its ordination on a PCA as well as the p-values of the inputted traits, selecting only those that are significant. Community weighted means were calculated using the function CWM in the R package 'FD' (Laliberté et al., 2014).

For our phylogenetic analyses, we used a previously published species level phylogeny consisting of over 1300 wasp and bee species as the basis for our phylogenetic tree (Hedtke et al., 2013). We modified the original tree by adding any species from our study not already present on the original tree using the function `add.species.to.genus` in the R package 'Phytools' (Revell, 2012). Any species not found in our study was removed from the tree using the `drop.tip` function within the R package 'Ape' (Paradis et al., 2004). The resulting modified tree contained only taxa found in our study representing 239 species from 32 genera spread over five bee families. This tree was then used to calculate the phylogenetic signal of our three traits using Moran's I and Abouheif's C_{mean} which measure phylogenetic signal by estimating how closely trait evolution follows Brownian motion (Cachera and Le Loc, 2017) using the R package 'Adephylo' (Jombart et al., 2008). Output values are between -1 and 1 indicating no phylogenetic signal (-1) and total phylogenetic signal (1) (Cachera and Le Loc, 2017).

In order to explore changes within our wild bee phylogenetic diversity we chose two measures of phylogenetic structure that determine if species found within communities are more clustered (closely related) or more even (spread) across our phylogenetic tree. Using our modified phylogenetic tree, we first converted the tree into a distance matrix using 'Ape' and then used functions in the package 'Picante' to evaluate the phylogenetic diversity of each site (Kembel et al., 2010; Paradis

Table 1

Table denoting the examined functional traits used for analysis and how we defined the different types of traits.

Trait	Types	Definition	Function
Nesting	Ground	Nest is excavated in the ground; majority of species	Habitat requirement; impacts the richness and abundance of certain species as well as the overall diversity of the bee community
	Stem	Nest is excavated in pithy stems, wood, pre-made cavities, and dead wood	
Behavior	Parasitic	Host nest is invaded by bee, who then lays own egg inside	Can be used to indicate and monitor host populations (Hudson et al., 2006; Sheffield et al., 2013)
	Solitary	Individual female establishes and provides for offspring alone	
	Sub-social	Females may form loose colonies comprised of foundress and daughters	
Lecty	Eusocial	Establish colonies with divisions of labor	See parasitic nesting
	Parasitic	See above	
Lecty	Polylectic	Females are generalists and forage for pollen on a variety of plant taxa	Visits many different plants to collect nectar and pollen; have no morphological adaptations for pollen collection
	Oligolectic	Females are pollen specialists and forage for pollen on closely related	
	Parasitic	Females do not intentionally collect pollen	

et al., 2004). All calculations used abundance weighted data matrices to account for differences in species abundance. We ran a mean pairwise distance (MPD) analysis and a mean nearest taxon distance (MNTD) analysis using the `ses.mpd` and `ses.mntd` functions. Both of these functions compare the diversity observed at our sites to a randomly constructed null model. The resulting phylogenetic differences between the observed and the randomized communities divided by the standard deviation of the null phylogenetic distance are known as standard effect size (SES) values. P-values for both the MPD and the MNTD tests are given as quantiles. Positive SES values and high quantiles indicate that communities are more phylogenetically diverse (evenness), while negative output numbers and low quantiles indicate less phylogenetic diversity (clustering) (Kembel et al., 2010). Both SES values and significant p values (< 0.05) are reported (Kembel et al., 2010). For the pasture landscape and conventional farm, we ran Wilcoxon tests in order to find deficiencies of certain functional traits or specific genera at these sites. Following the phylogenetic diversity analysis, we ran an analysis for indicator species using the package ‘Indicspecies’ (De Cáceres and Legendre, 2009). We examined both the specificity, which indicates the predictive ability of a species for a specific environment, and the fidelity, which indicates how abundant a species is given a specific environmental type, of each species (De Cáceres and Legendre, 2009) in order to extrapolate which species were unique to management intensity and grazing presence.

3. Results

A total of 12,074 bee specimens from 239 species and 32 different genera were collected between 2015 and 2017. Un-grazed sites ($n = 10,650$; $n = 231$ respectively) had eight-fold more bee abundance and about two times more species richness than grazed sites ($n = 1395$; $n = 109$ respectively). Overall, while the effect of management intensity on wild bee abundance and richness was not significant (abundance: $X^2 = 2.45$ df = 2, $p = 0.29$; richness: $X^2 = 4.07$, df = 2, $p = < 0.131$), the interaction effect of management intensity and grazing pressure on wild bee communities was highly significant (abundance: $X^2 = 3285.72$, df = 2, $p = < 0.001$; richness: $X^2 = 18.85$, df = 2, $p = < 0.001$; Fig. 2b). Additionally, un-grazed sites had the greatest wild bee abundance and richness when compared to grazed sites ($X^2 = 7545.24$, df = 1, $p < 0.001$; $X^2 = 568.49$, df = 1, $p = < 0.001$; Fig. 2a). Since management intensity had no significant effect on bee community abundance or richness, we ran the phylogenetic analyses based on the presence or absence of grazing. No MNTD value was significant for any individual landscape ($1.95 \geq \text{SES} \geq 0.976$, $0.946 \geq p \geq 0.848$; Fig. 3a). When the MPD of individual landscapes were examined, all but the conventional ($\text{SES} = 1.15$, $p = 0.09$) and the pasture ($\text{SES} = -0.002$, $p = 0.452$) were significant ($\text{SES} > 1.5$,

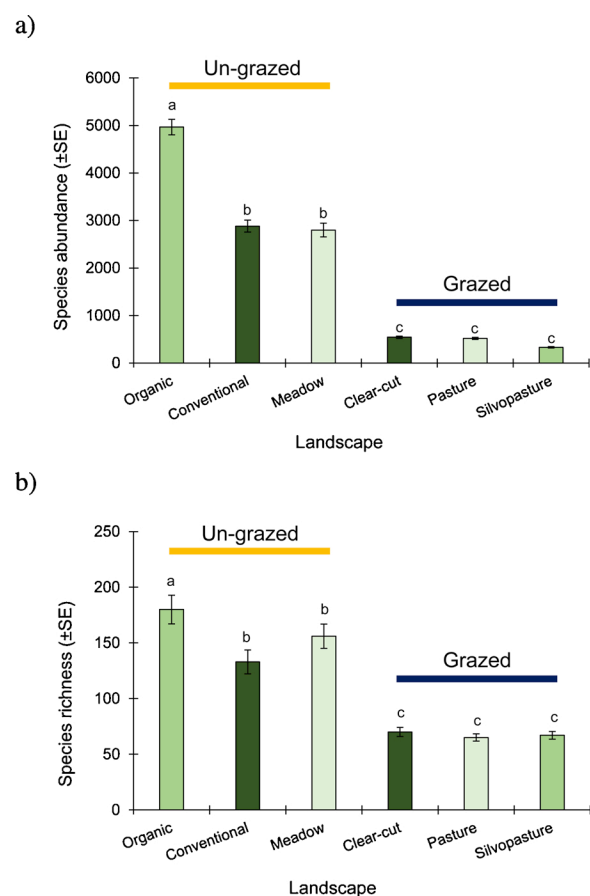


Fig. 2. Graphs representing species abundance and richness at all six sites. Different shades of green denote different management intensities: Light green for low intensity, green for moderate intensity, and dark green for high intensity. Both wild bee abundance (a) and species richness (b) were affected negatively by the presence of grazing. Wild bee abundance and richness were significantly affected by moderate management intensity but only in un-grazed sites (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

$p > 0.95$; Fig. 3b). We then further investigated the community composition of both these landscapes and found that the pasture landscape was depauperate of *Andrena* species ($X^2 = 13.285$, df = 5, $p = 0.021$; Fig. 4). Of the 65 species found at the pasture, only five were in the genus *Andrena*. For conventional farmland, although the results were not significant ($X^2 = 0.4234$, df = 2, $p = 0.80092$; Fig. 5) we found an

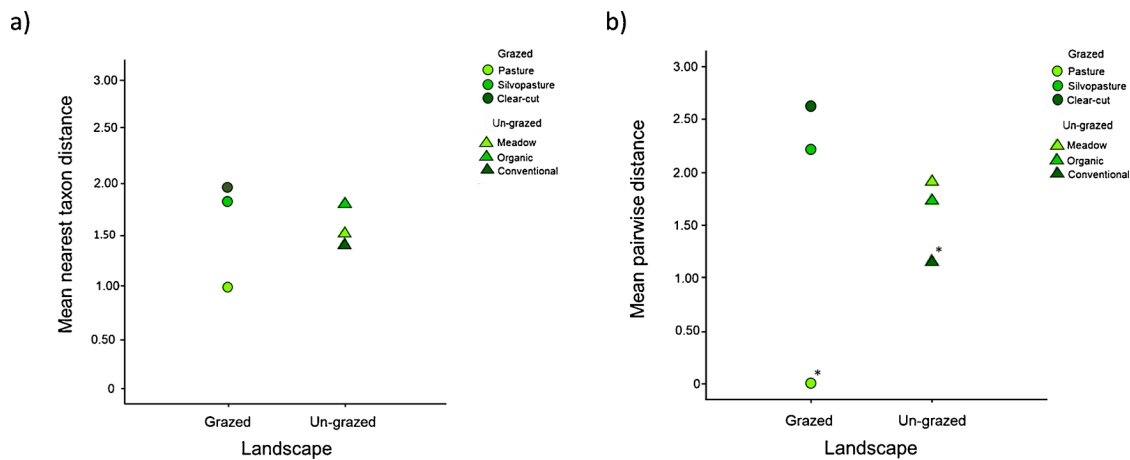


Fig. 3. a) Phylogenetic results for Mean Nearest Taxon Distance (MNTD) indicate that sites have expected levels of species groupings. b) Mean Pairwise Distance (MPD) analysis indicate that all landscapes except pasture and conventional farmland (denoted by asterisks) exhibited more diversity than expected from a null model.

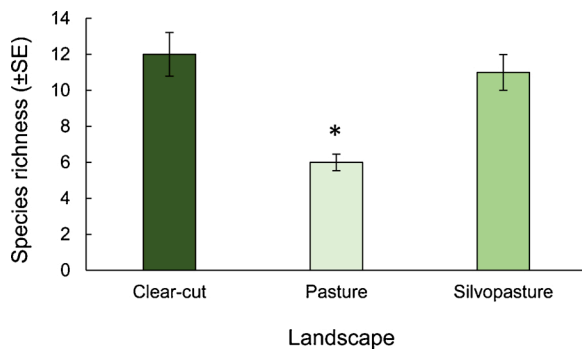


Fig. 4. The species richness of *Andrena* for grazed landscapes. Pasture sites are depauperate in *Andrena* species compared to other grazed landscapes.

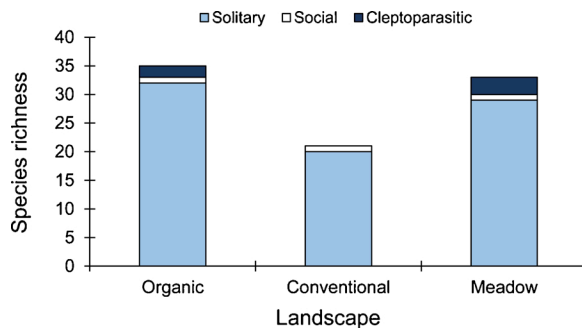


Fig. 5. The observed richness of only stem nesting species found at the three un-grazed landscapes. There are no cleptoparasitic stem nesting species, genus *Coelioxys*, in conventional farmland sites.

overall reduction of stem nesting species in comparison. Furthermore, we observed no cleptoparasitic species at conventional farmland.

3.1. Functional trait diversity

When the wild bee community was grouped by nesting biology, we found no interaction between management intensity and wild bee abundance and richness. Only nesting biology had a significant effect on abundance ($X^2 = 38.761$, $df = 1$, $p < 0.001$) and richness ($X^2 = 43.679$, $df = 1$, $p < 0.001$). There was also no interaction effect between grazing and nesting biology; however both grazing alone (abundance: $X^2 = 47.466$, $df = 1$, $p < 0.001$; richness: $X^2 = 38.761$, $df = 1$, $p < 0.001$) and nesting biology alone (abundance:

$X^2 = 23.109$, $df = 1$, $p < 0.001$; richness: $X^2 = 52.118$, $df = 1$, $p < 0.001$) had significant effects on wild bee abundance and richness.

For behavior, there were no interaction effects between management intensity and behavior for abundance ($X^2 = 0.194$, $df = 4$, $p = 0.9956$) nor for richness ($X^2 = 0.619$, $df = 4$, $p = 0.9609$). Like with nesting biology, only behavior was significant (abundance: $X^2 = 81.644$, $df = 2$, $p < 0.001$; richness: $X^2 = 78.598$, $df = 2$, $p < 0.001$). When examining grazing and behavior, grazing alone and behavior alone had significant effects on wild bee abundance (grazing: $X^2 = 68.454$, $df = 1$, $p < 0.001$; behavior: $X^2 = 109.615$, $df = 2$, $p < 0.001$) and richness (grazing: $X^2 = 42.576$, $df = 1$, $p < 0.001$; behavior: $X^2 = 113.448$, $df = 2$, $p < 0.001$).

For trait conservatism, we found that nesting biology had the strongest phylogenetic signal ($I = 0.825$, $C_{mean} = 0.826$), followed by behavior ($I = 0.766$, $C_{mean} = 0.768$), and finally lecty ($I = 0.721$, $C_{mean} = 0.722$). All of these results had p values less than 0.001 (Table 2).

Our PCA results indicate that presence or absence of grazing explains most of the variation in wild bee abundance at our six sites (Fig. 6). Furthermore, analysis on the community weighted means of our measured functional traits indicated that nesting alone ($p = 0.024$) was a significant driver of bee assemblages in grazed landscapes.

3.2. Indicator species

A total of 17 species were found to be highly significant indicators of un-grazed landscapes and when investigated further, six of these indicator species were found to have both high specificity and fidelity (Table 3). These six species contained three species of *Bombus* (*B. griseocollis*, *B. bimaculatus*, *B. impatiens*), one *Lasiglossum* (*L. leucozonium*), one *Hylaeus* (*H. affinis*), and one *Ceratina* (*C. mikmaqi*). *Bombus griseocollis*, specifically, was found to be the best predictor of un-grazed landscapes. With the exception of *B. bimaculatus* and *H. affinis*, these species were among the most commonly found and had frequencies greater than 100 individuals captured overall at un-grazed sites. Three species were found to be indicators of different management intensities

Table 2

Results from the phylogenetic signal tests on the combined set of the traits and the individual subcomponents using both Moran's I and Abouheif's C_{mean} .

Model	Moran's I	Abouheif's C_{mean}	p-value
Phylogeny ~ nesting	0.825	0.826	< 0.001
Phylogeny ~ behavior	0.766	0.768	< 0.001
Phylogeny ~ lecty	0.721	0.722	< 0.001

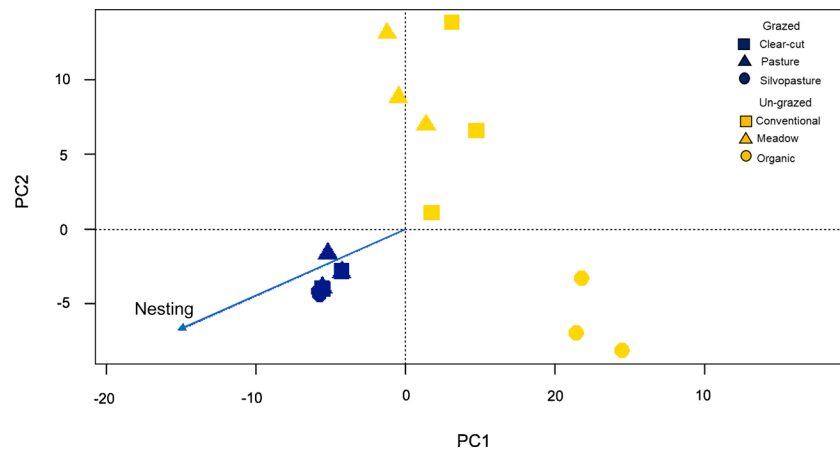


Fig. 6. PCA showing communities of wild bees in six different landscape types and separated by year. Nesting was the only trait found to be significantly correlated with the parameters of the PCA.

(Table 3). *Lasioglossum versatum* was indicative of both high and low intensities, *Lasioglossum lineatulum* was an indicator for moderate management only, and *Hylaeus modestus* was indicative of low and moderate intensities. Both nesting biologies (ground and stem) were represented by these three species and all have solitary behavior.

4. Discussion

In this study, we investigated how management intensity and grazing presence shapes different aspects of wild bee communities. We document how different levels of landscape management and the presence or absence of grazing influences the functional trait and phylogenetic diversity of wild bee populations. Our data revealed that the interaction between grazing presence and management intensity highly influences wild bee abundance and richness but does not reduce overall phylogenetic diversity. Finally, we determined a set of indicator species as potential bio-monitors for grazed landscapes and different levels of land use management.

4.1. Management intensity and grazing presence

Our results indicate that management intensity with no grazing presence supports the most abundant wild bee communities. The large number of bee species and individuals found at un-grazed managed landscapes was most likely due to the accumulation of wild flowers and other plant material in the absence of grazing (Forrest et al., 2015; Tucker and Rehan, 2018). Our findings provide further support for the growing body of literature that indicates the importance of farming practices that maintain heterogeneous landscapes that support wild

bees (Forrest et al., 2015; Tscharrntke et al., 2005; Tucker and Rehan, 2017, 2018; Winfree, 2010). Landscape heterogeneity has been shown to be favored by wild bees due to its ability to provide enough resources which maintain floral specialists and generalists as well as all nesting guilds (Forrest et al., 2015; Mallinger et al., 2016; Potts et al., 2003; Steckel et al., 2014; Vulliamy et al., 2006). Of the three un-grazed landscapes, conventional farmland was the only landscape found to have low phylogenetic diversity which was due to a landscape wide reduction in all stem nesting species. Furthermore, because stem nesting cleptoparasitic species, namely those in the genus *Coelioxys*, were absent from conventional farmland, we can infer the total health of the stem nesting community. The complete absence of *Coelioxys* implies that the overall stem nesting community is unstable and not healthy enough to support the tertiary trophic level occupied by parasitic life histories (Sheffield et al., 2013). High intensity management homogenizes the landscape by removing excessive vegetation and reducing natural landscapes, all of which provide the nesting resources for stem nesting bees (Williams et al., 2010). Together, the findings from our phylogenetic, abundance, and richness data suggest that moderate management intensity of landscapes is beneficial for wild bee communities.

Wild bee abundance and species richness was significantly negatively impacted by the presence of grazing. We found that grazed landscapes had bee communities that were eight-fold less abundant and two times less rich than un-grazed landscapes. This suggests that grazing pressure is a major driving force in shaping wild bee community composition. Indeed, our results are further supported by our PCA and community weighted means which clearly separated grazed from un-grazed sites. Further, nesting biology was the only trait that was a

Table 3

Table denoting the eleven indicator species for un-grazed landscapes and management intensity. These species were selected as indicators due their high specificity for marked landscapes or management intensity and abundant nature within those environments. Multiple “X”s denote species that are found in both.

Family	Species	Nesting biology	Behavior	Un-grazed landscapes	Low management intensity	Moderate management intensity	High management intensity
Apidae	<i>Bombus bimaculatus</i>	Ground	Social	x			
	<i>Bombus griseocolis</i>	Ground	Social	x			
	<i>Bombus impatiens</i>	Ground	Social	x			
	<i>Ceratina mikmaqi</i>	Stem	Solitary	x			
Colletidae	<i>Hylaeus affinis</i>	Stem	Solitary	x			
	<i>Hylaeus modestus</i>	Stem	Solitary		x	x	
Halictidae	<i>Halictus rubicundus</i>	Ground	Social	x			
	<i>Lasioglossum hitchensi</i>	Ground	Social	x			
	<i>Lasioglossum leucozonium</i>	Ground	Solitary	x			
	<i>Lasioglossum lineatulum</i>	Ground	Social			x	
	<i>Lasioglossum versatum</i>	Ground	Social		x		x

significant parameter of the PCA. Soil compaction, the destruction and removal of stems and twigs, and the reduction of floral resources are all disturbances bee face due to grazing (Kearns et al., 1998; Noy-Meir, 1995; Sugden, 1985). Bees are obligate florivores and have been found to choose areas based on their floral density (Sjödén, 2007). Grazing not only reduces floral density but also simplifies plant diversity and alters floral composition (Debano, 2006; Kruess and Tschardt, 2002; Xie et al., 2008). Changes in plant communities can then induce changes in pollinator communities causing shifts in plant-pollinator interactions, such as reducing the number of floral specialists within the community and ultimately weakening important ecological functions (Debano, 2006; Kimoto et al., 2012a, 2012b; Yoshihara et al., 2008). The low abundance and richness of wild bees found at our grazed sites indicate that the bee community is responding negatively to grazing pressures.

Despite the overall low abundance and richness at the grazed sites, only one grazed landscape (pasture) was found to show less species diversity than what is expected in a randomly generated model in our phylogenetic analysis. We found that the pasture lacked species of *Andrena* and this most likely accounts for the low levels of phylogenetic diversity in this landscape. Members of the genus *Andrena* are important pollinators of early spring blooming plants and contain many floral specialists (Mitchell, 1960). Of the three grazed landscapes, pasture sites lacked the early floral resources needed to support a diverse population of spring and specialist *Andrena* species despite other grazed landscape sites containing twice as many *Andrena*. Furthermore, all five of the *Andrena* species (*A. carlini*, *A. commoda*, *A. cressonii*, *A. vicina*, *A. wilkella*) found at the pasture site are generalists and have long foraging seasons that extend into middle and late summer. Unlike floral specialists which are tied to a select number of floral species and a specific blooming period, these generalists are able to forage on any available flowers and are unconstrained by specific seasonality. The severe lack of *Andrena* specifically at the pasture site mirror the findings of Hendrix et al. (2018), who also noted phylogenetic clustering in communities lacking *Andrena*. In their study, Hendrix et al. (2018) noted that landscapes that were lacking diverse floral resources were also scarce of *Andrena* species and that *Andrena* overall may be more impacted at landscape scales by changes in plant communities. Furthermore, using phylogenetic diversity estimates, Grab et al. (2019) found that species of *Andrena* are particularly sensitive to changes in land use. Our results support those by Grab et al. (2019) and Hendrix et al. (2018) and further suggest that *Andrena*, in particular, may be more susceptible to changes in floral communities brought on by grazing pressure.

4.2. Functional trait diversity

While past studies have found weak relationships between functional trait and phylogenetic diversity (Arnan et al., 2017; Devictor et al., 2010; Losos, 2008; Webb et al., 2002) it is known that the functional traits for nesting biology and behavior in wild bees is genetically conserved, thus linking together functional trait diversity with phylogenetic output (Grundel et al., 2010; Ricketts et al., 2008; Williams et al., 2010). Furthermore, previous research has indicated that conserved traits in closely related species should have detectible phylogenetic signals (Cachera and Le Loc, 2017). We estimated the phylogenetic signals of three different functional traits that are known to be conserved (nesting biology, behavior, and lecty) using Moran's I and Abouheif's C_{mean} and found relatively strong signals for each trait. This finding provides support that nesting biology, behavior and lecty are most likely genetically coded traits and are thus passed along through evolution. Findings from Losos (2008); Pearman et al. (2008) and Cachera & Le Loc'h (2017) indicate that certain functional traits are evolutionary conserved within a functional niche while most others are not and our results further bolster this conclusion.

4.3. Indicator species

The presence of indicator species allows for improved future monitoring of how wild bee populations respond to changes occurring in their environments. We found eight indicator species of un-grazed landscapes and an additional three species indicative of landscape management intensity, mainly in low to moderate intensity. These eleven species represent two behavior types (solitary, eusocial) and both types of nesting biology measured in this study (ground, stem). Many common and easily identified species were selected as indicators for un-grazed habitats, including three species of bumble bee. The bumble bee species identified as indicators in this study could be used as a possible conservation tool to assess the effects of grazing animals to pollinator populations. Bumble bees, specifically, are ideal indicators because many species can be identified by non-experts using available guides, making them appealing for use in conservation and restoration. Indicator species can be used to gauge the impact of management and whether alternative practices should be considered.

5. Conclusions

Landscape alteration has major impacts on wild bees and understanding how communities respond to disturbance can inform sustainable land use, restoration and conservation practices. We found that grazing presence has the most negative impact on wild bee community abundance and richness, but interestingly little to no impact on landscape phylogenetic diversity. Additionally, we found that landscapes featuring, low to moderately intensive management schemes supported more abundant and species rich wild bee populations. Our data suggest that regional landscapes are able to maintain their phylogenetic diversity despite low levels of species abundance and richness. Moreover, the finding of common and easily identified wild bee species as indicators facilitates their adoption as an important tool for assessing the status of changing landscapes.

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