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Relative bee abundance varies by collection method and flowering richness: Implications for understanding patterns in bee community data

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Abstract

1. Recent declines in wild bee populations have led to increases in conservation actions and monitoring of bee communities. Pan traps are a commonly used sampling method for monitoring bee populations due to their efficiency and low cost. However, potential biases inherent in different sampling techniques may result in misleading characterizations of bee communities across space and time.

2. In this paper, we examined how bee communities sampled using pan traps and aerial nets changed seasonally, and if they were affected by the availability of floral resources.

3. We found strong seasonal changes in the abundance, but not the richness, of bees captured in pan traps. Notably, we captured the fewest bees during weeks in spring when most flowering plant species were in bloom, suggesting that floral resource availability influences pan trap captures. We also compared patterns of bee abundance in pan traps to those captured by aerial netting. Bee richness in pans and nets was positively correlated, but relative abundances in pan and net samples were dominated by different bee genera. Furthermore, most genera decreased in pans with increasing floral richness, but patterns were mixed for nets. When using presence/absence data, rather than abundance, community composition was more similar between netted and pan-trapped bee communities and changed less substantially across the floral richness gradient.

4. Overall, these differences led to sampling substantially different bee community compositions in pan traps versus nets, especially when using abundance-based methods to characterize the bee community. By examining multiple years of intensive seasonal sampling of plant and bee communities, we document potential pitfalls with methods commonly used to sample bee communities.

5. We suggest that pan trapping and aerial netting provide similar estimates of bee species richness and community composition when using presence/absence data, but that practitioners should interpret pan-trapped bee abundance data with caution especially when comparing bee communities between sites where plant communities may differ.

1 | INTRODUCTION

Concern about declining bee populations (Cameron et al., 2011; Potts et al., 2010; Zattara & Aizen, 2021) has led to increased use of bee sampling and monitoring protocols using pan (i.e. bowl) traps (LeBuhn et al., 2013; Westphal et al., 2008). The choice of sampling methods can shape our understanding of ecological communities, and subsequently influence conservation efforts and management decisions. When sampling methods are standardized, repeatable and efficient, studies conducted by different researchers or in different geographical contexts are comparable and can provide information that accurately informs the research questions. Pan trapping – catching bees in coloured bowls filled with soapy water – generally meets these requirements. For example, pan trapping can be easily standardized, making it useful for comparisons across sites or regions (LeBuhn et al., 2016). Pan trapping is also simple to implement, reliable, inexpensive and efficient (LeBuhn et al., 2016; Wilson et al., 2008). As a passive collection method, it eliminates the need for highly trained surveyors, reducing collector bias (Cane et al., 2000; Nielsen et al., 2011).

Pan trapping, however, does have several known biases. First, certain groups may be over- or underrepresented in pan traps (Cane et al., 2000; Roulston et al., 2007; Toler et al., 2005; Wilson et al., 2008). Whether this reflects their relative abundance in the environment, or their affinity for pan traps is unclear (Portman et al., 2020) and may lead to a mischaracterized bee community composition. Second, the availability of flowers may influence the relative attractiveness of pan traps to bees (Cane et al., 2000; Nielsen et al., 2011; O'Connor et al., 2019; Toler et al., 2005). For example, as floral resources increase, the number of bees caught in pan traps may decrease, and vice versa. Baum and Wallen (2011) found differences in bee species richness and abundance in pan traps between years with low and high floral abundance during their 2-year study. However, Smith DiCarlo et al. (2020) did not detect a significant correlation between floral abundance or richness and abundance of bees in pan traps. Thus, while potential biases of pan trapping are recognized, it remains unclear how these biases may shape our understanding of ecological communities, due in part to a lack of empirical data addressing this issue.

Targeted aerial netting of bees from flowers is a method often used alone or in conjunction with pan trapping. Aerial netting can provide information on the community composition of foraging bees and is particularly useful for determining bees' floral associations, since bees are collected directly from flowers rather than passively sampled, as is the case for pan traps. Netting bees requires training and even trained samplers differ in their skill or ability to detect and capture insects, introducing potential biases that may affect sample sizes and species diversity (Nielsen et al., 2011). However, Cane et al. (2013) found that trained samplers of varying expertise collected similar proportions of bee species to one another at target flowers despite differences in bee abundance, and that net sampling reliably reflected the spatial and temporal variability of bee communities on focal plant species. Another bias of aerial netting is that flowers need to be present or obvious enough that they can be detected by samplers in order to net bees from them. Bees can be present in areas without floral resources (e.g. at nesting sites or dispersing), especially in early spring when bees can emerge before flowers (Meiners et al., 2017) or between major bloom periods. As such, aerial net sampling on flowers may only provide accurate information on community composition for bees that are actively foraging.

Knowing the limitations and biases of a sampling method has consequences for interpreting the results of field studies. Researchers can consider their findings within the context of these biases when they are known in advance; unknown biases, however, can result in misleading conclusions. As outlined above, the availability of floral resources has been recognized as potentially biasing pan trap data. One recent study, using a well spatially replicated study in European agricultural system, did convincingly show that floral resource availability can bias pan trap results (O'Connor et al., 2019). However, it is still unknown how generalizable this result is across other systems, particularly natural systems that might vary seasonally in the availability of resources.

In this paper, we combined three multi-year datasets from 20 plots spread across a 6000-ha intermountain grassland location in western Montana; one each of flowering phenology, bee pan trap collections, and bee aerial netting collections. We examine whether pan trap captures may be influenced by seasonal floral resource availability, measured as the richness of flowering plant species (hereafter 'floral richness' or 'flowering richness'), in natural and semi-natural intermountain grasslands in western Montana, USA. Specifically, we address the question: (1) Is seasonal variation in floral richness correlated with bee abundance or richness captured in pan traps? A negative correlation between floral richness and bee abundance or richness would suggest that during time periods when floral resources are scarce, bees or certain species are disproportionately captured in pan traps or nets.

However, a positive correlation between these variables would suggest that the sampling method provides a reasonable estimate of bee abundance at a site. We also examine whether bee communities sampled in pan traps are similar to those sampled using aerial netting. Because sampling efforts often differ substantially between passive and active methods, we focus on richness to ask: (2) Is richness of bee species captured in pans correlated with bee richness captured in nets? Finally, because abundance and richness do not provide information on taxa-specific responses to flower availability, we ask: (3) Do bee community compositions, measured as relative abundances at a plot, sampled in pans versus nets change differently across a floral richness gradient, and how sensitive are these metrics using abundance versus presence/absence data? If communities in pans and nets change consistently with floral richness, this would suggest that the pan traps and nets are comparable methods for sampling bees. If they are different, it would suggest that the two methods measure bee communities in relation to floral richness differently. For this question, we compared changes in the relative abundances of the nine most common genera captured in pans and nets.

2 | MATERIALS AND METHODS

2.1 | Study system

Our plots are located on MPG Ranch, a 6000-ha conservation property in the Bitterroot Valley and Sapphire Mountains of Missoula County, Montana. Elevation ranges from 975 m above sea level (asl) to 1860 m (asl). Mean annual precipitation ranges from 300 mm at the valley floor to 350 mm on mountain summits. West-central Montana lies within the Rocky Mountain Lower Montane, Foothill and Valley Grassland ecological system (Montana Field Guide, 2017) and is characterized by short, dry summers, cold winters, and cool, wet springs. Habitats at MPG Ranch include riparian bottomlands, dry open forests, intermountain grasslands, and montane mixed-conifer forest. The intermountain grasslands that dominate MPG Ranch are characterized by cool season bunchgrasses (e.g. *Pseudoroegnaria spicata* (Pursh) A. Love, *Festuca idahoensis* Elmer, *Poa secunda* J. Presl, *Koeleria macrantha* (Ledeb.) Schult.) and a diverse suite of perennial forbs (e.g. *Balsamorrhiza sagittata* (Pursh) Nutt., *Lupinus sericeus* Pursh, *Castilleja hispida* Benth., *Antennaria rosea* Greene) and occasional shrubs (e.g. *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem, *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom and G. I. Baird, *Chrysothamnus viscidiflorus* (Hook.) Nutt.). MPG Ranch has a rich bee fauna (Kuhlman & Burrows, 2017) with higher bee richness than would be expected for its size (Meiners et al., 2019).

For over a century prior to 2009, the property was managed for livestock and agricultural crop production. Some of the lower elevation native grassland had been replaced with irrigated crops or introduced forage grasses, but these are now undergoing restoration treatments to return them to a more natural state. Restoration actions (2009–present) include integrated weed management using biological, mechanical and chemical controls, revegetation efforts using live plant material and direct broadcast and drill seeding. Native ungulates (elk, mule deer and whitetail deer) and feral horses now comprise the majority of vertebrate grazers on the property.

2.2 | Bee sampling

Bee sampling occurred every 2–4 weeks throughout the growing season for 4 years at 20 plots on MPG Ranch. The bee sampling plots were selected from a larger grid of points used for various monitoring projects at MPG Ranch. Plots were selected to be representative of grassland habitats on the ranch and to span a range of elevations. Other plot characteristics were not considered during plot selection. Plots were separated by a minimum of 250 m and a maximum of 5000 m. We surveyed bees using a modified version of the protocol outlined in LeBuhn et al. (2003), reducing netting time from two 60-min periods per sampling day to one 30-min period per sampling day due to field crew availability. At each plot, we laid out two, perpendicular, 50 m transects which intersected to create an X. We deployed 21, 66 mL plastic condiment cups (Solo Cup Co., Urbana, IL, USA) at each plot, filled about two-thirds full with soapy water and placed them 5 m apart along the transects. Seven cups of each of colour (fluorescent blue, fluorescent yellow, white) were used at each plot. We placed these pan traps out at all plots on the same day between 0700 and 0900 h and collected the contents between 1500 and 1700 h, providing a snapshot of the bee species composition for that day. We visited plots in the same order when setting out traps and when collecting traps, so traps were open at each plot for approximately 8 h on sampling days. Upon collecting the samples, we strained trapped bees from the pan traps in the field and transferred them into 120 mL Whirl-Pak bags (Nasco Sampling/Whirl-Pak, Madison, WI, USA) with 70% isopropanol or 70% ethanol.

We returned to the plots while pan traps were open and netted bees using 30 cm diameter aerial insect nets (BioQuip Products, Rancho Dominguez, CA, USA). Samplers netted for 30 mi at each plot (or 15 min each, if there were two samplers) between 1000 and 1500 h on each collection day in 2015, 2016 and 2017. Netting and pan trapping occurred on the same days, except in 2014 when there was no net sampling. Samplers walked haphazardly throughout the plot netting from as many different flowers as possible within the time frame. Samplers did not stop timers while placing bees in kill jars, but processed specimens at the end of the netting session to minimize processing time. Netted bees were killed with ethyl acetate and kept frozen in labelled collection tubes. All pan-trapped and netted samples were sent to the USDA-ARS Pollinating Insects Research Unit in Logan, UT, USA, for processing, identification and curation.

We sampled plots seven times in 2014 (1 May, 15 May, 12 June, 10 July, 31 July, 28 August and 17 September), nine times in 2015 (21 April, 4 May, 18 May, 8 June, 29 June, 20 July, 10 August, 1 September and 23 September), eight times in 2016 (11 April, 27 April, 18 May, 6 June, 27 June, 18 July, 8 August and 29 August), and six times in 2017 (4 May, 23 May, 21 June, 13 July, 2 August and 23 August). In 2014, no netting was performed, but both netting and pan trapping occurred in all subsequent years.

Higher level taxonomy (family, genus, subgenus) follows Michener (2007), except for some of the *Lasioglossum* subgenera, which follow Gibbs et al. (2013). Species and morphospecies determinations and the taxonomic keys used are detailed in Kuhlman and Burrows (2017).

2.3 | Flowering richness sampling

We visited each plot weekly from March through November 2014–2017 and recorded the presence of plant species in flower. Plants were considered 'flowering' when individuals at a plot displayed mature reproductive structures (i.e. anthers, stigma, petals). A list of plant species is detailed in Durham et al. (2017). Bees rely primarily on pollen and nectar produced by flowers to meet their nutritional needs as adults and larvae (but see Meiners et al., 2017). Although bees are known to use graminoid pollen as a food resource; this behaviour is not well characterized (Saunders, 2018). Thus, we included only flowering forbs and shrubs and excluded graminoids in our analyses. Due to the number of sites and frequency of visits, it was not logistically feasible to record floral abundance. We recognize not being able to include floral abundance, which some studies have shown to be an important predictor of bee communities, may be a drawback of our study.

2.4 | Statistical analyses

To answer our first question whether seasonal variation in floral richness is correlated with bee abundance and/or richness captured in pan traps, we correlated abundance of bees caught in pan traps and floral richness across the entire season, then we examined relationships between these variables for early season (April until early July) and late season (mid-July through October). We chose week 28 (early July) as an ecologically relevant cut-off between early and late seasons because spring flowering is largely finished then and dry-down has begun (Durham et al., 2017). To calculate floral richness, we summed the number of species flowering during each survey period. Only weeks when both flower richness sampling and bee sampling occurred were included in the analyses. Similarly, for bee abundance we summed the number of individuals captured in all bowls at all plots during a surveying period. We pooled our samples across all plots by sampling date ($n = 30$ sampling dates across the 4 years). All Pearson's correlations were conducted in R (R Core Team, 2019) using the cor.test function in the base package. We conducted these same analyses using bee richness captured in pans, rather than abundance.

To answer our second question whether bee richness captured in pans was correlated with bee richness captured in nets, we performed a Pearson's correlation of these two variables using the cor.test function. These analyses were also conducted on the data pooled across the entire study per sampling date as above. However, we did not net bees in 2014, so these analyses only use three years of data ($n = 23$ sampling dates).

For our third question about whether bee community compositions sampled in pans versus nets change differently across a floral richness gradient, we compared the abundance of bees caught in pan traps versus nets for nine bee genera that were most abundant in both pan traps and nets. For this analysis, we used plot-level data ($n = 20$ plots sampled across all 3 years for which we had netting data). Many of the genera were rare, and representation in the net samples was low, particularly in the late season. Because we are specifically interested in potential changes in community composition, measured as relative abundances of species within a plot, this analysis required reasonable sample sizes in both pans and nets. Therefore, we restricted this analysis to early season based on the higher abundance of bees and flowers in the spring/early summer. Additionally, we included only nine common genera that had captures in pans and nets on at least five sampling dates so that we had enough captures in both pans and nets to robustly compare the methods. These genera are *Andrena* Fabricius, *Anthophora* Latreille, *Apis* Linnaeus, *Bombus* Latreille, *Halictus* Latreille, *Lasioglossum* Curtis, *Nomada* Scopoli, *Osmia* Panzer and *Sphecodes* Latreille. Since many bee functional traits, including body size, plant fidelity and visitation rates have a strong phylogenetic signal (Grab et al., 2019), we believe that pooling by genus accurately captures differences in life history and functional traits among genera.

We constructed a generalized linear mixed model with a Poisson distribution. Bee abundance was included as the response variable and collection method (pan vs. net), bee genus, floral richness, and all interactions were predictor variables. Random effects included, nested in order from plot, collection method, genus and year. Additionally, we included an individual-level random effect to account for overdispersion (Harrison, 2014). Models were fit using the *glmer* function in the lme4 package (Bates et al., 2015). As outlined for our first question, for example, a negative correlation between floral richness and bee abundance in pans would suggest that when floral resources are scarce, bees are disproportionately attracted to pan traps. However, a positive correlation between floral richness and bee abundance would suggest that pan traps provide a reasonable estimate of bee abundance at a plot. Any interaction involving bee genus would suggest a change in community composition (i.e. species relative abundances) as per the analytical framework outlined in Jackson et al. (2012) and employed, for instance, in Hahn and Orrock (2015). For example, a significant interaction between floral richness and bee genus would indicate that bee genera show different patterns (slopes) of correlation with floral richness and would suggest that different sampling techniques would result in different estimates of bee community composition (i.e. relative abundances). Furthermore, a significant interaction between collection method and floral richness would indicate that these correlations differ between collection methods. For example, if bee abundance and floral richness are negatively correlated for pan traps but positively (or neutral) for net samples, this would suggest that bees are disproportionately trapped in pans when floral richness is low. For significant interaction terms, we used the emmeans functions in the emmeans package (Lenth et al., 2020) in R to estimate mean abundance at different levels of floral richness. Model fit was assessed by examining simulated
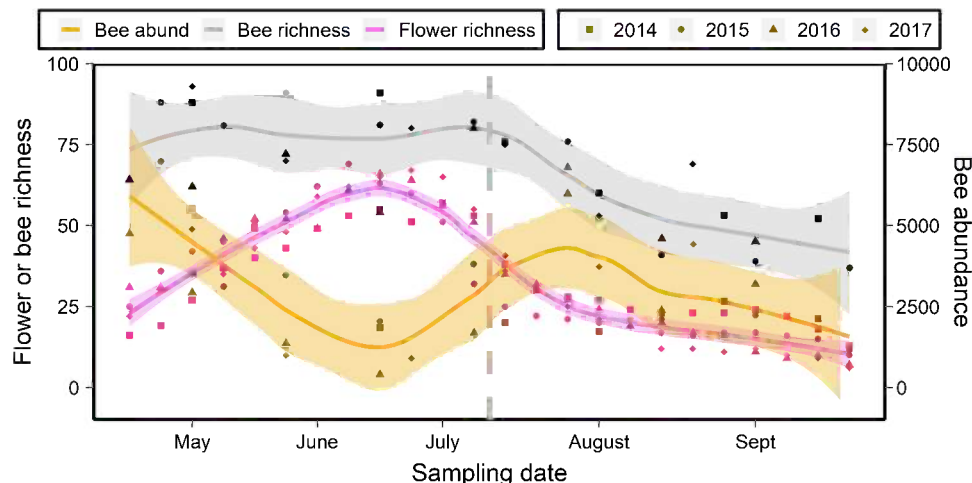
FIGURE 1 Flowering and bee species richness (primary *y*-axis) and bee abundance (secondary *y*-axis) as a function of time of year. All bee metrics are from pan traps. The dashed vertical line indicates the cutoff between early and late season. Note that the data points represent values summed across all plots

residuals using the simulateResiduals() function in the DHARMa package (Hartig & Lohse, 2020).

Related to the above analysis, we constructed a model identical to the above but used presence/absence data (binomial distribution) instead of abundance as the response variable to compare the sensitivity of the abundance metrics to presence/absence metrics. All fixed and random effects were the same, although we did not need to include an observation-level random effect to correct for overdispersion.

3 | RESULTS

3.1 | Bee sampling and flowering phenology

We caught a total of 95,436 bees (94,266 in pan traps and 1170 in nets) over the 4-year period. This includes 251 species and morphospecies (247 in pan traps and 110 in nets) from 38 genera and 5 families. Only one species occurred in nets that did not also occur in pans: *Megachile frigida* Smith. We documented flowering phenology of 174 species of forb and shrubs across the ranch from April through October. Flowering richness peaks in mid-June (Figure 1), which matches observations of a late spring/early summer bloom period in western Montana (Durham et al., 2017; Pearson, 2009).

3.2 | Seasonal variation in bee abundance and richness

Overall, bee abundance in pan traps trended towards being inversely correlated with flowering richness ($r = -0.34$, $df = 28$, $p = 0.066$). We found a strong inverse correlation ($r = -0.80$, $df = 14$, $p < 0.001$) between early season bee abundance in pan traps and flowering richness (Figure 2a) and no relationship between these variables for late season bee abundance in pan traps ($r = 0.12$, $df = 12$, $p = 0.65$; Figure 2b).

We found a moderate positive correlation ($r = 0.58$, $df = 28$, $p < 0.001$) between bee richness in pan traps and floral richness across the season. There was no significant relationship between bee richness in pan traps and floral richness for the early season ($r = -0.20$, $df = 14$, $p = 0.46$; Figure 2c). However, we found a strong positive correlation ($r = 0.68$, $df = 12$, $p < 0.001$) between late season bee richness and floral richness (Figure 2d). Bee richness captured in pan traps was positively correlated with bee richness captured in nets over the entire season ($r = 0.58$, $df. = 21$, $p = 0.004$, Figure 3).

3.3 | Changes in bee community composition in pan traps and nets

All termsin the abundance model were significant (Table 1). On average, more bees were captured in pan traps compared to nets, except for *Apis* and *Bombus*, which had more captures in nets than pans (Figure 4). Five of the nine genera (*Andrena*, *Anthophora*, *Apis*, *Nomada*, and *Sphecodes*) showed similar patterns in the pan traps and nets with regard to floral richness (Figure 4a). Importantly, four of the nine genera showed significantly different patterns with regard to floral richness in the pans versus the nets (Figure 4a). *Halictus* and *Lasioglossum* exhibited a negative correlation between bee abundance and floral richness that was stronger for pans versus nets. *Bombus* and *Osmia* each exhibited a positive correlation in nets but a negative correlation in pans (Figure 4a). The significant three-way interaction indicates that community composition (i.e. relative abundances) also changes between collection methods and with changes in floral richness (Figure 5a,b). In nets, *Apis*, *Bombus* and *Andrena* were the most common species captured, and *Andrena* and *Bombus* increased substantially in relative abundance, whereas *Halictus* and *Nomada* decreased, from low to high floral richness plots (Figure 5a). In pans, *Lasioglossum* accounted for over 50% of all captures and *Halictus* accounting for about 25%. Both of these genera decreased slightly in relative abundance from low to
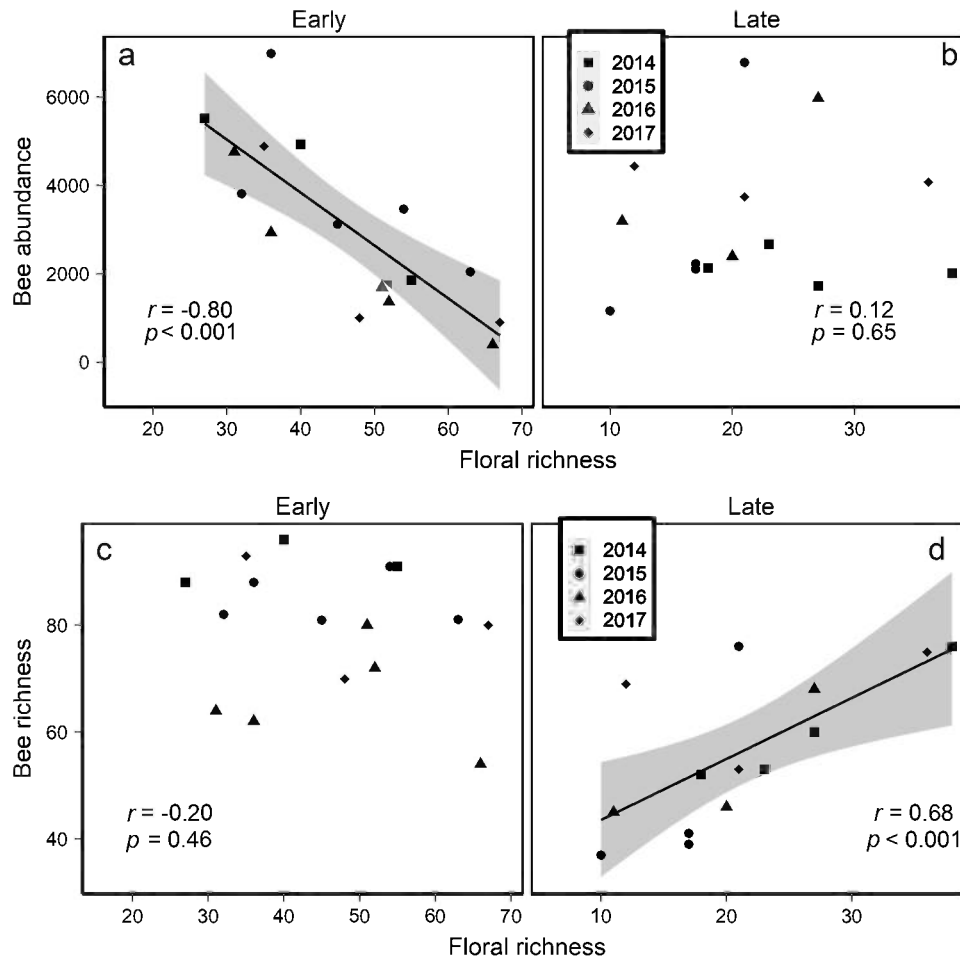
FIGURE 2 Correlation between bee abundance in pan traps and flowering species richness, divided into (a) early and (b) late seasons. Correlations between bee species richness and flowering species richness, divided into (c) early and (d) late seasons. Note that the data points represent values summed across all plots

TABLE 1 Full analysis of deviance tables for fixed effects and variance components for random effects for the Poisson abundance model and the binomial presence/absence model

| Fixed effects	Abundance model			Presence/absence model		
	χ^2	df	p	χ^2	df	p
Collection method	398.8	1	< 0.001	129.1	1	< 0.001
Genus	933.5	8	< 0.001	313.3	8	< 0.001
Floral richness	41.1	1	< 0.001	5.3	1	0.021
Collection method × Genus	408.8	8	< 0.001	190.2	8	< 0.001
Collection method × floral richness	17.0	1	< 0.001	7.5	1	0.006
Genus × floral richness	24.8	8	0.002	13.2	8	0.104
Collection method × genus × floral richness	16.8	8	0.032	19.3	8	0.013
Random Effects	Variance component			Variance component		
Observation term	1.16			NA		
Year × Genus × Collection × Plot	0.00			0.00		
Genus × Collection × Plot	0.27			0.29		
Collection method × Plot	0.00			0.00		
Plot	0.01			0.02		
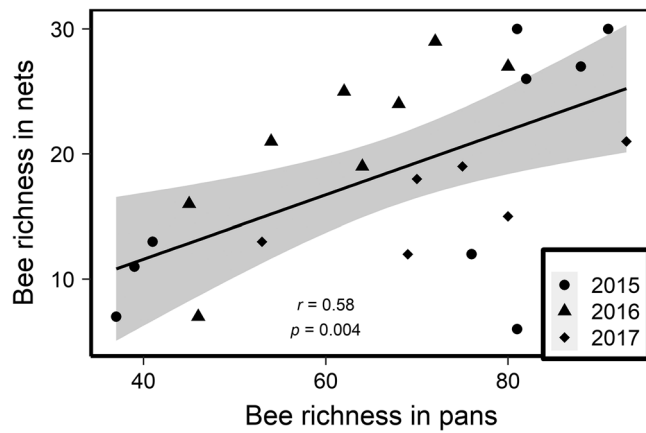
FIGURE 3 Correlation between bee species richness collected in pan traps versus nets. Note that the data points represent values summed across all plots

high floral richness plots, where *Andrena* increased in relative abundance from low to high floral richness plots (Figure 5a). All other genera made up very small proportion of captures in pans (Figure 5a).

All terms except for the two-way interaction between genus and floral richness were significant in the presence/absence model (Table 1). The results for how frequency of captures for each genus correlated with floral richness mirrored the abundance data (Figure 3). As with the

abundance model, the significant three-way interaction indicates that community composition (i.e. relative presence) also changes between collection methods and with changes in floral richness. In nets, *Apis*, *Bombus* and *Andrena* were the most frequently genera captured (Figure 4b), similar to the abundance data. In pans, the most frequently captured genera were *Andrena*, *Halictus*, *Lasioglossum* and *Osmia*. However, most genera were fairly evenly represented in both nets and pans and changes across the floral richness gradient were much more subtle (as indicated by the non-significant genus-by-richness interaction, Figure 5b).

4 | DISCUSSION

In this paper, we examined how pan trapping and netting, common techniques for sampling bee communities, change seasonally and respond to flowering species richness. We document strong seasonal changes in bee abundance, but not bee richness, captured in pan traps. Interestingly, pan traps had low bee captures in spring when most plant species are in bloom (Figure 1). That is, we captured the lowest number of bees in pans when the highest number of plant species were in bloom. We also compared patterns of bee abundance in pan traps versus aerial netting. Bee richness in pans and nets were positively correlated (Figure 3), suggesting both trapping methods provide similar information regarding the number of bee species present; a
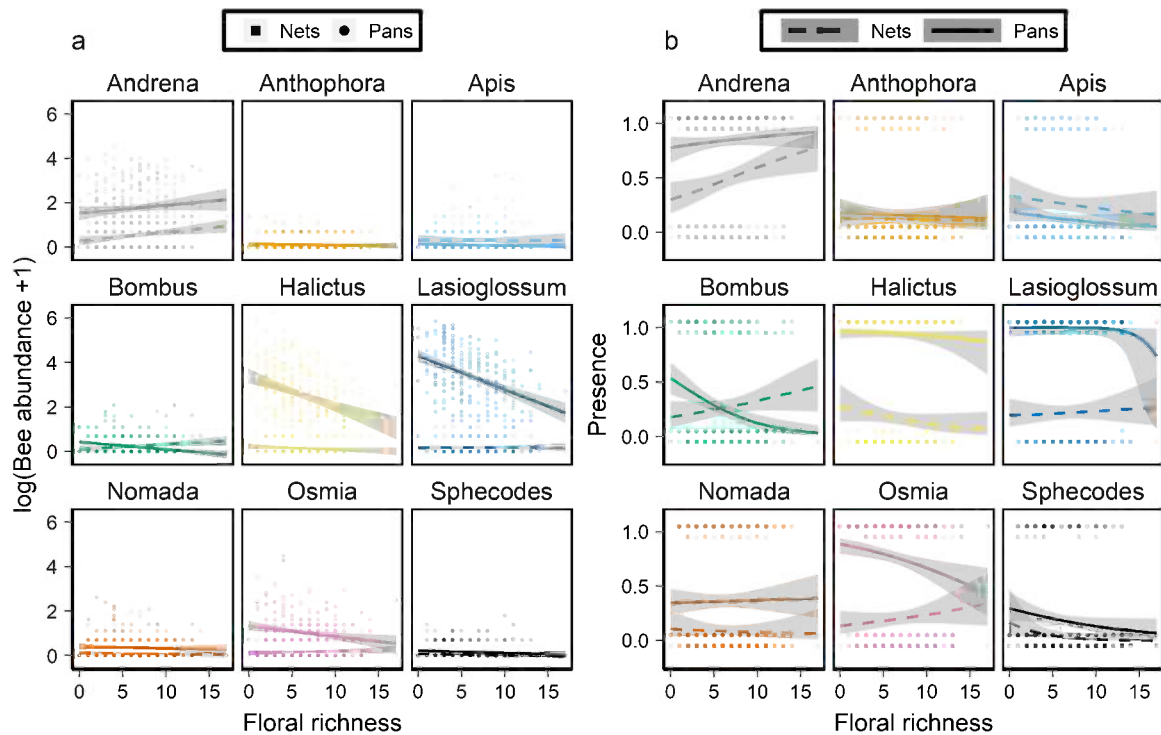

FIGURE 4 (a) Shows the abundance of bees captured in pan traps and nets as a function of floral richness at all sites during each survey session. Lines are best fit linear regression on log (+1) transformed data. (B) Shows the presence of bees captured in pan traps and nets as a function of floral richness at all sites during each survey session. Lines are best fit binomial regressions. Data are jittered above (pans) and below (nets) the 0/1 for visual clarity. In all panels, dots are partially transparent (alpha = 0.1) such that overlapping points appear darker. Data are only for early season, which is when bees were most abundant and diverse, and only for the nine most abundant genera
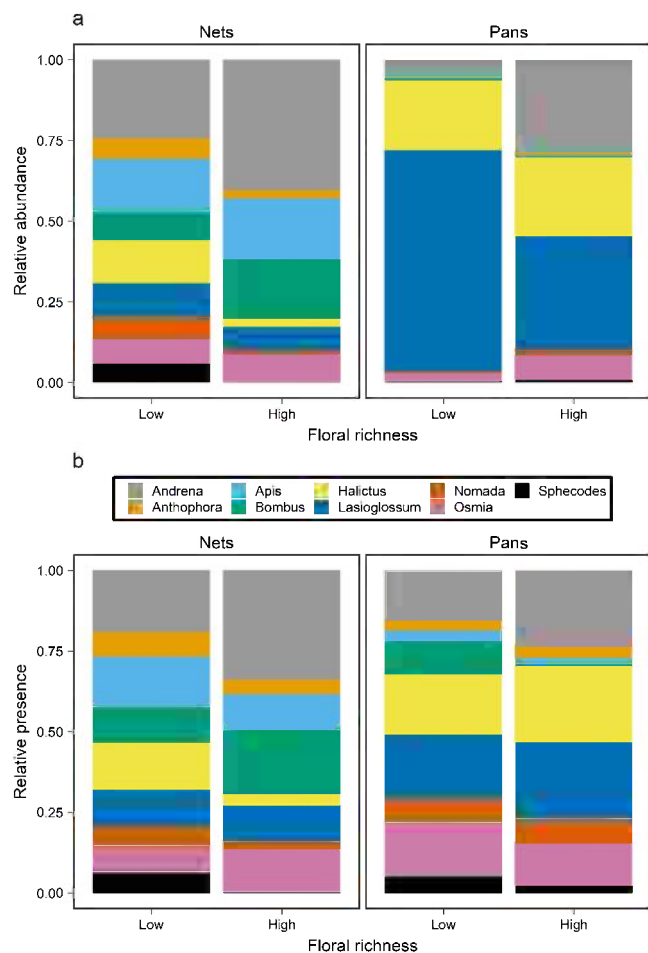
FIGURE 5 (a) Relative abundance from the Poisson abundance model and (b) relative presence from the binomial presence/absence model of the nine genera captured in pans or nets at low floral richness (one species in bloom per plot) or high floral richness (15 species in bloom per plot). Note that floral richness was included as a continuous variable in our statistical model, but here we show the extremes for low and high richness

finding consistent with other systems (O'Connor et al., 2019; Westphal et al., 2008). Abundances in pan traps were skewed towards a few genera (*Andrena*, *Halictus* and *Lasioglossum*) that accounted for up to 90% of the individuals captured in pans, whereas nets were dominated by *Andrena* and *Apis*. Abundances of most bee genera collected in pans decreased with increasing floral richness, but patterns were mixed for nets (Figure 4). The differences in bee captures across the floral richness gradient resulted in unique changes to bee community compositions (i.e. relative abundances) in pan traps versus aerial nets (Figure 5a). However, changes in bee presence/absences across the floral richness gradient were much more similar between pans and nets (Figure 5b), suggesting that presence/absence data are not as sensitive to biases towards species that are most attracted to pan traps. By combining intensive seasonal sampling of plant and bee communities over multiple years, we identify potential pitfalls with sampling bee communities. Below we discuss the implications of inferring changes in community composition from these different methods that should be considered in future studies.

4.1 | Seasonal relationships between bee abundance/richness and flowering richness

In our Montana foothills and grasslands location, we found that overall, the seasonal abundance of bees caught in pan traps had an inverse relationship to floral richness. In fact, at the peak of floral richness (mid-June), we caught the lowest numbers of bees in pan traps (Figure 1). The strength of the relationship varied between the early and late halves of the season. In the early season, when most plant species bloom in our system (Durham et al., 2017), we found a strong inverse relationship between bee abundance and floral richness, while later season showed no relationship. Our results confirm anecdotes from previous studies that floral richness may influence pan trap capture numbers (Baum & Wallen, 2011; Cane et al., 2000; Roulston et al., 2007; Wilson et al., 2008). O'Connor et al. (2019) found a similar effect in their study using short-term monitoring across large spatial scales, though it was particular to flowering agricultural crops in Europe. To the best of our knowledge, our study is the first to document this pattern using multi-year, seasonal monitoring in North American grasslands of the intermountain west.

Pan traps seem to work well to inventory species and document species richness, rather than measure bee abundance in an area, as has been suggested elsewhere (Nielsen et al., 2011; Westphal et al., 2008). We found that seasonal variation of bee richness in pan traps stayed relatively stable at both higher and lower levels of floral richness compared to bee composition in nets. This may be because pan traps can detect bees regardless of floral resource availability, including when there is a complete absence of vegetation (Rivers et al., 2018), whereas netting relies heavily on the availability of flowers from which the collector can sample (Cane et al., 2000; Gibbs et al., 2017; Nielsen et al., 2011).

When comparing bee richness found in pans to bee richness found in nets, we found an overall positive correlation (Figure 3). Sampling effort differed substantially between the different capture methods (192 h of pan trapping versus 12 h of netting per sampling day) and this likely affected our results, in that more species were caught with pans than with nets. In addition, approximately 99% of our bees were collected in pan traps, which is high when compared to other studies that combine pan trapping and aerial netting. For example, Roulston et al (2007) caught 17% of bees in pans, and Wilson et al (2008) caught 86% of bees in pans. These differences likely reflect our greater effort for pans versus nets. Nevertheless, the finding of richness being positively correlated between sampling methods provides further support that either method is reasonable for inventorying bee species' presence/absences.

4.2 | Interactions between bee abundance, flowering richness, and bee genera

Abundance of bees in pan traps is often used as a proxy measure of abundance in a given habitat (Rivers et al., 2018) and to estimate community composition (Mallinger et al., 2016; O'Connor et al., 2019; Smith DiCarlo et al., 2020; Westphal et al., 2008). Our work shows

that this relationship is complex and that pan traps are potentially problematic for community metrics that rely on abundance measurements. We found that abundance patterns of bee genera often differed with the capture method and that some bee genera responded strongly to either pans traps or nets. For example, approximately 50% or more of the individuals in our early-season pan traps were *Lasioglossum* and approximately 25% were *Halictus* (Figure 5a). The overwhelming abundance of these two genera likely represents an affinity for pan traps rather than their super-abundance in the environment (Leong & Thorpe, 1999; Portman et al., 2020; Roulston et al., 2007). Additionally, bees in these genera tend to be common, generalist foragers, and some species exhibit a degree of social behaviour (Michener, 2007), which may also partially explain their abundance in pan traps. Genera that were captured in low abundance may reflect either (1) their low relative abundance in the bee community (e.g. *Chelostoma*), (2) genera that have low affinity for pan traps (e.g. *Colletes*) or (3) genera that might easily escape pan traps (e.g. *Apis* or *Bombus*). In contrast to our findings in pan traps, bee community composition in nets was dominated by *Bombus* and *Apis*. Several factors may help explain this finding. Both of these groups consist of medium- to large-bodied bees which may be able to climb out of pan traps more easily than smaller bees (Cane et al., 2000; Westphal et al., 2008). These two genera are broadly recognized as bees by most people, and some samplers may be more inclined to net these more conspicuous bees (Nielsen et al., 2011).

We also found a strong overall inverse relationship between bee abundance in pan traps and flowering richness in early season, suggesting that floral richness can influence the traps' reliability in predicting true bee abundance in the environment as floral resources change spatially or throughout the season. O'Connor et al. (2019) documented similar patterns of total bee abundance changing across a gradient of flower density differently for pans versus counts via walking transects in European agricultural systems. However, they found generally greater abundance in the walking transects compared to pans, likely due to greater efforts invested in the walking transects. Additionally, we found differences among genera in how they changed in abundance in regard to floral richness in both pans and nets. *Halictus*, *Lasioglossum* and *Osmia* decreased with increased floral richness in pans but not nets. *Bombus* and *Andrena* increased in nets but not pans across the floral richness gradient (Figure 4). This means that despite differences in abundance between our two methods, bee community composition changed substantially across the floral richness gradient between pans and nets for these genera. Thus, estimates of community composition based on abundances in pan traps likely represents a mixture of abundance in the community coupled with affinity or susceptibility of capture in pan traps and available floral resources. When examining changes in frequency of capturing using presence/absence data, our results mirrored our findings for overall abundance. That is, the most abundant genera were also captured in greater frequency among plots (Figure 4). However, changes in bee community composition, measured as the relative presence/absence among the nine genera, was much more consistent both between nets and pans as well as changes across the floral richness gradient (Figure 5). Therefore, inferences based on changes in community composition using presence/absence data from

pan traps should provide less biased results that are more comparable to other methods (netting, in our study) when compared to using abundance-based metrics.

4.3 | Implications for comparing bee communities using pan traps and aerial nets

Any insect sampling method will have inherent biases that need to be considered when interpreting results of the sample. Pan traps are widely recognized as a passive collection method that is simple and efficient, with low sampler bias, and useful in a variety of landscapes (LeBuhn et al., 2016; Nielsen et al., 2011; Portman et al., 2020; Westphal et al., 2008; Wilson et al., 2008). We agree that this is the case, but there are also important biases to consider when interpreting pan trap data. Recently, Portman et al. (2020) suggested that pan traps were not suitable for abundance-based bee monitoring. Based on our findings, we concur that that abundance-based diversity metrics may not be appropriate. In our study system, we found that pan traps were well-suited for documenting bee richness and community composition based on measures of presence/absence, but may underestimate bee abundance during periods of high floral richness. We also found that bee genera differed in patterns of abundance between pan traps and nets, increasing the complexity of interpreting pan trap abundance results. These findings add to the growing body of evidence that pan traps can be an unreliable method for reflecting true bee abundance in the environment (Cane et al., 2000; Droege et al., 2010; O'Connor et al., 2019). We suggest that presence/absence data may be reliable to estimate changes in community composition from pan traps. Presence/absence data can be used in logistic regressions or binomial generalized linear (mixed) models, as we used. Although model-based approaches to analysing community data can be more informative than traditional ordination methods (Warton et al., 2015), when using multivariate procedures to compare communities, practitioners should consider avoiding abundance-based metrics such as Bray–Curtis distance matrices and instead use presence/absence based indices such as Sorensen's or Raup-Crick distance matrices (Oksanen et al., 2019). However, alternative sampling methods may provide more informative results than pan traps and researchers should consider adopted alternatives. Season-long, multi-year monitoring programs using multiple sampling methods, as we employed here, can help uncover the seasonal patterns of bee and floral communities that are particular to a landscape. Although low bee abundance in pan traps may be an indication of high floral richness nearby, unless practitioners have several years of data for comparison, it could instead signal a true decline in bee populations that may go otherwise undetected during other parts of the year when pan-trapped bee abundance and floral richness are not strongly associated.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

DM, PR and MK conceived project ideas. MK adapted bee collection methods and collected field data. SB identified the bees. MK and PH analysed the data. MK and PH led the writing of the manuscript. All authors contributed to the drafts and approve of the final version of the manuscript.

DATA AVAILABILITY STATEMENT

All data and R code associated with this manuscript are available in Dryad: https://doi.org/10.5061/dryad.2z34tmpmd (Kuhlman et al., 2021).

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