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Evaluating nesting microhabitat for ground-nesting bees using emergence traps

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Abstract

Nesting resources structure native bee communities and the availability of suitable nests may enhance population abundance and persistence. Nesting rates of ground-nesting bees have proven challenging to assess due to a lack of standardized methods. We quantified the abundance of ground-nesting native bees using emergence traps over a seven-month study period. We then compared specimens captured in emergence traps with pan- and net-collected specimens. We hypothesized that ground-nesting bees would be highly similar to bees found foraging within our study site. However, the species assemblage of ground-nesting bees collected from emergence traps was significantly dissimilar from the assemblages collected with aerial nets and pan traps, indicating different sampling methods target different components of the species assemblage. We then examined the importance of nesting resources found at each emergence trap on the abundance of ground-nesting bees collected from emergence traps. Quantification of potential nesting resources, such as percent bare soil, has been proposed as a proxy of nesting habitat for ground-nesting guilds. Sloped ground and soil compaction were the most predictive nesting resources at the community-level. Further, spatial distribution of nesting resources within the study landscape also affected nesting rates, although this varied by species. Bees occurred in 85% of emergence traps, with sampling date strongly affecting the number of bees collected. Emergence traps provide a useful method of sampling the ground-nesting native bee community and investigating nesting incidence.

Zusammenfassung

Nistgelegenheiten strukturieren Bienengemeinschaften, und die Verfügbarkeit von geeigneten Nestern kann die Abundanz und Persistenz von Populationen befördern. Es hat sich gezeigt, dass die Brutzahlen von bodennistenden Bienen schwer zu bestimmen sind, da standardisierte Methoden fehlen. Wir quantifizierten die Abundanz von bodennistenden Bienen, indem wir Schlüpffallen während einer 7-monatigen Untersuchungsperiode einsetzten. Wir verglichen dann die mit Schlüpffallen gefangenen Individuen mit Farbschalen- und Streifnetzfängen. Wir postulierten, dass die bodennistenden Bienen den Bienen, die wir auf unserer Untersuchungsfläche sammelnd antrafen, sehr ähnlich sein würden. Indessen unterschied sich die Artengemeinschaft der bodennistenden Bienen aus Schlüpffallen signifikant von den mit den beiden anderen Methoden erhaltenen Gemeinschaften, was anzeigt, dass unterschiedliche Sammelmethoden unterschiedliche Ausschnitte der Artengemeinschaft erfassen. Wir untersuchten dann die Bedeutung von Nestressourcen, die von den einzelnen Schlüpffallen erfasst wurden, für die Abundanz der mit Schlüpffallen gefangenen bodennistenden Bienen. Quantifizierungen von potentiellen Nestressourcen,

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wie z.B. der Anteil kahlen Bodens, wurden als Näherungsvariblen für Nisthabitate der bodennistenden Gilden eingeführt. Bodenneigung und Bodenverdichtung waren die vorhersagestärksten Nestressourcen auf der Gemeinschaftsebene. Darüber hinaus beeinflusste auch die räumliche Verteilung der Nestressourcen innerhalb der Untersuchungsfläche die Nistraten, wenn auch in artspezifischer Weise. Bienen traten in 85% der Schlüpffallen auf, wobei das Sammeldatum die Anzahl der gefangenen Bienen stark beeinflusste. Schlüpffallen stellen eine nützliche Methode zur Beprobung der Gemeinschaft der bodennistenden Bienen und zur Untersuchung ihrer Nisthäufigkeit dar.
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Keywords: Apiformes; Community dissimilarity; Hymenoptera; Aerial netting; Pan traps; Zero-altered model

Introduction

Wild, unmanaged pollinators are effective, often critical contributors to pollination services in natural and managed systems (Garibaldi et al., 2013; Klein et al., 2007). Of these, native bees are the most important pollinator group (Kearns, Inouye, & Waser, 1998). Interest in native bee conservation has risen in tandem with honey bee (*Apis mellifera* L.) decline (Menz et al., 2010; Winfree, 2010), and with increasing evidence of native bee population declines and local extinctions (e.g. Cameron et al., 2011). Yet little is known about one of the primary contributors to native bee life-history, nesting resources. As central-place foragers, native bees return to the same nest site after foraging bouts; therefore nest location is a key determinant of the distribution of pollination services in a given landscape (Lonsdorf et al. 2009).

Direct assessments of native bee nesting have focused on twig- and cavity-nesting guilds that readily occupy trap nests (e.g. Steffan-Dewenter & Schiele, 2008; Williams & Kremen, 2007). These guilds comprise less than 15% of all bee species; instead, the majority of native bees are solitary ground-nesters (Cane, 1991; Michener, 2007).

Ground-nesting bees can be assessed using tent traps that cover a portion of the ground, known as emergence traps (e-traps). E-traps have rarely been used to assess ground-nesting rates (e.g. Kim, Williams, Kremen, 2006). Standard bee collection techniques are pan-traps (colored bowls filled with soapy water) and aerial netting at flowers (Westphal et al., 2008), but these methods do not directly capture bees from their nests. Therefore the ability of habitat to support nesting is often inferred from (1) the presence of bee species from specific nesting guilds (e.g. Morandin & Kremen, 2013), or (2) the presence of potential nesting resources (e.g. Potts et al., 2005; Grundel, Frohnapple, Glowacki, Scott, & Pavlovic, 2010). The first inference assumes that bees found at a location must be nesting somewhere within a distance corresponding to their foraging range (Lonsdorf et al. 2009), which ranges from 300 m for small-bodied bees (e.g. *Lasioglossum*) to 2000 m for larger bees (e.g. *Bombus*; Greenleaf, Williams, Winfree, & Kremen, 2007). The second inference assumes that the availability of nesting resources affects the ability of native bees to nest in a given area.

Nesting resources have only recently emerged as factors potentially governing native bee community composition (Potts et al., 2005), persistence (Keitt, 2009), and response to disturbance (Williams et al., 2010). Nests can be challenging to locate therefore proxies are used as a means of quantifying potential nesting resources and habitat conditions within a landscape. Within-site characteristics, such as exposed bare ground (Potts et al., 2005), litter cover (Grundel et al., 2010), soil compaction (Wuellner, 1999), sloping ground (Burkle & Alarcon, 2011), and number of potential nesting cavities (cracks or holes in the ground; Potts et al., 2005), have been correlated to native bee community structure, but they have not been explicitly linked to within-site nesting incidence. Additionally, the distribution of nesting resources within a site may influence the distribution of within-site nesting, particularly if species have strong nesting preferences (Michener, Lange, Bigarella, & Salamuni, 1958; Potts & Willmer, 1997; Wcislo, 1996; Wuellner, 1999). Habitats may not be uniform in their ability to support populations of nesting bees (Grundel et al., 2010), however, models increasingly use nesting proxies and expert opinion regarding nesting suitability of land cover types to predict bee abundance in agricultural landscapes (Lonsdorf, Kremen, Ricketts, Winfree, & Williams, 2009; Kennedy et al., 2013). To improve these models and enhance conservation efforts, it is critical to test the accuracy of nesting proxies.

We used e-traps to examine whether species found nesting in our study site were similar to those detected using pan traps and aerial netting. We then determined which nesting resource proxies were correlated with native ground-nesting bee incidence. We hypothesized that: (1) species collected in e-traps would be a subset of the community collected using other sampling methods, however we expected to detect more similarities between e-trap and netted specimens because netting indicates direct use of within-site floral resources whereas pan traps may attract bees from a wider area (Morandin & Kremen, 2013); (2) specific nesting resources would be associated with higher nesting incidence and bee abundance in e-traps; and (3) nesting resources would be unevenly distributed throughout the study site, displaying spatial structuring, resulting in clustering of ground-nesting species utilizing those resources.

Table 1. Nesting variables used for quantifying nesting resources within emergence traps (adapted from Potts et al., 2005).

Nesting variable	Metric
Bare ground	% Bare exposed soil
Cavities	Any kind of hole in the ground, divided into two categories: number of small (<2 cm) and large (>2 cm)
Cracks	% of plot with cracks, for example, if a crack spanned the length of the trap but was <1 cm it would be marked as 1%
Litter	% Dead vegetation or leaf litter
Slope	Divided into three categories: percent slope in plot <30°, 30–60°, >60°. Slopes >60° were typically protrusions in soil
Soil compaction	A measure of surface soil resistance (0–4.5 kgf cm^2) taken with a soil penetrometer (Model no. 77114, Forestry Suppliers, Inc., Jackson, MS, USA)
Vegetation	% Living vegetative cover

Materials and methods

Our study was conducted in mixed chaparral gray pine habitat in the Capay Valley in Yolo Co., California (see Appendix A: Fig. 1). We delineated a 1 m × 1 m grid over an 40 m × 120 m area and placed 40 e-traps (BugDorm, 1.2 m^2; see Appendix A: Fig. 2) in randomly selected grid cells. We deployed e-traps continuously for the study duration, from May to October 2011. E-traps were staked down and edges secured with rebar to prevent bees from entering or exiting. Each e-trap contained a kill jar at its apex filled with 70% ethanol, which was changed approximately every 12 days, for a total of 11 sampling rounds. On days when e-trap kill jars were changed, we set out 24 pan traps (alternating blue, white and yellow) along 4 parallel 120 m transects for 4 h starting at 09:00 (see Appendix Fig. 3). Immediately following pan trap set-up, we netted all bee species visiting flowers within the study area for 40 minutes using variable transect walks (Westphal et al., 2008). We stopped the clock during specimen handling and between floral patches; netting usually lasted 1–1.5 h, from 09:30–11:00. Pan and net sampling was conducted on days with clear skies, temperatures above 18 °C, and wind speeds below 2.5 m/s (Morandin & Kremen, 2013). We quantified nesting proxies (Table 1) in each e-trap following Potts et al. (2005) in May.

Statistical methods

We characterized species richness of the entire community and for each collection method using a Chao1 (abundance-based) estimator of richness which corrects for undetected species (Chao, Chazdon, Colwell, & Shen, 2004) from the R package vegan (Oksanen et al., 2012; R core development team 2012). We compared Bray–Curtis, Chao and Jaccard dissimilarities between species assemblages of ground-nesting bees and parasites of ground-nesters collected by different sampling methods. First we calculated pairwise dissimilarities of the assemblages collected by each sampling method over the entire study period. Then, using perMANOVAs (Oksanen et al., 2012), which calculate dissimilarities between all sampling methods simultaneously, we assessed differences in species collected with each method for every sampling date, after removing all sampling date-method combinations in which fewer than 5 specimens were collected. We visualized the dissimilarities between methods using non-metric multidimensional scaling (NMDS). We then calculated the sample coverage of each sampling method by dividing the number of species collected by each method by the total number of species collected over the course of our study (Westphal et al., 2008).

The nesting data includes many e-trap samples with no bees (see Appendix A: Fig. 4); therefore to test our second hypothesis (specific resources are associated with bee nesting) we used a zero-altered model developed to deal with high number of zeros typical of count data. Zero-altered models contain two parts: a zero-altered model that models the binomial probability of observing a zero, and a count model that models the non-zero observations (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We first tested whether a Poisson or negative binomial distribution would better fit our data. Both the likelihood ratio test ($\chi^2 = 118.86$, $P = <0.001$) and AIC scores (Poisson model 750.6624, negative binomial model 633.8002) indicated that a negative binomial distribution was more appropriate for our data, suggesting a degree of overdispersion. We therefore modeled bee abundance in e-traps over the entire study period using a zero-altered negative binomial model using the R package pscl (Zeileis, Kleiber, & Jackman, 2008).

We assessed nesting proxies by first removing any variables that were significantly correlated (see Appendix A: Table 1), after visually assessing the results of a principle components analysis to confirm that correlated variables fell along similar major axes. Within an e-trap, slope categories summed to 100%, therefore this classification led to strong negative correlations between the slope covariates ($\rho = -0.968$). Since slopes 30–60° and >60° fell along the opposite major axis from slope <30°, which also included the nesting proxy pre-existing cavities, we used only Slope <30° as a predictor in our model.

We centered the variables included in the count model (mean subtracted from value) to facilitate interpretation. We hypothesized that two factors contributed to the number of zeros observed in our data: sampling date, which affects bee seasonality (Morandin & Kremen, 2013), and e-trap location, which was randomly placed in a single grid cell over the study period possibly missing adjacent bee nests. Therefore these variables were included in the zero-altered portion of the model. We simplified the model by dropping terms from both the count and zero-altered portions of the model following

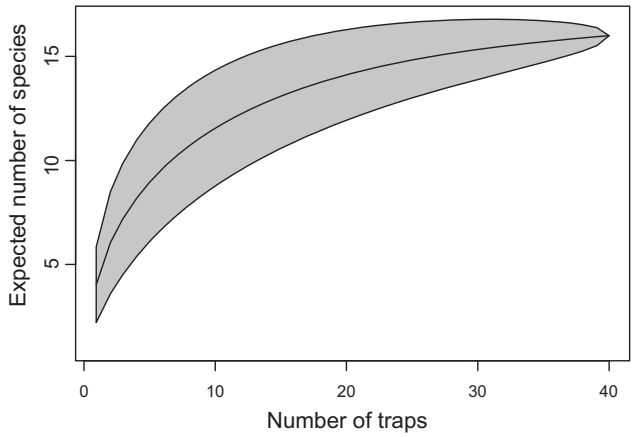

Fig. 1. Rarefaction by the number of traps shows that the number of species begins to saturate at a high number of traps. These data represent the number of species accumulated across the 7-month sample period in each trap. Shaded areas are 95% confidence intervals.

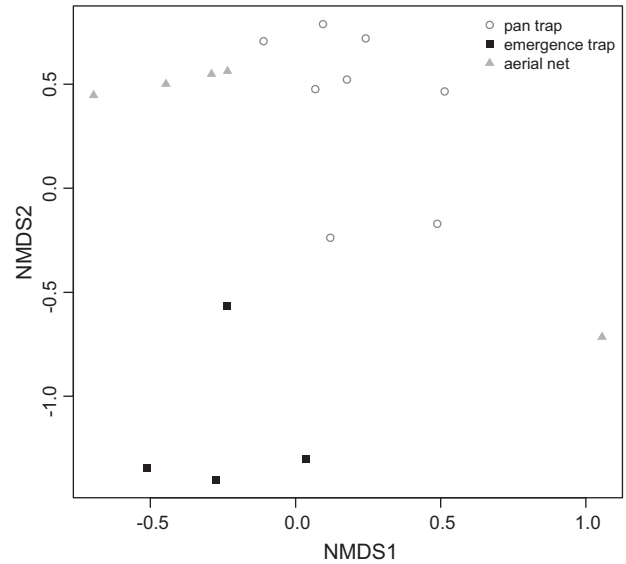

Fig. 2. NMDS plot of Bray–Curtis dissimilarities of species assemblages collected by pan trapping, aerial netting and emergence traps during 11 sampling events during the study period (NMDS, stress = 0.10501). Samples with fewer than 5 individuals were removed from analysis.

the protocol in Zuur et al. (2009). The final model contained all reduced candidate nesting proxy covariates (percent bare ground, percent cracks, number of pre-existing cavities, slope, soil surface compaction, and percent vegetation) in the count model, but only sampling date in the zero-altered portion of the model. We assessed the variance inflation factors (VIF) of nesting proxies included in the model to ensure they were not collinear. All VIF were below 3.0 (Zuur, Ieno, & Smith, 2007), indicating that reduction of correlated variables eliminated collinearity between model covariates.

Next, we examined whether nesting incidence (presence–absence) or abundance of the entire community of nesting bees collected in e-traps could be explained by the spatial pattern of nest location or was correlated to the distribution of nesting resources within the site, using multiple regression on Bray–Curtis distance matrices (Lichstein, 2006; Mandelik, Winfree, Neeson, & Kremen, 2012), which is an extension of the Mantel test in the R package ecodist (Goslee & Urban, 2007). We repeated this test for the genus *Lasioglossum*, which was the most commonly collected genus in e-traps, and also for individual species with incidence >5% of all samples.

Results

85% of e-traps collected bees over the duration of our study. Estimating species accumulation by rarefaction indicated that the detection of new species had begun to level out toward a higher number of traps over our 7 month study period (Fig. 1). Our study site had an observed species richness across all sample techniques of 54 species, with a Chao1 species richness estimate of 61.5 ± 6.2 (mean ± SE). Pan traps had the highest sample coverage, collecting 452 individuals from 35 species (Chao1 = 40 ± 12.724); netting produced 97 individuals from 26 species (Chao1 = 71.3 ± 62.5). E-traps collected 252 ground-nesting bees (164 females and 88 males) representing 15 species (Chao1 = 15.333 ± 1.870; see Appendix A: Table 2). The majority (97%) of bees in e-traps were small-bodied Halictidae, predominantly from the *Lasioglossum* and *Halictus* genera. Conversely, species collected in pan and net samples had a wider range of body sizes (from large-bodied *Bombus* to tiny *Perdita*).

The ground-nesting species assemblages and their parasites collected by pans, netting and e-traps were all significantly dissimilar from one another (Bray–Curtis: $F = 4.8566$, $P = 0.001$; Chao: $F = 4.4113$, $P = 0.001$; Jaccard: $F = 3.7945$, $P = 0.001$; Fig. 2). Overall, there was little overlap between species collected by different methods (Bray–Curtis pairwise dissimilarity pan-net: 0.8353, pan-e-trap: 0.8148, net-e-trap: 0.7492; Fig. 3). Further, the numbers of species collected by different sampling methods varied by season (Fig. 4.; see Appendix A: Table 2).

Slopes <30° (−0.0912 ± 0.0371, estimate ± SE, $P = 0.0141$), surface soil compaction (−2.9324 ± 1.2417, $P = 0.0182$), and pre-existing holes (−0.2170 ± 0.0880, $P = 0.0137$) were negatively associated with native bee nesting abundance, whereas percent bare ground was slightly positively associated with nesting (0.0281 ± 0.0167, $P = 0.0925$), although only marginally significant. Sampling date strongly influenced the number of zeros we observed, with fewer zeros earlier in the year (May–June).

We did not detect spatial patterns in nesting incidence or abundance for the ground-nesting community or the genus *Lasioglossum* in relation to nest location or nesting resources (Table 2). Variability of sloped ground among

Table 2. We constructed distance matrices using a multiple regression on Bray–Curtis distance matrices to evaluate the spatial distribution of resources on nesting incidence and abundance for species with occurrences >5. The values are Bray–Curtis dissimilarities. A complete table may be found in the Appendix (Table 4).

Model	Location	Bare ground	Cavities	Cracks	Slope	Soil compaction	Vegetation	r^2	F	Overall P
All community-abundance					0.3087*			0.21	25.7	0.11
All community-presence								0.04	3.82	0.82
All-*Lasioglossum*-abundance					0.4902*			0.44	79.25	0.04*
All-*Lasioglossum*-presence								0.03	*3.56*	0.85
Halictus tripartitus								0.07	7.24	0.46
Lasioglossum Dialictus sp.C	−308.78*				0.1842*			0.19	22.79	0.16
L. Dialictus.sp.D1			0.0758*	0.5870*	0.1094*			0.69	224.59	0.12
L. Dialictus ssp.								0.03	3.17	0.87
L. Evylaeus ssp.					0.2088*	0.8890*		0.72	250.41	0.08
L. incompletum								0.06	6.34	0.46

* $p < 0.05$.

e-traps significantly affected the abundance of some nesting *Lasioglossum* species (Table 2).

Discussion

Direct assessments of native bee nesting at the community-level are scarce due to a lack of standardized methods. As we here demonstrate, e-traps are a viable method for quantifying native bee nesting rates and associating ground-nesting species with specific nesting resources. E-traps had a high collection rate over the study duration and within each sample period, despite numerous instances in which no ground-nesting bee was found. Furthermore, e-traps had a low estimated number of unseen species particularly when compared to estimates of unseen species from pan and net samples. We found eight species in e-traps that were never captured in either pan or net surveys, indicating further that the method may compliment existing bee surveying techniques (Fig. 3).

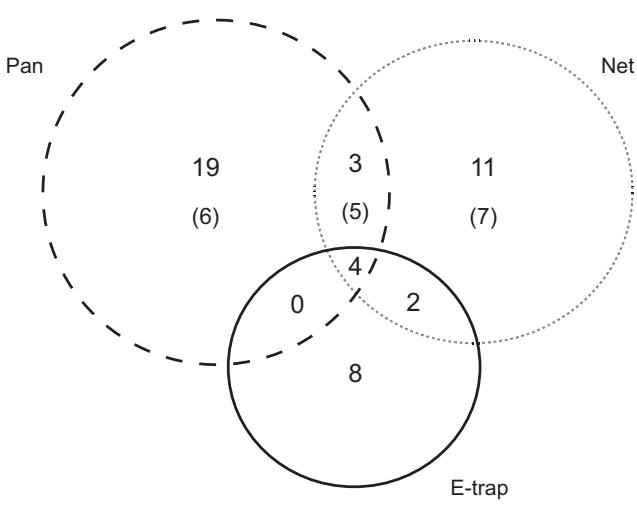

Fig. 3. Shared species collected by pan trapping, aerial netting and emergence traps. Number in parentheses indicate above-ground nesting species whereas all other numbers refer to below-ground nesting species.

Contrary to our hypothesis, e-traps collected markedly different species than pan and net samples. The high levels of dissimilarity we observed in species assemblages collected using different sampling methods could be attributable to biases associated with these methods or differences in sampling effort related to how the methods are implemented.

It is challenging to compare sampling effort across different methods. Pan traps are a passive method whose effectiveness varies given the abundance of adjacent floral resources (e.g. Morandin & Kremen, 2013). We collected higher numbers of species in pan traps toward the end of our study period (Fig. 4), which coincided with a sharp decline in floral resources. Conversely, the efficacy of aerial netting may benefit from presence of floral resources, but can vary with collector skill (Westphal et al., 2008). Our study area had low floral species richness, and we only found bees foraging on 5 of the 11 plant species in bloom over the course of the study (see Appendix A: Table 3). Trap nests, a passive collection method that measure nesting rates, of twig- and cavity-nesting bees, have low sample coverage when compared to pan and net. E-traps are a passive method that also quantify nesting rates, however in our study, e-traps had nearly twice the sample coverage Westphal et al. (2008) found trap nests to have (e-trap = 27.8%, trap nests = 14%).

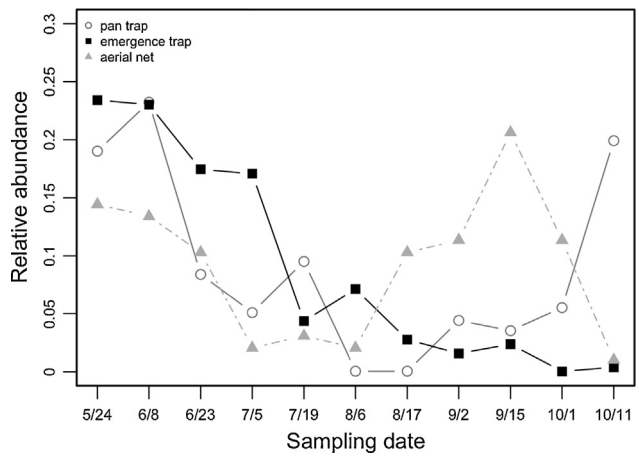

Fig. 4. Relative abundance of specimens collected over the study period using pan traps, netting, and emergence traps.

Other factors may have contributed to the levels of dissimilarity we observed between collection methods. For example, the unique species collected in the e-traps may have been the only individuals present in our study landscape, preventing them from being collected by other sampling methods. E-traps covered only a fraction of the study landscape (<1%), therefore it would be surprising if they collected all the individuals of a species in our study locale. Alternately, bees found foraging and flying in our study site could have come from surrounding areas. Our study area was smaller than the predicted foraging ranges of the species collected, however, even if it encompassed foraging ranges, species nesting outside the study area could still visit the study area if their nests were adjacent. Finally, e-traps were set out for the duration of our study, therefore bees collected in e-traps were those emerging from nests initiated the year prior to our study. The assemblage of species in the e-traps may have better matched community composition in the previous year, contributing to the high levels of dissimilarity between sampling methods we observed. Because we did not sample the year before we conducted our study, we cannot test this prediction nor disentangle it from biases associated with other sampling methods. Previous research has shown that bee communities can be highly variable between years, experiencing high rates of species turnover (Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008; Williams, Minckley, & Silveira, 2001). To eliminate this temporal issue in future studies we suggest collecting data on the flying community in the prior year to e-trap sampling or moving e-traps during the study period. With the latter method male bees would then need to be excluded from analyses as they may not represent ground-nest bees emerging from nests but may instead be resting in vegetation (Kim et al., 2006).

Our study is the first to confirm directly the importance of the availability and distribution of ground nesting resources for native bee ground-nesting incidence at the community level. In our study, surface soil compaction decreased the number of nesting bees within e-traps. Ground-nesting bees have a wide range of documented tolerances for soil compaction, tending toward softer soils, however their preferences can change depending on factors including adjacent nest density (Potts & Willmer, 1997).

Many species of ground-nesting bees display a wide range of nesting preferences (e.g. Potts & Willmer, 1997). It may therefore be challenging to identify specific nesting characteristics influencing nesting incidence on a species by species basis. Indeed, Grundel et al. (2010) found that differences in nesting resources across a range of sites influenced the community composition of bees present within those sites. Similarly, the importance of nesting resources may vary with community composition. Variability both within and among sites may be key to promoting diverse bee communities. Although our study occurred in a single site, we found that the distribution of nesting resources influenced nesting incidence of some species. For example, steeper slopes were not evenly distributed in our study area, thus bees preferring sloped ground displayed evidence of spatial clustering.

The inter-correlation we detected between existing nesting proxies suggests that ongoing assessment of nesting resources is warranted. For example, following Potts et al. (2005), we created categories for variables such as slope. It might be more meaningful to use continuous rather than discrete measurements to facilitate estimation of the degree of sloped ground that best supports bee nesting. Additionally, nesting resources may not be stable over time. We quantified nesting resources once during our study period; to link resources available to different bees more accurately, it may be necessary to repeat assessments over each distinct flight period.

Despite the limitations of our sampling procedures, our results show that e-traps can be used to directly associate native bee ground-nesting to within-site nesting resources. E-traps can be used over a wide range of habitat types to evaluate the ability of existing nesting proxies to predict within site nesting. E-traps can help illuminate spatial patterns of nesting and highlight discrepancies between the species utilizing within-site floral resources versus those nesting and reproducing at the site. Further, e-traps may be able to help address key questions in bee biology, including whether the spatial distribution of nesting resources limits native bee nesting. These kinds of direct, rather than correlative, studies are necessary to assist in conserving and promoting ground-nesting bee populations in natural and managed landscapes.

Authors' contributions

H.S.S and C.K. designed research and analysis; H.S.S. performed research; H.S.S. analyzed data; and H.S.S. and C.K. wrote the paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2014.02.004.

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