Short Communication

SPECIAL ISSUE: Shaping the Future of Pollinators in Farmed Landscapes

DIFFERENT SEMI-NATURAL HABITAT TYPES PROVIDE COMPLEMENTARY NESTING RESOURCES FOR WILD BEES

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Abstract—Semi-natural habitats provide refuge for pollinating insects such as wild bees. Different types of semi-natural habitat can provide complementary floral resources throughout the year, but it is uncertain to what extent different semi-natural habitat types provide nesting habitat for wild bees. In this study, nesting resources for wild bees and nest-searching bees were surveyed visually in three different types of semi-natural habitat (i.e., hollow roads, tree rows, and forest edges). The composition of nesting resources for wild bees varied across the three types of semi-natural habitat. We also identified clear indicators of nesting resources within the different habitat types. We conclude that different types of semi-natural habitat provide varying and complementary nesting resources for wild bees. This study further highlights the importance of semi-natural habitat for pollinator conservation and emphasizes the need for further research to increase our understanding how different wild bee species use different habitat types for nesting.

Keywords—Land use, landscape composition, pollinators, biodiversity conservation

INTRODUCTION

Abundant and diverse resources across space and time are crucial for persistence of pollinator populations (Schellhorn et al. 2015). Habitat loss and agricultural intensification are among the main factors associated with declines of pollinator populations, as they drive loss and homogenization of floral resources (Kleijn et al. 2009; Goulson et al. 2015). Semi-natural habitat (SNH) provides a buffer against these changes, allowing pollinator populations to persist in agricultural landscapes, hence enhancing crop pollination services (Dainese et al. 2019; Eeraerts 2023). This is partly because SNH provides floral resources for pollinating insects throughout the year (Timberlake et al. 2019; Eeraerts et al. 2021). Recent studies show that landscapes with a variety of SNH types have further amplified supply of floral resources, whereby they support diverse pollinator communities (Martínez-Núñes et al. 2022; Maurer et al. 2022).

While our understanding of how floral resources structure pollinator communities is growing, the role of nesting resources is much less clear due to the challenges inherent in assessing this resource in different habitat types. Nesting habitat is required for wild bees to reproduce and maintain viable populations. Certain nesting resources like bare ground and existing nesting cavities have been shown to be important for structuring bee community composition in Mediterranean landscapes (Potts et al. 2005). In European fruit orchards, Eeraerts et al. (2021) found more abundant and diverse nesting resources in SNH compared to fruit orchards. This is expected to support greater diversity of wild bees due to the wide range of nesting habitat requirements among bee species (Harmon-Threatt 2020). Cavity-nesting bees can use a wide range of spaces found across landscapes including hollow *Rubus* stems in raspberry fields (Coates et al. 2022), snail shells in semi-natural habitat (Hopfenmüller et al. 2020) as well as artificial nesting cavities (Eeraerts et al. 2022). However, research on how nesting resources for bees are distributed across different habitat types is scarce and improving our understanding on this topic is essential to improve pollinator conservation.

A major challenge to the study of bee nesting is being able to quantify nesting resources in different habitats (MacIvor 2017; Antoine & Forrest 2021). Emergence cages have been used to collect bees emerging from nests in the ground, but these tend to yield very low numbers of insects (Sardiñas & Kremen 2014; Buckles & Harmon-Threatt 2019). They are also costly, and the captured insects reflect only one nesting guild since they do not allow for sampling of aboveground-nesting bees. Remote sensing has also been used for assessing soil slope, aspect and bareness in relation with wild bee activity (Ariza et al. 2022). While application of this approach is successful it is difficult to include more detailed nesting proxies such as hollow stems, snail shells, etc. Additionally, it requires detailed landcover maps and high-end programming capacity. The approach reported by Potts et al. (2005) provides a method for visual assessment of multiple nesting resources that may be used by bees, but that was used in xeric habitats without abundant vegetation. An adapted approach may be effective in temperate landscapes, but this has not been widely tested or compared among different habitat types. To this end, the dataset from Eeraerts et al. (2021) provides an opportunity to explore the differences in nesting resources provided by different types of SNH.

The goal of this study was to investigate how nesting resources for wild bees vary across different types of SNH common in temperate farmland. The specific research objectives were to determine 1) whether and how the nesting resources composition varies across different types of SNH, 2) identify which nesting resources are associated with certain types of SNH, and, 3) determine if the number of nest-searching bees is different across different types of SNH.

MATERIALS AND METHODS

DATA COLLECTION

The study was conducted in Flanders, Belgium, where intensive agriculture is widespread. Here, we selected 13 study landscapes, with a minimum distance of 2 km between each landscape (see Eeraerts et al. 2021 for details on study design). The main types of SNH embedded in these agricultural landscapes are hedgerows, hollow roads, tree rows, shrub vegetation, field margins and forests. In each landscape we selected one, two, or three SNH elements, depending on availability (11 hollow roads (HR), 7 tree rows (TR) and 6 forest edges (FE); all linear, perennial elements; Fig. S1). A HR road is a road eroded by leaching from rainwater and/or frequent use, placing the road between two slopes. They are historic landscape features that occur frequently in the study area. A TR is a row of human-planted trees, often along a road and/or agricultural plot. All selected SNH elements had well-developed vegetation layers (tree, shrub, and herbaceous vegetation) and had a loam and sandy-loam soil texture. In each element, a transect of 50 m was marked for data collection. In 2017 and 2018, we collected data in six and seven study landscapes, respectively (Table S1). According to Potts et al. (2005) we measured eight different proxies for nesting resources for wild bees: i) bare soil, ii) flat soil, iii) sloped soil, iv) steep soil, v) dead wood, vi) hollow stems, vii) cavities and viii) shells (see Table S2 for the method of measuring each nesting resource). Nesting resources were surveyed once at each site of every study landscape, during end of March-beginning of April in each year. Here, five 1 m^2 quadrats were placed at random along the 50 m transect, sampling the most southern-faced side for sloped soil. In each quadrat the different nesting resources were surveyed at ground level.

During the pollinator surveys in March-April of Eeraerts et al. (2021; net catching pollinators for one day in each transect, two times 30 minutes per day), we collected nest-searching solitary bees and bumble bees (O'Connor et al. 2017). Nest-searching bees display distinctive behaviors, including flying in low, zigzag patterns, and investigating holes in the ground between patches of vegetation. When a nest-searching bee was observed, it was caught with an insect net. After each 30-minute survey the specimens were identified to species level, and specimens that could not be identified were taken to the lab for species identification (identification key used: Falk & Lewington 2017).

DATA ANALYSES

For analyzing the diversity and composition of bee nesting resources, data from the five plots were pooled to obtain the mean value for each of the eight nesting resources. A generalized linear mixed-effects model (GLMM) with a negative binomial error distribution was used to test the influence of SNH type on the number of nesting resources per element, including landscape ID as a random factor. The diversity of nesting resources was calculated as the Shannon index of all nesting resources (function *diversity*, R package *vegan*; Oksanen et al. 2019). A linear mixed-effects model (LME) was used to test the influence of SNH type on the Shannon index per element, including landscape ID as a random factor. A Bray−Curtis dissimilarity matrix was created using the mean nesting resource values. We then used a permutation-based multivariate analysis of variance (PERMANOVA) to test the influence of habitat type on the composition of bee nesting resources (function *adonis2*, R package *vegan*). PERMANOVA detects compositional differences among groups for balanced designs (Anderson & Walsh 2013). As this study has an unbalanced design of SNH elements, it was necessary to check the multivariate homogeneity of group variance (i.e., dispersion) between habitat types. Before the PERMANOVA, the dispersion of nesting resource composition across SNH types was examined (function *betadisper*, R package *vegan*). Non-metric multidimensional scaling (NMDS) was used to visualize the composition of nesting resources between SNH types (function *metaMDS*, R package vegan). Pairwise comparisons were calculated with the function *adonis2* and a Bonferonni correction was applied ($P = 0.05/3 = 0.0167$). Additionally, we determined if certain nesting resource parameters are indicators of certain SNH types by calculating point-biserial correlation coefficients (r_{pb}) for each parameter (function *multtpath*, R package *indicspecies*; De Caceres et al. 2010). Year was not included as a fixed variable in any analyses because different sites were sampled in different years.

Nest-searching bee counts from the two 30-minute surveys in the first sampling period were pooled, to obtain the total number of nest-searching bees per habitat element. A GLMM with a negative binomial error distribution was used to test the influence of SNH type, with landscape ID as a random factor, on the number of nest-searching bee specimens (function *glmer.nb*, R package *lme4*; Bates et al. 2019). A second GLMM with a negative binomial error distribution was used to test the influence of the nesting resource Shannon index, with landscape ID as a random factor, on the number of nest-searching bee specimens. A Bray−Curtis dissimilarity matrix was created using the number of nest-searching bees per site. We then used a PERMANOVA to test the influence of habitat type on the composition of nest-searching bees (function *adonis2*, R package *vegan*). Before the PERMANOVA, the dispersion of nest-searching bee composition across SNH types was examined (function *betadisper*, R package *vegan*).

For the LME the model fit was evaluated visually by checking the normality of the model residuals (QQ-plot and plot of the residuals versus the fitted values). For the GLMMs, the residual diagnostics and goodness-of-fit tests from the DHARMa R package were used to evaluate the model fit (Hartig 2019). All analyses were performed with R version 4.2.0 (R Development Core Team 2020).

RESULTS

The total number of nesting resources was not different across SNH types (SNH type: $X^2 = 1.70$, $P = 0.43$, Fig. S2), yet the Shannon index for nesting resources was different across SNH types (SNH type: $F = 7.27$, $P = 0.013$). Post hoc comparisons revealed that the hollow roads had a slightly higher Shannon index compared to both tree rows and forest edges (Fig 1A; Table 1). PERMANOVA indicated that SNH type had a significant effect on nesting resource composition (Table 2). The NMDS further illustrated the different nesting resource composition across SNH habitat types (Fig. 1B). Dispersion across SNH types was not significantly different ($F = 0.45$, $P = 0.65$), which implies that PERMANOVA gives a conservative result for an unbalanced design (Anderson & Walsh 2013). Concerning the different nesting resource parameters, bare soil, steep ground, hollow stems and dead wood were strongly associated with HR (bare soil: $r_{pb} = 0.61$, $P < 0.01$; steep ground: $r_{pb} = 0.79$, $P < 0.01$; hollow stems: $r_{pb} = 0.61$, $p < 0.01$; and dead wood: $r_{pb} = 0.54$, $P = 0.02$). Flat soil was strongly associated with both FE and TR ($r_{pb} = 0.73$, $P < 0.01$).

A total of 71 nest-searching bees were detected, ranging from 0 to 7 per habitat element (3.10 ± 0.43; mean ± SE). The species richness and number of nest-searching bees was positively correlated (Spearman correlation: $\varrho = 0.94$, $P < 0.001$). Type of

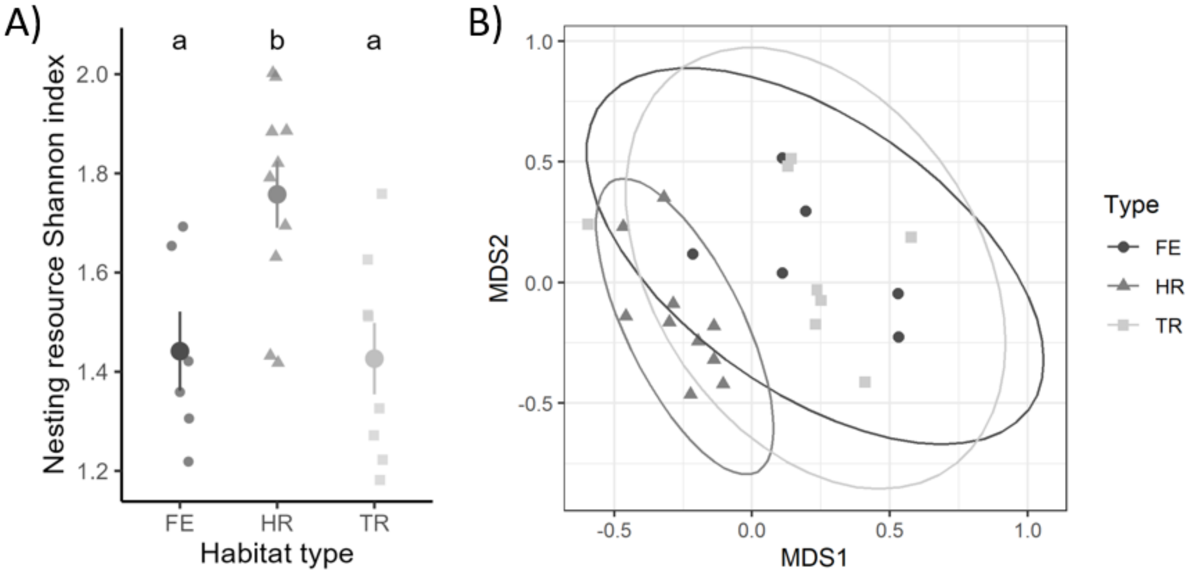

Figure 1: Shannon index for wild bee nesting resources in different SNH types (A; FE = forest edge, HR = hollow road, TR = tree row; the dots indicate the raw data, the dot with the bars indicates the mean and standard error). Letters in plot A indicate post hoc difference between SNH types. NMDS plot based on the Bray–Curtis dissimilarity data, to compare the composition of bee nesting resources between the SNH types (B). The NMDS plot represents the data with a stress of 0.10.

Table 1: Results of post hoc comparisons for nesting resource Shannon index in three habitat types around Belgian farms. Model statistics are reported: degrees of freedom (df), estimate, standard error, t-values and *P*-values.

Comparison	df	estimate	SE	t	P
FE versus HR	9	-0.32	0.11	-2.97	0.038
FE versus TR	9	0.02	0.11	0.14	0.99
HR versus TR	9	0.33	0.10	3.39	0.020

SNH and the Shannon index had no effect on the number of nest-searching bees (SNH type: X^2 = 0.57, *P* = 0.79, Fig. S3A; Shannon index: X^2 = 1.27, *P* = 0.26). PERMANOVA indicated that SNH type had no effect on the nest-searching bee community (F 0.65, *P* = 0.77; Fig S3B). Dispersion across SNH types was not significantly different (F = 0.14, *P* = 0.87).

Table 2: Results of PERMANOVA on Bray-Curtis distances for the composition of nesting resources in three habitat types around Belgian farms. Model statistics are reported: degrees of freedom (df), F-values and *P*-values.

Model parameter	df	F	P
Habitat type	2	6.08	< 0.001
Comparison			
FE versus HR	1	9.78	< 0.001
FE versus TR	1	-0.07	0.99
HR versus TR	1	8.95	< 0.001

DISCUSSION

Our study highlights that different SNH types provide a set of distinct, complementary nesting resources for wild bees, with indicator nesting types identified for certain SNH types. This further adds to the evidence which emphasizes the importance of SNH conservation to maintain bee populations and their pollination service (Winfree 2010; Eeraerts 2023).

This complementary resource provision for wild bees of different habitat types has been highlighted extensively for floral resources (Mandelik et al. 2012; Timberlake et al. 2019; Eeraerts et al. 2021; Maurer et al. 2022). Therefore, different habitat types support and enhance the diversity of the landscape-wide pollinator population (Mandelik et al. 2012; Martínez-Núñes et al. 2022). Regarding nesting resources for wild bees, SNH provides more abundant and diverse nesting resources compared to fruit orchards

(Eeraerts et al. 2021). The current study further illustrates how nesting resources for wild bees are distributed across different semi-natural habitat types. While our sample size is modest, this study is one of the first to investigate the distribution of nesting resources for wild bees across different types of SNH, and our findings provide clear evidence on this topic.

We found that the nesting resource Shannon index was slightly higher for HR compared to TR and FE, which in combination with the high number of indicator nesting resources suggests that HR provide a unique set of multiple nesting resources for wild bees. Similarly, Heneberg & Bogusch (2020) found that sunken lanes and sand pits provide unique nesting habitat and support nesting of rare bee and wasp species. Despite the disturbance, these historic landscape features seem to be very valuable elements for wild bees. Similarly, the added value of TR and FE might be providing more flat soil, and more vegetated parts (e.g., grass tussocks) which can be a valuable nesting resource for multiple bee species as well (Nichols et al. 2020; Tsiolis et al. 2022). Yet, more research is needed to increase our understanding between nesting resources and nesting activity of bees and other pollinating insects.

Including other habitat types and identifying which resources are essential for different bee taxa are among the future research needs for understanding how best to develop conservation strategies for these pollinators. Priority questions to address include: 1. How are nesting resources distributed across multiple other habitat types? (urban, grassland, arable land, forest interior, etc.), 2. Do other types of SNH provide additional sets of complementary resources?, and 3. How do bees respond to the availability of nesting resources including vegetative parameters like grass tussocks, straw bales, field borders, etc. (see Kells & Goulson 2003; Lindström et al. 2022; Tsiolis et al. 2022)?

As our understanding of nesting resource use by wild bees continues to expand, the linkages between complementary nesting and complementary floral resources across habitat types will be identified for key pollinator species (Mandelik et al. 2012; Eeraerts et al. 2021). We expect this will allow for more targeted conservation programs that incorporate the full ecological needs of these species, allowing for tailored approaches that enhance populations of species providing pollination services in different settings.

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DISCLOSURE STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data of this study are published as supplementary material together with the online version of this article (Eeraerts_Isaacs_data).

APPENDICES

Additional supporting information may be found in the online version of this article:

Fig. S1: Overview of the different woody semi-natural habitat elements

Table S1: Overview of the study landscapes

Table S2: Methods used for measuring each type of wild bee nesting resource

Fig. S2: Number of nesting resources present per habitat type

Fig. S3: The number of nest-searching bees in the different SNH types

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