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Evaluating wild bee diversity across key habitats of two Belgian National Parks

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Abstract. Protected areas are central to biodiversity conservation, but management efforts usually prioritise vertebrates or plant communities. The effectiveness of these initiatives in safeguarding insect diversity, particularly wild bees, remains poorly studied, and existing evidence shows contrasting results. To address this gap, we surveyed bee communities for five months in two recently established national parks in Belgium, namely the Semois Valley (SVNP) and Entre-Sambre-et-Meuse (ESEMNP), across a range of habitats. First, we evaluated whether mean alpha diversity (Hill numbers) and beta diversity varied across parks and habitats. Then we assessed whether threatened bee species (as categorized by the Belgian Red List) were associated with specific habitats or park. Collectively, these analyses enabled a comparative assessment of these two parks, highlighting their relative conservation value and identifying key habitats for wild bee conservation. We hypothesized that the mesic and calcareous grasslands would support the highest diversity in the national parks SVNP and ESEMNP respectively. Overall, we recorded 2278 bee specimens belonging to 153 species, including 30 threatened species, with the Semois Valley National Park harbouring higher overall mean alpha diversity than the Entre-Sambre-et-Meuse National Park. While no significant differences in alpha diversity were observed among habitats in the first National Park, calcareous grasslands and hay meadows in the second National Park supported the highest alpha diversity of wild bees, emphasizing the high conservation value of these habitats. Conversely, tall-herb habitats consistently showed the lowest alpha diversity across both national parks. Ensuring the persistence of these parks and their key habitats through targeted management and connectivity measures, will be essential for maintaining bee diversity in Belgium.

Key words. Bumblebee, pollinator, Red list, IUCN, Wallonia.

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Introduction

With around 1 million of described species, insects represent a substantial fraction of global biodiversity and biomass in terrestrial ecosystems, and play essential roles in their functioning through pollination, decomposition, and food-web support (Stork 2018; Rosenberg *et al*. 2023). Yet, mounting evidence indicates abrupt declines in both their abundance and diversity across many regions of the world (Hallmann *et al*. 2017; Wagner *et al*. 2021). These declines are primarily driven by anthropogenic pressures, including habitat loss and fragmentation, agricultural intensification, pesticide use, climate change, and the spread of invasive species (Ghisbain *et al*. 2021; Wagner *et al*. 2021; Gekière *et al*. 2025). The erosion of insect populations not only threatens ecological stability but also undermines key ecosystem services on which human societies depend (Potts *et al*. 2016; Cardoso *et al*. 2020).

Establishing protected areas is one of the main strategies to mitigate biodiversity loss (Rodrigues *et al*. 2004; Watson *et al*. 2014). A protected area is defined by the International Union for Conservation of Nature as "*a clearly defined geographical space, that is recognized, dedicated, and managed through legal or other effective means, to achieve the long term conservation of nature*" (Dudley 2008). However, management plans for these areas typically prioritise vertebrates, plant communities or ecosystems as a whole. While the protection of habitats can indirectly benefit the species associated with them, conservation objectives rarely consider insect diversity or explicitly evaluate how insects respond to protection (Chowdhury *et al*. 2023a). This represents a missed opportunity, as protected areas could play a key role in mitigating insect declines (van Klink *et al*. 2020), although evidence for this is mixed, partly because areas are rarely designated by a careful selection process to conserve insects (Chowdhury *et al*. 2023b; Fiordaliso *et al*. 2025). In particular, little is known about the extent to which protected areas support wild bees, despite their recognised importance as pollinators for various terrestrial ecosystems (Garibaldi *et al*. 2013; Senapathi *et al*. 2021). Several studies have highlighted that many protected areas were not originally designed with insects in mind, and that centres of highest insect diversity often lie outside protected zones (Casanelles-Abella *et al*. 2023; Chowdhury *et al*. 2023a, 2023b). To address this conservation paradox, there is a need for more standardised studies focusing on insect populations within protected areas.

Belgium has recently established two new national parks, namely the Semois Valley National Park (SVNP) and the Entre-Sambre-et-Meuse National Park (ESEMNP). Following a standardised protocol, preliminary lists of bee species have recently been compiled for each of these national parks (Gérard *et al*. 2025). They represent the first national parks in Wallonia, the southern region of the country, and provide a unique opportunity to evaluate their conservation potential – particularly for insects, and wild bees as key pollinators. In Wallonia, the designation 'National Park' does not in itself confer legal protection. Nevertheless, within these two parks there are many areas that are formally protected, such as Natura 2000 sites, as well as sites that are not automatically legally protected but can have conservation plans in place, such as the 'Sites of Great Biological Interest' (SGBI). Together, legally protected and SGBI sites make up 54 % of the surface area in SVNP and 31.8% in ESEMNP. In this context, our primary objective is to provide a baseline assessment of bee diversity through a standardised sampling programme across habitats of both national parks, while testing how habitat types structure bee communities. To study these communities of the two national parks, we conducted a five-month sampling campaign in both parks, focusing on specific habitats. Most habitats were classified using the European Nature Information System (EUNIS) codes, a standardised habitat classification system in Europe (Chytrý *et al*. 2020). Among these, calcareous and mesic grasslands, when extensively managed, are known to host diverse bee communities (Klaus *et al*. 2021; Parmentier *et al*. 2025). We also included habitats that are generally overlooked in the literature on bee conservation, such as tall-herb communities or wet grasslands, to ensure a comprehensive evaluation of conservation value across contrasting habitat types. We evaluated the conservation potential of all these habitats using multiple complementary approaches, both on the combined dataset of the two parks and separately within each national park. We quantified biodiversity patterns across multiple scales. Specifically, we first compared overall species richness (γ-diversity) between parks, providing a regional-scale baseline of species composition. We then assessed local-scale variations in mean α-diversity between national parks and among habitats. Next, we compared compositional dissimilarities (β-diversity) of bee communities among sites. We hypothesized that the mesic and calcareous grasslands would support the highest diversity in SVNP and ESEMNP, respectively, as these habitats typically provide a rich and continuous supply of floral resources, a high amount of nectar per unit area, and suitable nesting sites, which together promote greater bee species richness and functional diversity (Morandin *et al*. 2007; Hopfenmüller *et al*. 2014; Baude *et al*. 2016). Finally, using the IUCN Red List categories (Rodrigues *et al*. 2006) and the Belgian Red List of bees (Drossart *et al*. 2019), we assessed whether the proportion of specimens belonging to threatened species were associated with specific parks or within-park habitats. Together, these complementary metrics provide a robust framework for characterising the diversity of wild bees in newly established protected areas.

Material and methods

National parks and sites description

On 9 December 2022, following a call for projects, the Walloon government officially designated the first two national parks in Wallonia, namely the Semois Valley National Park (SVNP) and the Entre-Sambre-et-Meuse National Park (ESEMNP). SVNP covers 28 903 ha across the provinces of Namur and Luxembourg. It is predominantly forested (86.5%) but also includes a rich wetland ecosystem along the Semois River, grasslands, and habitats shaped by historical human activities such as abandoned slate quarries. ESEMNP extends over 22 129 ha in the provinces of Hainaut and Namur. Among its most emblematic habitats are the calcareous grasslands of the Calestienne, which form a unique landscape in Wallonia. The park also contains extensively managed meadows and wet habitats along the Viroin, Eau Noire and Eau Blanche rivers.

To obtain a representative picture of wild bee diversity in the studied habitat types, we selected 32 sampling sites in each national park (Fig. 1). For each national park, the 32 sites were divided into four habitat categories, with eight sites per category. In SVNP, one category comprised ‘Mesic grasslands’ (EUNIS E2), open habitats with low to moderate fertilisation that support a high diversity of plant species. Two other categories were associated with wetlands: ‘Seasonally wet and wet grasslands’ (E3) and ‘Moist or wet tall-herb communities’ (E5.4). The former are open habitats that can be temporarily or permanently wet, typically occurring on nitrogen- and mineral-rich soils, while the latter are moist habitats dominated by dense, tall, broad-leaved vegetation, especially during summer. The final category, ‘Other habitats,’ included more heterogeneous sites that could provide valuable resources for wild bees but were not frequent enough in the park to form a separate category. The specific habitat types grouped under this last category are listed in Table 1. In ESEMNP, the first category consisted of ‘Perennial calcareous grasslands’ (E1.2), open and thermophilous habitats on calcium carbonate-rich soils that host a particularly diverse flora. The second category comprised ‘Sub-Atlantic lowland hay meadows’ (E2.2), open habitats developing under mild climatic conditions on well-drained soils, traditionally mown once a year and supporting a mixture of grasses and broad-leaved herbs. The third category, ‘Moist or wet tall-herb communities’ (E5.4), was the same as in SVNP, while the final category again grouped heterogeneous sites under ‘Other habitats’ (Table 1).

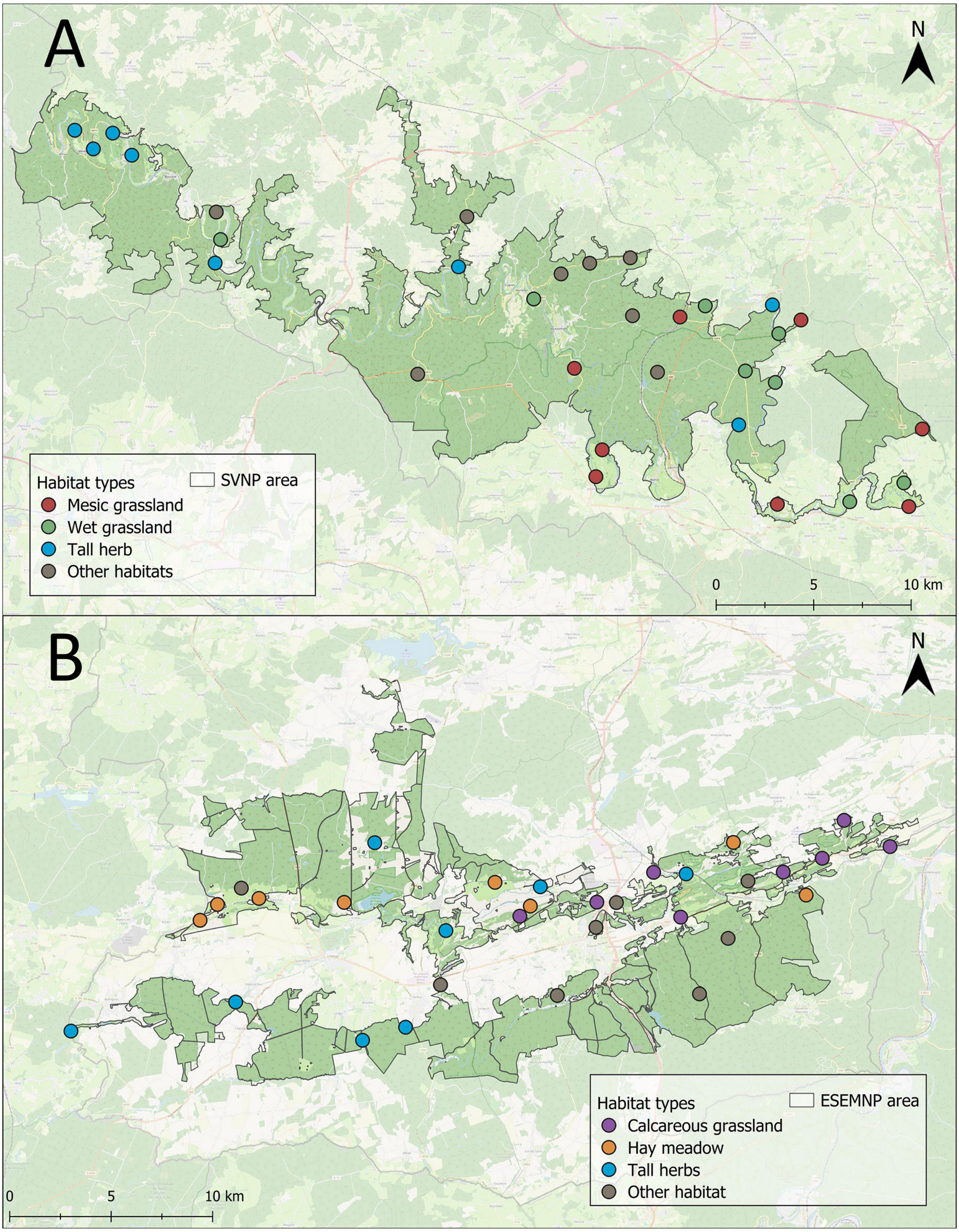

Figure 1 – Distribution of the 32 sampling sites for each national park (Wallonia, Belgium). **A**. The Semois Valley National Park. **B**. The Entre-Sambre-et-Meuse National Park. The colour code represents the habitat type at each sampling site.

TABLE 1

List of habitat types included in the 'Other habitats' category, in which of the two national parks they occur and their corresponding EUNIS (European Nature Information System) codes (where applicable). SVNP: Semois Valley national park. ESEMNP: Entre-Sambre-et-Meuse national park.

Type of habitat	**National park**	**EUNIS code**	**Number of sites**
Slate (schist) quarries	SVNP	Unclassified	6
Dry heaths	SVNP	F4.2	1
Dry grasslands	SVNP	E1	1
Riverine and fen scrubs	SVNP	F9	1
Valley and transition mires	SVNP	D2	1
Permanent mesotrophic pastures	ESEMNP	E2.1	1
Salix and fen scrubs	ESEMNP	F9.2	1
Inland cliffs and rock pavements	ESEMNP	H3.2	1
Dry heaths	ESEMNP	Unclassified	1
Quarries (calcareous and sandstone)	ESEMNP	Unclassified	2
Apple orchards	ESEMNP	Unclassified	2

Sampling sites were separated by at least 800 m, which minimises spatial autocorrelation and reduces the risk of collecting individuals from the same nest, as the foraging range of bees is generally well below 800 m (Gathmann & Tscharntke 2002). The surface area of sites ranged from 0.15 ha to 12.39 ha (mean = 1.92 ha; median = 1.16 ha). Access arrangements were secured beforehand: private landowners were notified, and the Département Nature et Forêt (DNF) was consulted for state or publicly owned plots. Collection permits were issued for all sites by the Service Public de Wallonie (SPW).

Sampling protocol

Both national parks were sampled from April to August, in 2024 for the SVNP and in 2025 for the ESEMNP. This period covers the peak flight season of wild bees in Belgium (Duchenne *et al.* 2020). Across the 32 sites, sampling was carried out once a month, resulting in five visits to each site during the survey period, with at least 20 days between two sampling sessions of the same site. A standardised protocol was applied to maintain comparability between sites and national parks. On each visit, collecting was performed for 40 minutes of effective sampling per plot, which means that the stopwatch was paused while handling specimens to allow their transfer into vials and to record associated data before resuming the search.

Bees were sampled exclusively by netting, a method particularly effective for most species (Leclercq *et al.* 2022). A flexible transect approach was employed, whereby the collector moved freely within the site to focus on patches of floral resources or potential nesting areas, rather than following a strict linear transect. Such an adaptive method improves species detection by concentrating effort where bee activity is the highest (Westphal *et al.* 2008). Specimens were placed in vials with ethyl acetate-soaked paper to ensure rapid euthanasia. For every individual collected, information including GPS coordinates, altitude, site code, behavioural context (e.g., flying, foraging), and visited plant species was documented in a database. Sampling was restricted to favourable weather, specifically between 09:00 and 17:00 on days above 15°C, without rainfall.

Specimens were processed the day after collection. Identifications were conducted under a stereo microscope using taxonomic keys and subsequently validated by expert taxonomists for each family: Apidae (Frédéric Carion, Maxence Gérard, Guillaume Ghisbain, Achik Dorchin; identification keys: Smit 2018; Rasmont *et al*. 2021), Megachilidae (Clément Tourbez; identification key: Pauly 2019a), Halictidae (Thomas Brau, Simone Flaminio; identification keys: Amiet *et al*. 2001; Pauly 2019b), Andrenidae (William Fiordaliso, Maxence Gérard, Thomas Wood; identification key: Wood 2023), Colletidae (Maxence Gérard, Romain Le Divelec; identification key: Amiet *et al*. 2014), and Melittidae (Maxence Gérard; identification key: Amiet *et al*. 2020).

Statistical analyses

First, we illustrated the gamma diversity with a Venn diagram showing the number of shared and unique bee species between the two parks. Then, to compare the mean alpha diversity of bee communities between national parks and among habitats within each park, we calculated Hill numbers of different orders q (i.e., the effective number of species, where species are weighted by their relative abundances, with increasing leverage on dominant species as q increases) for three diversity orders, namely (i) species richness (N0, $q=0$), which counts all species equally without accounting for their relative abundances; (ii) Hill-Shannon diversity (N1, $q=1$), representing the effective number of common species (i.e., the exponential of Shannon entropy); and (iii) Hill-Simpson diversity (N2, $q=2$), representing the effective number of dominant species (i.e., the inverse of the Simpson index). Hill numbers can also be interpreted as indices of mean rarity (i.e., the inverse of relative abundance), with orders 0, 1 and 2 corresponding to arithmetic, geometric and harmonic means, respectively (Chao *et al*. 2014; Hsieh *et al*. 2016; Roswell *et al*. 2021; Fiordaliso *et al*. 2025). To ensure meaningful comparisons, Hill numbers were standardised using coverage-based rarefaction and extrapolation, a method that adjusts for differences in sample completeness rather than sample size and provides more reliable diversity estimates (Chao & Jost 2012). Data from the five sampling events were pooled for each site. We excluded three sites from the analyses because their inclusion would have significantly reduced the standardised sample size due to their insufficient coverage (Appendix 1). Then, the 61 remaining sampling sites were standardized to a maximum coverage of 72%. Calculations of Hill numbers and coverage-based standardization were performed using the estimateD() function from the *iNEXT* package (Hsieh *et al*. 2016).

As Hill numbers represent effective species counts, we compared the alpha diversity of bee communities using generalised linear models (GLMs) fitted with a negative binomial error distribution (linear parameterisation) and a log link function. In addition, we compared the number of specimens belonging to threatened species between national parks and among habitats within each park, based on their IUCN status from the latest Belgian Red List (Drossart *et al*. 2019). Conservation status was treated as a binary variable, with species classified as vulnerable (VU), endangered (EN) or critically endangered (CR) and considered as “threatened,” whereas all other species not belonging to any of these categories were considered as “not threatened.” The numbers of specimens belonging to threatened species were compared using GLMs with a binomial error distribution and a logit link function.

For comparisons between national parks and among habitats within each national park, the models included “park” and “site area” as fixed effects. Models were fitted using the glmmTMB() function from the *glmmTMB* package (Brooks *et al*. 2017). Model assumptions were assessed using the simulateResiduals() and testDispersion() functions from the *DHARMa* package (Hartig 2024). To assess the significance of fixed effects in our GLMs, we performed analysis of deviance using Type-II Wald chi-square tests with the Anova() function from the *car* package (Fox & Weisberg 2019). When significant differences were detected between parks, model coefficients were back-transformed by exponentiation to facilitate interpretation (i.e., multiplicative change in expected counts for negative binomial models and odds ratio in binomial models). For significant effects of habitats within a park, we performed *post-*

hoc pairwise comparisons with false discovery rate (FDR) adjustment using the emmeans() function from the *emmeans* package (Lenth 2025).

The composition of bee communities (i.e., beta diversity) was compared between national parks and among habitats within each national park using Principal Coordinates Analysis (PCoA) to visualise patterns of community similarity in a reduced two-dimensional space. PCoA was performed with the wcmdscale() function in the *vegan* package (Oksanen *et al*. 2025). Pairwise dissimilarities were calculated using the Bray-Curtis index, which was then square-root transformed to meet Euclidean properties required for PCoA (Borcard *et al*. 2018). To statistically test for differences in community composition, we used permutational multivariate analysis of variance (perMANOVA) implemented with the adonis2() function in the *vegan* package (Oksanen *et al*. 2025), with 999 permutations to assess significance. Separate perMANOVA models were run to test for differences between national parks and differences among habitats within each park. For significant effects of habitat within a park, we performed *post-hoc* pairwise comparisons using the pairwiseAdonis() function (available on GitHub). Because perMANOVA can be sensitive to heterogeneity of dispersion, we also evaluated whether within-group variation (i.e., the average distance of sampling sites to their group centroid in multivariate space) differed between national parks or among habitats within each park. This was done with the betadisper() function in the *vegan* package (Oksanen *et al*. 2025). Finally, we conducted indicator species analysis using the multipatt() function in the *indicspecies* package (Cáceres & Legendre 2009) with 999 permutations to determine the bee species associated with each national park or with each habitat within each national park.

Results

General bee sampling results

A total of 2278 bee specimens were collected across the two national parks, with 1119 specimens from the Semois Valley National Park (SVNP) and 1159 specimens from the Entre-Sambre-et-Meuse National Park (ESEMNP). Sampling was conducted evenly throughout the season, ensuring a representative temporal coverage of bee activity (Appendix 2). All specimens are currently hosted at the research collection of the Laboratory of Zoology, University of Mons (Belgium). The two parks harboured all six bee families recorded in Europe, 26 genera, and 153 species, including 30 threatened species (19% of the total number of collected species) covering 161 or 7% of the collected specimens. Species richness was slightly higher in SVNP, which hosted 120 species, compared with 101 species in ESEMNP. Of these species, 52 were unique to the SVNP, 33 were unique to the ESEMNP, and 68 species were shared between the parks (Appendix 3A). At the genus level, four genera were only detected in the SVNP, two were only detected in the ESEMNP, and 20 genera were common in both parks (Appendix 3B). All six bee families were present in both parks. More details on the most common species observed in these national parks, as well as on rare species and their ecology, can be found in Gérard *et al*. (2025, 2026).

Diversity between national parks

The predicted species richness N0 was 142 (95% CI: 123–162) and 108 (95% CI: 86–131), the predicted number of common species N1 was 53 (95% CI: 48–58) and 34 (95% CI: 31–37), and the predicted number of dominant species N2 was 25 (95% CI: 21–29) and 15 (95% CI: 13–16) for SVNP and ESEMNP, respectively. We found significant differences in bee mean alpha diversity between the two national parks, with the SVNP showing approximately 1.4 times higher values across all diversity metrics, including species richness N0 (GLM; $e^{\beta} = 1.38$, 95% CI: 1.11–1.71, $p = 0.003$; Fig. 2A), the number of common species N1 (GLM; $e^{\beta} = 1.44$, 95% CI: 1.17–1.76, $p < 0.001$; Fig. 2B), and the number of dominant species N2 (GLM; $e^{\beta} = 1.48$, 95% CI: 1.22–1.81, $p < 0.001$; Fig. 2C). By contrast, we found no significant effect of the size of the site area on species richness N0 (GLM; $e^{\beta} = 1.01$, 95% CI: 0.97–

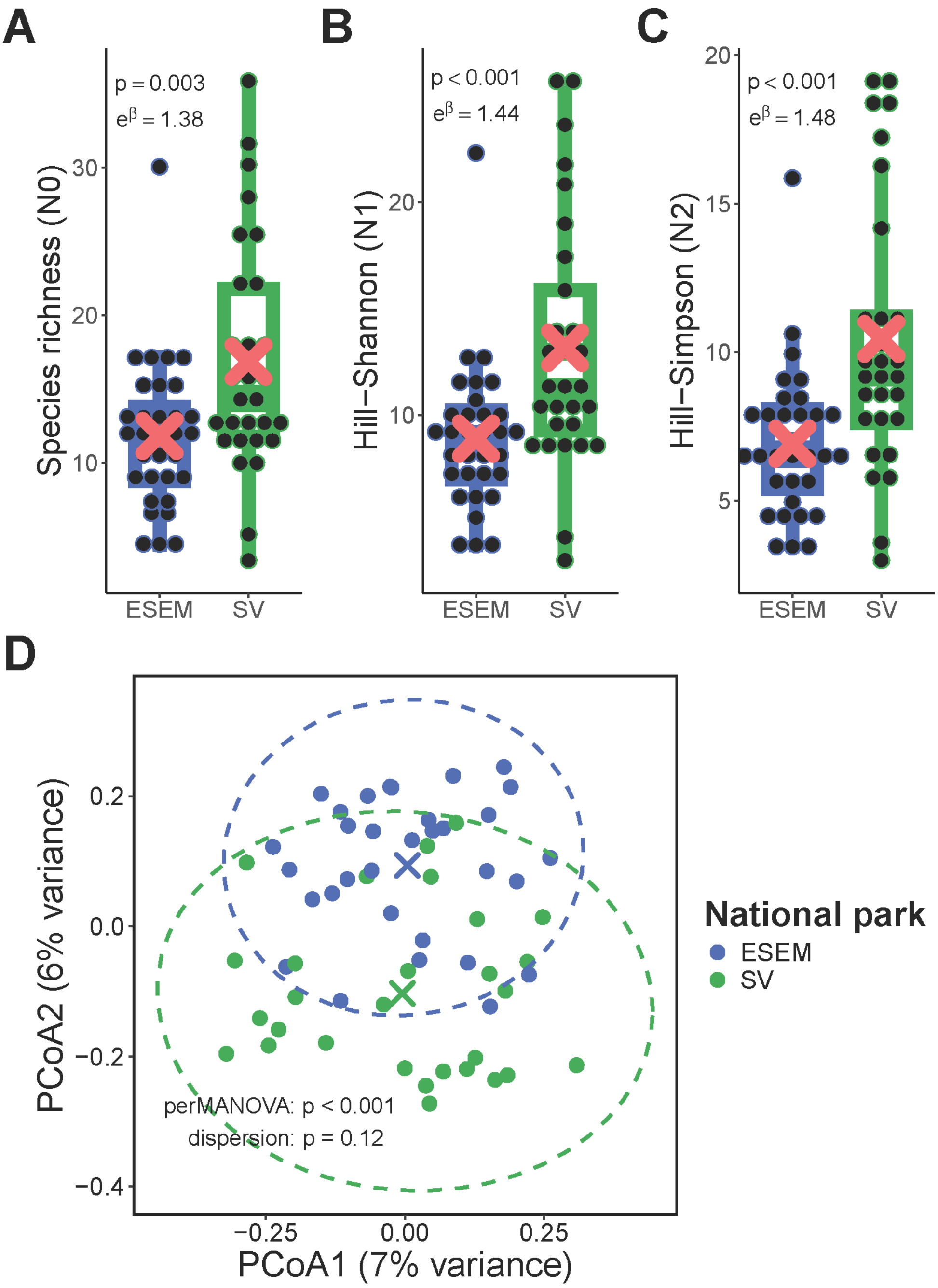

Figure 2 – Alpha and beta diversities of each national park, ESEM national park (ESEMNP) and SV national park (SNVP). Crosses represent the means. P-values and exponentiated coefficients ($\exp(\beta)$; back-transformed from the log scale of negative binomial models with a log link) are reported. The $\exp(\beta)$ values represent multiplicative differences between national parks. P-values smaller than 0.05 indicate significant differences between the two national parks. **A**. Species richness (N0) represents the total number of species. **B**. Hill-Shannon diversity (N1) reflects the effective number of common species. **C**. Hill-Simpson diversity (N2) reflects the effective number of dominant species. **D**. Principal coordinates analysis (PCoA) of bee beta diversity in the two national parks, ESEM national park (ESEMNP; shown in blue) and SV national park (SNVP; shown in green). Points represent the different sampling sites (32 for ESEMNP and 29 for SVNP). Ellipses show 95% confidence intervals around park centroids (illustrated as crosses). Axes display the percentage of variance explained by each coordinate. P-values from perMANOVA (i.e., between-park heterogeneity) and dispersion test (i.e., within-park heterogeneity) are also provided.

1.05, $p = 0.65$), the number of common species N1 (GLM; $e^{\beta} = 1.01$, 95% CI: 0.98–1.05, $p = 0.45$), or the number of dominant species N2 (GLM; $e^{\beta} = 1.02$, 95% CI: 0.98–1.06, $p = 0.33$). We observed a significant difference in bee community composition between national parks (perMANOVA; $F = 2.47$, $R^2 = 0.04$, $p < 0.001$). This result can be interpreted with confidence, since the test of multivariate dispersion indicated no difference in within-park heterogeneity ($p = 0.12$), suggesting that the perMANOVA result reflected differences in centroid locations rather than differences in within-park dispersion (Fig. 2D). Although bee community composition differed between national parks, the indicator species analysis did not identify any species being significantly associated with a particular park (all p-values > 0.05).

The absolute number of threatened species was relatively similar between parks, with ESEMNP and SVNP harbouring 18 and 22 threatened species, respectively (18% of the species in each park). We found no significant difference in the probability of an individual belonging to a threatened species between parks (GLM; odds ratio = 1.14, 95% CI: 0.83–1.57, $p = 0.43$), with both parks showing 8% of threatened specimens (77/1159 for the ESEMNP and 84/1119 for the SVNP). Likewise, site area size had no effect on the probability of an individual belonging to a threatened species (GLM; odds ratio = 1.02, 95% CI: 0.95–1.09, $p = 0.66$).

Diversity among habitats within each national park

In SVNP, the number of bee species varied among habitats, with 81 species recorded in mesic grasslands, 66 in "other habitats", 50 in tall-herb communities, and 62 in wet grasslands. The predicted species richness N0 was 95 (95% CI: 78–113), 64 (95% CI: 47–80), 64 (95% CI: 29–100) and 75 (95% CI: 56–93); the predicted number of common species N1 was 52 (95% CI: 45–59), 36 (95% CI: 30–41), 21 (95% CI: 15–27) and 37 (95% CI: 31–43), and the predicted number of dominant species N2 reached 34 (95% CI: 29–39), 23 (95% CI: 18–27), 10 (95% CI: 7–13) and 21 (95% CI: 17–25) for mesic grasslands, wet grasslands, tall-herb communities and "other habitats", respectively.

We found no significant differences in mean alpha diversity among habitats, whether measured by species richness N0 (GLM; $p = 0.24$; Fig. 3A), the number of common species N1 (GLM; $p = 0.15$; Fig. 3B) or the number of dominant species N2 (GLM; $p = 0.11$; Fig. 3C). Likewise, we found no significant effect of the size of the site area on species richness N0 (GLM; $e^{\beta} = 0.98$, 95% CI: 0.92–1.05, $p = 0.58$), the number of common species N1 (GLM; $e^{\beta} = 0.99$, 95% CI: 0.93–1.05, $p = 0.75$), or the number of dominant species N2 (GLM; $e^{\beta} = 1.00$, 95% CI: 0.94–1.06, $p = 0.96$). By contrast, a significant difference was observed in bee community composition among habitats (perMANOVA; $F = 1.50$, $R^2 = 0.15$, $p < 0.001$), with mesic grasslands harbouring distinct communities compared to tall herbs and 'other habitats', and wet grasslands showing overlap with mesic grasslands and 'other habitats'. This result is well supported, since the test of multivariate dispersion indicated no difference in within-habitat heterogeneity ($p = 0.07$), suggesting that the perMANOVA resulted reflect differences in centroid locations rather than differences in within-habitat dispersion (Fig. 3D). Although bee community composition differed among habitats, the indicator species analysis did not identify any species being significantly associated with a particular habitat type (all p-values > 0.05).

The absolute number of threatened species – based on red list categories – was relatively similar among habitats, with 15 threatened species in mesic grasslands (19% of species in this habitat), 10 threatened species in wet grasslands (16% of species in this habitat), 8 threatened species in tall herbs (16% of species in this habitat) and 9 threatened species in 'other habitats' (14% of species in this habitat). We observed a significant difference in the probability of an individual belonging to a threatened species among habitats (GLM; $p = 0.03$), with mesic grasslands harbouring a higher proportion of threatened specimens (11%; 35/327) than 'other habitats' (5%; 13/291), while no significant differences were observed for wet grasslands (8%; 20/254) or tall herbs (7%; 16/247). By contrast, the size of site areas had no effect on the probability of a given individual belonging to a threatened species (GLM; odds ratio = 0.95, 95% CI: 0.84–1.07, $p = 0.38$).

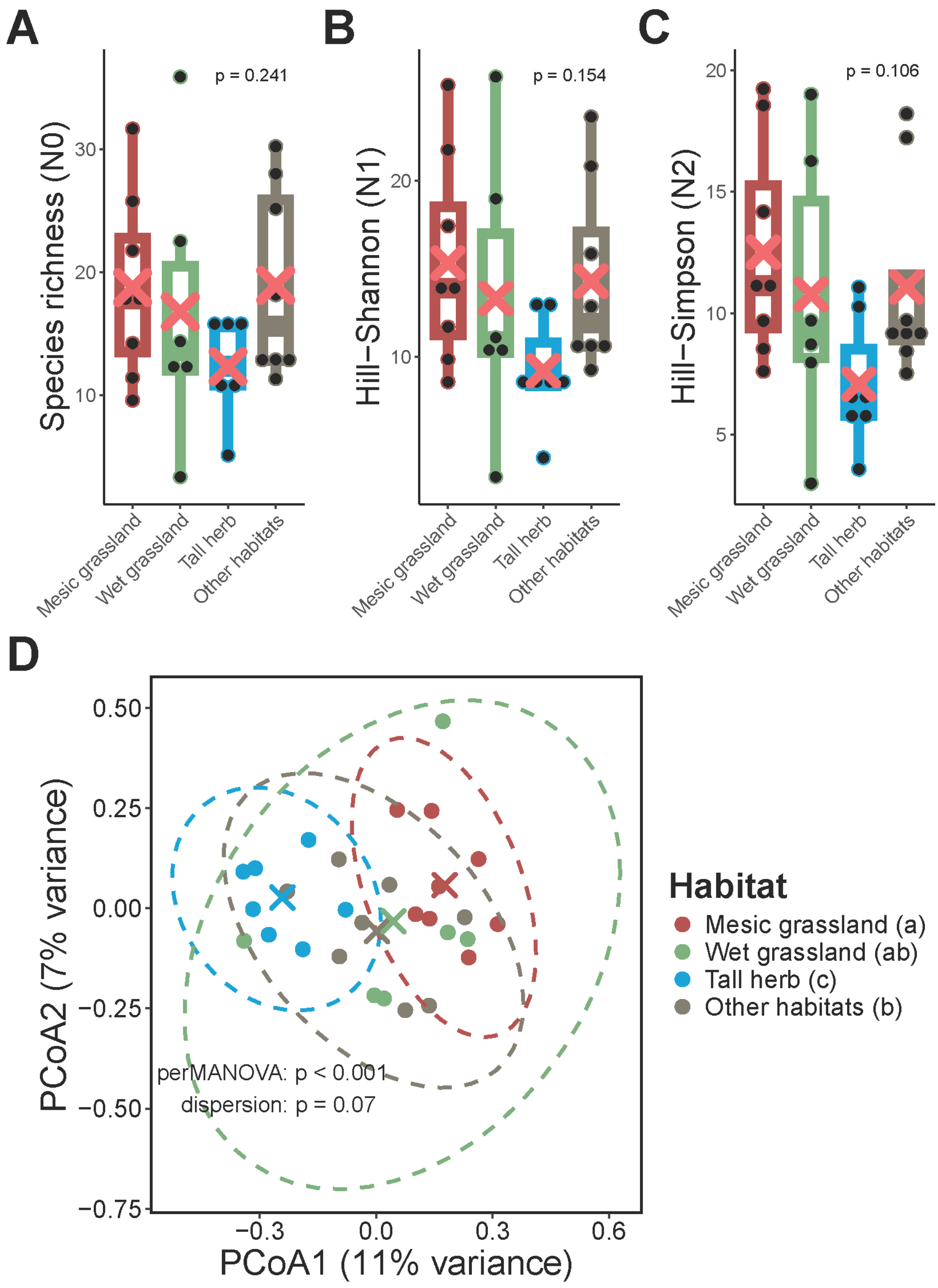

Figure 3 – Alpha and beta diversities across habitats within the Semois Valley national park (SVNP; Mesic grassland: n = 8; Wet grassland: n = 6; Tall herb: n = 7; Other habitats: n = 8). Crosses represent the means. P-values are from generalised linear models (negative binomial, log link). P-values smaller than 0.05 indicate significant differences between habitats. **A**. Species richness (N0) represents the total number of species. **B**. Hill-Shannon diversity (N1) reflects the effective number of common species. **C**. Hill-Simpson diversity (N2) reflects the effective number of dominant species. **D**. Principal coordinates analysis (PCoA) of bee beta diversity among habitats. Points represent the different sampling sites and colours indicate habitats. Ellipses show 95% confidence intervals around habitat centroids (illustrated as crosses). Axes display the percentage of variance explained by each coordinate. P-values from perMANOVA (i.e., between-habitat heterogeneity) and dispersion test (i.e., within-habitat heterogeneity) are also provided. Two habitats not sharing the same letter are statistically different (pairwise comparisons with FDR adjustment).

In ESEMNP, the number of bee species varied among habitats, with 65 species recorded in calcareous grasslands, 56 in "other habitats", 42 in tall-herb communities, and 59 in hay meadows. The predicted species richness N0 was 87 (95% CI: 50–124), 75 (95% CI: 45–105), 46 (95% CI: 27–64) and 62 (95% CI: 47–77), the predicted number of common species N1 was 37 (95% CI: 31–42), 25 (95% CI: 20–30), 18 (95% CI: 15–22) and 24 (95% CI: 20–28), and the predicted number of dominant species N2 21 (95% CI: 18–24), 12 (95% CI: 10–15), 10 (95% CI: 8–12) and 11 (95% CI: 8–14) for calcareous grasslands, hay meadows, tall-herb communities and "other habitats", respectively.

We detected significant differences in mean alpha diversity among habitats, as measured by species richness N0 (GLM; $p = 0.013$; Fig. 4A), the number of common species N1 (GLM; $p = 0.009$; Fig. 4B), and the number of dominant species N2 (GLM; $p = 0.040$; Fig. 4C). Overall, calcareous grasslands and hay meadows harboured higher diversity than tall herbs, while 'other habitats' showed intermediate diversity. In contrast, there was no significant effect of the size of the site areas on species richness N0 (GLM; $e^{\beta} = 0.99$, 95% CI: 0.94–1.04, $p = 0.635$), the number of common species N1 (GLM; $e^{\beta} = 0.99$, 95% CI: 0.93–1.04, $p = 0.618$), or the number of dominant species N2 (GLM; $e^{\beta} = 0.98$, 95% CI: 0.92–1.05, $p = 0.610$). In addition, we obtained a significant difference in bee community composition among habitats (perMANOVA; $F = 1.34$, $R^2 = 0.13$, $p = 0.001$), with calcareous grasslands and hay meadows harbouring a different community as compared to each other and to tall herbs or 'other habitats' (Fig. 4D). This result is statistically supported as the test of multivariate dispersion indicated no difference in within-habitat heterogeneity ($p = 0.14$), suggesting that the perMANOVA result reflected differences in centroid locations rather than differences in within-habitat dispersion (Fig. 4D). Although bee community composition differed among habitats, the indicator species analysis did not identify any species being significantly associated with a particular habitat (all p-values > 0.05).

The absolute number of threatened species – based on red list categories – was relatively similar among habitats, with 9 threatened species in calcareous grasslands (14% of species in this habitat), 10 threatened species in hay meadows (17% of species in this habitat), 7 threatened species in 'other habitats' (13% of species in this habitat) and 4 threatened species in tall herbs (10% of species in this habitat). There was a significant difference in the probability of an individual belonging to a threatened species among habitats (GLM; $p = 0.02$), with calcareous grasslands (9%; 27/295) and hay meadows (8%; 27/331) harbouring a higher proportion of threatened specimens than tall herbs (3%; 8/244), while no significant differences were observed with 'other habitats' (5%; 15/289). By contrast, the size of the site area had no effect on the probability of an individual belonging to a threatened species (GLM; odds ratio = 0.96, 95% CI: 0.85–1.08, $p = 0.469$).

Discussion

In this study, we quantified bee diversity across the two recently established national parks in Belgium, sampling over 2,200 specimens representing 153 species. The Semois Valley National Park (SVNP) supported significantly higher alpha diversity than the Entre-Sambre-et-Meuse National Park (ESEMNP) across all Hill numbers, although the proportion of threatened species was similar in both national parks. Species diversity within the surveyed habitats recorded during a five-month period represents more than one-third of the Belgian bee species, and probably around half of the species known from Wallonia (Vertommen *et al*. 2024). For comparison, a study conducted in the industrial belt of Hainaut, Belgium, over three years and across 112 sites, recorded 180 species (Fiordaliso *et al.* 2022). Another survey carried out in the same region as the ESEMNP during a single year and across 20 sites, but using an additional trapping method (pan traps), reported 96 species (Vandaudenard 2023). Although methodological differences make direct comparison difficult, the overall order of magnitude in our study remains similar to these studies. In the region of the ESEMNP, historical records dating back to the early 20th century list a total of 257 species (Vandaudenard 2023). In addition, a two-year study conducted in

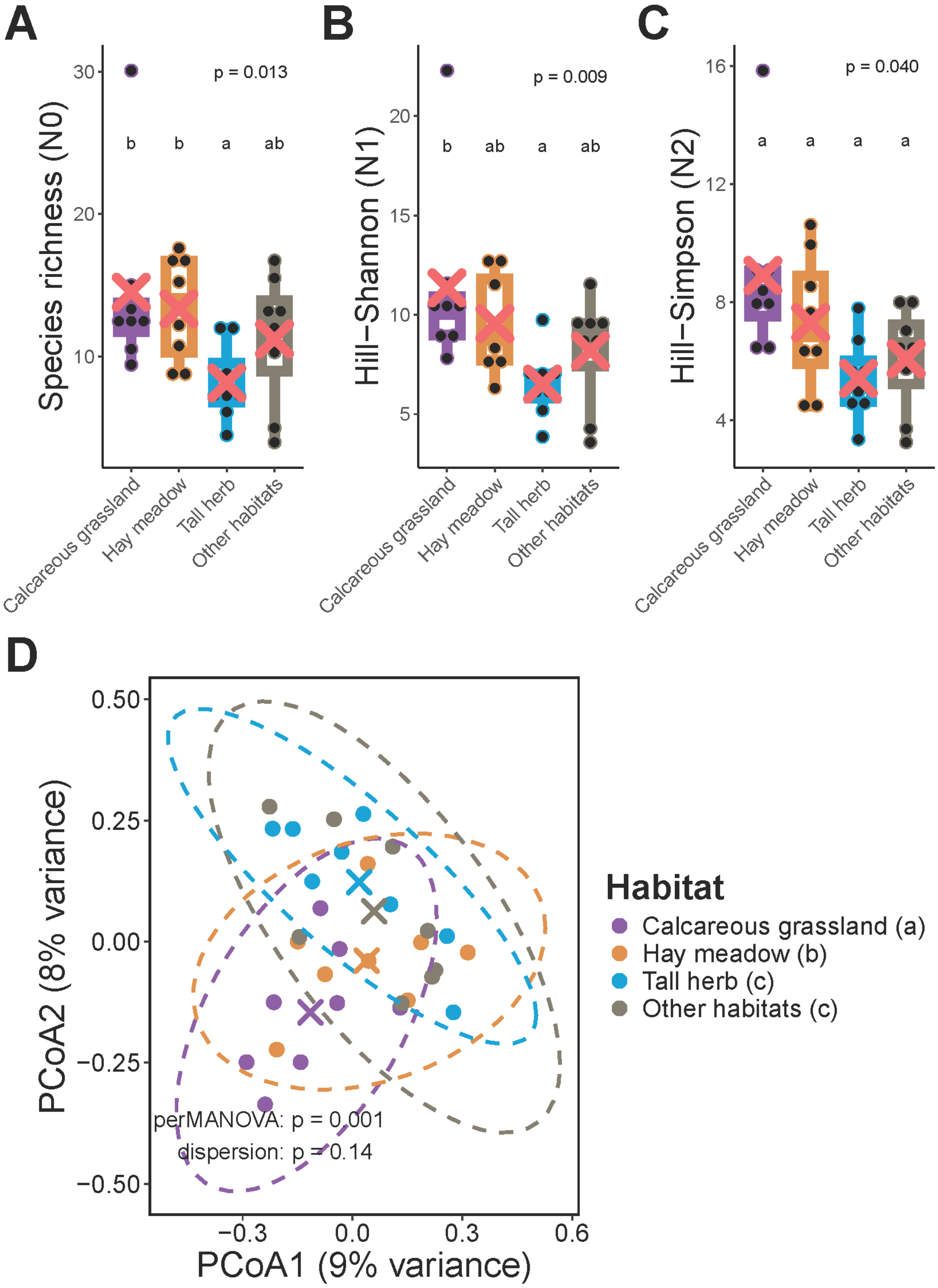

Figure 4 – Alpha and beta diversities across habitats within the Entre-Sambre-et-Meuse national park (ESEMNP; Calcareous grassland: n=8, Hay meadow: n=8, Tall herb: n=8, Other habitats: n=8). Crosses represent the means. P-values are from generalised linear models (negative binomial, log link). P-values smaller than 0.05 indicate significant difference among habitats. **A**. Species richness (N0) represents the total number of species. **B**. Hill-Shannon diversity (N1) reflects the effective number of common species. **C**. Hill-Simpson diversity (N2) reflects the effective number of dominant species. Two habitats not sharing the same letter are statistically different (pairwise comparisons with FDR adjustment). **D**. Principal coordinates analysis (PCoA) of bee beta diversity among habitats. Points represent sampling sites and colours indicate habitats. Ellipses show 95% confidence intervals around habitat centroids (illustrated as crosses). Axes display the percentage of variance explained by each coordinate. P-values from perMANOVA (i.e., between-habitat heterogeneity) and dispersion test (i.e., within-habitat heterogeneity) are also provided. Two habitats not sharing the same letter are statistically different (pairwise comparisons with FDR adjustment).

an agricultural landscape located less than 100 km from the two national parks, reported lower species richness (89 species) and the presence of only three threatened species based on the Belgian Red List of bees (Noel *et al*. 2021). That study also combined pan-traps with netting, a method that can increase species detectability, indicating that the number of species recorded in both national parks using netting alone in our study is particularly high and illustrates the importance of their diverse habitats. Taken together, these comparisons indicate that our survey achieved a high level of species richness relative to both sampling duration, sampling method and spatial effort, highlighting the ecological value of the studied habitats.

Within parks, bee diversity varied among habitats, with no significant differences detected in SVNP – though the alpha-diversity was overall higher in the mesic grasslands – whereas calcareous grasslands and hay meadows in ESEMNP supported the most diverse communities, emphasizing their high conservation value. In contrast, tall herb sites consistently supported the lowest diversity in both parks, although the differences were not always significant. The conservation value of these habitats is further supported by significantly higher probability of encountering individuals belonging to threatened species in calcareous grasslands and hay meadows than in tall-herb communities in ESEMNP, and in mesic grasslands as compared to other habitats in SVNP, as well as by the highest absolute numbers of threatened species recorded in hay meadows in ESEMNP (n = 10) and in mesic grasslands in SVNP (n = 15), respectively. Calcareous grasslands tend to favour thermophilous bee species, whose occurrence reflects the warmer and drier microclimatic conditions of these habitats (Klaus *et al*. 2021). In addition, the preservation of flora in calcareous and hay meadows is probably facilitated by existing protection measures, such as Natura 2000 sites and conservation plans, which contribute to maintaining habitats favourable to bees (Poniatowski *et al*. 2020). The abundance of host plants and pollen sources is known to strongly influence bee patch occupancy (e.g., Franzén *et al*. 2009), and the restoration of calcareous grasslands has been shown to markedly increase the diversity of available pollen resources (Poniatowski *et al*. 2020). In the literature, patch size emerged as a key factor: Klaus *et al*. (2019) demonstrated that large calcareous grassland patches (> 8.4 ha) supported more than twice as many solitary bee species as smaller ones (< 3 ha). However, this pattern was not observed in our study. One possible explanation is that the patches we surveyed were often smaller than 2 ha, preventing us from detecting the positive effect of large patch size. Alternatively, local habitat quality and floral resource availability may have played a stronger role than patch size in shaping bee assemblages in our study. Moreover, a key aspect linking hay meadows and calcareous grasslands is their low to intermediate nutrient concentration in their soils, particularly the low concentrations of phosphorus and nitrogen that typify calcareous systems. Such conditions limit the dominance of competitive plant species and thereby promote high floral diversity, which in turn supports a richer community of wild bees (Van den Berg *et al*. 2010; Chytrý *et al*. 2020; Balfour *et al*. 2025). This is especially relevant in the current context of widespread habitat degradation driven by agricultural intensification, where fertiliser inputs and atmospheric nitrogen deposition alter soil chemistry and reduce plant and pollinator diversity (Stevens *et al*. 2004; Rasmont *et al*. 2021; Balfour *et al*. 2025). Together, these findings highlight that both floral diversity and nutrient concentration must be considered when designing effective conservation measures.

Several environmental and anthropogenic factors may contribute to the higher species diversity in SVNP. A large proportion of SVNP is covered by forest, which can enhance bee diversity at forest edges (Eckerter *et al*. 2022), particularly early in the season when early flowering trees provide resources (Watson *et al*. 2011; Inari *et al*. 2012). Additionally, this large dominance of extensive forest patches could limit the availability of suitable foraging sites, which may have concentrated bee activity in the scarce open areas, resulting in locally high diversity. In contrast, ESEMNP offered a greater availability and spatial continuity of open habitats. Under these conditions, bees could have been more evenly distributed across the landscape, leading to lower apparent densities per site despite similar or even higher overall population sizes. The SVNP also borders the “Belgian Lorraine” region, a geological region that is the only one in Belgium dating from the Jurassic period. This region is characterised by distinctive geology and a warmer microclimate than most other parts of Belgium (Van der Perre *et al.* 2015), which could contribute to influencing the observed bee species community. It harbours species that are otherwise rare in Belgium, sometimes representing their only strongholds in the country, such as the Sand Lizard (*Lacerta agilis* Linnaeus, 1758) or the Brown-banded carder bumblebee (*Bombus humilis* Illiger, 1806) observed in our study. The SVNP may also act as a northern colonisation front for species expanding from the south. In Belgium, many of these bee species occur close to the northern edge of their distribution, while being more widespread in France and further south. Among bees, this was recently exemplified by the first records of the Splay-footed carpenter bee *Xylocopa valga* Gerstaecker, 1872, documented through citizen science observations that were later validated by experts (from the observations.be platform), although the species is otherwise common across the Mediterranean region. The persistence of these species is further supported by a dense network of protected areas (e.g., numerous Natura 2000 sites) and by a 2023 EU LIFE project, which has helped maintain a mosaic of open habitats that have become rare elsewhere due to agricultural intensification (Van Nieuwenhuyse & De Middeleer 2024). Urbanisation in both national parks and the intensity of surrounding agricultural practices should be formally quantified to assess their potential effects on species diversity. While habitats such as the calcareous grasslands of the ESEMNP contains a noteworthy bee diversity for Wallonia, they may be embedded within a matrix of more intensively managed crops, which is a major driver of bee declines in this region and across Europe more broadly (Dicks *et al.* 2021; St-Clair *et al.* 2022). Intensively managed crops have oversimplified landscapes over the last century, reducing floral and nesting resources and exposing bees to pesticides and other agrochemicals, thereby disrupting foraging, reproduction, and survival (Potts *et al.* 2010; Dicks *et al.* 2021; Ghisbain *et al.* 2025). Nevertheless, compared to other areas in the Hainaut and Namur provinces, the ESEMNP is not characterised by intensive agriculture, limiting the likelihood of this factor being a major driver here.

Species composition differed significantly between most habitats in both national parks, probably reflecting variations in floral resources, nesting substrates, and microclimatic conditions among habitat types. These environmental differences can favour distinct bee guilds with specific foraging and nesting requirements, leading to habitat-specific assemblages. This pattern is particularly evident in the category 'other habitats', which encompasses highly diverse assemblages of habitats. Indeed, given that the category 'other habitats' includes sites as diverse as slate quarries, dry heaths, and fen scrubs, such variation is expected. No significant differences in the proportion of specimens belonging to threatened species were observed between the two national parks, and the overall proportion of threatened species was relatively similar across parks. This suggests that although SVNP has higher overall species richness and harbours more threatened species in absolute terms, the relative proportion of specimens belonging to threatened species remains broadly consistent. These threatened species are represented by 160 specimens in total, corresponding to 7.51% of the specimens from SVNP and 6.56% from ESEMNP, respectively. These values indicate a relatively high proportion of individuals belonging to threatened species. For comparison, in the more urbanised Hainaut industrial belt in Belgium, with less semi-natural sites, (Fiordaliso *et al.* 2022), only 2.03% of the specimens belonged to species listed as threatened in the Belgian national Red List (Drossart *et al.* 2019). Among the different habitats in our study, mesic grasslands (SVNP), calcareous grasslands, and hay meadows harboured the highest proportion of threatened specimens, indicating that habitats with the greatest alpha diversity also supported the largest proportion of specimens from threatened species, thereby reinforcing their critical conservation value.

Certain methodological biases cannot be entirely ruled out in our study. Sampling was conducted over two different years by different collectors, and spring weather conditions in SVNP were particularly poor, potentially reducing species detectability. This may have led to an underestimation of spring-active species in the SVNP, suggesting that actual species richness could be even higher than recorded. However, all collectors had a comparable level of experience at the start of the sampling programme, as they were students conducting their first field season, which probably limited potential collectorrelated bias. In addition, bee species richness in Belgium typically peaks later in the season, around June (Duchenne *et al*. 2020), while spring assemblages are generally less diverse, which may further mitigate the impact of unfavourable spring weather on overall diversity estimates. Another limitation of our study could also be the relatively low sample coverage at three of the surveyed sites, which were therefore excluded from the analyses. This suggests that the current dataset likely underrepresents the true species diversity at some sites. Consequently, it is clear that additional sampling will reveal species not yet detected, meaning that the observed patterns should be interpreted with caution. In addition, in SVNP in 2024, unfavourable weather conditions, with frequent rain and low temperatures, most likely restricted bee foraging activity to a few suitable days. During these brief favourable periods, bees may have been particularly active, temporarily inflating apparent diversity. In contrast, in 2025, more stable and favourable weather conditions may have allowed foraging to occur over a longer period, resulting in a more even temporal distribution of bee activity. Finally, although our sampling design covered a representative range of habitat types, the limited number of sites per habitat (eight) may have constrained our ability to detect statistically significant differences in bee diversity among them. For example, while mesic grasslands clearly supported the highest diversity in the SVNP, no significant differences were detected. Given the high spatial variability typical of bee assemblages, a larger number of replicated sites within each habitat type would likely increase the robustness and resolution of our results, providing a more reliable assessment of habitat-specific patterns in species richness and composition.

Key habitats for bees such as calcareous grasslands are declining due to threats including habitat fragmentation and high levels of agricultural nutrient enrichment. Targeted conservation measures could be implemented at the most favourable sites to evaluate their effects on species diversity and long-term persistence. For example, it is crucial to connect protected areas and to promote host plants for specific species, such as the vulnerable solitary mining bee *Andrena pandellei*, which forages exclusively on plants of the genus *Campanula*. Furthermore, at the European level, conservation programmes should broaden their scope to better address pollinator protection. To date, only 0.4% of LIFE projects have focused on this issue (European Court of Auditors 2020). As LIFE projects are designed to implement EU environmental policies and to protect and restore biodiversity, they could play a crucial and practical role in improving pollinator health. Finally, the long-term effectiveness of conservation efforts will largely depend on sustained financial and institutional support. With potential budget cuts looming over the management of national parks and biodiversity monitoring in Wallonia, the recruitment of qualified personnel beyond 2026 remains uncertain. This is a major concern, as consistent monitoring is essential to detect population trends, evaluate the success of current conservation measures, and adjust management actions accordingly. Given that our study highlights a substantial proportion of threatened species in both national parks, ensuring long-term investments in these programmes is critical to secure their persistence within these newly established areas.

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Competing interests

The authors declare that they have no competing interests.

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References

Amiet F., Hermann M., Müller A. & Neumeyer R. (2001). Apidae 3: *Halictus*, *Lasioglossum*. Fauna Helvetica. 1, 6. CSCF & Schweizerische Entomologische Gesellschaft. Available from https://identification-resources.github.io/catalog/detail/?id=B602 [accessed 28 April 2026].

Amiet F., Müller A. & Neumeyer R. (2014). Apidae 2: *Colletes*, *Dufourea*, *Hylaeus*, *Nomia*, *Nomioides*, *Rhophitoides*, *Rophites*, *Sphecodes*, *Systropha*. Fauna Helvetica. 2, 4. CSCF & Schweizerische Entomologische Gesellschaft.
Available from https://identification-resources.github.io/catalog/detail/?id=B601 [accessed 28 April 2026].

Amiet F., Hermann M., Müller A. & Neumeyer R (2020). Apidae 5: *Ammobates*, *Ammobatoides*, *Anthophora*, *Biastes*, *Ceratina*, *Dasypoda*, *Epeoloides*, *Epeolus*, *Eucera*, *Macropis*, *Melecta*, *Melitta*, *Nomada*, *Pasites*, *Tetralonia*, *Thyreus*, *Xylocopa*. Fauna Helvetica. 2, 20. CSCF & Schweizerische Entomologische Gesellschaft. Available from
Available from https://identification-resources.github.io/catalog/detail/?id=B605 [accessed 28 April 2026].

Balfour N.J., Harris C., Storkey J. & Ratnieks F.L.W. (2025). Trade-off between pollinator-wildflower diversity and grassland yields. *Npj Biodiversity* 4: e1. https://doi.org/10.1038/s44185-024-00070-6

Baude M., Kunin W.E., Boatman N.D., Conyers S., Davies N., Gillespie M.A.K. *et al*. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* 530: 85–88. https://doi.org/10.1038/nature16532

Borcard D., Gillet F. & Legendre P. (2018). *Numerical Ecology with R, Second Edition*. Springer International Publishing, Collection "Use R!", Cham, Switzerland.

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

Cáceres M.D. & Legendre P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology* 90: 3566–3574. https://doi.org/10.1890/08-1823.1

Cardoso P., Barton P.S., Birkhofer K., Chichorro F., Deacon C., Fartmann T. *et al*. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation* 242: e108426. https://doi.org/10.1016/j.biocon.2020.108426

Casanelles-Abella J., Fontana S., Meier E., Moretti M. & Fournier B. (2023). Spatial mismatch between wild bee diversity hotspots and protected areas. *Conservation Biology* 37: e14082. https://doi.org/10.1111/cobi.14082

Chao A. & Jost L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93: 2533–2547. https://doi.org/10.1890/11-1952.1

Chao A., Gotelli N.J., Hsieh T.C., Sander E.L., Ma K.H. & Colwell R.K. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84 (1): 45–67. https://doi.org/10.1890/13-0133.1

Chowdhury S., Jennions M.D., Zalucki M.P., Maron M., Watson J.E.M. & Fuller R.A. (2023a). Protected areas and the future of insect conservation. *Trends in Ecology & Evolution* 38: 85–95. https://doi.org/10.1016/j.tree.2022.09.004

Chowdhury S., Zalucki M.P., Hanson J.O., Tiatragul S., Green D., Watson J.E.M. & Fuller R.A. (2023b). Three-quarters of insect species are insufficiently represented by protected areas. *One Earth* 6: 139–146. https://doi.org/10.1016/j.oneear.2022.12.003

Chytrý M., Tichý L., Hennekens S.M., Knollovà I., Janssen J.A.M., Rodwell J.S. *et al.* (2020). EUNIS habitat classification: Expert system, characteristic species combinations and distribution maps of European habitats. *Applied Vegetation Science* 23: 648–675. https://doi.org/10.1111/avsc.12519

Dicks L.V., Breeze T.D., Ngo H.T., Senapathi D., An J., Aizen M.A., *et al.* (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution* 5: 1453–1461. https://doi.org/10.1038/s41559-021-01534-9

Drossart M., Rasmont P., Vanormelingen P., Dufrêne M., Folschweiller M., Pauly A., Vereecken N., Vray S., Zambra E. & D'Haeseleer J. (2019). *Belgian Red List of Bees*. Presse universitaire de l'Université de Mons, Mons, Belgium.

Duchenne F., Thébault E., Michez D., Gérard M., Devaux C., Rasmont P., Vereecken N. & Fontaine C. (2020). Long-term effects of global change on occupancy and flight period of wild bees in Belgium. *Global Change Biology* 26: 6753-6766. https://doi.org/10.1111/gcb.15379

Dudley N. (2008). Guidelines for applying protected area management Categories. *In*: Stolton S.W., Shadie P. & Dudley N. (eds) *IUCN WCPA Best Practice Guidance on Recognising Protected Areas and Assigning Management Categories and Governance Types, Best Practice Protected Area Guidelines Series No. 21*: 1–86. Gland, Switzerland.

Eckerter T., Braunisch V., Buse J. & Klein A.M. (2022). Open forest successional stages and landscape heterogeneity promote wild bee diversity in temperate forests. *Conservation Science and Practice* 4: e12843. https://doi.org/10.1111/csp2.12843

European Court of Auditors. (2020). *Protection of Wild Pollinators in the EU – Commission Initiatives Have not Borne Fruit.* (Special Report) (p. 61p). Publications Office of the European Union, Luxembourg.

Fiordaliso W., Reverté S., Wood T.J., Barbier Y., Rasmont P., Lefèbvre A., Loockx M., Reese A., Ruelle E. & Michez D. (2022). Inventaire et conservation des abeilles sauvages (Hymenoptera: Anthophila) du sillon industriel hainuyer (Belgique). *Belgian Journal of Entomology* 132: 52–52. Available from https://www.srbe-kbve.be/cm/sites/default/files/publications/BJE/BJE%202022/BJE_132_Fiodaliso%20et%20al._2022.pdf [accessed 29 April 2026].

Fiordaliso W., Reverte S., Ghisbain G., Wood T., Ruelle E., Lefèbvre A., Reese A., Loockx M., Michez D. & Tougeron K. (2025). Reconciling community-level responses of wild bees to highly anthropized landscapes. *Landscape and Urban Planning* 259: e105347. https://doi.org/10.1016/j.landurbplan.2025.105347

Fox J. & Weisberg S. (2019). *An R Companion to Applied Regression, Third edition*. Sage, Thousand Oaks CA. Available from https://www.john-fox.ca/Companion/ [accessed 29 April 2026].

Franzen M., Larsson M. & Nilsson S.G. (2009). Small local population sizes and high habitat patch fidelity in a specialised solitary bee. *Journal of Insect Conservation* 13: 89–95. https://doi.org/10.1007/s10841-007-9123-4

Garibaldi L.A., Steffan-Dewenter I., Winfree R., Aizen M.A., Bommarco R., Cunningham S.A. *et al.* (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339: 1608–1611. https://doi.org/10.1126/science.1230200

Gathmann A. & Tscharntke T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology* 71: 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Gekière A., Gérard M., Potts S.G., Michez D. & Ghisbain G. (2025). Underlying mechanisms shaping wild bee decline. *Biological Journal of the Linnean Society* 145: blaf043. https://doi.org/10.1093/biolinnean/blaf043

Gérard M., Fiordaliso W., Ferrais L., Fournier C., Hairault M., Lheureux L., Rosa P. & Ghisbain G. (2025). Wild bee diversity of the National Park of the Semois Valley (Belgium). *Biodiversity Data Journal* 13: e144223. https://doi.org/10.3897/BDJ.13.e144223

Gérard M., Beaubois V., Fiordaliso W., Gautier F., Guillaume A., Peduzzi J., Ghisbain G. (2026). Wild bee diversity in the Entre-Sambre-et-Meuse National Park (Belgium). *Biodiversity Data Journal* 14: e176439. https://doi.org/10.3897/BDJ.14.e176439

Ghisbain G., Gérard M., Wood T.J., Hines H.M. & Michez D. (2021). Expanding insect pollinators in the Anthropocene. *Biological reviews* 96: 2755–2770. https://doi.org/10.1111/brv.12777

Ghisbain G., Chittka L. & Michez D. (2025). Bumblebees. *Current Biology* 35: 206–211. https://doi.org/10.1016/j.cub.2025.01.041

Hallmann C.A., Sorg M., Jongejans E., Siepel H., Hofland N., Schwan H., Stenmans W., Müller A., Sumser H., Hörren T., Goulson D. & de Kroon H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* 12: e0185809. https://doi.org/10.1371/journal.pone.0185809

Hartig F. (2024). DHARMa: residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.7. Available from http://florianhartig.github.io/DHARMa/ [accessed 29 April 2026].

Hopfenmüller S., Steffan-Dewenter I. & Holzschuh A. (2014). Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS ONE* 9: e104439. https://doi.org/10.1371/journal.pone.0104439

Hsieh T.C., Ma K.H. & Chao A. (2016). iNext: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7: 1451–1456. https://doi.org/10.1111/2041-210X.12613

Inari N., Hiura T., Toda M. J. & Kudo G. (2012). Pollination linkage between canopy flowering, bumble bee abundance and seed production of understorey plants in a cool temperate forest. *Journal of Ecology* 100: 1534–1543. https://doi.org/10.1111/j.1365-2745.2012.02021.x

Klaus F., Tscharntke T., Uhler J. & Grass I. (2021). Calcareous grassland fragments as sources of bee pollinators for the surrounding agricultural landscape. *Global Ecology and Conservation* 26: e01474. https://doi.org/10.1016/j.gecco.2021.e01474

Leclercq N., Marshall L., Weekers T., Anselmo A., Benda D., Bevk D., Bogusch D. *et al*. (2022). A comparative analysis of crop pollinator survey methods along a large-scale climatic gradient. *Agriculture, Ecosystems & Environment* 329: e107871. https://doi.org/10.1016/j.agee.2022.107871

Lenth R. (2025). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.11.2-80001. Available from https://rvlenth.github.io/emmeans/ [accessed 29 April 2026].

Morandin L.A., Winston M.L., Abbott V.A. & Franklin M.T. (2007). Can pastureland increase wild bee abundance in agriculturally intense areas. *Basic and Applied Ecology* 8: 117–124. https://doi.org/10.1016/j.baae.2006.06.003

Noel G., Bonnet J., Everaerts S., Danel A., Calderan A., de Liedekerke A., *et al*. (2021). Distribution of wild bee (Hymenoptera: Anthophila) and hoverfly (Diptera: Syrphidae) communities within farms undergoing ecological transition. *Biodiversity Data Journal* 9: e60665. https://doi.org/10.3897/BDJ.9.e60665

Oksanen J., Simpson G.L., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., *et al*. (2025). vegan: an R package for community ecologists – ordination methods, diversity analysis and other functions for community and vegetation ecologists. R package version 2.8-0. Available from https://vegandevs.github.io/vegan/ [accessed 29 April 2026].

Parmentier L., Van Kerckvoorde A., Couckuyt J., van Calster H., Smagghe G. & Haesaert H. (2025). Sinus management: meandering mowing as a novel method to improve pollinator biodiversity and habitat heterogeneity in mesic grasslands. *Agriculture, Ecosystems & Environment* 382: e109478. https://doi.org/10.1016/j.agee.2025.109478

Pauly A (2019a). *Clés illustrées pour l'identification des abeilles de Belgique et des régions limitrophes (Hymenoptera: Apoidea) II. Megachilidae*. Available from https://geonature.arb-idf.fr/sites/default/files/articles/documents/ClefIdent/Hymenopteres/Pauly_2015_clé_Megachilidae_Belgique.pdf [accessed 29 April 2026].

Pauly A (2019b). *Abeilles de Belgique et des régions limitrophes (Insecta: Hymenoptera: Apoidea). Famille Halictidae*. Faune de Belgique, Royal Belgian Institute of Natural Sciences.

Poniatowski D., Stuhldreher G., Helbing F., Hamer U. & Fartmann T. (2020). Restoration of calcareous grasslands: the early successional stage promotes biodiversity. *Ecological Engineering* 151: e105858. https://doi.org/10.1016/j.ecoleng.2020.105858

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

Potts S.G., Imperatriz-Fonseca V., Ngo H.T., Aizen M.A., Biesmeijer J.C., Breeze T.D. *et al*. (2016). Safeguarding pollinators and their values to human well-being. *Nature* 540: 220–229. https://doi.org/10.1038/nature20588

Rasmont P., Ghisbain G. & Terzo M. (2021). *Bumblebees of Europe and Neighbouring Regions*. NAP Editions, Verrières-le-Buisson.

Rodrigues A.S., Andelman S.J., Bakarr M.I., Boitani L., Brooks T.M., Cowling R.M. *et al*. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature* 428: 640–643. https://doi.org/10.1038/nature02422

Rodrigues A.S., Pilgrim J.D., Lamoreux J.F., Hoffmann M. & Brooks T.M. (2006). The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution* 21: 71–76. https://doi.org/10.1016/j.tree.2005.10.010

Rosenberg Y., Bar-On Y.M., Fromm A., Ostikar M., Shoshany A., Giz O. & Milo R. (2023). The global biomass and number of terrestrial arthropods. *Science Advances* 9: eabq4049. https://doi.org/10.1126/sciadv.abq4049

Roswell M., Dushoff J.& Winfree R. (2021). A conceptual guide to measuring species diversity. *Oikos* 130: 321–338. https://doi.org/10.1111/oik.07202

Senapathi D., Fründ J., Albercht M., Garratt M.P.D., Kleijn D., Pickles B.J. *et al*. (2021). Wild insect diversity increases inter-annual stability in global crop pollinator communities. *Proceedings of the Royal Society B* 288: e20210212. https://doi.org/10.1098/rspb.2021.0212

Smit J. (2018). Identification key to the european species of the bee genus *Nomada* Scopoli, 1770 (Hymenoptera: Apidae), including 23 new species. *Entomofauna Monographs* 3: 1–253. Available from http://www.insecta-web.org/MWM/html_stat/entomofauna/2018.htm [accessed 129 April 2026].

St-Clair A.L., Zhang G., Dolezal A.G., O'Neal M.E. & Toth A. (2022). Agroecosystem landscape diversity shapes wild bee communities independent of managed honey bee presence. *Agriculture, Ecosystems & Environment* 327: e107826. https://doi.org/10.1016/j.agee.2021.107826

Stevens C.J., Dise N.B., Mountford J.O. & Gowing D.J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science* 303: 1876–1879. https://doi.org/10.1126/science.1094678

Stork N.E. (2018). How many species of insects and other terrestrial arthropods are there on Earth? *Annual Review of Entomology* 63: 31–45. https://doi.org/10.1146/annurev-ento-020117-043348

Vandaudenard T. (2023). *Étude des populations d'abeilles sauvages du Parc naturel Viroin-Hermeton*. Université catholique de Louvain. Available from http://hdl.handle.net/2078.1/thesis:42287 [accessed 29 April 2026].

Van den Berg L.J.L., Vergeer P., Rich T.C.G., Smart S.M., Guest D. & Ashmore M.R. (2010). Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. *Global Change Biology* 17: 1871–1883. https://doi.org/10.1111/j.1365-2486.2010.02345.x

Van der Perre R., Bythell S., Bogaert P., Claessens H., Ridremont F., Tricot C. *et al*. (2015). La carte bioclimatique de Wallonie: un nouveau découpage écologique du territoire pour le choix des essences forestières. *Forêt-Nature* 135: 47–58.
Available from https://www.fichierecologique.be/resources/FO135-47-58.pdf [accessed 29 April 2026].

van Klink R., Bowler D.E., Gongalsky K.B., Swengel A.B., Gentile A. & Chase J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368 : 417–420. https://doi.org/10.1126/science.aax9931

Van Nieuwenhuyse D. & De Middeleer L. (2024). Spectacular increase of Red-Backed Shrike (*Lanius collurio*) in Gaume, Southern Belgium – Evidence for northward expansion due to structural climate change. *European Journal of Ecology* 10: 79–92. https://doi.org/10.17161/eurojecol.v10i.23247

Vertommen W., Vanormelingen P., D'haeseleer J., Wood T.J., Baugnée J., De Blanck T. *et al*. (2024). New and confirmed wild bee species (Hymenoptera: Apoidea: Apiformes) for the fauna of Belgium, with notes on the rediscovery of regionally extinct species. *Belgian Journal of Entomology* 149: 1–63. Available from https://www.srbe-kbve.be/cm/sites/default/files/publications/BJE/BJE%202024/BJE_149_Wild%20bees%20Belgium_Vertommen%20et%20al.pdf [accessed 29 April 2026].

Wagner D.L., Grames E.M., Forister M.L., Berenbaum M.R. & Stopak D. (2021). Insect decline in the anthropocene: death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America* 118: e2023989118. https://doi.org/10.1073/pnas.2023989118

Watson J.C., Wolf A.T. & Ascher J.S. (2011). Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environmental Entomology* 40: 621–632. https://doi.org/10.1603/EN10231

Watson J.E.M., Dudley N., Segan D.B. & Hockings M. (2014). The performance and potential of protected areas. *Nature* 515: 67–73. https://doi.org/10.1038/nature13947

Westphal C., Bommarco R., Carré G., Lamborn E., Morison N., Petanidou T., Potts S.G., Roberts S.P.M., Szentgyörgyi H., Tscheulin T., Vaissière B.E., Woyciechowski M., Biesmeyer J.C., Kunin W.E., Settele J. & Steffan-Dewenter I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs* 78: 653–671. https://doi.org/10.1890/07-1292.1

Wood T. (2023). The genus *Andrena* in Belgium: revisions, clarifications, and a key for their identification (Hymenoptera: Andrenidae). *Belgian Journal of Entomology* 135: 1–64. Available from https://hdl.handle.net/20.500.12907/46437 [accessed 29 April 2026].

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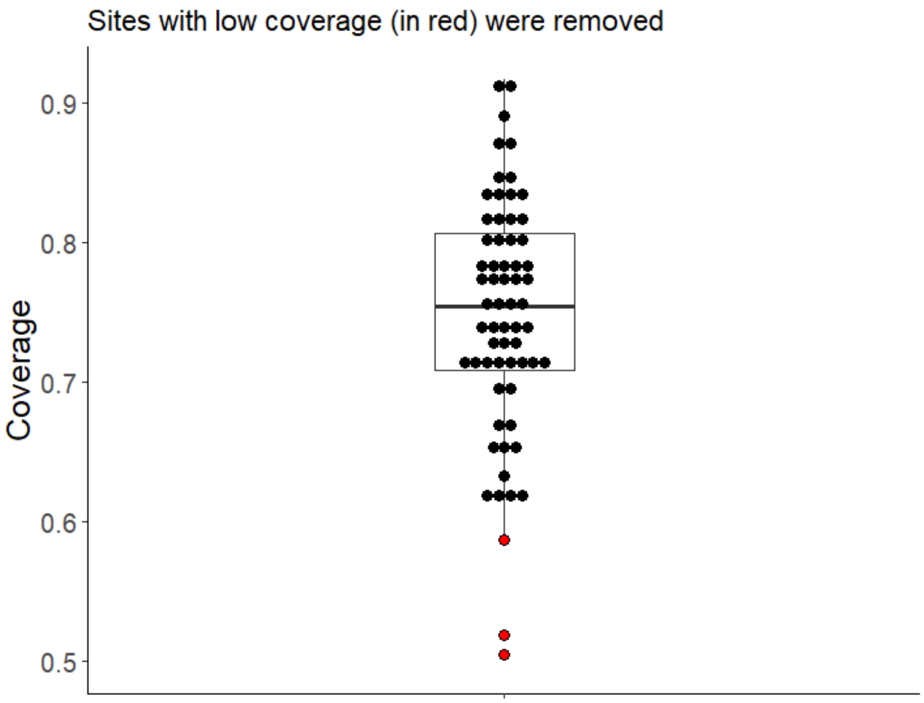
Appendix 1

Site removal for statistical analyses

The initial dataset comprised 64 sites with sample coverages ranging from 50% to 92%, with a total of 2278 bee individuals.

We first applied a coverage-based standardisation across all 64 sites, which yielded a standardised coverage of 59% and a standardised sample size of 1005 individuals. This loss was substantial since more than half of the original dataset was excluded after standardisation. This reduction was mainly driven by three sites with very low coverage values (50%, 51%, and 59%; see figure below). These sites exerted a strong influence on the standardisation procedure, leading to significant rarefaction in the other sites.

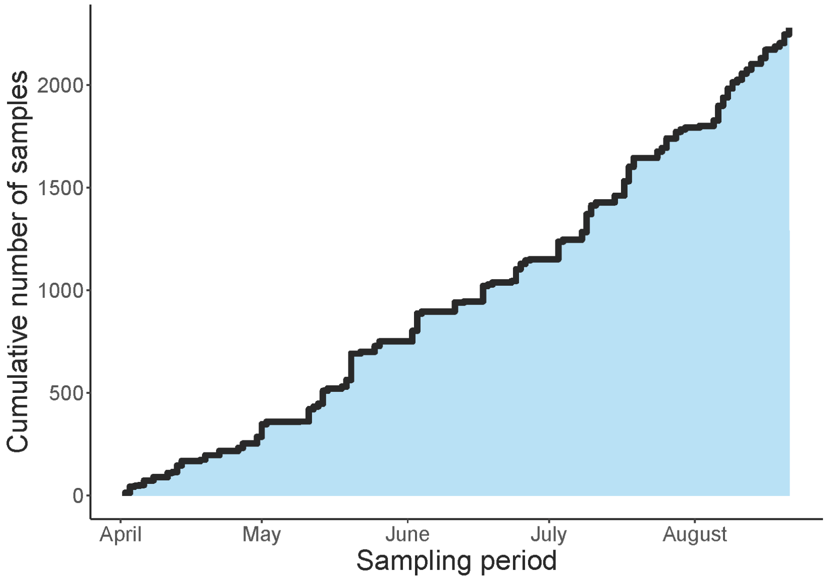
To mitigate this effect, we excluded these three low-coverage sites and re-did the standardisation analyses on the remaining 61 sites. This increased the standardised coverage to 72% and the standardised sample size to 1760 individuals. Hence, removing these three sites improved both the coverage and the sample size following standardisation.



No additional sites were removed. Excluding the next site with the lowest coverage (61%) would have reduced the standardised sample size to 1744 individuals. This number would have been lower than the 1760 individuals retained with only three sites removed, thereby offering no benefit for data standardisation.

Appendix 2

Sampling effort across the two national parks over two years.



Appendix 3

Unique and shared number of bee species **(A)** and genera **(B)** between the two National parks. Entre-Sambre-et-Meuse National Park (ESEMNP) and Semois Valley National Park (SVNP).