

ARTICLE

Influence of a local bioclimatic gradient on wild bees in boreal forest clearcuts

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Abstract

Variation in wild bee assemblages along climatic gradients is still poorly known, particularly in eastern Canada. In this study, we assessed wild bee communities in forest stands that were recently clearcut along a latitudinal bioclimatic gradient. The analyses were conducted at two taxonomic levels: first at the genus level for bees as a whole (*Anthophila*) and then at the species level for bumble bees (*Bombus* spp. Latreille) (Hymenoptera: Apidae). Coloured pan traps were used to catch bees and a point-intercept method was used to survey floristic composition at each site. Abundance and richness of *Anthophila* genera and abundance of bumble bee species were inversely related to latitude, but richness of bumble bee species was not, being instead associated with sections of the gradient. These results indicate that the relationship between wild bee diversity and latitude varies among taxa and that climate and floristic resources probably each play a role. *Bombus terricola*, a species of concern in eastern Canada, was found in relatively high numbers throughout the study area. To our knowledge, this study provides the first assessment of wild bees in clearcuts in the province of Quebec, showing a clear differentiation of the communities along a spatial bioclimatic gradient.

Résumé

Les variations dans les assemblages d'abeilles sauvages le long de gradients climatiques sont encore mal connues, en particulier dans l'est du Canada. Dans cette étude, nous avons évalué les communautés d'abeilles sauvages dans des peuplements forestiers ayant été récoltés récemment le long d'un gradient bioclimatique latitudinal. Les analyses ont été menées à deux niveaux taxonomiques : d'abord au genre pour l'ensemble des abeilles (*Anthophila*), puis au niveau de l'espèce pour les bourdons (*Bombus* spp. Latreille) (Hymenoptera : Apidae). Des pièges bols colorés ont été utilisés pour capturer les abeilles et une méthode par points d'interception a été utilisée pour étudier la composition floristique de chaque site. L'abondance et la richesse spécifique des genres d'*Anthophila* et l'abondance des bourdons étaient inversement liées à la latitude, mais pas la richesse spécifique des espèces de bourdons, ceux-ci étant plutôt associées à des sections du gradient. Ces résultats suggèrent que la relation entre la diversité des abeilles sauvages et la latitude varie selon les taxons, et que le climat et les ressources floristiques jouent probablement tous les deux un rôle. *Bombus terricola*, une espèce dont le statut est préoccupant dans l'est du Canada, a été trouvé en nombre relativement élevé dans toute la zone d'étude, ce qui pourrait s'expliquer en partie par le fait que les sites étudiés sont situés loin des activités humaines autres que l'exploitation forestière. À notre connaissance, cette étude fournit une première évaluation des abeilles sauvages dans les coupes à blanc de la province de Québec, démontrant une nette différenciation des communautés selon un gradient bioclimatique spatial.

Introduction

Insect pollinators are crucial for the successful sexual reproduction of more than 80% of the world's flowering plants (Ollerton *et al.* 2011; Kremen 2018). The pollination services provided are vital to maintaining biodiversity in natural ecosystems and also for human food security (Ollerton 2017). Insect pollinators are known to increase the production of a considerable number of crop species (Klein *et al.* 2006; Vanbergen and the Insect Pollinators Initiative 2013; Kremen 2018). Bees (Apoidea: Anthophila) are considered the most important pollinators, with 20 000 species (Michener 2007) that vary in their use of floral resources and are distributed across many ecosystems worldwide.

Bees are facing major threats, such as climate change and habitat loss caused by disturbances (Sánchez-Bayo and Wyckhuys 2019; Wagner 2020). Evidence of bee decline has been recorded in recent decades across Europe and North America (Williams and Osborne 2009; Cameron *et al.* 2011, 2016; Bartomeus *et al.* 2013; Mathiasson and Rehan 2019; Soroye *et al.* 2020). Multiple climatic variables impact bee physiology (Wagner 2020) and could be responsible in part for these declines. Temperature is one determining factor in bees' development rate, survival, reproductive success, flight activity, and foraging patterns (Rader *et al.* 2013; Whitfield *et al.* 2013). Climatic variables also influence the productivity and dispersion of flowering plants (Pyke *et al.* 2016). Variations in temperature and precipitation can reduce phenological synchrony between bees and plants, resulting in declines in the abundance of some species and in shifts in species' ranges (Williams *et al.* 2014; Pyke *et al.* 2016).

Human activities such as the exploitation of natural resources can drastically reshape natural environments in ways that affect bees (Memmott *et al.* 2004). Landscape disturbances leading to changes in the availability of flower resources, nesting sites, and overwintering habitats particularly can impact bees, eventually resulting in species loss (Zurbuchen *et al.* 2010a; Williams *et al.* 2014). Because bee species vary in their nesting requirements, these impacts are expected to be species specific.

The boreal forest is the northernmost forested ecosystem on the planet. It is one of the widest spanning biomes on earth, forming a mostly uninterrupted belt across Canada, Alaska, Russia, Finland, and Scandinavia (Henry 2002). It is characterised by a cold climate that allows the growth of mostly coniferous trees. Disturbances such as fires and defoliating insect outbreaks are common in the boreal forests and contribute to their natural cycle (Shugart *et al.* 2005). Logging is also a major anthropogenic disturbance type affecting boreal ecosystems. Even though bees are often studied in agricultural or urban environments, open or recently disturbed forests that are rich in understorey flowering plants constitute an important habitat for many bee species. Anthropogenic disturbances such as logging create early succession habitats that are potentially suitable for many species (Romey *et al.* 2007; Pengelly and Cartar 2010; Taki *et al.* 2013; Zitomer *et al.* 2023). Several studies have shown that vegetation development following logging activities can positively impact wild bee communities in temperate forests (Romey *et al.* 2007; Taki *et al.* 2013; Rubene *et al.* 2015; Rodríguez and Kouki 2017; Chase *et al.* 2023a, 2023b; Davies *et al.* 2023). Specifically, the creation of canopy openings increases light penetration, which stimulates understorey herbaceous flowering plants (Hanula *et al.* 2015). Because they feed exclusively on pollen and nectar at every developmental stage (Whitfield *et al.* 2013), bees are highly dependent on the availability of floral resources. The increased amounts of woody debris, dead plant materials, and exposed soil after forest harvesting also create specific nesting habitats that can be used by ground-, cavity-, and wood-nesting bees (Hanula *et al.* 2016; Chase *et al.* 2023a). The presence in clearcuts of a wide variety of nesting habitats and floral resources benefits bees because they must return to their nest several times a day while foraging (Zurbuchen *et al.* 2010a).

Studies conducted on wild bees in managed boreal forests have mainly focused on the effect of elevation, floral and nesting resources, or management practices (Rubene *et al.* 2015; Rodríguez and Kouki 2017; Westerfelt *et al.* 2018; Luna Santa-María 2021). How climate drives the

assemblage of bee communities along latitudinal gradients in forest environments remains unknown, particularly at the regional scale. Specifically, bee communities present in recent clearcuts may vary depending on climatic and environmental conditions present in different regions. A better understanding of how bee communities vary along spatial bioclimatic gradients could help forecast potential impacts of climate change. Indeed, current climate change models predict that an increase in both average temperatures and their variability, as well as decreased seasonality, will be more pronounced at higher latitudes in the Northern Hemisphere (Intergovernmental Panel on Climate Change 2014). Wild bees, which are nonmigratory organisms, may be strongly affected by these changes (Pyke *et al.* 2016), especially given their limited heat tolerance (Gonzalez *et al.* 2024). Negative consequences of climate change have been documented at the community and population levels (Rafferty 2017; Kammerer *et al.* 2021), especially for bumble bees (Jackson *et al.* 2022; Liczner *et al.* 2023). The consequences include reduction of species-distribution ranges (Sirois-Delisle and Kerr 2018), reductions in floral-resource availability (Phillips *et al.* 2018), and phenological mismatches between bees and their feeding resources, thereby reducing the breadth of their diet (Memmott *et al.* 2007; Forrest 2015). Assessing wild bee communities' potential response to spatial climate variation would facilitate evaluation of their potential sensitivity to climate change (Lebuhn *et al.* 2013).

The overall aim of the present study was to, respectively, assess the effects of climate and floristic composition on wild bee diversity in clearcuts in the province of Quebec along a single local latitudinal bioclimatic gradient. We used recent clearcuts as a study ecosystem to uniformise the disturbance history of the different sites along this gradient and to facilitate the analysis of bee community responses to the variables of interest, climate and flowering plants.

We first assessed Anthophila communities at the genus level and then pursued our evaluation to the species level specifically for bumble bee communities (*Bombus* spp. Latreille) (Hymenoptera: Apidae). We conducted species-level analyses for this genus because it contains species that are potential indicators of climate change (Williams *et al.* 2014; Kerr *et al.* 2015). We hypothesised that wild bee diversity would be inversely related to latitude; according to McCabe *et al.* (2019), cold environments can act as environmental filters on bee communities. Moreover, as the seasonal activity period is variable among Anthophila taxa (Packer *et al.* 2007), a higher diversity of genera is expected in regions where the growing season is longer (Ogilvie and Forrest 2017). To test our hypothesis, we first compared bee abundance, richness, and diversity for three forest areas located in different bioclimatic domains in Quebec, Canada. Second, we highlighted indicator, dominant, and exclusive taxa using bee distribution patterns along the same gradient. Third, we explored the influence of local floristic composition on bee community assemblages. These steps also allowed us to identify which Anthophila genera and which bumble bee species were the most abundant in boreal and mixed forests in the province of Quebec, a region where post-disturbance bee communities have been little studied to date.

Material and methods

Study sites

We conducted our study during the summer of 2020 in three study areas positioned in three adjacent bioclimatic domains located at the interface between the boreal and temperate forest zones in the province of Quebec, Canada (Fig. 1): the balsam fir–yellow birch domain (southern area), the balsam fir–white birch domain (central area), and the black spruce–moss domain (northern area; Berteaux *et al.* 2014). Besides the dominant tree species representative of each bioclimatic domain – *Abies balsamea* (Pinaceae), *Betula alleghaniensis* (Betulaceae), *B. papyrifera* (Betulaceae), *Picea mariana* (Pinaceae) – boreal species aspen, *Populus tremuloides* (Salicaceae), and jack pine, *Pinus banksiana* (Pinaceae), tend to be sparsely present across the three study areas, whereas relatively thermophilic species such as red maple, *Acer rubrum* (Sapindaceae), yellow

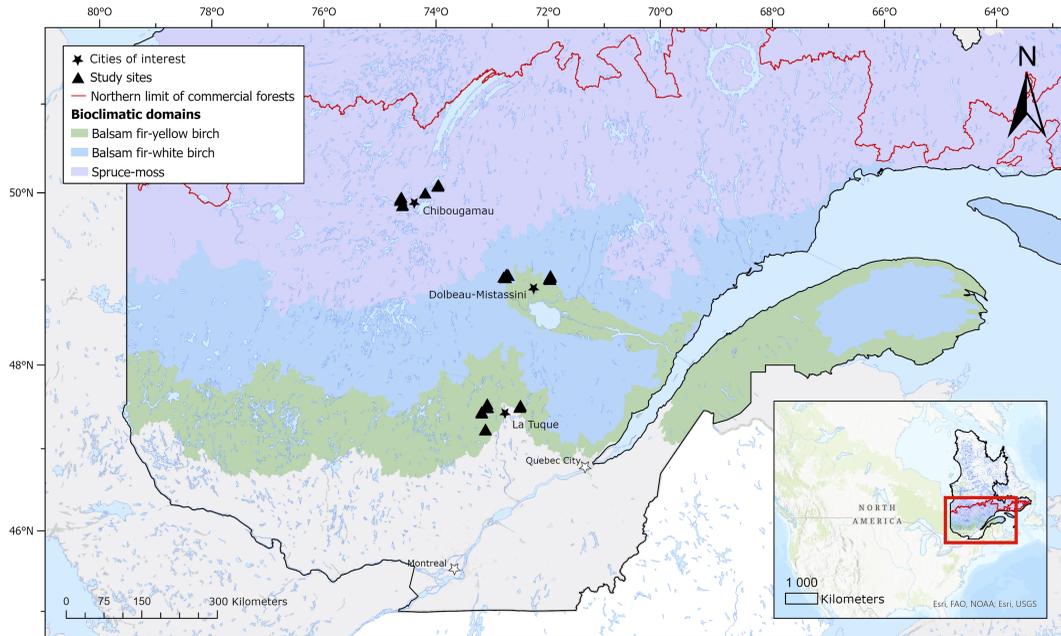


Figure 1. Distribution of study sites (black triangles; $n = 33$) across three bioclimatic domains in the province of Quebec, Canada.

birch, *B. alleghaniensis*, and sugar maple, *A. saccharum* (Sapindaceae), are found only in the southern area. Forests in these regions are managed, generally using clearcutting, followed by natural regeneration of the harvested stands, with tree planting being used only when natural regeneration is insufficient. Partial cuts are also used, primarily in tolerant hardwood stands of the southern area.

Thirty-three sampling sites were established within 50 km of three towns, each located in a different bioclimatic domain: 12 sites around La Tuque (47.43° N, 72.78° W), 10 sites around Dolbeau-Mistassini (48.88° N, 72.23° W), and 10 sites around Chibougamau (49.91° N, 74.36° W). These towns, located at least 150 km apart, were chosen because of their proximity to recent logging activities and their geographical location along the gradient. Each sampling site was positioned inside a forest stand that had been clearcut 3–10 years before. The sites were positioned at least 5 km from power lines and agricultural lands to avoid any bias related to their floral resources or pesticides. The sites were also positioned at least 0.5 km apart (generally more than 1 km) to ensure a relative spatial independence in wild bee communities (Zurbuchen *et al.* 2010b). In general, all sites were located on glacial tills with loamy textures and that were more than 50 cm thick over bedrock. On average, for the three areas, from south to north, mean growing season lengths were 215.86 days, 203.43 days, and 179.67 days; mean annual temperatures were 2.93 °C, 1.78 °C, and –4.2 °C; and mean annual precipitations were 958.9 mm, 925.79, and 921 mm, respectively, for the 2014–2020 period (Environment and Climate Change Canada; <https://climat.meteo.gc.ca>). Mean elevation for the sites of the southern, central, and northern areas was 354 m, 257 m, and 403 m, respectively. Further details on site characteristics, including clearcut year, clearcut size, and ecological type, are provided in Supplementary material, Table S1.

On each site, we established a 2000-m² plot in which two parallel 40-m-long transects were positioned 20 m apart. To minimise a potential edge effect, a buffer of approximately 50 m was kept around plots from the nearest active secondary road and from the forest margin. Following plot installation, areas were surveyed every two weeks from mid-June to the end of August. During



Figure 2. Pictures of the pan-trapping setup shown side-by-side, showing blue and yellow 12-oz plastic bowls secured in a tomato cage with binder clips. Transparent plastic saucers fastened on top of the cages prevented rain from filling the bowls and spilling their contents.

each survey, all the sites of an area were visited within 2–3 consecutive days. At each visit to a plot, two sampling protocols were performed, starting with the gathering of captured insects and followed by a survey of floral resources. In the southern and central study areas, five sampling surveys were performed over the course of the whole summer. In the northern area, only four surveys were carried out because of the shorter growing season.

Wild bee sampling

Bees were collected using coloured pan traps (Fig. 2). We used blue, white, and yellow 12-oz plastic PartyCity party bowls (7.5 inches diameter \times 1.5 inches deep; \sim 19 cm \times \sim 4 cm). These colours are known to attract bees and are the most used in North American pan trap sampling (Droege *et al.* 2010; Whitfield *et al.* 2013). Three pan traps (one of each colour) were set 10 m apart along the two transects, for a total of six coloured pan traps per plot. For each trap, binder clips were used to secure a bowl approximately 20 cm above the ground in a tomato cage. We prevented rain from filling the bowl and spilling its contents by fastening a transparent plastic saucer on top of the cage, about 20 cm above the bowl. Approximately 120 mL of propylene glycol was used to catch and preserve specimens in the bowls because it does not evaporate like soapy water and slows the decomposition of dead insects (Whitfield *et al.* 2013). This also allowed us to leave the traps operational in the field between visits, thereby accounting for the fact that active periods are variable between bee species and can be affected by daily weather (Packer *et al.* 2007). At each visit, the traps were reinstalled and refilled with propylene glycol after the caught specimens had been collected from the bowls. This way, traps were continually deployed for the entire growing season, from mid-June to the end of August.

Before identification, captured specimens were stored in 40% ethanol. They were then washed and pinned. All specimens were identified at least to the genus level. Identification was pursued to the species level for the *Bombus* spp. specimens. Packer *et al.* (2007), Williams *et al.* (2014), Wilson and Carril (2015), Ascher and Pickering (2020), and Milam *et al.* (2020) were used as keys. Difficult bee genera and *Bombus* species were confirmed with the assistance of expert taxonomists (see [Acknowledgements](#)). Voucher specimens were deposited at Université Laval (laboratory of Valérie Fournier, Québec, Quebec, Canada) and at the Collection d'insectes du Québec (Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec, Québec, Quebec, Canada).

Floral-resource sampling

The floral resources were surveyed following the FIREMON point-intercept sampling method (Caratti 2006). Two transects of 18 sampling rods (3 mm diameter) were established along those of the pan traps, with 2 m between each, for a total of 36 rods per site. Along the transects, we considered each flowering plant species touching a pole as a “hit.” The point-intercept method allowed us to statistically consider the seasonal species turnover in floral composition.

Relative species abundance Rel_{abond} of floristic species i at a site j was obtained using the rule of proportion:

$$Rel_{abond_{ij}} = \mu_{Obs_{ij}} \sum_i \mu_{Obs_{ij}} \times 100$$

where the mean number of observations μ_{Obs} of each floristic species i encountered within the site j was calculated as:

$$\mu_{Obs_{ij}} = \sum Obs_{ij} (36 \text{ rods} \times k_j)$$

where Obs_i corresponds to the number of hits for species i within site j and k_j corresponds to the number of surveys that could be done on that same site.

Flowering plants were identified in the field to the lowest possible taxonomic level using the keys of Frère Marie-Victorin *et al.* (2002), Larivière and Villeneuve (2014), Leboeuf (2016), and Brouillet (2024). The recurring visits allowed us to confirm the identification of some annual species that were insufficiently developed in early spring.

Data analyses

All analyses were first performed at the genus level for the whole Anthophila group, including bumble bees, and then performed a second time for bumble bees only. Data from the whole sampling season were pooled to best assess the factors influencing spatial variation in wild bee populations. Sites are considered as replicates for the three bioclimatic areas. The effectiveness of the sampling effort was assessed by computing species accumulation curves in the Anthophila data and in the bumble bee data using the function *specaccum* from the *vegan* package, version 2.5-7, in R (Oksanen *et al.* 2020; R Core Team 2021). Accumulation curves assess the increase in the number of species observed according to the sampling effort. Mean species accumulation curves and their standard deviations were obtained from repeated richness accumulations in random order from 999 permutations or subsampling without replacement (Gotelli and Colwell 2001).

Assessing community diversity

Abundance (number of individuals) and richness (number of genera for Anthophila; number of species for bumble bees) were calculated for each site and were used to compare community diversity between the three areas. Shannon’s H' diversity index (Hill 1973) and Pielou’s J' evenness index (Pielou 1975) were similarly calculated for each site and were used as diversity indexes to quantify how diversified and equally distributed the communities of wild bees were across sites and along the bioclimatic gradient. The two indexes are complementary, which ensures thorough interpretation of the results. Indexes were computed using the function *diversity* from the *vegan* package (Oksanen *et al.* 2020). Shannon’s diversity index considers the total number of species (S) and the individual abundance within each species. Compared to a community dominated by a sole species (minimal value of 0), a community with perfectly codominant species will have a maximum index value ($\ln S$, $\log S$, or $\log_2 S$, depending on the choice of the logarithm base) and will be considered the most diversified (Hill 1973). Pielou’s evenness index indicates the extent to

which species are proportional in numbers on each site along the gradient; a value of 1 indicates a perfectly balanced community (same number of individuals for each species), whereas a value of 0 indicates an unbalanced community where only one species surpasses all the others in numbers (Pielou 1975).

Abundance and richness were compared between areas using generalised linear models with the *glm* function from the *stats* package in R (R Core Team 2021), using a log-link function in both models. Overall significance ($P < 0.05$) of the categorical factor “area” was assessed by performing a likelihood ratio test by comparing the model containing that variable with the null model. For cases where the difference was significant, pairwise comparisons were computed by changing the base level. Shannon’s diversity and Pielou’s evenness indexes were compared between areas using one-way analyses of variance with the *lm* function from the *stats* package, version 4.1.1, in R. When results were significant, multiple pairwise comparisons were computed using the *joint_tests* and *emmeans* functions from the *emmeans* package and the *cld* function from the *multcomp* package in R (Hothorn *et al.* 2008; Lenth 2021). Shannon’s diversity data were log-transformed to be normally distributed.

Indicator, dominant, or exclusive taxa

The Dufrière–Legendre indicator species analysis (IndVal index) was used to determine if any and, if so, which Anthophila genera and bumble bee species were significantly associated with any of the studied bioclimatic domains along the latitudinal gradient. The IndVal index calculates the indicator value of species within clusters of sites by combining their specificity (highest mean abundance within a group compared to the other groups) and fidelity (presence in most sites of that group; Dufrière and Legendre 1997). The index values were computed using the *indval* function from the *labdsv* package, version 2.0-1, in R (Roberts 2019). The IndVal index was also applied to the floristic data to corroborate the observed floristic assemblage within each area with published findings.

To highlight the differences in Anthophila abundance among sites and along the gradient, we also plotted heatmaps with the *phheatmap* package in R (Kolde 2019). The heatmaps allowed us to visualise the distribution of highly dominant taxa and to identify Anthophila genera and bumble bee species that were exclusively captured in specific parts of the gradient.

Influence of floristic composition

We used a redundancy analysis, a constrained ordination (Legendre *et al.* 1998), to determine the effect of floristic composition on Anthophila and bumble bee communities along our gradient. The Hellinger transformation was applied to our bee matrix using the *decostand* function from the *vegan* package in R (Oksanen *et al.* 2020). The Hellinger transformation is particularly well suited for species abundance data because it gives low weights to variables with low counts and many zeros (Legendre and Gallagher 2001). The tested explanatory variables were floristic species, based on their relative abundance on each site. Colinearity of our redundancy analysis model was assessed using variance inflation factor scores. The *step* function (from the *vegan* package) was used with forward selection, based on both the Akaike information criterion and the Bayesian information criterion, to determine which floristic species best explain bee community composition. We performed an analysis of variance–like permutation test on our redundancy analysis to assess the significance of constraints and axis using the *anova.cca* function from the *vegan* package. Anthophila genera and bumble bee species with fewer than 10 individuals were not used in the analysis, given their scarcity. Floristic species with a relative abundance less than 1% were also omitted.

Table 1. List of the 21 bee genera collected along a bioclimatic gradient in the province of Quebec, Canada, from early June to late August 2020, with their abundance in each studied area. The genera are sorted according to their corresponding family.

Family	Genus	Taxonomic authority	Abundance by area		
			South	Central	North
Andrenidae	<i>Andrena</i> spp.	Fabricius, 1775	77	15	21
	<i>Pseudopanurgus</i> spp.	Cockerell, 1897	0	1	0
Apidae	<i>Anthophora</i> spp.	Latreille, 1803	16	2	0
	<i>Ceratina</i> spp.	Latreille, 1802	29	2	0
	<i>Melissodes</i> spp.	Latreille, 1829	21	2	0
	<i>Nomada</i> spp.	Scopoli, 1770	9	0	1
	<i>Bombus</i> spp.	Latreille, 1802	345	265	253
Colletidae	<i>Colletes</i> spp.	Latreille, 1802	11	19	5
	<i>Hylaeus</i> spp.	Fabricius, 1793	33	26	8
Halictidae	<i>Augochlora</i> spp.	Smith, 1853	9	0	0
	<i>Augochlorella</i> spp.	Sandhouse, 1937	25	0	0
	<i>Dufourea</i> spp.	Lepelletier, 1840	1	1	0
	<i>Halictus</i> spp.	Latreille, 1804	52	19	5
	<i>Lasioglossum</i> spp.	Curtis, 1833	1866	630	264
	<i>Sphecodes</i> spp.	Latreille, 1804	17	14	35
Megachilidae	<i>Coelioxys</i> spp.	Latreille, 1809	2	1	1
	<i>Epeolus</i> spp.	Latreille, 1802	2	1	0
	<i>Hoplitis</i> spp.	Klug, 1807	7	2	1
	<i>Megachile</i> spp.	Latreille, 1802	43	6	2
	<i>Osmia</i> spp.	Panzer, 1806	48	19	16
	<i>Stelis</i> spp.	Panzer, 1806	3	2	0

Results

General results

Overall, we retrieved a total of 328 samples from the pan traps in the southern area, 263 from the central area, and 264 from the northern area. The number of consecutive trap days for each area was 76, 71, and 55, respectively. We collected a total of 4255 specimens belonging to the Anthophila group, corresponding to 21 genera in five families (Table 1). The most abundant genus was *Lasioglossum* spp. Curtis (Hymenoptera: Halictidae), with a total of 2760 individuals, representing 65% of all collected bees. Bumble bees (*Bombus* spp.) represented the second most abundant genus (20%), with 863 individuals. All other Anthophila genera combined represented only 15% of all collected individuals. Within bumble bees, 10 species were found (Table 2). *Bombus ternarius* Say was the most abundant, with 339 individuals, representing 39% of all caught bumble bees. *Bombus terricola* Kirby was the second most abundant, with 173 individuals (20%), followed by *B. sandersoni* Franklin, with 170 individuals (19.7%), and *B. vagans* Say, with 93 individuals (10.78%).

Table 2. List of the 10 bumble bee species collected along a bioclimatic gradient in the province of Quebec, Canada, from early June to late August 2020, with their abundance for each studied area. Species are presented in alphabetical order.

Genus	Subgenus	Species	Taxonomic authority	Abundance by area		
				South	Central	North
<i>Bombus</i>	(<i>Subterraneobombus</i>)	<i>borealis</i>	Kirby, 1837	7	1	2
	(<i>Psithyrus</i>)	<i>flavidus</i>	Eversmann, 1852	3	7	15
	(<i>Pyrobombus</i>)	<i>frigidus</i>	Smith, 1854	0	0	17
	(<i>Psithyrus</i>)	<i>insularis</i>	Smith, 1861	1	1	5
	(<i>Pyrobombus</i>)	<i>perplexus</i>	Cresson, 1863	17	11	0
	(<i>Cullumanobombus</i>)	<i>rufocinctus</i>	Cresson, 1863	1	0	0
	(<i>Pyrobombus</i>)	<i>sandersoni</i>	Franklin, 1913	64	42	64
	(<i>Pyrobombus</i>)	<i>ternarius</i>	Say, 1837	78	133	128
	(<i>Bombus</i>)	<i>terricola</i>	Kirby, 1837	122	29	22
	(<i>Pyrobombus</i>)	<i>vagans</i>	Say, 1837	52	41	0

Sampling effort. The accumulation curves for both taxonomic levels, Anthophila genera (Supplementary material, Fig. S1A) and bumble bee species (Supplementary material, Fig. S1C), reached saturation, which indicates a sufficient sampling effort. Accumulation curves by area reached a plateau only in the southern area for Anthophila genera (Supplementary material, Fig. S1B) and in the northern area for the bumble bee species (Supplementary material, Fig. S1D), which suggests that richness in the other areas might have been slightly higher if more sampling sites were established.

Community diversity

Anthophila communities. For the Anthophila communities, diversity measures decreased from the south to the north of the gradient. According to the results of our generalised linear model analyses, the effect of *area* was significant in both the models for abundance and richness. Abundance (P -value < 0.0001; Fig. 3A) and genera richness (P -value < 0.0001; Fig. 3B) both differed significantly between all three areas. Total abundance was higher in the southern area, with 2616 individuals, followed by the central area, with 1027 individuals, and the northern area, with 612 individuals. A mean abundance of 218 ± 79.09 (standard deviation) was obtained for the southern area, 102.7 ± 44.16 (standard deviation) for the central area, and 55.64 ± 23.59 (standard deviation) for the northern area. Total genera richness was higher in the southern area (20 genera), followed by the central area (18 genera), and the northern area (13 genera). A mean richness of 11.58 ± 2.84 (standard deviation) was obtained for the southern area, 8.2 ± 2.57 (standard deviation) for the central area, and 5.9 ± 1.3 (standard deviation) for the northern area.

Regarding diversity indexes, Shannon's diversity for Anthophila communities did not differ significantly between the areas ($F_{2,30} = 1.354$, P -value = 0.2736; Fig. 3C). Mean Shannon's diversity was 1.07 ± 0.31 (standard deviation) in the southern area, 0.95 ± 0.4 (standard deviation) in the central area, and 1.18 ± 0.22 (standard deviation) in the northern area. However, Pielou's evenness index differed significantly between the northern area and the two other areas ($F_{2,30} = 24.029$, P -value < 0.0001; Fig. 3D), which were themselves not significantly different from one another. Anthophila community evenness was highly unbalanced along the whole gradient ($J' < 0.5$). Mean Pielou's evenness was 0.19 ± 0.05 (standard deviation) for the southern area,

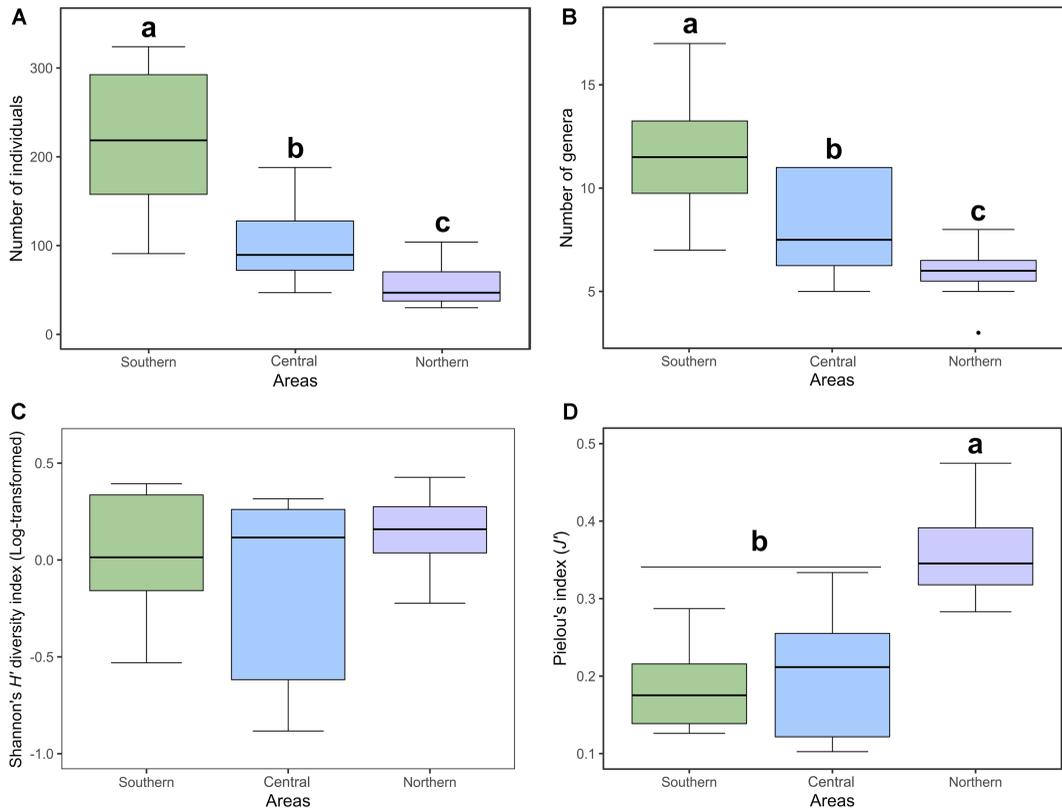


Figure 3. **A**, Mean abundance; **B**, mean genera richness; **C**, mean Shannon's diversity index; and **D**, mean Pielou's evenness index of *Anthophila* from clearcut sites in three studied areas along a bioclimatic gradient in the province of Quebec, Canada. Letters represent the *post hoc* result (P -value < 0.0001), showing significant differences between the three areas for diversity measures (abundance and richness) and for Pielou's evenness index. Shannon's diversity index data were log-transformed to be normally distributed and to respect homogeneity of variance.

0.2 ± 0.08 (standard deviation for the central area, and 0.36 ± 0.06 (standard deviation) for the northern area.

Bumble bee communities. For the bumble bee communities, the generalised linear model analyses indicate that the effect of *area* was significant only for the abundance model (P -value = 0.0247; Fig. 4A). Bumble bee species richness showed no relationship to area (P -value = 0.6756; Fig. 4B). Abundance was higher in the southern area than in the northern area (P -value = 0.0070). A total abundance of 345 individuals was obtained in the southern area, 265 individuals in the central area, and 253 individuals in the northern area. Mean abundance of bumble bees was 28.75 ± 17.14 (standard deviation) for the southern area, 26.5 ± 34.97 (standard deviation) for the central area, and 23 ± 9.24 (standard deviation) for the northern area. Total species richness was similar between areas, with nine species in the southern area, eight species in the central area, and seven species in the northern area. A mean richness of 4.75 ± 1.42 (standard deviation) was obtained for the southern area, 4 ± 1.89 (standard deviation) for the central area, and 4.64 ± 0.81 (standard deviation) for the northern area.

Diversity indexes showed no relation between bumble bee communities and area. Neither Shannon's diversity index ($F_{2,30} = 1.598$, P -value = 0.219; Fig. 4C) nor Pielou's evenness index ($F_{2,30} = 2.864$, P -value = 0.0727; Fig. 4D) differed significantly between areas. Mean Shannon's

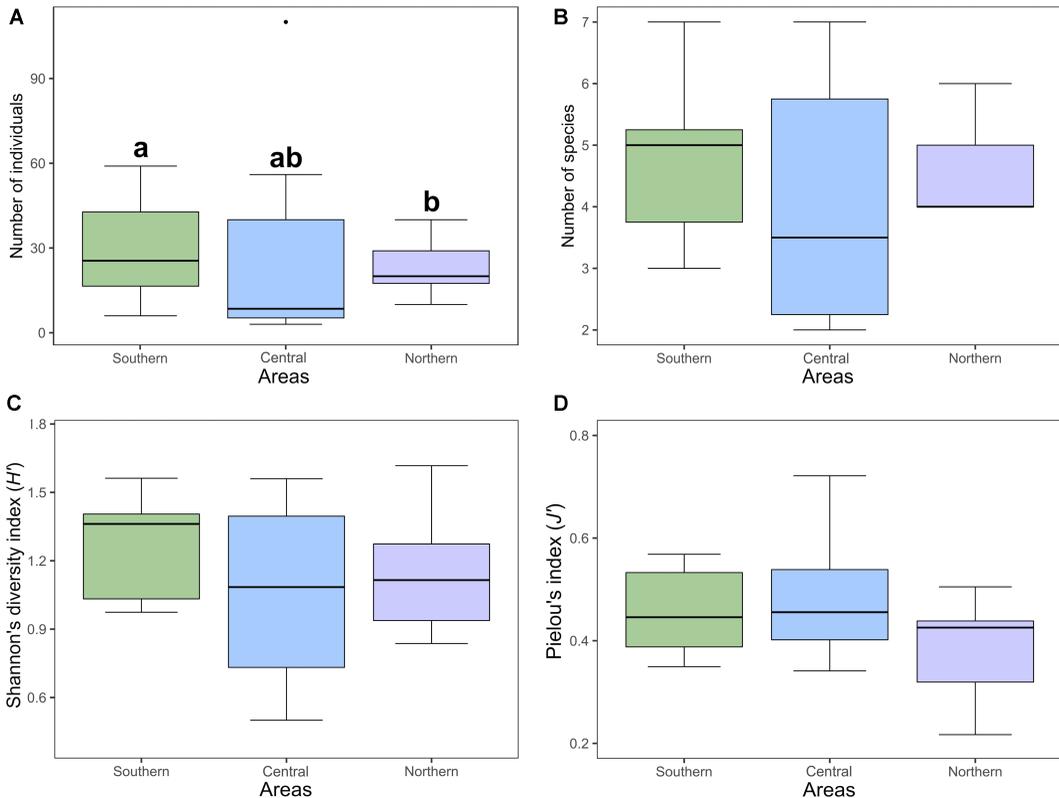


Figure 4. **A**, Mean abundance; **B**, mean species richness; **C**, mean Shannon's diversity index; and **D**, mean Pielou's evenness index of bumble bees (*Bombus* spp.) from clearcut sites in three studied areas along a bioclimatic gradient in the province of Quebec, Canada. Letters represent the *post hoc* result (P -value < 0.0001), showing significant differences between the southern and northern areas for abundance.

diversity was 1.27 ± 0.21 (standard deviation) for the southern area, 1.06 ± 0.38 (standard deviation) for the central area, and 1.13 ± 0.24 (standard deviation) for the northern area. Mean Pielou's evenness was 0.46 ± 0.77 (standard deviation) for the southern area, 0.49 ± 0.12 (standard deviation) for the central area, and 0.39 ± 0.09 (standard deviation) for the northern area.

Indicator, dominant, and exclusive taxa

Anthophila communities. Results from the IndVal analysis of Anthophila identified 10 genera as indicators in the southern area (*Ceratina* Latreille, *Augochlorella* Sandhouse, *Andrena* Fabricius, *Lasioglossum*, *Megachile* Latreille, *Halictus* Latreille, *Melissodes* Latreille, *Osmia* Panzer, *Nomada* Scopoli, and *Augochlora* spp. Smith), with *Ceratina* spp. having the highest value (Table 3). The central and northern areas had a single indicator genus each, *Colletes* spp. Latreille and *Sphecodes* spp. Latreille, respectively.

According to the abundance heatmap (Supplementary material, Fig. S2), *Lasioglossum* and *Bombus* spp. were predominant genera along the whole gradient. *Lasioglossum* had the highest abundance at every site except one, where it was surpassed by the genus *Bombus*. *Lasioglossum* spp. was particularly abundant in the southern area and the first half of the central area (Supplementary material, Fig. S2A). Distribution patterns of the 19 other genera (Supplementary material, Fig. S2B) showed that, overall, the three study areas shared 11 genera. Six genera were

Table 3. List of indicators obtained from the Dufrene–Legendre indicator species analysis for Anthophila genera and bumble bee species from clearcuts along a bioclimatic gradient in the province of Quebec, Canada. Studied areas were clustered. Taxonomic groups are sorted according to their indicator value and area.

Taxonomic group	Area	Genus or species	Indicator value	P-value	Frequency
Anthophila genera	Southern	<i>Ceratina</i> spp.	0.693	0.001	11
		<i>Augochlorella</i> spp.	0.667	0.001	8
		<i>Andrena</i> spp.	0.653	0.001	27
		<i>Lasioglossum</i> spp.	0.641	0.001	33
		<i>Megachile</i> spp.	0.616	0.004	15
		<i>Halictus</i> spp.	0.594	0.003	21
		<i>Melissodes</i> spp.	0.524	0.003	9
		<i>Osmia</i> spp.	0.499	0.039	27
		<i>Nomada</i> spp.	0.372	0.013	6
	<i>Augochlora</i> spp.	0.333	0.031	4	
	Central	<i>Colletes</i> spp.	0.407	0.043	14
Northern	<i>Sphecodes</i> spp.	0.530	0.011	27	
Bumble bee species	Southern	<i>Bombus terricola</i>	0.675	0.002	29
	Northern	<i>Bombus frigidus</i>	0.455	0.003	5
		<i>Bombus flavidus</i>	0.429	0.036	14

found in the southern and central areas but not in the northern area; these were *Anthophora* Latreille, *Ceratina*, *Dufourea* Lepeletier, *Epeolus* Latreille, *Melissodes*, and *Stelis* spp. Panzer). Two genera – *Augochlora* and *Augochlorella* spp. – were collected exclusively in the southern area, and the only specimen of *Pseudopanurgus* spp. Cockerell was caught in the central area. *Nomada* spp. was collected in limited numbers in both in the southern and northern areas but was absent from the central area.

Bumble bee communities. For the bumble bee communities, results from the IndVal index analysis identified *B. terricola* as the only indicator species in the southern area (Table 3). *Bombus frigidus* Smith and *B. flavidus* Eversmann were indicator species in the northern area. No indicator species was detected in the central area.

According to the abundance heatmap of bumble bee species (Supplementary material, Fig. S2C), *B. ternarius* was a dominant species along the latitudinal gradient, as were *B. sandersoni* and *B. terricola*, which were also well distributed along the whole gradient. *Bombus terricola* was generally dominant in the southern area, whereas *B. sandersoni* tended to dominate in the central and northern areas. Overall, the three areas shared six species. Two species were collected only in a specific area – *B. frigidus* in the northern area and *B. rufocinctus* Cresson in the southern area. *Bombus perplexus* Cresson and *B. vagans* were found in both the southern and central areas but not in the northern area.

Influence of floristic composition

Floristic composition along the gradient. A total of 51 floristic species were recorded during our sampling season (Supplementary material, Table S2). The most abundant species along the whole gradient were *Kalmia angustifolia* Linnaeus (Ericaceae) (10.35%), *Vaccinium angustifolium* Aiton

(Ericaceae) (10.12%), *Prunus pensylvanica* Linnaeus *filis* (Rosaceae) (9.76%), *Diervilla lonicera* Miller (Caprifoliaceae) (9.44%), and *Rubus idaeus* Linnaeus (Rosaceae) (8.61%).

In the southern area, 36 floristic plant species were recorded. Floristic composition of sites within the area was dominated by *Prunus pensylvanica* (16%), *Rubus idaeus* (15.56%), and *Diervilla lonicera* (11.41%). Five floristic species were significant indicators (IndVal index, P -value < 0.05) of the southern area: *Prunus pensylvanica*, *Rubus idaeus*, *Eurybia macrophylla* (Linnaeus) Cassini (Asteraceae), *Maianthemum canadense* Desfontaines (Asparagaceae), and *Fallopia cilinodis* (Michaux) Holub (Polygonaceae). See Supplementary material, Table S3 for the complete indicator species list with values.

In the central area, 36 floristic plant species were recorded. Floristic composition of sites within the area was dominated by *Kalmia angustifolia* (13.55%), *Diervilla lonicera* (11.39%), *Vaccinium angustifolium* (11.11%), and *Cornus canadensis* Linnaeus (Cornaceae) (10.84%). Nine floristic species were significant indicators (IndVal index, P -value < 0.05) of the central area: *Viburnum cassinoides* Linnaeus (Viburnaceae), *Cornus canadensis*, *Linnaea borealis* Linnaeus (Caprifoliaceae), *Diervilla lonicera*, *Clintonia borealis* (Aiton) Rafinesque (Liliaceae), *Ilex mucronata* (Linnaeus) M. Powell, V. Savolainen and S. Andrews (Aquifoliaceae), *Aralia hispida* Ventenat (Araliaceae), *Epigaea repens* Linnaeus (Ericaceae), and *Viola* spp. Linnaeus (Violaceae).

In the northern area, 20 floristic plant species were recorded. Floristic composition of sites within the area was dominated by *Rhododendron groenlandicum* (Oeder) Kron and Judd (Ericaceae) (23.83%), *Kalmia angustifolia* (23.74%), and *Vaccinium angustifolium* (23.74%). Three species were significant indicators (IndVal index, P -value < 0.05) of the northern area: *Rhododendron groenlandicum*, *Gaultheria hispidula* (Linnaeus), Muhlenberg ex Bigelow (Ericaceae), and *Chamaedaphne calyculata* (Linnaeus) Moench (Ericaceae).

Anthophila communities. Using the redundancy analysis, we found that only three of the 51 floristic species sampled along our gradient significantly described the relative abundance of Anthophila genera: *Diervilla lonicera* (DIE, $F_{1,29} = 13.649$, P -value < 0.001), *Rhododendron groenlandicum* (LEG, $F_{1,29} = 5.722$, P -value = 0.001), and *Vaccinium angustifolium* (VAA, $F_{1,29} = 2.178$, P -value = 0.076). Only the first axis of the redundancy analysis was significant (Axis 1: $F_{1,29} = 19.202$, P -value < 0.001). Our model explained 42.6% of Anthophila genera relative abundance, with an adjusted R^2 -value of 0.36, leaving approximately 57.4% unexplained. The genera omitted from the analysis due to their scarcity in the dataset ($n < 10$) were *Augochlora*, *Coelioxys* Latreille, *Dufourea*, *Epeolus*, *Hoplitis* (Klug), *Nomada*, *Pseudopanurgus*, and *Stelis* spp.

As presented in Figure 5A, the genera *Lasioglossum* and *Bombus* spp. tend to be associated with different floral communities. The relative abundance of *Lasioglossum* spp. seems related to the presence of *Diervilla lonicera*. The genera *Bombus* and *Sphecodes* spp. are positively correlated with sites from the northern area, and their relative abundance appears, respectively, correlated with *Vaccinium angustifolium* and *Rhododendron groenlandicum*.

Bumble bee communities. Using redundancy analysis, we found that eight of the 51 floristic species sampled along the gradient significantly described the relative abundance of bumble bee species: *Maianthemum canadense* ($F_{1,22} = 9.216$, P -value < 0.001), *Eurybia macrophylla* ($F_{1,22} = 6.450$, P -value < 0.001), *Prunus pensylvanica* ($F_{1,22} = 5.761$, P -value < 0.001), *Oclemena acuminata* (Michaux) Greene (Asteraceae) ($F_{1,22} = 4.902$, P -value < 0.001), *Kalmia angustifolia* ($F_{1,22} = 3.481$, P -value = 0.009), *Aralia nudicaulis* Linnaeus (Araliaceae) ($F_{1,22} = 3.289$, P -value = 0.013), *Linnaea borealis* ($F_{1,22} = 2.475$, P -value = 0.042), and *Acer rubrum* Linnaeus (Sapindaceae) ($F_{1,22} = 2.382$, P -value = 0.053). The first three axes of the redundancy analysis were significant (Axis 1: $F_{1,24} = 17.839$, P -value < 0.001;

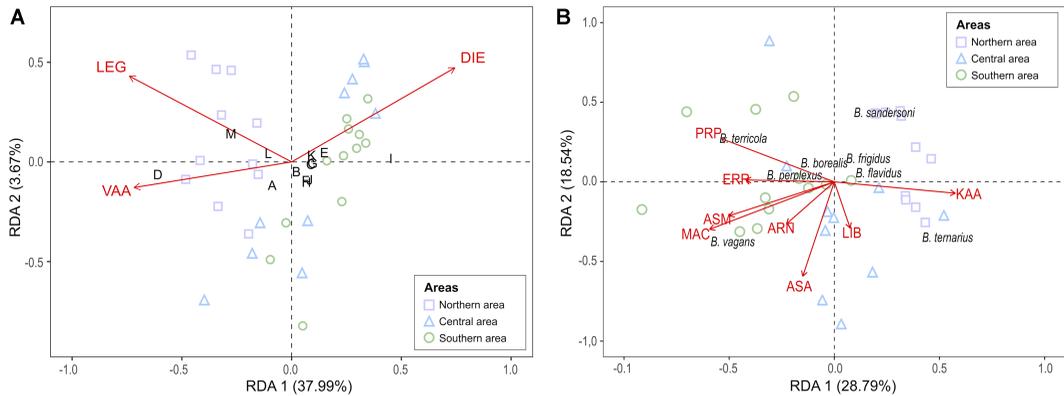


Figure 5. Redundancy analysis (RDA) triplots of Hellinger-transformed bee data explained by **A**, three significant plant species for Anthophila, and **B**, eight significant plant species for bumble bees. Anthophila genera code (panel **A**) appears in black capital letters: A, *Andrena* spp.; B, *Anthophora* spp.; C, *Augochlorella* spp.; D, *Bombus* spp.; E, *Ceratina* spp.; F, *Colletes* spp.; G, *Halictus* spp.; H, *Hylaeus* spp.; I, *Lasioglossum* spp.; J, *Megachile* spp.; K, *Melissodes* spp.; L, *Osmia* spp.; and M, *Sphecodes* spp. The floristic species code appears in red capital letters: ARN, *Aralia nudicaulis*; ASA, *Oclemena acuminata*; ASM, *Eurybia macrophylla*; ERR, *Acer rubrum*; DIE, *Diervilla lonicera*; KAA, *Kalmia angustifolia*; LEG, *Rhododendron groenlandicum*; LIB, *Linnaea borealis*; MAC, *Maianthemum canadense*; PRP, *Prunus pensylvanica*; and VAA, *Vaccinium angustifolium*. Site icon colour and shape reflect the three areas.

Axis 2: $F_{1,24} = 11.485$, P -value < 0.001 ; Axis 3: $F_{1,24} = 6.062$, P -value = 0.001). Our model explained 61.2% of bumble bee species relative abundance, with an adjusted R^2 -value of 0.48, leaving approximately 38.7% unexplained. The bumble bee species omitted from the analysis due to their scarcity in the dataset ($n < 10$) were *B. rufocinctus* and *B. insularis* Smith.

As presented in Fig. 5B, a strong negative correlation is suggested between *B. terricola* and *B. ternarius*. They are, respectively, linked with *Prunus pensylvanica* and *Kalmia angustifolia*. A strong negative correlation is also suggested between *B. sandersoni* and *B. vagans*. *Bombus sandersoni*, *B. frigidus*, and *B. flavidus* are positively correlated with sites from the northern area. Also, because it is the bumble bee species correlated with the most floral species, including two significant indicators of the southern area (*i.e.*, *M. canadense*, *E. macrophylla*, and *A. nudicaulis*), *B. vagans* seems positively correlated with floristic species from temperate forests.

Discussion

To our knowledge, our study is the first to assess the influence of a regional bioclimatic gradient on wild bee communities in managed boreal forests. We found that climate and floristic resources are key factors driving community assemblages for both Anthophila and bumble bees along this spatial gradient. Our hypothesis that wild bee diversity would be inversely related to latitude was partially supported at the genus level for Anthophila communities and at the species level for bumble bee communities. Communities at both taxonomic levels were unbalanced along the gradient, which could be explained by the dominance of a small number of competitive taxa. We were able to identify taxa that were exclusive to, or representative of, specific areas. Finally, several floristic species were found to play a determinant role in the relative abundance of some taxa within wild bee communities.

Anthophila communities

Our hypothesis was partially supported in the assessment of Anthophila genera. Abundance and richness were both inversely related to latitude, but Shannon's diversity index and Pielou's

evenness index were not. The north–south latitudinal gradient in forest characteristics in the province of Quebec is driven by climatic conditions that become colder towards the north, with a corresponding decrease in forest productivity (Berteaux *et al.* 2014). Indeed, in the study areas, post-clearcut vegetation development tended to be more advanced in the southern part of the gradient (L.C.G., unpublished data). In most study sites in the southern area, a young tree layer had already established, which often overshadowed the understorey herbaceous and shrub layers. In contrast, in the northern area, the vegetation was low and consisted mainly of shrubs and herbaceous plants. The arborescent layer was not yet well developed because of the slow growth of the coniferous species typical of this climate. These observations in clearcuts indicate that the growth speed of regeneration and time-lapse between ecological successions depend on the latitudinal situation along the spatial gradient (De Frenne *et al.* 2012). It is possible that wild bee communities observed in clearcuts in the south of our gradient are typical of more advanced forest succession than those observed in clearcuts to the north.

The floristic composition of the sites of the northern area had up to 1.8 times fewer floristic species than those in the other two, more southerly areas. Moreover, it was largely dominated by three Ericaceous shrubs: *Rhododendron groenlandicum*, *Kalmia angustifolia*, and *Vaccinium angustifolium*. The more diverse floral communities in the southern and central areas of our gradient may have played a determinant role in Anthophila genera richness and abundance. As shown previously, a sufficient variety of floral species must be present to support diverse and abundant wild bee communities (Venjakob *et al.* 2016). Floristic diversity is known to be critical to ensuring overlapping blooms throughout the entire season (Fortuin and Gandhi 2021). Anthophila taxa have variable seasonal activity periods, from early season to full season, and sometimes emerge and forage within only a short 4- to 6-week window (Packer *et al.* 2007). Bloom patterns are therefore one of the environmental factors limiting Anthophila taxa within open forest habitats (Fortuin and Gandhi 2021).

The Pielou's evenness index results indicate that, in the southern and central areas, Anthophila communities are composed of a high number of rare genera but are dominated by one genus – *Lasioglossum* spp. In the northern area, Anthophila communities are also composed of a great number of rare genera, but the genus *Lasioglossum* spp. is codominant with the genus *Bombus*. *Lasioglossum* spp. was by far the most abundant genus captured in clearcuts in our study. This genus is very common throughout temperate and boreal forests (Packer *et al.* 2007) and was also the most abundant genus caught in other wild bee studies in clearcuts (Romey *et al.* 2007; Gibbs 2010; Proctor *et al.* 2012; Fortuin and Gandhi 2021). The genus *Lasioglossum* has been described as indicative of recently disturbed landscapes and open forested areas (Proctor *et al.* 2012), mainly because most *Lasioglossum* species are ground nesters (Wilson and Carril 2015). Proctor *et al.* (2012), Rubene *et al.* (2015), and Fortuin and Gandhi (2021) observed that regenerating clearcuts tend to favour groundnesting bee groups because the percent cover of warm bare soil is consistently higher there than what is found in undisturbed forests.

It is noteworthy that results of the Anthophila analyses would have been different if performed at the species level. For example, the lower evenness levels observed in the southern and central areas are probably explained in part by the disproportionate abundance of *Lasioglossum* spp. in those areas. However, because this is known to be a speciose genus (Gibbs 2010), the evenness index results could have changed dramatically and even flipped (*i.e.*, they could have been higher in the southern area) if the analyses were made at the species level.

Bumble bee communities

Regarding the bumble bee communities, our hypothesis was only partially supported at the species level for the genus *Bombus*. Neither richness nor Shannon's diversity index decreased from south to north, revealing no significant relationship with latitude. The results of Pielou's evenness

index, which also did not differ significantly between areas, showed that bumble bee communities along the entire gradient are generally composed of a few competitive species that dominate a greater number of rare species. Only abundance decreased from the southern to the northern area.

Many factors could explain the absence of the expected decreasing relationship of richness to latitude. For example, bumble bees are known to include species that are particularly well adapted to colder climates (Williams *et al.* 2014), and some have even been seen foraging at temperatures close to the freezing point (Goulson 2010). Their large bodies are covered by thick and dense coats of hairs. They can shiver their flight muscles, which allows them to produce their own body heat (Heinrich and Esch 1994). The flight muscles can disconnect from the wings, thereby saving energy during shivering (Whitfield *et al.* 2013; Wilson and Carril 2015).

Despite these genus-level adaptations, individual bumble bee species tend to be limited to relatively narrow climatic niches (Kerr *et al.* 2015). This may explain how, instead of finding decreasing bumble bee diversity as latitude increased, we observed relatively distinct species assemblages in each bioclimatic domain. Different bumble bee species are known to be differentially distributed in eastern Canada (Laverty and Harder 1988).

All bumble bee species that we observed were already recognised as part of the boreal fauna, but we lacked a clear understanding of how these boreal species sort themselves within the boreal habitat. Our study reveals specific niche requirements for bumble bees within this important zone, which is one of the most vulnerable to climate change. The distribution of bumble bee abundances in our captures suggests that *B. sandersoni*, *B. terricola*, and *B. ternarius* may possess larger climatic niches than the other bumble bee species within our study areas: those three species were well distributed along the entire gradient. Only a few observations of *B. sandersoni* have been documented to date in the province of Quebec (Bumble Bee Watch 2022; Global Biodiversity Information Facility 2022); our results provide substantial new information on the distribution of this species and its potential response to climate, *B. sandersoni* being the third most abundant species among our bumble bee captures.

Bombus terricola was the second most abundant species among our bumble bee specimens. This was unexpected because the species has been reported to be declining in parts of its range in North America (Grixti *et al.* 2009; Cameron *et al.* 2011; Bartomeus *et al.* 2013). NatureServe (2022) and the IUCN Red List (Hatfield *et al.* 2015) register *B. terricola* as “vulnerable.” The status of *B. terricola* in the province of Quebec is undetermined because a large part of the species’ distribution range remains sparsely surveyed. Pathogen spillover from domestic bumble bees used in greenhouses and pesticides such as neonicotinoids are correlated with the species’ decline throughout its North American range and appear to be some of the most significant threats to this species (Hopwood *et al.* 2012; Szabo *et al.* 2012). However, the remote environment examined in the present study may still be exempt from such influences. The important presence of *B. terricola* in clearcuts in our study also implies that this kind of altered environment could support the species, at least in the short term, by providing an adequate habitat that is free of those threats. Competition with other bumble bees has also been shown to impact this vulnerable species: Butler *et al.* (2021) observed that the array of floral species visited by *B. terricola* in Michigan, United States of America, consistently narrowed when *B. ternarius* was also present. As a well-known generalist, *B. ternarius* has a wide dietary breadth, which includes most of the floral species favoured by *B. terricola* (Butler *et al.* 2021). In our study, the abundance of *B. terricola* was greater than that of *B. ternarius* on most sites in the southern area, indicating that dense regeneration in clearcuts might attenuate the competitive impact of *B. ternarius*. Furthermore, *B. ternarius* is a common bumble bee species in the northeastern boreal forest and is known to inhabit many open woodland and wetland habitats within natural and disturbed landscapes (Williams *et al.* 2014). Our results suggest that although *B. ternarius* has great versatility in terms of choice of habitat and floral resources, *B. terricola* can outcompete it in clearcuts with a dense arborescent floral composition.

Effect of sampling method

Concerns about potential biases from using only the pan-trapping method for bee collection are raised throughout the literature (e.g., Popic *et al.* 2013; Fortuin and Gandhi 2021). Captures of bumble bees and other large-bodied bee groups are limited when using pan traps (Romey *et al.* 2007), and thus, the dominance of small bees within our samples (~75% of captures) may be related to this bias. A combination of pan trapping and netting is suggested to obtain samples with the greatest diversity of bees in flower-rich areas (Tucker and Rehan 2017). However, hand netting was impractical in most of our settings, considering the density and height of the vegetation on multiple sites. Also, unpredictable weather during our tight-scheduled surveys shortened the time frame during which hand netting was feasible because this method cannot be performed when the vegetation is wet (Popic *et al.* 2013). Another inadvertent sampling bias is mentioned in the literature. Because bees use visual colour cues to navigate to flowers, some studies warn that traps visible from a greater distance are more likely to catch bees than traps that have visual obstructions (Song *et al.* 2015). Bees might also be underrepresented in traps that are situated in understorey vegetation when foraging resources are available in the canopy (Urban-Mead *et al.* 2021). Even though visual obstruction and canopy resources did not seem to affect our catch rates, caution suggests accounting for possible bias, and therefore, the wild bee diversity metrics documented here should not be considered absolute.

Conclusion

For the two taxonomic levels investigated, our study demonstrates that latitudinal dissimilarities in climate and floristic composition are determinant factors of wild bee community assemblages within boreal forest clearcuts. In general, wild bee communities were unbalanced in that they tended to be dominated by a few taxa. The results of the present study also show that disturbed forests are a critical habitat for bees and that this information could be used in forest planning, in particular by using interventions that might affect floral diversity.

As revealed by the results, abundance and richness of Anthophila genera and abundance of bumble bee species were inversely related to latitude in clearcuts along a bioclimatic gradient in the province of Quebec. However, this relationship was not observed for the richness of bumble bee communities. Divergent results between the two taxonomic levels suggest an underlying complexity that may be masked by the predominance of a sole taxon. Bees of each genus will need to be analysed at the species level because wild bee taxa are highly diverse in terms of their life histories, social structures, and nesting biology (Michener 2007; Wilson and Carril 2015). Also, to maintain pollination services and advise policymakers regarding the migration capabilities of these taxa in the context of climate change, further research is needed to deepen basic knowledge on wild bee dispersion ranges within the boreal forest. To our knowledge, the present study provides the first assessment of wild bees in clearcuts in the province of Quebec and could be used as a baseline for the study of environmental changes on these organisms.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.4039/tce.2025.11>.

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Competing interests. The authors declare that they have no competing interests.

References

- Ascher, J.S. and Pickering, J. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila) [online]. Available from http://www.discoverlife.org/mp/20q?guide=Apoidea_species [accessed 26 September 2021].
- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., and Winfree, R. 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences*, **110**: 4656–4660. <https://doi.org/10.1073/pnas.1218503110>.
- Berteaux, D., Casajus, N., and de Blois, S. 2014. Changements climatiques et biodiversité du Québec: vers un nouveau patrimoine naturel [Climatic changes and biodiversity of Quebec: towards a new natural history]. Presses de l'Université du Québec, Québec, Quebec, Canada.
- Brouillet, L. 2024. Database of vascular plants of Canada (VASCAN). Version 37.14 [online]. Global Biodiversity Information Facility, Copenhagen, Denmark. Available from <https://www.gbif.org/dataset/3f8a1297-3259-4700-91fc-acc4170b27ce> [accessed 1 May 2024].
- Bumble Bee Watch. 2022. Bumble bee sightings map: *Bombus sandersoni* [online]. Available from https://www.bumblebeewatch.org/app/#/bees/map?filters=%7B%22sightingstatus_id%22:%5B%22%22%5D,%22species_id%22:%5B32%5D,%22province_id%22:%5B%2211%22%5D%7D [accessed 15 April 2022].
- Butler, R.G., Lage, C., Dobrin, S.E., Staples, J.K., Venturini, E., Frank, J., and Drummond, F.A. 2021. Maine's bumble bees (Hymenoptera: Apidae). Part 2: Comparisons of a common (*Bombus ternarius*) and a rare (*Bombus terricola*) species. *Environmental Entomology*, **50**: 1358–1369. <https://doi.org/10.1093/ee/nvab100>.
- Cameron, S.A., Lim, H.C., Lozier, J.D., Duennes, M.A., and Thorp, R. 2016. Test of the invasive pathogen hypothesis of bumble bee decline in North America. *Proceedings of the National Academy of Sciences*, **113**: 4386–4391. <https://doi.org/10.1073/pnas.1525266113>.
- Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F., and Griswold, T.L. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, **108**: 662–667. <https://doi.org/10.1073/pnas.1014743108>.
- Caratti, J.F. 2006. Point intercept (PO). In FIREMON: Fire Effects Monitoring and Inventory System. General Technical Report RMRS-GTR-164-CD. Edited by D.C.K. Lutes, E. Robert, J.F. Caratti, C.H. Key, N.C. Benson, S. Sutherland, and L.J. Gangi. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, United States of America. P. PO-1-17.
- Chase, M.H., Charles, B., Harmon-Threatt, A., and Fraterrigo, J.M. 2023a. Diverse forest management strategies support functionally and temporally distinct bee communities. *Journal of Applied Ecology*, **60**: 2375–2388. <https://doi.org/10.1111/1365-2664.14513>.

- Chase, M.H., Fraterrigo, J.M., Charles, B., and Harmon-Threatt, A. 2023b. Wild bee response to forest management varies seasonally and is mediated by resource availability. *Forest Ecology and Management*, **548**: 121426. <https://doi.org/10.1016/j.foreco.2023.121426>.
- Davies, C.B., Davis, T.S., and Griswold, T. 2023. Forest restoration treatments indirectly diversify pollination networks via floral- and temperature-mediated effects. *Ecological Applications*, **33**: e2927. <https://doi.org/10.1002/eap.2927>.
- De Frenne, P., Graae, B.J., Brunet, J., Shevtsova, A., De Schrijver, A., Chabrierie, O., *et al.* 2012. The response of forest plant regeneration to temperature variation along a latitudinal gradient. *Annals of Botany*, **109**: 1037–1046. <https://doi.org/10.1093/aob/mcs015>.
- Droege, S.A.M., Tepedino, V.J., Lebuhn, G., Link, W., Minckley, R.L., Chen, Q., and Conrad, C. 2010. Spatial patterns of bee captures in North American bowl trapping surveys. *Insect Conservation and Diversity*, **3**: 15–23. <https://doi.org/10.1111/j.1752-4598.2009.00074.x>.
- Dufrène, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**: 345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAAI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAAI]2.0.CO;2).
- Forrest, J.R.K. 2015. Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? *Oikos*, **124**: 4–13. <https://doi.org/10.1111/oik.01386>.
- Fortuin, C.C. and Gandhi, K.J.K. 2021. Functional traits and nesting habitats distinguish the structure of bee communities in clearcut and managed hardwood and pine forests in southeastern USA. *Forest Ecology and Management*, **496**: 119351. <https://doi.org/10.1016/j.foreco.2021.119351>.
- Frère Marie-Victorin, E.C., Brouillet, L., Rouleau, E., Goulet, I., Hay, S., Brouillet, L., *et al.* 2002. Flore laurentienne. Troisième édition [Laurentian Flora. Third edition]. G. Morin, Boucherville, Québec, Canada.
- Global Biodiversity Information Facility. 2022. Occurrences in Quebec (CA): *Bombus sandersoni* [online]. Available from https://www.gbif.org/occurrence/map?taxon_key=1340339&occurrence_status=present&gadm_gid=CAN.11_1 [accessed 15 April 2022].
- Gibbs, J. 2010. Revision of the metallic *Lasioglossum* (*Dialictus*) of Canada (Hymenoptera, Halictidae, Halictini). *Zootaxa*, **2591**: 1–382. <https://doi.org/10.11646/zootaxa.2591.1.1>.
- Gonzalez, V.H., Herbison, N., Robles Perez, G., Panganiban, T., Haefner, L., Tscheulin, T., *et al.* 2024. Bees display limited acclimation capacity for heat tolerance. *Biology Open*, **13**: bio060179. <https://doi.org/10.1242/bio.060179>.
- Gotelli, N.J. and Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**: 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Goulson, D. 2010. *Bumblebees: Behaviour, Ecology, and Conservation*. Second edition. Oxford University Press, Oxford, United Kingdom.
- Grixti, J.C., Wong, L.T., Cameron, S.A., and Favret, C. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation*, **142**: 75–84. <https://doi.org/10.1016/j.biocon.2008.09.027>.
- Hanula, J.L., Horn, S., and O'Brien, J.J. 2015. Have changing forests conditions contributed to pollinator decline in the southeastern United States? *Forest Ecology and Management*, **348**: 142–152. <https://doi.org/10.1016/j.foreco.2015.03.044>.
- Hanula, J.L., Ulyshen, M.D., and Horn, S. 2016. Conserving pollinators in North American forests: a review. *Natural Areas Journal*, **36**: 427–439. <https://doi.org/10.3375/043.036.0409>.
- Hatfield, R., Jepsen, S., Thorp, R., Richardson, L., and Colla, S. 2015. *Bombus terricola*, yellow-banded bumblebee. The International Union for Conservation of Nature Red List of Threatened Species, **2015**: e.T44937505A46440206. <https://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T44937505A46440206>.

- Heinrich, B. and Esch, H. 1994. Thermoregulation in bees. *American Scientist*, **82**: 164–170. <https://www.jstor.org/stable/29775151>.
- Henry, J.D. 2002. *Canada's Boreal Forest*. Smithsonian Institution Press, Washington, D.C., United States of America.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**: 427–432. <https://doi.org/10.2307/1934352>.
- Hopwood, J., Vaughan, M., Shepherd, M., Biddinger, D., Mader, E., Black, S.H., and Mazzacano, C. 2012. Are Neonicotinoids Killing bees? A review of research into the effects of neonicotinoid insecticides on bees, with recommendations for action. Xerces Society for Invertebrate Conservation, Portland, Oregon, United States of America.
- Hothorn, T., Bretz, F., and Westfall, P. 2008. Simultaneous inference in general parametric models. *Biometrical Journal*, **50**: 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Intergovernmental Panel on Climate Change. 2014. *Climate Change 2014 Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Intergovernmental Panel on Climate Change, Genève, Switzerland.
- Jackson, H.M., Johnson, S.A., Morandin, L.A., Richardson, L.L., Guzman, L.M., and M'Gonigle, L.K. 2022. Climate change winners and losers among North American bumblebees. *Biology Letters*, **18**: 20210551. <https://doi.org/10.1098/rsbl.2021.0551>.
- Kammerer, M., Goslee, S.C., Douglas, M.R., Tooker, J.F., and Grozinger, C.M. 2021. Wild bees as winners and losers: relative impacts of landscape composition, quality, and climate. *Global Change Biology*, **27**: 1250–1265. <https://doi.org/10.1111/gcb.15485>.
- Kerr, J.T., Pindar, A., Galpern, P., Packer, L., Potts, S.G., Roberts, S.M., *et al.* 2015. Climate change impacts on bumblebees converge across continents. *Science*, **349**: 177–180. <https://doi.org/10.1126/science.aaa7031>.
- Klein, A., Vaissière, B., Cane, J., Steffan-Dewenter, I., Cunningham, S., Kremen, C., and Tscharntke, T. 2006. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **274**: 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kolde, R. 2019. pheatmap: Pretty heatmaps. R package. Version 1.0.12. Available at <https://cran.r-project.org/web/packages/pheatmap/pheatmap.pdf> [accessed 26 March 2025].
- Kremen, C. 2018. The value of pollinator species diversity. *Science*, **359**: 741–742. <https://doi.org/10.1126/science.aar7614>.
- Larivière, R. and Villeneuve, M. 2014. *Plantes sauvages de la forêt boréale : identifier, déguster, soigner [Wild plants of the boreal forest: identify, taste, care]*. L'ABC de l'édition, Rouyn-Noranda, Québec, Canada.
- Laverty, T.M. and Harder, L.D. 1988. The bumble bees of eastern Canada. *The Canadian Entomologist*, **120**: 965–987. <https://doi.org/10.4039/Ent120965-11>.
- Leboeuf, M. 2016. *Arbres et plantes forestières du Québec et des Maritimes [Forest trees and plants of Quebec and the Maritimes]*. Éditions Michel Quintin, Waterloo, Québec, Canada.
- Lebuhn, G., Droege, S., Connor, E.F., Gemmill-Herron, B., Potts, S.G., Minckley, R.L., *et al.* 2013. Detecting insect pollinator declines on regional and global scales. *Conservation Biology*, **27**: 113–120. <https://doi.org/10.1111/j.1523-1739.2012.01962.x>.
- Legendre, P. and Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**: 271–280. <https://doi.org/10.1007/s004420100716>.
- Legendre, P., Legendre, L., and Legendre, L. 1998. *Numerical Ecology*. Second English edition. Elsevier, Amsterdam, The Netherlands.
- Lenth, R.V. 2021. *Emmeans: Estimated Marginal Means, a.k.a., least-squares means*. R Package. Version 1.7.0.

- Liczner, A.R., Schuster, R., Richardson, L.L., and Colla, S.R. 2023. Identifying conservation priority areas for North American bumble bee species in Canada under current and future climate scenarios. *Conservation Science and Practice*, **5**: e12994. <https://doi.org/10.1111/csp2.12994>.
- Luna Santa-María, J.R. 2021. Diversity patterns and composition of wild bee communities (Hymenoptera: Anthophila) in Swedish boreal forests under different management regime. M.Sc. thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Mathiasson, M.E. and Rehan, S.M. 2019. Status changes in the wild bees of northeastern North America over 125 years revealed through museum specimens. *Insect Conservation and Diversity*, **12**: 278–288. <https://doi.org/10.1111/icad.12347>.
- McCabe, L.M., Cobb, N.S., and Butterfield, B.J. 2019. Environmental filtering of body size and darker colouration in pollinator communities indicate thermal restrictions on bees, but not flies, at high elevations. *PeerJ*, **7**: e7867. <https://doi.org/10.7717/peerj.7867>.
- Memmott, J., Craze, P.G., Waser, N.M., and Price, M.V. 2007. Global warming and the disruption of plant–pollinator interactions. *Ecology Letters*, **10**: 710–717. <https://doi.org/10.1111/j.1461-0248.2007.01061.x>.
- Memmott, J., Waser, N.M., and Price, M.V. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**: 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>.
- Michener, C.D. 2007. *The Bees of the World*. Second edition. Johns Hopkins University Press, Baltimore, Maryland, United States of America.
- Milam, J., Johnson, D.E., Andersen, J.C., Fassler, A.B., Narango, D.L., and Elkinton, J.S. 2020. Validating morphometrics with DNA barcoding to reliably separate three cryptic species of *Bombus* Cresson (Hymenoptera: Apidae). *Insects*, **11**: 669. <https://doi.org/10.3390/insects11100669>.
- NatureServe. 2022. *Bombus terricola*: yellow-banded bumble bee [online]. Available from https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.806567/Bombus_terricola [accessed 15 April 2022].
- Ogilvie, J.E. and Forrest, J.R.K. 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, **21**: 75–82. <https://doi.org/10.1016/j.cois.2017.05.015>.
- Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., *et al.* 2020. *Vegan: Community Ecology Package*. R Package. Version 2.5–7.
- Ollerton, J. 2017. Pollinator diversity: distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*, **48**: 353–376. <https://doi.org/10.1146/annurev-ecolsys-110316-022919>.
- Ollerton, J., Winfree, R., and Tarrant, S. 2011. How many flowering plants are pollinated by animals? *Oikos*, **120**: 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Packer, L., Genaro, J., and Sheffield, C. 2007. The bee genera of eastern Canada. *Canadian Journal of Arthropod Identification*, **3**: 1–32. <https://doi.org/10.3752/cjai.2007.03>.
- Pengelly, C.J. and Cartar, R.V. 2010. Effects of variable retention logging in the boreal forest on the bumble bee–influenced pollination community, evaluated 8–9 years post-logging. *Forest Ecology and Management*, **260**: 994–1002. <https://doi.org/10.1016/j.foreco.2010.06.020>.
- Phillips, B.B., Shaw, R.F., Holland, M.J., Fry, E.L., Bardgett, R.D., Bullock, J.M., and Osborne, J.L. 2018. Drought reduces floral resources for pollinators. *Global Change Biology*, **24**: 3226–3235. <https://doi.org/10.1111/gcb.14130>.
- Pielou, E.C. 1975. *Ecological Diversity*. John Wiley, New York, New York, United States of America.
- Popic, T., Davila, Y., and Wardle, G. 2013. Evaluation of common methods for sampling invertebrate pollinator assemblages: net sampling outperforms pan traps. *PLOS One*, **8**: e66665. <https://doi.org/10.1371/journal.pone.0066665>.

- Proctor, E., Nol, E., Burke, D., and Crins, W.J. 2012. Responses of insect pollinators and understorey plants to silviculture in northern hardwood forests. *Biodiversity and Conservation*, **21**: 1703–1740. <https://doi.org/10.1007/s10531-012-0272-8>.
- Pyke, G.H., Thomson, J.D., Inouye, D.W., and Miller, T.J. 2016. Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. *Ecosphere*, **7**: e01267. <https://doi.org/10.1002/ecs2.1267>.
- R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R., Reilly, J., Bartomeus, I., and Winfree, R. 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology*, **19**: 3103–3110. <https://doi.org/10.1111/gcb.12264>.
- Rafferty, N.E. 2017. Effects of global change on insect pollinators: multiple drivers lead to novel communities. *Current Opinion in Insect Science*, **23**: 22–27. <https://doi.org/10.1016/j.cois.2017.06.009>.
- Roberts, D.W. 2019. labdsv: Ordination and Multivariate Analysis for Ecology. R package. Version 2.0-1. Available from <https://rpkgs.net/package/labdsv> [accessed 20 April 2025].
- Rodríguez, A. and Kouki, J. 2017. Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecological Applications*, **27**: 589–602. <https://doi.org/10.1002/eap.1468>.
- Romey, W.L., Ascher, J.S., Powell, D.A., and Yanek, M. 2007. Impacts of logging on midsummer diversity of native bees (Apoidea) in a northern hardwood forest. *Journal of the Kansas Entomological Society*, **80**: 327–338.
- Rubene, D., Schroeder, M., and Ranius, T. 2015. Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat, and surrounding landscape. *Biological Conservation*, **184**: 201–208. <https://doi.org/10.1016/j.biocon.2015.01.029>.
- Sánchez-Bayo, F. and Wyckhuys, K.A.G. 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation*, **232**: 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>.
- Shugart, H.H., Leemans, R., Bonan, G.B., and Payette, S. 2005. A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, United Kingdom.
- Sirois-Delisle, C. and Kerr, J.T. 2018. Climate change-driven range losses among bumblebee species are poised to accelerate. *Scientific Reports*, **8**: 14464. <https://doi.org/10.1038/s41598-018-32665-y>.
- Song, B., Niu, Y., Stöcklin, J., Chen, G., Peng, D.-L., Gao, Y.-Q., and Sun, H. 2015. Pollinator attraction in *Cornus capitata* (Cornaceae): the relative role of visual and olfactory cues. *Journal of Plant Ecology*, **8**: 173–181. <https://doi.org/10.1093/jpe/rtv012>.
- Soroye, P., Newbold, T., and Kerr, J. 2020. Climate change contributes to widespread declines among bumble bees across continents. *Science*, **367**: 685–688. <https://doi.org/10.1126/science.aax8591>.
- Szabo, N.D., Colla, S.R., Wagner, D.L., Gall, L.F., and Kerr, J.T. 2012. Do pathogen spillover, pesticide use, or habitat loss explain recent North American bumblebee declines? *Conservation Letters*, **5**: 232–239. <https://doi.org/10.1111/j.1755-263X.2012.00234.x>.
- Taki, H., Okochi, I., Okabe, K., Inoue, T., Goto, H., Matsumura, T., and Makino, S.I. 2013. Succession influences wild bees in a temperate forest landscape: the value of early successional stages in naturally regenerated and planted forests. *PLOS One*, **8**: e56678. <https://doi.org/10.1371/journal.pone.0056678>.
- Tucker, E.M. and Rehan, S.M. 2017. High-elevation refugia for *Bombus terricola* (Hymenoptera: Apidae) conservation and wild bees of the White Mountain National Forest. *Journal of Insect Science*, **17**: 4. <https://doi.org/10.1093/jisesa/iiew093>.
- Urban-Mead, K.R., Muñoz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M., *et al.* 2021. Bees in the trees: diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management*, **482**: 118903. <https://doi.org/10.1016/j.foreco.2020.118903>.

- Vanbergen, A.J. and the Insect Pollinators Initiative. 2013. Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment*, **11**: 251–259. <https://doi.org/10.1890/120126>.
- Venjakob, C., Klein, A.-M., Ebeling, A., Tschardtke, T., and Scherber, C. 2016. Plant diversity increases spatio-temporal niche complementarity in plant–pollinator interactions. *Ecology and Evolution*, **6**: 2249–2261. <https://doi.org/10.1002/ece3.2026>.
- Wagner, D.L. 2020. Insect declines in the Anthropocene. *Annual Review of Entomology*, **65**: 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>.
- Westerfelt, P., Weslien, J., and Widenfalk, O. 2018. Population patterns in relation to food and nesting resource for two cavity-nesting bee species in young boreal forest stands. *Forest Ecology and Management*, **430**: 629–638. <https://doi.org/10.1016/j.foreco.2018.08.053>.
- Whitfield, J.B., Purcell, A.H., and Daly, H.V. 2013. *Daly and Doyen's Introduction to Insect Biology and Diversity*. Third edition. Oxford University Press, New York, New York, United States of America.
- Williams, P.H. and Osborne, J.L. 2009. Bumblebee vulnerability and conservation worldwide. *Apidologie*, **40**: 367–387. <https://doi.org/10.1051/apido/2009025>.
- Williams, P.H., Thorp, R.W., Richardson, L.L. and Colla, S. 2014. *Bumble Bees of North America: An Identification Guide*. Princeton University Press, Princeton, New Jersey, United States of America.
- Wilson, J.S. and Carril, O.M. 2015. *The Bees in Your Backyard: A Guide to North America's Bees*. Princeton University Press, Princeton, New Jersey, United States of America.
- Zitomer, R.A., Galbraith, S.M., Betts, M.G., Moldenke, A.R., Progar, R.A., and Rivers, J.W. 2023. Bee diversity decreases rapidly with time since harvest in intensively managed conifer forests. *Ecological Applications*, **33**: e2855. <https://doi.org/10.1002/eap.2855>.
- Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S., and Dorn, S. 2010a. Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology*, **79**: 674–681. <https://doi.org/10.1111/j.1365-2656.2010.01675.x>.
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., and Dorn, S. 2010b. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, **143**: 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>.