Trees, degrees, wasps and bees: The microclimatic effects of forest cover in agricultural land and impacts on the nesting success of solitary cavity-nesting bees and wasps

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Abstract

Forests buffer temperatures to create cooler, more stable thermal environments, or 'microclimates'. Agricultural landscapes can be severely lacking in thermal-buffering features (like forest cover) and can become very hot environments in summer. Solitary cavity-nesting bees and wasps occur in agricultural landscapes and provide crucial ecosystem services (pollination, pest control). It is well documented that high temperatures disrupt the reproduction and development of insects, but there remain unanswered questions about how solitary, cavity-nesting bees and wasps that occur in agricultural landscapes are impacted by forest microclimates and high temperatures, especially in terms of their nesting success. In this study, I investigated the impacts of forest cover in agricultural landscapes on temperature inside bee and wasp cavity-nests in margins adjacent to crop fields, and the impacts of forest cover plus nest temperature on the nesting of solitary cavity-nesting bees and wasps. I observed two scales of forest cover: at the scale of 1 km-radius landscapes and at the local, field-margin scale, where margins were either forested or open. My first objective was: (1) to assess the effect of forest cover in agricultural landscapes on nest temperatures. Next, I investigated the impact of forest cover and nest temperatures on (2) nest abundance and richness, (3) brood cell number and (4) developmental success. Daily maximum, mean and range of nest temperatures were significantly lower in forested field margins, but forest cover at a larger scale (in 1-km radii) had no effect on nest temperature. Cavity-nests in forested margins had greater probability of developmental success, but forest cover (neither scale) and nest temperature were not associated with any changes in nest richness or brood cell number. Cavity-nesting bees were more associated with open margins, while wasps were more associated with forested margins. These findings point to the potential of incorporating both forested and open habitat types in agricultural landscapes to better support solitary cavity-nesting bees and wasps.

Keywords: Nesting success, Nesting habitat, Cavity-nesting bees, Cavity-nesting wasps, Agriculture, Agroecosystem, Field margins, Temperature, Forest cover, Thermal ecology.

Résumé

Les forêts atténuent les températures pour créer des environnements thermiques moins chaud et plus stables, ou « microclimats ». Les paysages agricoles peuvent manquer cruellement d'attributs de régulation thermique (comme la couverture forestière) et, en été, ils peuvent devenir des environnements très chauds. Les abeilles et les guêpes solitaires nichant dans les cavités sont présentes dans les paysages agricoles et fournissent des services écosystémiques essentiels (pollinisation, consommation de ravageurs). Il est bien connu que les températures élevées peuvent perturber la reproduction et le développement des insectes, mais il reste des questions sans réponse sur la manière dont les abeilles et les guêpes solitaires nichant dans les cavités et présentes dans les paysages agricoles peuvent être affectées par les températures élevées et les microclimats des forêts, en particulier sur la manière dont la reproduction (succès de la nidification) est affecté. Dans cette étude, j'ai étudié les impacts de la couverture forestière dans les paysages agricoles sur la température à l'intérieur des nids d'abeilles et de guêpes dans les marges adjacentes aux champs, et les impacts de la couverture forestière et de la température des nids sur la nidification des abeilles et des guêpes solitaires nichant dans des cavités. Mon premier objectif était de : (1) évaluer l'effet du couvert forestier dans les paysages agricoles sur la température des nids. Ensuite, j'ai étudié l'impact du couvert forestier et des températures des nids sur (2) l'abondance et la richesse des nids, (3) le nombre de cellules de nids (4) le succès du développement. Les températures quotidiennes maximales, moyennes et étendues des nids étaient significativement inférieures dans les marges boisées, mais la couverture forestière à l'échelle des paysages (dans un rayon de 1 km) n'avait aucun effet sur la température du nid. Les nids dans les marges boisées avaient une plus grande probabilité de succès de développement, mais la couverture forestière (ni l'échelle) ni la température du nid n'étaient associées à des changements dans la richesse du nid ou dans le nombre de cellules du couvain. Les nids creux des abeilles étaient davantage associés aux lisières ouvertes, tandis que ceux des guêpes étaient davantage associés aux lisières forestières. Ces résultats soulignent le potentiel d'incorporer les habitats boisés et ouverts dans les paysages agricoles pour mieux soutenir les abeilles et les guêpes nichant dans les cavités.

Mots clés: Succès de nidification, Habitat de nidification, Abeilles nichant dans les cavités, Guêpes nichant dans les cavités, Agriculture, Bordures de champs, Température, Couvert forestier, Écologie thermique.

Acknowledgements

Long before my study area was converted to agricultural land, it was inhabited and stewarded by Algonquin, Anishinaabeg, Haudenosaunee and Mohawk peoples. Much of western science, including ecology, was adapted from traditional ways of knowing that indigenous people in North America (Turtle Island) honed over many generations. European colonizers killed and displaced millions of indigenous peoples in North America and drained resources and wealth from the land that they stole. Today, descendants of indigenous people endure transgenerational trauma, poverty, and institutional racism. When in the field, I was reminded of the history that took place in my study sites. I feel that all ecologists should acknowledge indigenous history, learn about the contributions of indigenous people to western sciences, and help to contribute to a better future for indigenous people.

My supervisors, Dr. Ilona Naujokaitis-Lewis (ECCC) and Dr. Jessica Forrest (uOttawa) contributed invaluable expertise, support and time to my thesis project, and even worked over weekends to edit drafts or join me in the field. I am thoroughly grateful for the trust and support of my supervisors, and I feel that this project could not have been successful without their valuable insight. My thesis advisory committee, Dr. Lenore Fahrig and Dr. Heather Kharouba, provided helpful feedback during my degree.

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Figure S1. Map of study sites (N= 17 crop field sites) located outside of Ottawa city limits. The minimum distance between study sites was 3.2 km.

Figure S2. Cavity-nesting bees and wasps at field sites and on nest blocks (artificial nesting habitat). A: Female *Megachile* bee leaving the cavity-nest entrance. B: Female *Megachile* bee returning to her cavity-nest with pollen on her abdominal scopa (hairs specialized for collecting pollen). Other megachilid bees (e.g. *Chelostomoides* spp., *Heriades* spp., *Hoplitis* spp., *Osmia* spp.) carry pollen in the same manner. C: Eumenine wasp that recently emerged from its cavity-nest. D: Eumenine wasp flying into a cavity-nest entrance.

Chapter One: Introduction

Local air temperature is influenced by the presence of abiotic and biotic attributes that can buffer or amplify heat from the sun. Topography, water bodies, sun exposure, vegetation (e.g. tree canopy, understorey plants ; Bramer et al., 2018 ; Maclean et al., 2021) and anthropogenic structures (e.g. buildings ; Wong et al., 2016) directly impact local air temperature (Bramer et al., 2018) to such an extent that air temperatures within their influence vary substantially from free-air macroclimates. We can refer to these thermally-distinct local environments as microclimates (Geiger et al., 1995 ; Bramer et al., 2018). To understand how land use impacts organisms, we must first discover how local landscape features contribute to microclimates, and how those microclimates affect organism survival and fitness.

Forest canopies can block solar radiation, precipitation, wind, etc., from reaching the sub-canopy environment, and create a distinct microclimate within (Chen et al., 1999; von Arx et al., 2012 ; De Frenne et al., 2019). During the summer, in temperate regions, canopies have peak foliage density (Park & Jeong, 2021; Hes et al., 2024), which blocks solar radiation, resulting in lower understorey temperatures relative to temperatures outside of forest cover (Hes et al., 2024 ; De Lombaerde et al., 2022). Trees also perform evapotranspiration, by pulling water from the soil and releasing it into the air. In the summer, the water they release absorbs heat from the air, making the local temperature beneath forest cover cooler. In their global review of forest microclimate studies, De Frenne et al., (2019) demonstrated that forest cover significantly lowered local average temperatures, maximum temperatures, and overall temperature fluctuation.

The scale of land that organisms interact with in their lifetime is species-specific, and so, the spatial scale of microclimatic effects can be more or less biologically meaningful to different species. This is why, when studying microclimates, it is important to consider spatial scale.

A small forest patch, or even a single tree, can lower or stabilize temperatures in the area directly beneath its canopy (Baker et al., 2016 ; Hofmeister et al., 2019)—an area that could be biologically meaningful for a small animal. However, forest cover can also influence temperature on a larger spatial scale (Saunders et al., 1998). For example, a large piece of land (e.g. multiple hectares) with higher forest cover should consequently have more shade and higher evapotranspiration. These factors could mediate more thermal buffering throughout the land, resulting in landscape-wide temperature that is, on average, cooler and less variable than temperature averaged across an equal-size landscape with lower forest cover (De Frenne et al. 2019).

Forest microclimates at any scale may be a crucial habitat resource in agricultural landscapes, which generally lack thermal-buffering attributes (e.g. tree cover, water bodies, or variable topography, etc.). Without these attributes, open agricultural landscapes and the organisms within can be exposed to the full heat of the sun. Additionally, climate change is making summertime temperatures hotter (Vogel et al., 2019 ; Lin & Wang, 2022) and increasing the intensity and frequency of heat waves (Frich et al., 2002 ; IPCC, 2007 ; Brown, 2020). Organisms in agricultural landscapes likely will endure warmer temperatures, and potentially more heat stress, than they have experienced or are adapted to.

Agricultural landscapes contain a variety of managed or unmanaged woody features, including linear woodlots (also called forested margins, hedgerows, etc.). These features were historically implemented to provide wind protection (Burel, 1996) and prevent soil erosion (Sobieraj-Betlińska et al., 2023) but can also buffer temperature to produce microclimates (Forman & Baudry, 1984 ; Sánchez et al., 2010 ; Vanneste et al., 2020). Forested margins, therefore, could serve as beneficial habitat to organisms in agricultural land looking to evade extremely high temperatures.

Many bees and wasps occur in agricultural landscapes, where they provide valuable ecosystem services and potentially endure extreme heat exposure. High temperatures are lethal to bees and wasps when they surpass the insects' physiological limits (Scheffers et al., 2014) and cause irreparable damage to essential enzymes and genetic material (González-Tokman et al., 2020 ; Nacko et al., 2023). The threshold at which an animal loses muscle control and dies is known as the critical thermal maximum (Lutterschmidt & Hutchison, 1997 ; Lighton & Turner, 2004). The critical thermal maxima of *Megachile* bees (Megachilidae) and *Vespula* wasps (Vespidae) are between 45℃ and 48℃ (Hamblin et al., 2017 ; Käfer et al., 2012). While local air macroclimate temperatures might never reach CT_{max} levels, bees and wasps are still at risk of experiencing such extremes, because muscular activity (Sotavalta, 1954 ; Kammer & Heinrich, 1974) and solar radiation can raise body temperature substantially (Digby, 1955). In open, hot agricultural landscapes, the risk of lethal heat exposure may be substantial.

Heat exposure can interfere with insect demography and have consequences to fitness. More specifically, heat exposure can disrupt reproduction (i.e. male fertility (Nguyen et al., 2013 ; El-Sabrout et al., 2021 ; Martinet et al., 2021) and development (Melone et al., 2024) in bees and wasps. In juvenile bees and wasps, heat exposure can disrupt developmental rates (Storey & Storey, 2004 ; González-Tokman et al., 2020) and reduce survival (Radmacher & Strohm, 2011 ; CaraDonna et al., 2018 ; Melone et al., 2024). While adult bees and wasps are mobile (flying), juveniles are mostly immobile and are confined to their nests until they reach adulthood (Krombein, 1967 ; Michener, 2000), and are less likely to overheat from muscular activity or direct sun exposure. Still, there are disadvantages to being immobile and confined to a nest, especially for solitary bees and wasps as opposed to social ones. Solitary bee and wasp species do not perform parental care of larvae, and parents do not facilitate thermoregulatory cooling of brood (Jones & Oldroyd, 2006). Therefore, juvenile solitary bees and wasps are forced to endure the thermal conditions of their nest environment.

In addition to temperature extremes, temperature fluctuations might also impact the survival, reproduction or development of bees and wasps. Radmacher & Strohm, (2011) found that both high and fluctuating temperatures sped up juvenile development and dramatically increased adult mortality of *Osmia bicornis*, a cavity-nesting bee. Previous work looking at temperature and bees/wasps has tended to focus on the impacts of constant temperature extremes (Hamblin et al., 2017; Kemp & Bosch, 2005 ; Käfer et al., 2012) or heat shocking (Melone et al., 2024) and there remain unanswered questions about the impacts of temperature fluctuation—which, as noted above, may be greater in landscapes lacking thermal buffering features.

Forest understorey microclimates could contribute to more abundant and/or more diverse bee and wasp communities relative to nearby unforested areas. Some bees select nest locations based on thermal factors, like sun exposure (seen in *Megachile* spp., Wilson et al., 2020). Some wasps may have similar temperature-based criteria when selecting nest location; *Polistes* wasps, for example, select wind-sheltered nesting locations or build their nests to face the morning sun, resulting in warmer nest microclimates (Kovac et al., 2023).

Forest microclimates may also provide non-thermal benefits to bees and wasps in agricultural lands. For example, numerous woodland plants cannot exist in open (hotter) agricultural land, but can persist in (cooler) forest microclimates (McCollin et al., 2000 ; Van Den Berge et al., 2018). With these distinct plant communities, forest patches in agricultural landscapes may support a larger, or unique, community of bees and wasps (Bartual et al., 2019 ;

Holzschuh et al., 2009), relative to nearby agricultural land without forest cover. Second, some bees forage on flowering trees (Sheffield, 2014 ; Urban-Mead et al., 2021) and may choose to nest nearby. Additionally, the prey of many solitary wasps are insects or spiders, which can be abundant in forested areas (Fateryga, 2020). More work is needed to explore what roles forest microclimates play in agricultural landscapes and how they impact the diversity and nesting success of solitary bees and wasps.

Today, there is a growing body of literature on the effects of heat exposure on the reproduction or development of social bees, including honey bees (*Apis* spp., Wang et al., 2016 ; Abou-Shaara et al., 2017 ; Rousseau et al., 2020) and bumblebees (*Bombus* spp., Guiraud et al., 2021 ; Campion et al., 2023 ; Sepúlveda et al., 2024). But the vast majority of bee and wasp species are solitary, not social (Batra, 1984). Further, a subset of solitary bee and wasp species are cavity-nesters; that is, they nest in above-ground cavities, like holes in dead wood or reeds. By nesting above-ground, these species may be more exposed to thermal stress than ground-nesting species. There is a general lack of knowledge regarding how heat exposure can impact solitary, cavity-nesting bees; even less is known about its impacts on solitary wasps. Furthermore, it is unclear whether forest microclimates can effectively limit heat exposure in cavity-nesting bees and wasps.

Cavity-nesting bees and wasps provide important ecosystem services and their vulnerability to heat exposure or temperature fluctuations should be of concern. Some cavity-nesting bees are commercial crop pollinators (Ballantyne et al., 2017), like *Osmia* spp. (orchard fruits: apple, nectarine) and *Megachile rotundata* (alfalfa; Pitts-Singer & Cane, 2011). Solitary bees also pollinate most of the world's wild flowering plants (Klein et al., 2018), including wild plants in agricultural land (Blaauw & Isaacs, 2014 ; Lowe et al., 2024). Solitary wasps are predators to many prolific crop pests (Udayakumar et al., 2022), and provide massive benefits to crop yield globally (Southon et al., 2019). While wasps are not as effective pollinators as bees, many plants still benefit from (Ivey et al., 2003 ; Brock et al., 2021) or rely on their pollination services (Mant et al., 2002 ; Hallett et al., 2017). Collectively, bees and wasps have major impacts on plant diversity, the human diet and the economy (Klein et al., 2018). From conservation and economic perspectives, the nesting biology of wild bees and wasps should be a central concern.

In this study, I investigated the impacts of forest cover in agricultural landscapes on local temperature in margins adjacent to crop fields, and the consequences of forest cover, plus resulting thermal fluctuation, for the nesting success and richness of solitary cavity-nesting bees and wasps. I assessed the impact of forest cover at two scales: at the scale of 1 km-radius landscapes (henceforth referred to as "percent forest cover"), and at the local, field-margin scale (henceforth "margin type", where margins were either forested or open). My first objective was: (1) to assess the effect of forest cover (percent forest cover and margin type) in agricultural landscapes on nest temperatures. Next, I investigated the impact of forest cover (percent forest cover and margin type) and local temperatures on (2) nest abundance and richness, (3) brood cell number and (4) developmental success of cavity-nesting bees and wasps in crop field margins.

Chapter Two: Methodology

Study area and site selection

The study took place in eastern Ontario, outside Ottawa, Canada, from April to November 2023 (Appendix I: Figure S1). The study area is predominantly agricultural land, and all of my study sites consisted of field margins adjacent to crop fields. Agriculture in the region is dominated by soy, corn, wheat, and alfalfa or alfalfa mixtures (Government of Canada, 2022). Summer climate in this region is warm and humid (Government of Canada, 2023). During the hottest month in this region (July), maximum daytime temperatures average 27℃ and minimum temperatures average 15℃ (Government of Canada, 2023).

Land surface temperatures were obtained from the U.S. Geological Survey (earthexplorer.usgs.gov) on May 5, 2021, the optimal measurement day with lowest cloud cover. Woody features shapefiles were obtained from Ontario's Ministry of Natural Resources, and used to describe the % forest cover, or the total area within a 1 km buffer with woody features, across my study region. I used these data to select 17 crop fields with a broad range of % forest cover (1.9 to 83.5 %; mean 27.1% ± SD 23.3) and land surface temperature (25.6℃ to 37.9℃; mean 30.6℃ ± SD 3.2℃) within a 1 km radius. I chose a minimum inter-site distance of 3.2 km to minimize the potential for the same individual insects to occur in multiple sites.

I selected fields with commonly grown crops in the region, such as soy, corn, and wheat (Statistics Canada, 2021), plus one site with clover (rotation crop). I required crop fields with a 50-m section of field edge that contained a dense canopy of mature deciduous and coniferous trees, and a 50-m section that was free of mature trees or shrubs, but could include tall grasses and forbs (henceforth, “forested” and “open” margins, respectively).

All observations of bees, wasps, and temperature took place in these margins. To confirm the difference in canopy cover between margin types, I analyzed spherical photographs of the canopy directly above a nest block and temperature logger set-up (Figure 1A), taken using a smartphone camera with a fish-eye lens attachment. Open margin canopy cover ranged from 0.0 to 9.8% cover and averaged (mean ± SD) 1.8 ± 3.1% (n = 17). Forested margins ranged from 76.3% to 94.4% cover and averaged 88.1 ± 5.3% (n = 17). It is likely that all margins in my study were exposed to pesticides that were sprayed onto crops.

Study organisms

A number of solitary, cavity-nesting bee and wasp species will nest inside “nest blocks” (also named “trap nests”, “bee hotels”, “bee boxes”, or “bee condos”; MacIvor, 2017). Nest blocks are human-made, standardized nesting habitat, useful for studying nesting rates and behaviours of solitary cavity-nesting bees and wasps because the researcher can decide the location of nesting habitat, rather than needing to locate natural bee or wasp nests in the field (MacIvor, 2019). However, nest blocks only capture a subset of bee and wasp species: those that seek out pre-existing cavities in wood, *and* that will accept human-made cavities (Cane et al., 2007). I acknowledge that my method of sampling excludes the majority of locally-occurring solitary bees and wasps.

Solitary female bees and wasps build their nests individually. After mating, a cavity-nesting female bee or wasp will select a nest cavity. Then, over a few days, she constructs a single-file row of brood cells inside the cavity (see Figure 1B), in which each cell contains an egg plus food provisions (Krombein, 1967). Mated females can construct multiple separate cavity nests in succession. Depending on the species, bees and wasps separate brood cells within a nest using materials they collect and process into nest ‘walls’, such as foliage, mud, tree resin, or rocks (Krombein, 1967). For example, many *Megachile* spp. (“leaf-cutter bees”; Figure S2 A-B) use fragments of foliage to build partitioning walls (Krombein, 1967). To complete a nest, the females add a final, enclosing wall to the cavity entrance.

Bees provision offspring with pollen and nectar; wasps provision with paralyzed spiders or insects, such as lepidopteran caterpillars, beetle larvae, or aphids. Each offspring will complete its development inside the brood cell constructed by its mother (Krombein, 1967). Bee and wasp offspring are vulnerable to, and targeted by, a range of predators and parasites (Krombein, 1967). They are also vulnerable to excess moisture and mold. However, if the larva survives, once it is sufficiently grown, or once all provisions are eaten, it spins a cocoon. In temperate zones, including Ontario, many bees and wasps go dormant after spinning their cocoon, and will overwinter at this (prepupal) stage and then undergo pupation and emerge as adults in spring (Krombein, 1967). Other species, including *Osmia* bees, will overwinter inside their cocoons as adults. Others, including eumenine wasps (Figure S2C-D), are facultatively bivoltine, meaning that wasps that emerge in spring/summer can produce progeny which emerge and also reproduce during the same summer.

Nest blocks

To study diversity and nesting success (i.e. nest abundance, brood cell number and developmental success of brood cells) of cavity-nesting bees and wasps, I constructed and installed nest blocks in open and forested field margins and conducted observations of nest occupancy throughout summer 2023. Nest blocks were installed over a period of one month (April 10 to May 16, 2023) and then collected over a period of three weeks (October 15 - November 8, 2023) with the exception of blocks from one site which were collected September

22. Later, I collected and dissected bee and wasp nests from nest blocks to identify occupants and quantify progeny development.

To construct nest blocks, I cut untreated 5 cm × 15 cm softwood lumber into 15 cm lengths. In each piece, I drilled five holes of three different sizes (two of diameter 6.35 mm, two 7.94 mm and one 9.52 mm) through the entire length of the wood. Offering multiple cavity sizes can attract a diversity of cavity-nesting bees and wasps. I coated all blocks with four coats of water-based polyurethane (including inside of cavities) to protect from water and sun damage. Next, I bound two 15 cm lengths of wood together with zip ties to create one nest block containing 10 cavities (four small, four medium and two large). I placed paper straws of different sizes (inner straw diameters: 4.60 mm, 6.35 mm and 7.80 mm), that were folded closed at the rear end, in all cavities. This way, any nests made by bees or wasps were contained inside the straws, which I could easily retrieve during nest observations. In the following, I consider the complete contents of a straw to be an individual bee or wasp nest—except for cases where a nest was usurped by another individual and so a straw contained two nests.

I plugged the rear end of all nest block cavities with a small amount of black silicon caulking to protect nests from exposure and water damage. The opposite ends of cavities were left unplugged to allow bees and wasps to enter straws and construct their nests. Anecdotal evidence suggests that *Osmia* spp. prefer blackened wood cavities over light wood. For this reason, I scorched the unplugged sides of nest blocks with a blow torch (prior to the polyurethane treatment) and sprayed black paint on the outward ends of paper straws. I attached 'roofs' (8.9 cm by 17.8 cm pieces of plastic-coated medium-density fibreboard) to the top of each nest block to minimize water damage.

Nest blocks were attached to wooden stakes at a height of 0.7 m. To prevent nest predation by ants and earwigs, I applied Tanglefoot® resin to the bottom of each wooden stake. In all, I installed 68 nest blocks (two per margin, two margins per site, 17 sites).

During summer 2023, I checked for new nests on a monthly basis, and evicted any non-bee or non-wasp occupants, such as spiders, earwigs or ants. Also, I frequently removed paper straws and re-drilled holes to repair wood shrinkage due to rain and sun exposure.

Nest dissections

In November 2023, I collected all nest blocks from the field and dissected all bee and wasp nests. The goals of nest dissections were to determine the taxonomic identity of the insect that had constructed each nest, count the number of brood cells, and assess the developmental success of each offspring. I identified nest occupants by opening one end of each paper straw and looking inside to inspect nest characteristics, such as construction materials, construction methods, leftover food provisions, and cocoon characteristics (See Table 1 for details). I was capable of identifying most bee nests to genus level; however, I could not identify some wasp nests or parasitoid cocoons beyond family or subfamily level (i.e., Chrysididae, Eulophidae, Eumeninae, and Ichneumonidae). Some wasp nests (68 out of 563 nests) could not be identified to any taxonomic level and were excluded from nest richness analyses but were included in all nesting success analyses. I identified some parasitic wasps (i.e. Chrysididae, Eulophidae, and Ichneumonidae) using dead adults that remained inside nests. In some cases, I identified empty parasite cocoons as evidence of ichneumonid or chrysidid wasp occupants. Despite this, there are numerous examples of unidentified cocoons.

Next, I counted the number of brood cells. To do this, I cut open nest straws from end to end with microscissors (Figure 1B). With the nests of some taxa (e.g. eumenine wasps), brood cell number could be counted without dissection, simply by holding the straw in a dark place and shining a flashlight from one side. This illuminated the straw and highlighted individual cells and their partitioning walls, allowing me to count each cell. Some mothers include “vestibules” near the nest entrance or "intercalary cells", which are empty spaces between nest cells. These were distinguishable from true nest cells because they did not contain food provisions, and were not counted as nest cells. In some cases, all offspring had fully developed and left the nest prior to nest collection. To quantify the number of brood cells, I counted cocoons (which often remain adhered to the straw’s inner walls). I also referred to observational data of nest cell number, which I recorded on a monthly basis throughout the summer.

After counting the number of brood cells, I recorded the developmental stage that each offspring had reached, even if it had since died. I assumed offspring were still alive unless there were obvious signs of mortality, such as desiccation, dismemberment, mold, etc. To record development of brood cells, nest straws needed to be fully opened with microscissors. Because assessing offspring development was a time-consuming process, I opted to only assess offspring development in a stratified random subset of nests. I stratified nests by site, margin, taxon, and cavity size, and selected up to three random nests within each stratum, leaving me with a subset comprising 73.5% of all nests. The developmental stages that I observed were: egg, larva, cocoon, and adult. All egg-stage brood cells included an egg and food provisions. Larva-stage brood cells included a larva that had yet to spin a cocoon. These larvae could also be surrounded by uneaten provisions, suggesting they had not developed sufficiently for spinning their cocoons. Mold growth on pollen provisions sometimes prevented me from locating eggs or larvae, and the developmental stage of these offspring was labeled as “unknown”. I described host cocoons as "cocoon-stage" cells, but did not open individual cocoons. To detect cocoons in *Megachile* nests, I peeled away leaf material from around cocoons. Adult-stage offspring were fully-developed bees or wasps that had left their cocoon. In some cases, a nest cell contained only an empty cocoon, no remaining provisions, and holes in walls leading to the nest entrance, suggesting that an adult bee or wasp had left the nest. I counted these as adults.

Some offspring died due to predation, parasitism, mold, or unidentified causes. To the best of my ability, I recorded the cause of death for each offspring. Parasites included minute parasitoid wasps (*Melittobia* spp.; Eulophidae) and brood-parasitic wasps (e.g. *Sapyga* spp., Chrysididae). Predators included ants, earwigs, and other unidentified animals. All bee or wasp parasites were counted as nest occupants, and were included in analyses of nest richness, but brood predators were not included. Some offspring died after being chewed through by their emerging siblings. Regardless of an offspring’s cause of death, if it had spun a cocoon before death, its developmental stage was recorded as “cocoon”.

Table 1. Characteristics of nest construction and materials used by solitary cavity-nesting bees and wasps. Information from (Krombein, 1967 ; Matthews et al., 2009 ; Martynova, 2020 ; Holm, 2022) and personal observations.

Bee / Wasp	**Taxon**	**Occupant type**	**Nest materials and traits**	**Provisions**	**Nests observed (out of 680 cavities)**
Wasp	Eumeninae (Vespidae)	Cavity-nest builder	Walls constructed of mud, no trace of leaf material. Cocoons thin, beige, translucent, and normally occupying the full height and width (but not always length) of their cavity (straw) - unlike other cavity-nesting wasps.	Lepidopteran caterpillars, beetle larvae	209
	Isodontia spp. (Sphecidae)	Cavity-nest builder	Grass fronds only. Large translucent cocoons. Cocoon material thicker than that of Eumeninae.	Crickets, katydids	4
	Passaloecus spp. (Crabronidae)	Cavity-nest builder	Conifer resin. Larvae yellow. Colourless translucent cocoons. Sometimes aphid legs remain in cocoons.	Aphids	11
	Trypoxylon spp. (Crabronidae)	Cavity-nest builder	Mud walls to which narrow cocoons (narrower than straw) are attached at one end. Cocoons thin, beige or brown, more developed (i.e. thicker and more opaque) than those of Eumeninae.	Spiders	12
	Dipogon spp. (Pompilidae)	Cavity-nest builder	Cocoons are surrounded by loose dirt and sometimes vegetation. No partitioning between cells, but there are mud walls at the entrance and back of nest. Cocoons are opaque, white to beige, and more developed than cocoons of Eumeninae or	Spiders	14

			Isodontia spp.		
	Ichneumonidae	Parasitoid	Small narrow cocoons inside host cocoon or nest cell. Cocoons are white, beige, brown or reddish brown; often opaque and have polished surface.	N/A	N/A
	Eulophidae (likely *Melittobia* spp.)	Parasitoid	Minute (~1 mm) transparent, white cocoons with grey spots. Many dozen can be found inside host cocoon or nest cell. Sometimes adults are present amongst larvae and pupae. Adults are minute (~1.5 mm) black wasps.	N/A	N/A
	Chrysididae	Brood parasite	Brown or reddish brown cocoons with polished surface. May kill host before or after host spins cocoon.	N/A	N/A
	Sapyga spp. (Sapygidae)	Brood parasite	Translucent, brown cocoons. Brood parasites of megachilid bees, especially *Osmia* spp., in my study area.	N/A	N/A
Bee	*Hylaeus* spp. (Colletidae)	Cavity-nest builder	Thin, colourless, cellophane-like building material. Cocoons are transparent, such that larvae are visible from outside.	Pollen	23
	Megachile spp. (subgenera other than *Chelostomoides* ;Megachilidae)	Cavity-nest builder	Walls made with circular leaf pieces, sometimes mud/sand is incorporated, or sometimes made entirely of mud, depending on species. Cocoons are opaque beige or white and are covered with larval frass. Overwinter as larvae (prepupae) in cocoons.	Pollen	139
	Osmia spp. (Megachilidae)	Cavity-nest builder	Walls of masticated vegetation and/or mud/sand. Cocoons opaque, beige or brown.	Pollen	71

			Overwinter as adults in study region.		
	Hoplitis spp. (Megachilidae)	Cavity-nest builder	Walls of masticated vegetation and sometimes small rocks. Cocoons translucent, white. Overwinter as larvae (prepupae) in study region.	Pollen	11
	Megachile (Chelostomoides) spp. (Megachilidae)	Cavity-nest builder	Walls of resin and mud. Resin is translucent, thick and sticky. Cocoon thicker than in *Hylaeus* sp.	Pollen	2
	Heriades spp.	Cavity-nest builder	Walls of resin, usually 0.2 to 0.5 in thickness. Resin walls were opaque.	Pollen	1
	Coelioxys spp. (Megachilidae)	Brood parasite	Parasites of *Megachile* in our study region.	N/A	N/A

Nest temperature

I recorded temperatures inside nest boxes at all field margins throughout summer 2023 in every open and forested margin (N = 34; described above). I installed Thermochron iButton loggers (model: DS1925L, accuracy ± 0.45℃) inside small holes drilled into nest blocks (0.8 mm deep, 19 mm wide) before deploying the nest blocks into the field (Figure 1A). Logging frequency was 15 minutes. To prevent local vegetation influences on temperature measurements, I used hedge trimmers to cut down all vegetation within a 1 m radius of the loggers. I re-trimmed vegetation throughout the summer.

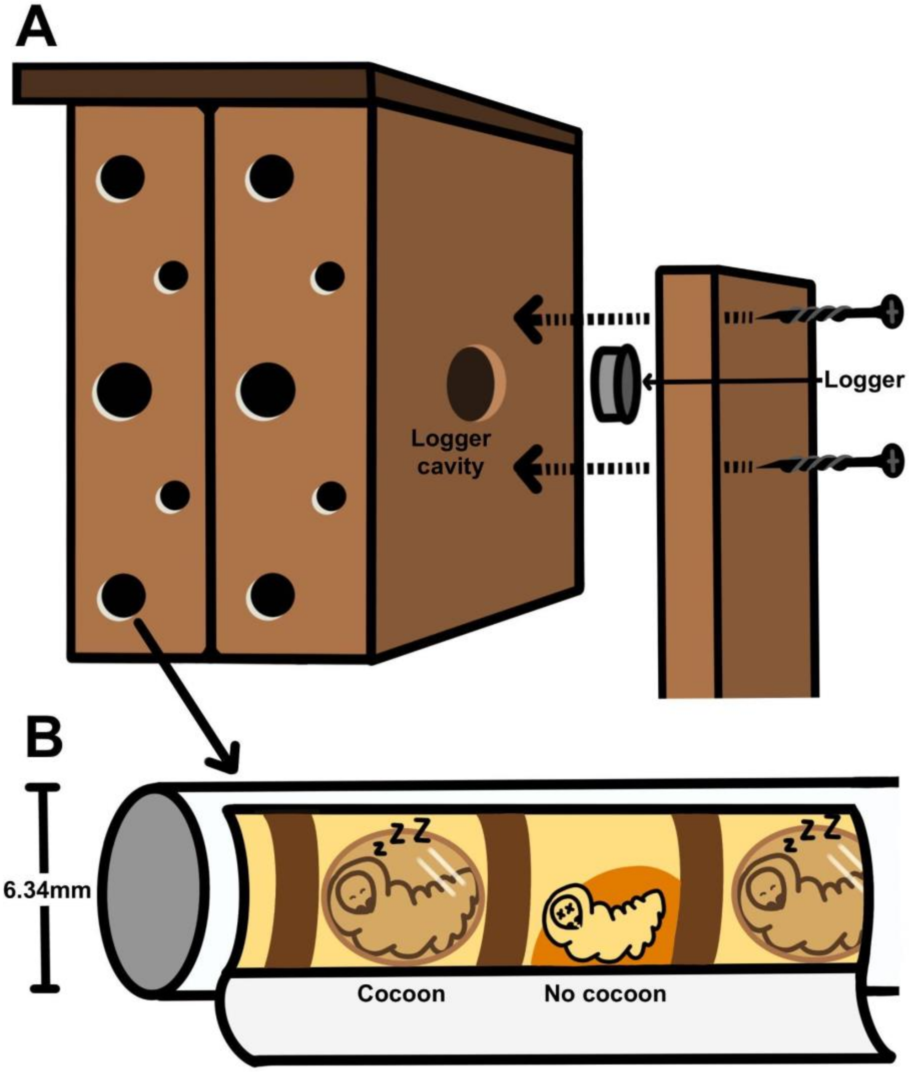

Figure 1. **A**: Nest block with a Thermochron iButton temperature logger. Loggers were placed in a cavity in between nest blocks and wooden stakes used to stake nest blocks into the ground. Each nest block contained 10 paper straw-lined cavities. Cavity-nesting bees and wasps built nests in paper straws within nest blocks during the study period (May to September 2023).

B: Longitudinal section of a straw with generic cavity-nester brood cells inside. Cavity-nesting bees and wasps build individual brood cells and place an egg plus food provisions inside each cell. At minimum, to have successful development, bees and wasps must go from egg to larva and spin a cocoon by the fall.

Statistical analyses

For all data wrangling, visualization and analysis I used R version 4.2.2 (R Core Team, 2022) . I used the following R packages for wrangling and summarizing data: car (J Fox & Weisberg, 2019), dplyr (Wickham, François, et al., 2023), readr (Wickham, Hester, et al., 2024), tibble (Müller et al., 2023), tidyr (Wickham, Vaughan, et al., 2024) and tidyverse (Wickham et al., 2019). To create and test significance of linear mixed models (LMMs) and generalized linear mixed models (GLMMs), I used the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) packages, and to create regression tables I used jtools (Long, 2023) and sjPlot (Lüdecke et al., 2024). I scaled all continuous model predictors by dividing by the standard deviation.

All model assumptions were verified for violations. Specifically, I used the DHARMa package (Hartig & Lohse, 2022) to simulate and plot residuals versus fitted values generated by all GLMMs and LMMs. I also used DHARMa to test for under/overdispersion in GLMMs. I inspected qq-plots for deviations from the expected trend line. I looked at point dispersion in residual versus fitted value plots to assess homoscedasticity. To assess multicollinearity amongst model variables, I generated variance inflation factors with the car package (J Fox & Weisberg, 2019). When two model terms have VIFs above 5, I considered this to be indicative of moderate to high collinearity (Kim, 2019).

To assess model goodness-of-fit, I used the MuMIn package (Bartoń, 2024) to generate conditional r-squared values of LMMs and conditional pseudo-r-squared values of GLMMs. For data visualizations, I used packages ggeffects (Daniel Lüdecke et al., 2024), ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2023) and RColorBrewer (Neuwirth, 2022). To create a map of all study sites (Appendix I: Figure S1) I used packages mapview (Appelhans et al., 2023), purrr (Wickham, Henry, et al., 2023) and sf (Pebesma, 2018).

Forest cover and nest temperature: I summarized data by field margin (N = 34) to obtain mean, maximum and minimum temperature values for every study day from May 21 to September 21, 2023. For each day, I subtracted daily minima from daily maxima to obtain a daily temperature range. Next, I averaged the three calculated temperature metrics (daily means, maxima, ranges) over all study days, to obtain a singular mean, maximum, and range value for all 34 margins. To address objective 1, I fitted three linear mixed models. The response variable of each model was one of the three focal temperature metrics: mean daily maximum, mean daily mean, or mean daily temperature range. All three models included two fixed predictor variables—percent forest cover within a 1 km radius (a continuous variable) and margin type (a binary variable, open or forested)—and site as a random effect (N = 17).

Nest abundance: I quantified nest abundance of cavity-nesting bees and wasps by counting the total number of nests made in all nest blocks in each margin. To assess the impact of forest cover on nest abundance (objective 2), I fit three LMMs to separately model the effect of each nest temperature variable: mean daily maximum, mean daily mean and mean daily range in temperature. All LMMs included nest abundance as the response variable, nest temperature, % forest cover and margin type as predictor variables, and site as a random factor (Table 2). Two of three nest abundance models (specifically 2.7 and 2.9) had VIFs over 5, reflecting moderate to high collinearity in temperature and margin type. I nevertheless kept margin type and temperature variables so that nest abundance models were analogous to nest richness models. However, I also ran a reduced LMM of nest abundance as a function of margin type and % forest cover (i.e. without any temperature metrics).

Nest richness: To quantify nest richness, I counted the number of taxa present in nests in the two nest blocks per margin. All nests that had at least one offspring (egg, larva, cocoon, or adult) were included, regardless of whether those offspring had died or emerged. I excluded any unidentified nest occupants (e.g. unknown wasps) from this analysis. To address objective 2, I fit three GLMMs with Poisson distribution to separately model the effect of each nest temperature variable. All GLMMs included nest richness as the response variable, nest temperature, % forest cover and margin type as predictor variables, and site as a random factor (Table 2). In the field, I observed that forested margins had noticeably lower local air temperatures. I expected that margin types would differ in nest temperature. I therefore fit "full" and "partial" GLMMs, i.e. ones that included and excluded the “margin type” predictor, as a way of testing the impact of local forest cover on richness independently of local temperature (e.g., Table 2, model 2.4 versus 2.5). Then, I calculated second-order AIC values (package MuMIn ; Bartoń, 2024) of all six models to compare the amount of variance explained by full versus partial models. Temperature and margin type predictor variables in some full richness models (specifically, 2.4 and 2.8) had moderately-high VIFs (between 5 and 7), however, both variables were necessary in the full models to allow comparisons with "partial" models.

Brood cell number: To address objective 3, I fit three GLMMs with Poisson distribution. As with previous analyses, I created three GLMMs to separately model each nest temperature metric as a predictor variable. All GLMMs included brood cell number (calculated per nest) as a response variable, nest temperature, % forest cover and margin type as predictor variables, plus site as a random factor (Table 2, models 3.1 to 3.3). I also added a random slope factor (“temperature metric | taxon” in R syntax) which allowed the effects of temperature on brood cell number to vary by taxon. Unidentified wasps were treated as a separate taxon ("unknown wasps"). The brood cells of parasites were excluded from this analysis. A total of seven bee and wasp types were included (**bees**: *Chelostomoides* spp., *Hylaeus* spp. *Hoplitis* spp., *Megachile* spp., *Osmia* spp.; **wasps**: Eumeninae, *Dipogon* spp., *Trypoxylon* spp., *Passaloecus* spp., *Isodontia* spp,. and unknown wasps).

Developmental success: I assessed developmental success of all primary (i.e. non-parasitic) nest occupants. In my study region, all cavity-nesting bees or wasps should have spun a cocoon well before the time of nest dissection (November 2023). Offspring that failed to spin a cocoon prior to dissection were considered to have not successfully developed, while those with complete cocoons were considered to have successfully developed. To quantify developmental success, I counted the number of brood cell occupants in each nest that lived to or beyond the cocoon stage, or the number of "successes". I then counted the number of brood cell occupants that did not live to cocoon stage as the number of "failures". I excluded cells made by parasites. Host cells that failed to make cocoons as a result of parasitism, mold, moisture, or other known disturbances (2.6% of cells) were also excluded. Sometimes, offspring were killed by parasites after they had spun a cocoon. In such cases, I still counted the host cocoon as having developed "successfully", but the parasite cocoon was not counted.

To address objective 4, I fit three GLMMs with Poisson distribution to separately model the effect of each nest temperature variable on developmental success. The response variable of all GLMMs was a matrix tabulating the numbers of successes and failures for each nest. The predictor variables of each model were nest temperature, % forest cover and margin type, and site as a random factor (Table 2, models 4.1 to 4.3). I added a random slope factor (“temperature metric | taxon” in R syntax) which allowed the effects of temperature on developmental success to vary by taxon.

Table 2. Models fitted to address research objectives 1 through 4 (See Introduction). "MD" stands for "mean daily" because all temperature metrics were calculated by averaging across all days of the study (MDMax, MDMean and MDRange).

Objective 1: Nest temperature (LMM)			
Response	**Predictors**	**Random effects**	**Model no.**
MDMax	% forest cover (continuous) + margin type (categorical)	1|site	1.1
MDMean	% forest cover + margin type	1|site	1.2
MDRange	% forest cover + margin type	1|site	1.3
Objective 2: Nest abundance (LMM, family = Gaussian) and nest richness (GLMM, family = Poisson)			
Nest abundance	MDMax + % forest cover + margin type	1|site	2.1
Nest abundance	MDMean% + forest cover + margin type	1|site	2.2
Nest abundance	MDRange + % forest cover + margin type	1|site	2.3
Nest richness	MDTempMax + % forest cover + margin type	1|site	2.4
Nest richness	MDTempMax + % forest cover	1|site	2.5
Nest richness	MDTempMean + % forest cover + margin type	1|site	2.6
Nest richness	MDTempMean + % forest cover	1|site	2.7
Nest richness	MDTempRange + % forest cover + margin type	1|site	2.8
Nest richness	MDTempRange + % forest cover	1|site	2.9
Objective 3: Brood cell number (GLMM, family = Poisson)			

Brood cell number	MDTempMax + margin type + % forest cover	MDTempMax | taxon, 1|site	3.1
Brood cell number	MDTempMean + margin type + % forest cover	MDTempMean | taxon, 1|site	3.2
Brood cell number	MDTempRange + margin type + % forest cover	MDTempRange | taxon, 1|site	3.3
Objective 4: Developmental success (GLMM, family = binomial)			
Successes : (Total cells – Successes)	MDTempMax + margin type + % forest cover	MDTempMax | taxon, 1|site	4.1
Successes : (Total cells – Successes)	MDTempMean + margin type + % forest cover	MDTempMean | taxon, 1|site	4.2
Successes : (Total cells – Successes)	MDTempRange + margin type+ % forest cover	MDTempRange | taxon, 1|site	4.3

Chapter Three: Results

Forest cover and nest temperature

Across all 17 sites, temperatures inside nest blocks were hotter and fluctuated more on a daily basis in open margins than in forested margins (Figure 2). On average, maximum temperatures were (mean ± SE) 31.1 ℃ ± 0.5 in open margins and 24.3℃ ± 0.2 in forested margins (LMM: Margin (open): Estimate = 6.7, SE = 0.51, df = 13, $t = 13$, $p < 0.0001$; Appendix II: Table S1). Daily mean temperatures were 20.4℃ ± 0.5℃ in open margins and 18.8℃ ± 0.1℃ in forested margins (LMM: Margin (open): Estimate = 1.4, SE = 0.16, df = 16 $t = 9.0$, $p < 0.0001$). Daily temperature range averaged 19.6℃ ± 0.6℃ in open margins and 10.7℃ ± 0.3 ℃ in forested margins (LMM: Margin (open): Estimate = 8.8, SE = 0.54, df = 14, $t = 16$, $p < 0.0001$). The highest recorded temperature at each site occurred in the open margin. In five open margins, the highest recordings were 45℃ or higher. I observed no effects of landscape-scale % forest cover on any metric of nest temperature (all $| t | \leq 1.5$, all $p > 0.1$).

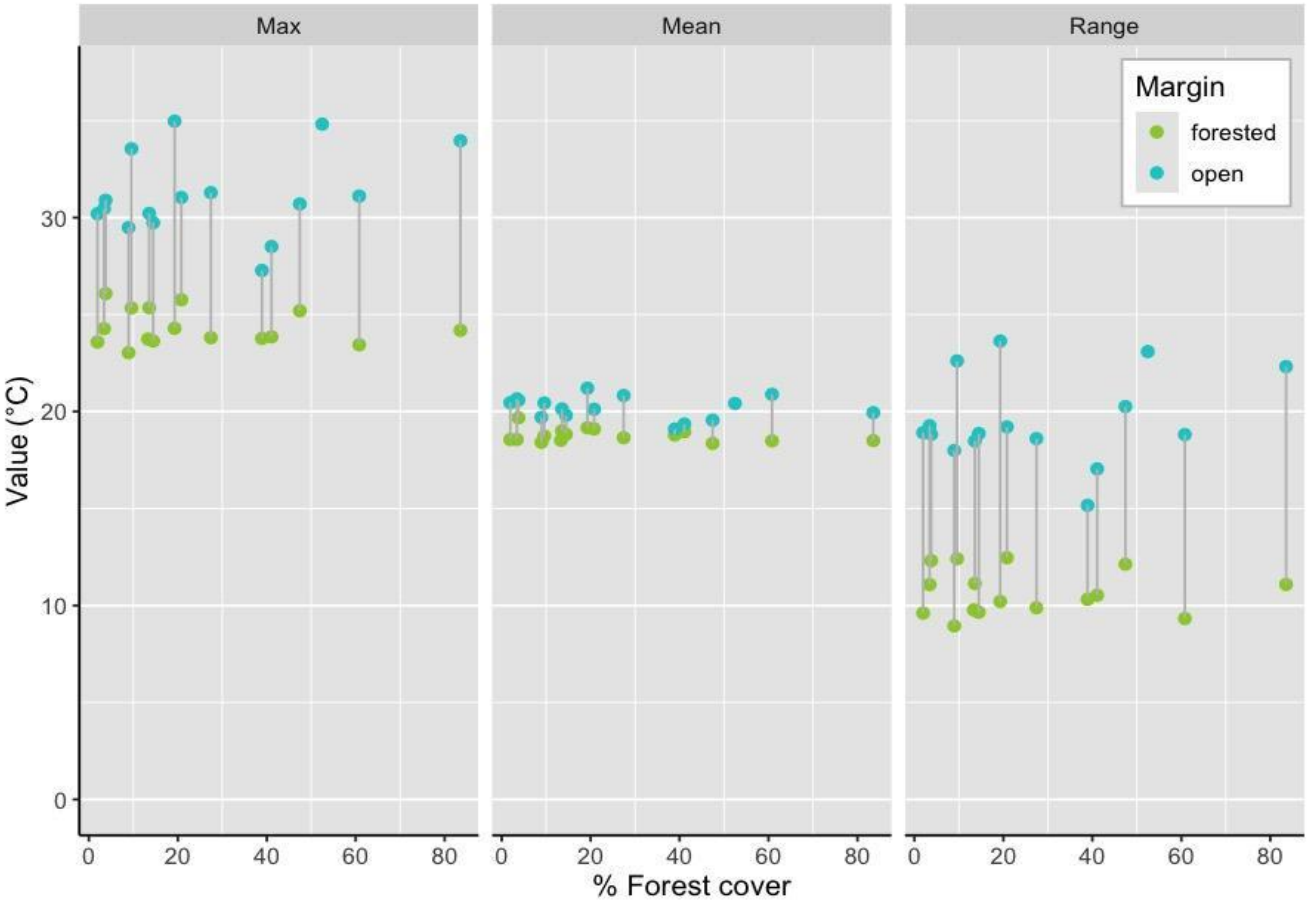

Figure 2. Nest temperature metrics (mean daily maximum, mean, and range) calculated from temperature data collected by data loggers (Thermochron iButtons) installed inside nest blocks. Each point is a value from one open or forested field margin (n = 32*) at one of 17 sites. In Max and Mean panels, each point is a value of averaged daily maximum or mean temperatures at each margin. In the Range panel, each point is an average of differences between daily maximum and minimum temperatures. Values of margins nested in the same study site are connected with a grey line. Each study site (crop field) had a unique level of percent forest cover at the landscape scale (i.e. % cover in 1 km radius). Temperature recording took place from May 21 to September 21, 2023. *Due to a technical problem, temperature data could not be extracted from two of the 34 data loggers.

Nest abundance and richness

Cavity-nesting bees and wasps built a total of 327 nests in open margins and 254 nests in forested margins. Nest abundance was significantly higher in open versus forested margins (LMM: Margin (open): Estimate: 4.3, SE = 1.4, df = 31, $t = 3.0$, $p = 0.006$). Percent forest cover was not associated with any changes in nest abundance. Eumenine wasps (37% of nests), *Megachile* (25%; excluding *Chelostomoides* spp.), and *Osmia* spp. (12.6%) were the most commonly observed taxa (Table 1 for numbers of nests per taxon). The most abundant nest parasites were eulophid wasps, likely *Melittobia* spp.

Per margin, richness values ranged from 3 to 10 taxa (genera or families) of bees, wasps, or parasitic wasps (Figure 3). In forested margins, richness averaged (mean ± SE) 5.3 ± 0.5 taxa per margin, and in open margins richness averaged 6.8 ± 0.4 taxa. Neither nest temperature, percent forest cover nor margin type was associated with any changes in nest richness (Poisson GLMMs: all $|z| < 1.3$, all $p > 0.1$, Appendix II: Table S3). Compared to models without margin type as a predictor, partial models had slightly lower AICc values (Appendix II: Table S3).

Richness did not differ by margin type, but some taxa were associated with one margin type more than another. Overall, most bee nests (77%) were built in open margins and most wasps nests (60%) were built in forested margins. In particular, *Megachile* bees and eumenines showed associations with opposite margin types; I observed only 1.4 ± 0.8 *Megachile* nests per forested margin (mean ± SE per site) vs. 7.4 ± 1.3 per open margin (Figure 4). In contrast, I observed an average of 7.3 ± 1.3 eumenine nests in forested margins, vs. 5.1 ± 0.9 in open margins).

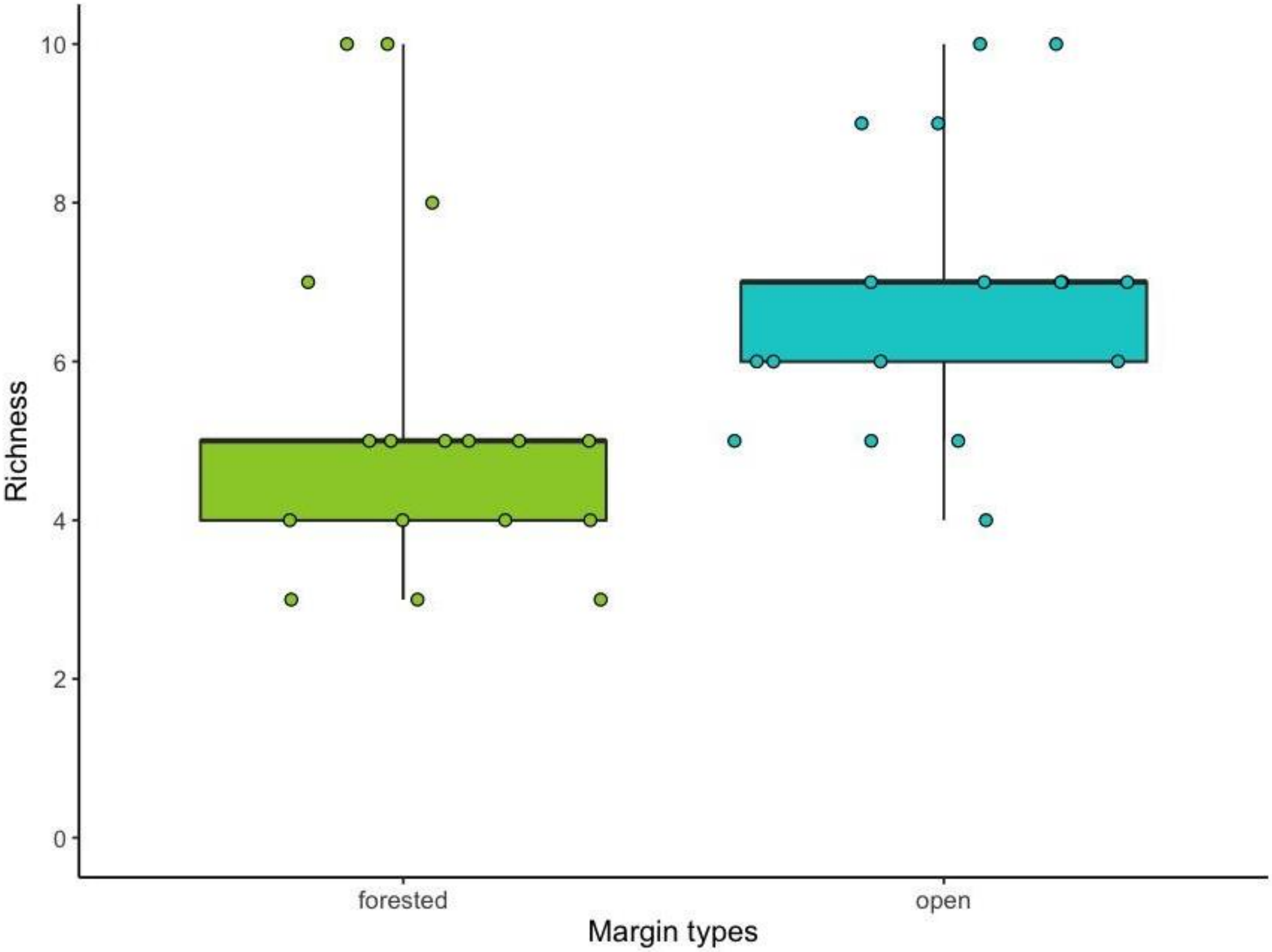

Figure 3. Average richness (number of taxa) of solitary cavity-nesting bees and wasps observed in nest blocks installed in forested and open field margins. Nests could only be identified to genus, sub-family or family level. Boxes demonstrate the interquartile ranges of richness and thick lines inside each box indicate median richness. Lower box whiskers extend to minimum values and upper whiskers extend to maximum values. Green and blue points are raw richness values (N = 34 margins).

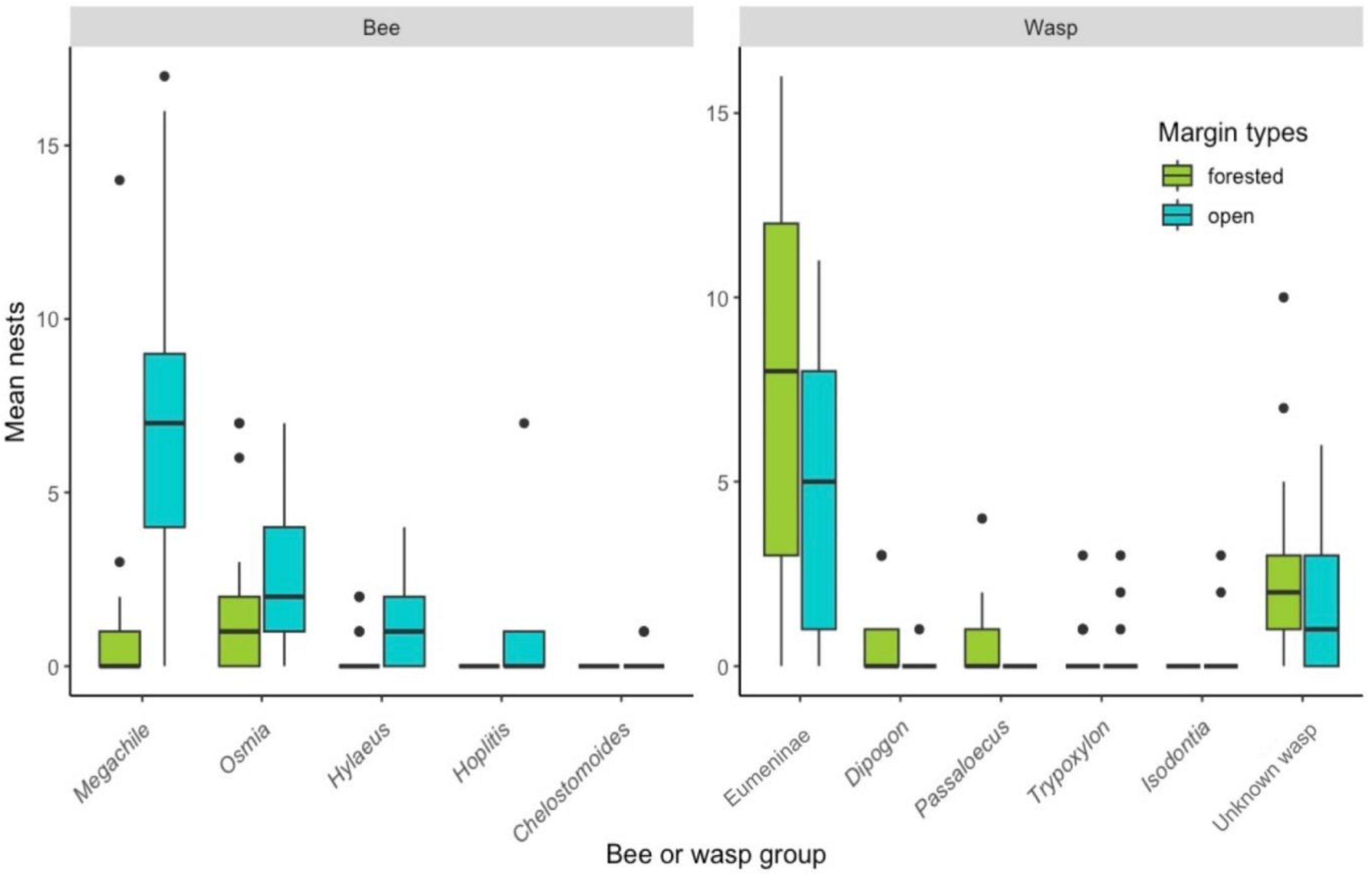

Figure 4. Mean numbers of bee and wasp nests produced in open and forested field margins. Only nests of solitary cavity-nesting bees or wasps with at least one brood cell were considered. Nests were identified to genus, subfamily or family level by assessing nest characteristics (Table 1). Some wasp nests could not be identified and are included here as "unknown wasp". Boxes demonstrate the interquartile ranges of nest number and thick lines inside each box indicate median nest number. Lower box whiskers extend to minimum values and upper whiskers extend to 1.5 times interquartile range. Black points are outliers (N = 563 nests).

Brood cell number

In the 563 bee and wasp nests analyzed here, there were a total of 3015 brood cells. The average number of brood cells per nest was (mean ± SE) 5.38 ± 0.15. None of the three metrics of nest temperature, nor margin type or percent forest cover, were associated with changes to the number of brood cells per nest (Poisson GLMMs: all $| z | < 1.7$, all $p > 0.1$; Figure 5A-C & Appendix II: Table S4).

Developmental success

Of the 2286 documented brood cell occupants, 91% made cocoons and were considered to have had successful development. Mean daily temperature range was positively associated with developmental success, but with borderline significance (binomial GLMM: Estimate = 1.1, SE = 0.55, $z = 2.0$, $p = 0.050$; Figure 5F). Mean daily maximum, mean daily mean temperature, and percent forest cover were not associated with any changes in developmental success (binomial GLMMs: all $| z | \leq 1.8$, all $p > 0.06$). Open margins were associated with up to 21% reduction in the probability of developmental success, depending on the specific temperature covariate (Table S5).

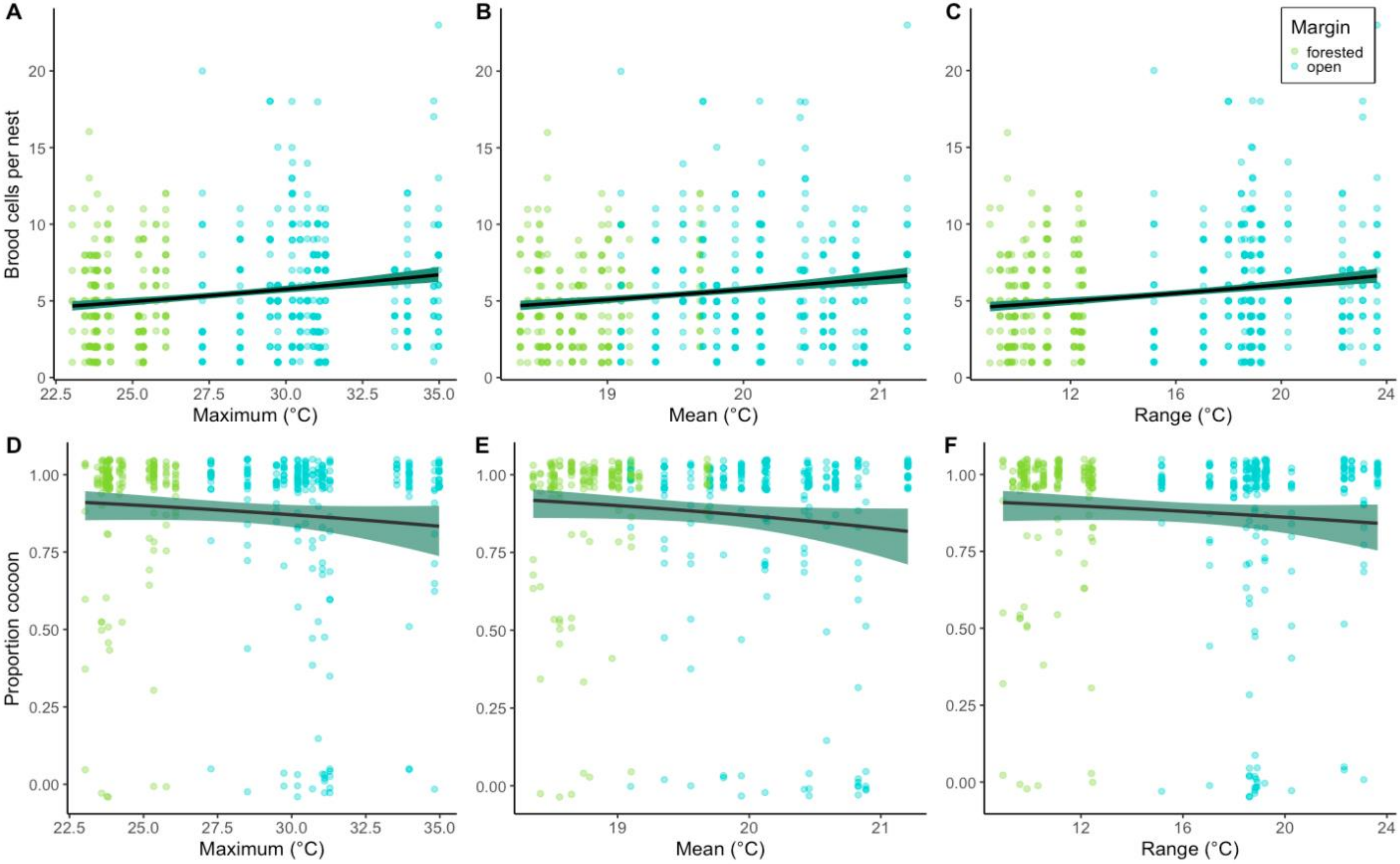

Figure 5. [A - C] Numbers of brood cells per nest (total nests = 437) versus nest temperatures (mean daily maximum [A] and mean temperatures [B] and range [C]). Individual nests were dissected to count the number of brood cells containing an egg, larva, pupa, or adult. **[D - F]** Proportions of brood cells that developed to cocoon stage (i.e. developmental success) versus nest temperatures (mean daily maximum [D] mean temperatures [E] and range [G]). Cocoon proportion values were calculated by dividing the number of cells with cocoons by the total number of cocoons, per nest (n = 414 nests dissected). Individuals that died after cocoon production were counted as having made cocoons. Lines are fitted linear regressions with 95% confidence intervals based on GLM fits; these may differ slightly from the statistical output of GLMMs reported in text and Table S3 and Table S4.

Chapter Four: Discussion

During the summer, organisms in open agricultural landscapes, including solitary cavity-nesting bees and wasps, might endure exceptionally high—and potentially harmful—temperatures. Agricultural landscapes in formerly forested landscapes can contain a variety of woody features, like forested field margins, which hold potential as a form of beneficial habitat that can support local biodiversity. Here, I explored how forest cover in agricultural landscapes impacted temperatures in bee and wasp nest habitat, and how forest cover plus temperature impacted nesting success of these insects. Specifically, I investigated how forest cover in agricultural landscapes can impact temperatures inside nests (objective 1), and how both forest cover and nest temperature impact nest abundance and richness (objective 2), brood cell number (objective 3) and development success of cavity-nesting bees and wasps (objective 4).

Forest cover and nest temperature

In this study, local-scale forest cover (i.e. margin type) reduced temperatures inside bee and wasp nest blocks. Daily thermal variability, or the mean daily range in temperature, was also significantly greater in open field margins. These findings align with previous work comparing local temperatures in places with more or less forest cover (Forman & Baudry, 1984 ; Sánchez et al., 2010 ; Vanneste et al., 2020). Other studies found that forested hedgerows, which were similar to the forested margins studied here and only a few meters in width, performed nearly as well as larger woodlands at buffering temperatures (Vanneste et al., 2020). Forested hedgerows or margins appear to have substantial buffering capacities while taking up relatively little area, making them an attractive form of provided natural habitat in agricultural landscapes, where cropped land, crop yield and monetary profit are prioritized.

Unlike local forest cover, landscape-scale forest cover (i.e. % cover in a 1 km radius), was not associated with any changes in nest temperature. This finding did not align with findings of other studies (Cohn et al., 2019 ; Sanczuk et al., 2023). For example, Cohn et al., (2019) assessed changes in air temperature due to deforestation, and found that landscape-scale forest cover loss (in 2 to 10+ km radii) raised local temperatures inside undisturbed wooded areas. However, variables other than percent cover can increase thermal-buffering, such as tree density (Ghafarian et al., 2024), stand height (Martens et al., 2000 ; Vanneste et al., 2020) and stand vertical complexity (Kovács et al., 2017), and may have impacted nest temperatures here. For example, Ghafarian et al., (2024) found that denser tree stands were associated with lower local temperatures. Taller tree stands are associated with more thermal-buffering because shading is positively related to tree height (Martens et al., 2000; Vanneste et al., 2020). A future study could have more sites, including repetition of landscape-forest cover values, and consider other landscape scale forest cover factors.

Nest abundance and richness

Unexpectedly, no metrics of forest cover or nest temperature were associated with nest richness of cavity-nesting bees and wasps. In this study, it was not possible for me to identify nests occupants beyond genus- or sub-family level. But when adults later emerged from their nests, I observed multiple "morphospecies" from a number of taxa (including eumenines, *Passaloecus* spp., *Megachile* spp., *Osmia* spp., and *Hylaeus* spp.). Possibly, relationships between richness and forest cover or nest temperature might have been detectable with a finer taxonomic resolution. The ideal study would allow time for offspring to reach adulthood so that all nests could be identified to species level (as in Barthell et al., 1998 , Diekötter et al., 2014 and, Drapeau Picard et al., 2024).

The bee and wasp assemblages observed here were affected by timing of nest block installation and phenology of local cavity-nesting bees and wasps. Nest blocks were available to occupants by mid-April (or mid-May for three sites). Some cavity-nesting bees and wasps, like *Passaloecus* spp., only begin their mating and nest building in late summer. By this time, many nest cavities had been filled. The high number of eumenine, *Megachile* spp., and *Osmia* spp. nests in the early season likely reduced opportunities to observe late-season cavity-nesters, like *Passaloecus* wasps, *Hylaeus* bees or *Heriades* bees, which are active from July onwards (Romankova, 2003). The scarcity of late-season species may have impacted the results here. A way to create nesting opportunities for late-season bees and wasps could have been to install additional nest blocks in each margin later in summer.

Because of drastic differences in forest cover between margin types, and its effect on nest temperature, there is an inherent challenge in distinguishing the temperature-mediated effects of local-scale forest cover on bee and wasp communities from other ("direct") effects of forest cover. Here, margin type, and all other predictor variables, were not associated with any changes in richness. Also, margin type also had a negligible impact to model goodness-of-fit (Appendix II: Table S3). To parse the direct effects of forest cover versus effects mediated by thermal buffering, additional work with an experimental approach is required. A suitable experiment to investigate this should have an orthogonal array of high and low forest cover treatments and high and low nest temperature treatments. This could be achieved by adapting my study design, and adding a set of modified nest block and logger apparatuses to each margin. Apparatuses could be placed beneath an artificial tree canopy, such as a white roof (with high albedo), which would provide shade without introducing non-thermal factors associated with forested margins, like different floral or nest resources. The design should likewise include nest blocks on the edge of a forested margin, where there is zero forest canopy, but there is potentially still an influence of non-thermal impacts of forested margins.

Associations of bees and wasps with local forest cover

Despite seeing no impact of forest cover or nest temperature on nest richness, I did observe that certain taxa were more associated with one margin type. Overall, the majority of bee nests were built in open margins and the majority of wasp nests were in forested margins. This pattern is largely driven by the high number of *Megachile* bee nests in open margins and high number of eumenine wasp nests in forested margins (Figure 4). But other bees and wasps also supported the trend: *Osmia* and *Hylaeus* bee nests were most abundant in open margins, while *Passaloecus* and *Dipogon* wasps were most abundant in forested margins (Figure 4).

For bees, open margins may have been more attractive nest sites because they were significantly hotter and (based on personal observations) sunnier than forested margins. Bees sometimes avoid nesting in hot areas because it can be harmful to brood development (Wilson et al., 2020 ; Xu & James, 2012 ; Ostap-Chec et al., 2021) but nest habitats with non-extreme, warm (Polidori et al., 2024) and sunny conditions (Everaars et al., 2011) are generally preferred by bees. These preferences can be strengthened by the fact that warm, sunny conditions are associated with more floral resources (Zaragoza-Trello et al., 2021). Warm, sunny climates also afford greater flight efficiency to bees (Roberts & Harrison, 1998 ; Glass et al., 2024).

Margin-type associations demonstrated by bees and wasps might also have been driven by differences in availability of nest resources. As central-place foragers, cavity-nesting bees and wasps must repeatedly transport nest resources, like food provisions and building materials, to their cavity-nest. It is therefore energetically favourable for them to minimize the distance between the nest resources and their nest. Open margins had greater flowering plant richness and more total flowers than forested margins (Appendix III), which may have made them more attractive to nesting bees. In contrast, wasps provision their brood with paralyzed insects or spiders (Krombein, 1967). Eumenine wasps, the most abundant wasps represented here, provision brood with phytophagous larvae, like Lepidopteran caterpillars or beetle larvae, that can be found eating the leaves of shrubs, trees or other vegetation (Krombein, 1967 ; Fateryga, 2020). If the provisions of eumenine wasps and other wasps were more abundant in forested margins, they could have driven wasps to build more nests in these margins.

It is interesting that wasps, despite being flower-reliant nectarivores, still built more nests in forested margins where there were fewer floral resources. Perhaps wasps prioritize proximity to nest-provisioning resources instead of flowers when selecting a nest location because carrying provisions to the nest is more energetically costly than foraging for nectar. Also, relative to bees, wasps are much less reliant on flowers for feeding young, which might explain why some tended to nest in forest microclimates, where adult health or survival might be greater. Some solitary cavity-nesting wasps might have thermal tolerances that are lower than those of cavity-nesting bees. To my knowledge, there are no records of the thermal optima or tolerances of the wasp taxa observed here (with the exception of *Isodontia* spp. ; O'Neill et al., 2023), and no studies that have examined how nest resources versus floral resources impact nest-site preferences of solitary wasps.

Brood cell number and developmental success

Forest cover and nest temperature were not associated with any changes in brood cell number, but nests in open margins had reduced developmental success. Specifically, the modeled probabilities of developmental success were up to 21% lower in open margins than forested ones. Daily temperature range might also have negatively impacted developmental success, but this effect was only borderline significant (Appendix II: Table S5), and might have been driven by the negative association between daily temperature range and margin type.

Temperatures in some open margins may have repeatedly exceeded thermal tolerances of the species observed here (Hamblin et al., 2017; Melone et al., 2024), but daily maximum temperatures were not associated with changes in brood cell number or developmental success. On average, maximum daily temperature in open margins was 31.1℃, and some open-margin nests reached 40℃ or higher on multiple occasions. Melone et al. (2024) reported that juvenile mortality doubled in *Osmia lignaria* nests treated with 37℃ "heatwaves". The lack of impact of temperature, but remaining negative impact of margin type suggests that there may be non-thermal qualities of open margins that have a negative impact on developmental success, potentially including the non-thermal qualities mentioned earlier: differences in floral resources or nest-provisioning resources.

Species-specific thermal tolerances likely impact the nest location of bees and wasps taxa observed here, and may have driven them to nest in cooler locations, like forest microclimates. In order to investigate species-specific variation in thermal tolerances, and how this impacts brood cell number or developmental success, specimens of the same species should be exposed to different temperature regimes, and to achieve this, a more experimental approach must be taken. The future study could involve collecting nests from nest blocks in the field, and storing them in incubators with different temperature regimes to mimic open and forested margin microclimates (Bosch & Kemp, 2004 ; O’Neill et al., 2023). This option would eliminate the influence of forest cover and of the maternal nesting preferences for tolerable microhabitats.

However, the nest temperature analysis used here is not ideal for assessing how extremely high temperatures impacted bees and wasps. Here, I calculated average temperature values, e.g. one maximum, mean and range value per margin (study site), and in doing so, I averaged away within-margin temperature variability which was likely influenced by forest cover and which may have been harmful, or even lethal, to cavity-nesting bees and wasps (e.g. CT_{max} temperatures ; Käfer et al., 2012 ; Hamblin et al., 2017 ; Melone et al., 2024). Additional work, likely in the form of an experimental study, is needed to investigate how local forest cover influences short-term temperature variables, such as the frequency or intensity of sudden extremely high temperatures (e.g. over CT_{max}). In such study, nesting success variables, such as nest abundance, brood cell number and developmental success, should be assessed repeatedly throughout an extreme temperature event (as in Melone et al., 2024).

Conclusions

Wild bees are in decline (Brown & Paxton, 2009 ; Cameron et al., 2011 ; Zattara & Aizen, 2021), and habitat loss (Goulson et al., 2015) is largely responsible. There is little to no consensus of the state of wasp populations because they are rarely the focus of field studies or monitoring efforts (Bell & Sumner, 2013). However, habitat loss (and other land use factors) is a driver of global insect declines (van Klink et al., 2020), and could be causing declines to wild wasp populations. The leading driver of natural habitat loss is agricultural expansion (ECCC 2021, Retrieved June 9, 2024). As more forest is converted to farmland, and wild habitat is removed, there is greater need for research into how restoration practices that do not interfere with agricultural practices (Rands & Whitney, 2010) can best support the habitat requirements of beneficial insects like bees and wasps.

My study yielded valuable observations about the impact of forests in agricultural landscapes on the nesting habitat of a group of insects that perform crucial ecosystem services in these landscapes. The findings presented here demonstrate that forested margins produce distinct microclimates, and point to the importance of incorporating both forested and open habitat types in agricultural landscapes to support cavity-nesting bees and wasps. Lastly, these findings serve as a jumping-off point to future work exploring the potential of field margins as beneficial habitat and thermal refugia for wild bees and wasps.

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Appendix I: Supplementary figures

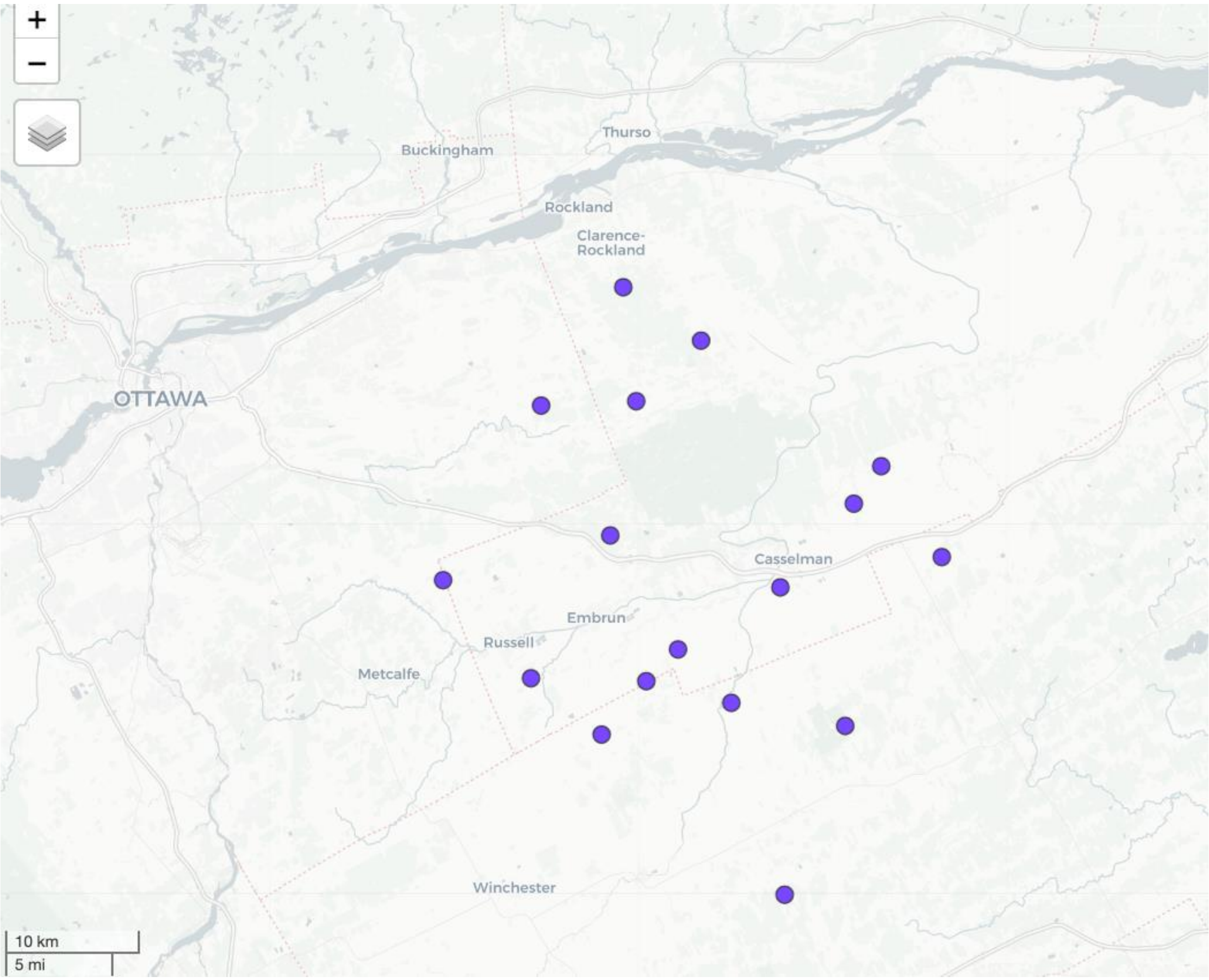

Figure S1. Map of study sites (N= 17 crop field sites) located outside of Ottawa city limits. The minimum distance between study sites was 3.2 km.

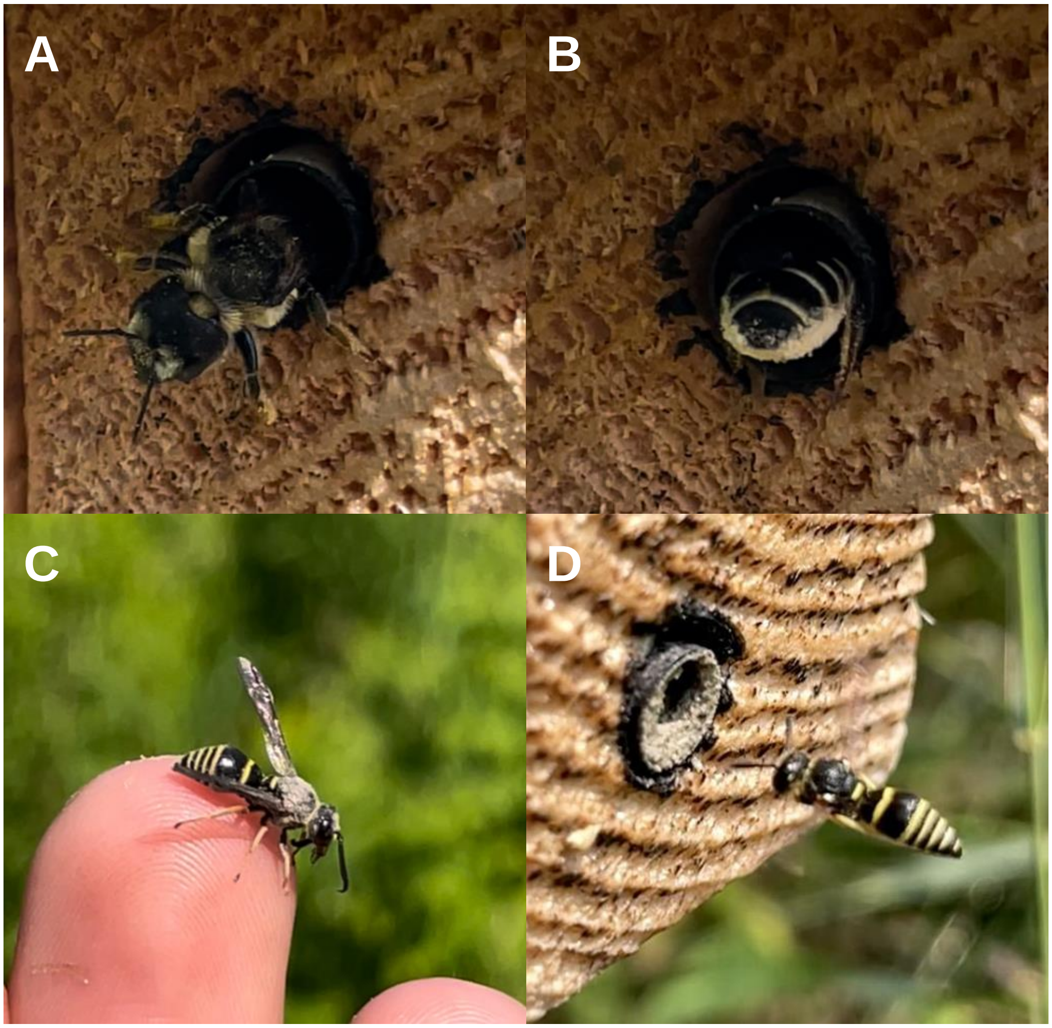

Figure S2. Cavity-nesting bees and wasps at field sites and on nest blocks (artificial nesting habitat). A: Female *Megachile* bee leaving the cavity-nest entrance. B: Female *Megachile* bee returning to her cavity-nest with pollen on her abdominal scopa (hairs specialized for collecting pollen). Other megachilid bees (e.g. *Chelostomoides* spp., *Heriades* spp., *Hoplitis* spp., *Osmia* spp.) carry pollen in the same manner. C: Eumenine wasp that recently emerged from its cavity-nest. D: Eumenine wasp flying into a cavity-nest entrance.

Appendix II : Supplementary information about models

Forest cover and nest temperature

Table S1. Output of LMMs fitted to test the impact of forest cover on three metrics of nest temperature: mean daily maximum temperature or "MDMax", MDMean and MDRange (N = 32 margins). There is one model for each nest temperature metric. Both metrics of forest cover are added as predictor variables: % forest cover (also referred to as landscape-scale forest cover) and margin type (categorical variable, open or forested margins). Site was included in all models as a random effect (17 sites). The "SE" column lists standard errors and "SD" are standard deviations. All significant *p*-values are bolded except for intercept p-values (*a* = 0.05). Model numbers are consistent with those in Table 2.

Model no.	**Response**	**Predictors**	**Estimate**	**SE**	**df**	***t***	***P***
1.1	MDMax	Intercept	24	0.42	26	57	0.0001
		% forest cover (scaled)	0.24	0.34	13	0.69	0.50
		Margin type (open)	6.7	0.51	13	13	**< 0.0001**
		1|Site	***Variance*** = 0.83 ***SD*** = 0.91				
1.2	MDMean	Intercept	19	0.12	28	160	<0.0001
		% forest cover (scaled)	0.12	0.09	15	-1.3	0.21
		Margin type (open)	1.4	0.16	16	9.1	**< 0.0001**
		1|Site	***Variance*** = 0.03 ***SD*** = 0.17				

1.3	MDRange	Intercept	11	0.46	26	23	<0.0001
		% forest cover (scaled)	0.25	0.38	14	0.66	0.52
		Margin type (open)	8.8	0.54	14	16.0	**< 0.0001**
		1|Site	***Variance*** = 1.1 ***SD*** = 1.04				

Nest richness and abundance

Table S2. Output of an LMM testing the impacts of forest cover (two scales: % forest over and margin type) and nest temperature on nest abundance, or the number of bee and wasp nests in artificial nest blocks installed in field margins (N= 34 margins).

Model no.	**Pseudo R^2**	**Predictors**	**Estimate**	**SE**	***df***	***t***	***P***
2.1	0.25	Intercept	15	1.9	28	7.7	< 0.0001
		% forest cover (scaled)	0.95	0.80	13	1.2	0.26
		Margin (open)	4.1	3.5	28	1.2	0.25
		MDMax (scaled)	0.18	1.8	27	0.10	0.92
		1|Site	***Variance*** = 1.5 ***SD*** = 1.2				
2.2	0.25	Intercept	15.4	1.6	28	9.6	< 0.0001
		% forest cover (scaled)	1.1	0.81	14	1.4	0.20
		Margin (open)	2.8	2.8	26	0.99	0.33

		MDMean (scaled)	1.0	1.4	28	0.70	0.49
		1|Site	***Variance*** = 1.50 ***SD*** = 1.20				
2.3	0.25	Intercept	15	2.2	28	6.7	< 0.0001
		% forest cover (scaled)	0.95	0.80	13	1.2	0.25
		Margin (open)	4.3	4.1	28	0.03	0.98
		MDRange (scaled)	0.07	2.1	27	0.03	0.98
		1|Site	***Variance =*** 1.40 ***SD*** = 1.20				

Table S3. Output of GLMMs testing the impacts of nest temperature and forest cover (two scales: % forest over and margin type) on nest richness, or the number of bee and wasp taxa observed in artificial nest blocks (N = 563 nests, family: Poisson). There are six models that are nested by three nest temperature predictor variables: MDMax, MDMean and MDRange. In each group, there is one full model with temperature, % forest cover and margin type as predictor variables, and a "partial" model with the margin type predictor removed. Margin type was added and removed to assess its impact on model goodness-of-fit.

Model no.	**AICc**	**Pseudo R^2**	**Predictors**	**Estimate**	**SE**	***z***	***P***
2.4	146	0.08	Intercept	1.8	0.17	10	< 0.0001
			MDMax (scaled)	-0.12	0.16	-0.77	0.40
			% forest cover (scaled)	0.06	0.07	0.86	0.30

			Margin type (open)	0.35	0.31	1.1	0.20
			1|Site	***Variance*** = 2.4 e-03 ***SD*** = 0.05			
2.5	144	0.06	Intercept	1.9	0.07	27	< 0.0001
			MDMax	0.04	0.07	0.54	0.60
			% forest cover (scaled)	0.05	0.07	0.75	0.40
			1|Site	***Variance*** = 5.0 e-03 ***SD*** = 0.07			
2.6	146	0.08	Intercept	1.8	0.15	12	< 0.0001
			MDMean (scaled)	-0.12	0.13	-0.91	0.30
			% forest cover (scaled)	0.04	0.07	0.52	0.60
			Margin type (open)	0.32	0.25	1.30	0.20
			1|Site	***Variance*** = 1.7 e-03 ***SD*** = 0.04			
2.7	144	0.05	Intercept	1.9	0.07	27	< 0.0001
			MDMean (scaled)	0.02	0.07	0.33	0.70
			% forest cover (scaled)	0.06	0.07	0.84	0.40
			1|Site	***Variance*** = 5.0 e-03 ***SD*** = 0.07			
2.8	146	0.07	Intercept	1.8	0.20	8.9	< 0.0001
			MDRange (scaled)	-0.11	0.19	-0.59	0.60
			% forest cover (scaled)	0.06	0.07	0.84	0.40
			Margin type (open)	0.33	0.36	0.91	0.40
			1|Site	***Variance*** = 2.7 e-03 ***SD*** = 0.05			

2.9	144	0.06	Intercept	1.9	0.07	27	< 0.0001
			MDRange (scaled)	0.05	0.07	0.68	0.50
			% forest cover (scaled)	0.05	0.07	0.74	0.50
			1|Site	***Variance*** = 4.9 e-03 ***SD*** = 0.07			

Brood cell number

Table S4. Output of GLMMs testing the impacts of nest temperature and forest cover (two scales: % forest over and margin type) on the number of brood cells per cavity nest (N = 563 nests, family: Poisson).

Model	**Pseudo R^2**	**Predictors**	**Estimate**	**SE**	***z***	***P***
3.1	0.34	Intercept	1.7	0.12	14	< 0.0001
		MDMax (scaled)	0.07	0.07	1.1	0.30
		% forest cover (scaled)	0.02	0.04	0.63	0.50
		Margin type (open)	-0.03	0.11	-0.24	0.80
		MDMax | Taxon	***Variance*** = 0.29 ***SD*** = 0.54			
		1|Site	***Variance*** = 0.017 ***SD*** = 0.13			
3.2	0.34	Intercept	1.6	0.11	15	< 0.0001
		MDMean (scaled)	0.04	0.06	0.72	0.50
		% forest cover (scaled)	0.04	0.04	0.99	0.30
		Margin type (open)	0.04	0.09	0.52	0.60
		MDMean | Taxon	***Variance*** = 3.6 ***SD*** = 1.90			
		1|Site	***Variance*** = 0.02 ***SD*** = 0.14			

3.3	0.34	Intercept	1.7	0.12	14.0	< 0.0001
		MDRange (scaled)	0.14	0.08	1.70	0.09
		% forest cover (scaled)	0.02	0.04	0.56	0.60
		Margin type (open)	-0.15	0.14	-1.1	0.30
		MDRange | Taxon	***Variance*** = 7.9 e-03 ***SD*** = 0.09			
		1|Site	***Variance*** = 0.018 ***SD*** = 0.14			

Developmental success

Table S5. Output of GLMMs testing the impacts of nest temperature and forest cover on the developmental success of cavity-nesting bees and wasps, or the proportion of brood cells per nest that reached cocoon stage (N = 437 nests, family = binomial). Estimate values are in log-odds format.

Model	**Pseudo R^2**	**Predictors**	**Estimate**	**SE**	***z***	***P***
4.1	0.85	Intercept	3.5	0.76	4.6	< 0.0001
		MDMax (scaled)	0.92	0.50	1.8	0.065
		% forest cover (scaled)	-0.32	0.22	-1.4	0.15
		Margin type (open)	-2.0	0.65	-3.1	**0.0018**
		MDMax | Taxon	***Variance*** = 74 ***SD*** = 8.6			
		1|Site	***Variance*** = 0.65 ***SD*** = 0.80			
4.2	0.85	Intercept	2.9	0.78	3.7	1.8e-4
		MDMean (scaled)	-0.0039	0.37	-0.011	1.0
		% forest cover (scaled)	-0.15	0.24	-0.64	0.53
		Margin type (open)	-1.2	0.48	-2.4	**0.015**

		MDMean | Taxon	***Variance*** = 255 ***SD*** = 16.0			
		1|Site	***Variance*** = 0.86 ***SD*** = 0.93			
4.3	0.85	Intercept	3.7	0.79	4.7	< 0.0001
		MDRange (scaled)	1.1	0.55	2.0	0.04998
		% forest cover (scaled)	-0.30	0.21	-1.4	0.16
		Margin type (open)	-2.4	0.77	-3.1	**0.0022**
		MDRange | Taxon	***Variance*** = 24 ***SD*** = 4.9			
		1|Site	***Variance*** = 0.59 ***SD*** = 0.77			

Appendix III: The effect of margin type on richness and abundance of flowers

Introduction

Heat exposure can be damaging to bee and wasp nesting, but the availability of floral resources can also heavily impact nesting success. Bees and wasps are extremely reliant on flowering plants to meet their energetic requirements. Most bees and wasps consume floral nectar as adults, and in Canada, all solitary (non-parasitic) bees provision their young with pollen and nectar (or, rarely, oil) that they harvest from flowers. It is well known that the availability of floral resources, namely diversity and abundance of flowers, can strongly influence bee and wasp community richness (Grundel et al., 2010), nest site selection (Cope et al., 2019), and reproductive output (Crone, 2013 ; Forrest & Chisholm, 2017). To investigate differences in floral abundance and diversity between forested and open field margins, I surveyed flowering plants at all study sites throughout the duration of this study.

Methodology

Floral surveys: In all field margins (N = 34), I established 50 m transects with the nest block set-up defining the midpoint of the transects. At three random positions along each transect, I placed a 1 m by 1 m quadrat and counted the number of flowers per species of flowering plant inside the quadrat. Any non-graminoid flowering plant that hung into the quadrat was included. This included herbaceous and woody plants, but excluded trees when they were too tall to be assessed. To determine if a flower was open, I looked for traces of pollen. A flower with fruit was considered past the flowering stage.

Every plant that fit my criteria was identified to the lowest possible taxonomic level, and the total number of open flowers present in the quadrat were counted. For most Asteraceae species, which can have hundreds of florets per capitula, capitula were counted rather than florets. Some plants have tiny flowers that are not conveniently organized into capitula, or have complex inflorescences made of many smaller inflorescences, like *Solidago* spp., making it impractical to count each flower or capitulum. For plants with abundant flowers, I counted capitula or flowers per inflorescence in four inflorescences of the same species. From this, I calculated an average number of flowers or capitula per inflorescence. Then, the number of total inflorescences from that species within the quadrat was counted and multiplied by the average number of flowers or capitula per inflorescence to obtain an estimate of total flowers/capitula per species. I repeated floral survey transects at every margin in June, July and August.

Statistical analyses: I combined floral survey data from all survey periods and quadrats and summarized by margin (N = 34). I calculated two summary floral resource variables: floral richness, i.e. the number of plant taxa in flower, and total flower number. I fit a GLMM with Poisson distribution to model floral richness as a function of margin type, with site as a random factor. Second, I fit an LMM to model total flower number as a function of margin type plus site as a random factor. Total flower number data were strongly right-skewed and so I applied a log transformation. I verified all model assumptions and found no signs of violations.

Results

Floral richness and abundance differed between the two margin types. Open margins had slightly higher floral richness than forested margins (mean ± SE: 7.65 ± 0.91 vs. 5.88 ± 0.74 species). The significance of this difference was borderline (Table S6, $p = 0.047$, $\alpha = 0.05$). The number of flowering inflorescences was also higher in open margins (3080 ± 989) than forested margins (347 ± 100; Table S7, df = 16, $t = 2.7$, $p = 0.015$).

Table S6. Output of GLMM evaluating the impact of margin type on floral resource richness (N = 34 margins, family = Poisson, Pseudo $R^2 = 0.46$).

Predictors	**Estimate**	**SE**	***z***	***P***
Intercept	1.7	0.13	13	< 0.0001
Margin type (open)	0.26	0.13	2.0	**0.047**
1|Site	***Variance*** = 0.12 ***SD*** = 0.34			

Table S7. Output of LMM evaluating the impact of margin type on total flower number (N = 34 margins, Pseudo $R^2 = 0.22$).

Predictors	**Estimate**	**SE**	**df**	***t***	***P***
Intercept	5.0	0.46	32	10.9	< 0.0001
Margin type (open)	1.7	0.64	16	2.7	**0.015**
1|Site	***Variance*** = 0.17 ***SD*** = 0.41				