RESPONSES OF BUMBLEBEES (*BOMBUS*) TO CLIMATE CHANGE

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Abstract

With over 1 million species facing extinction due to land use intensification and changing climatic patterns, the acceleration of extinction rates of flora and fauna worldwide is projected to continue to worsen. The swift pace of climate change limits opportunities for evolutionary adaptation, exposing species to conditions that challenge their ability to survive or fulfill essential functions. Bee populations, globally dwindling due to these environmental shifts, play a crucial role as wild pollinators responsible for over 80% of global pollination services. Of particular concern are declines in bumblebees (*Bombus*), a group of approximately 260 species. Rapid climate changes expose *Bombus* species to conditions surpassing their historical tolerances, with rising temperatures challenging thermoregulation, foraging, and reproduction efficiency. While models linking climate change to species losses rely on broad-scale observations and complex models, the interaction between climatic position and land use at both continent-wide and local scales remains understudied for bumblebees. This thesis investigates patterns in *Bombus* persistence across North America to elucidate the impacts of climate and land use on bumblebees and inform conservation initiatives. In Chapter 2, I identify broad-scale, continent-wide mechanisms behind *Bombus* climate vulnerability to involve spatio-temporal shifts. I find that shifts in activity timing, not only range shifts, have contributed to climate-driven bumblebee extirpations across North America for the last three decades. I determine that mechanisms of climate change and land use intensity vulnerability observed at a macroecological scale are relevant at a community scale in Southern Ontario, demonstrating the biological relevance of such drivers (Chapter 3). Then, I demonstrate that, among bumblebee species, vulnerabilities to these stressors have a quantifiable pattern with regards to life-history traits and evolutionary histories (Chapter 4). This work will improve predictions of how bumblebee species respond to changing environments and landscape and may suggest new avenues for conservation and management of these and other important pollinator species. By improving predictions of bumblebee responses to changing environments, this research offers insights for conservation and management strategies, with broader implications for understanding climate and land use change responses across taxa.

Statement of work

Chapter 2 has been published in the peer-reviewed journal *Biological Conservation*:

Koppel, O., Kerr, J. (2022). Strong phenological shifts among bumblebee species in North America can help predict extinction risk. *Biological Conservation.* DOI: 10.1016/j.biocon.2022.109675.

I have also had the opportunity to co-author an additional peer-reviewed publication and several reports resulting from my doctoral research and academic involvement with lab mates, peers from the Biology Graduate Student Association, and other collaborations from colleagues from McGill and Carleton University:

Reid, J.*, Koppel, O.*, Ednie, G.*, Piczak, M.*, Kapoor, T*. (2022). Foresight science in conservation: tools, barriers, and mainstreaming opportunities. *Ambio*. DOI: 10.1007/s13280-022-01786-0

Koppel, O. October 19, 2022. What a buzzkill: Early-ending winters disrupt bumblebee slumber. *The Conversation.* Reprinted in The National Post on October 20, 2022, and subsequently other news outlets. https://theconversation.com/what-a-buzzkill-early-ending-winters-disrupt-bumblebee-slumber-190885.

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Allison, J.*, Bretzlaff, T. *, Chisholm S.*, Gordon S.*, Kerr J.*, Koppel O.*, Leduc M. *, Leo S.*, Paradis, A.*, Sirois-Delisle, C.*, Soroye, P.* (2018). *The case for diversity in Canadian science.* iPolitics. https://www.ipolitics.ca/news/the-case-for-diversity-in-canadian-science. Angell, C.*, Dyck, A.*, Gordon, S.*,

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Chapter 1: General Introduction

The past four decades have seen declines, extirpations, and extinctions as a result, in part, from rapid global climate change (Parmesan 2006, Kerr et al. 2015). Over 1 million species currently face extinction due to human drivers, and acceleration of extinction is projected to increase (Finn et al., 2023). Global temperatures are projected to exceed over 1.5 degrees Celsius from pre-1970 levels between 2030 and 2052 (IPCC, 2023). These extinction rates are 10-100x higher than average extinction rates over the past 10 million years (Brondizio et al. 2019), and this rapid pace of climate change limits potential for evolutionary adaptation to shifting conditions. These environmental changes cause species to experience conditions that impair their capacity to survive or fulfill vital functions (Parmesan and Yohe 2003). The consequent reduction in biodiversity will result in ecosystems that are even less resilient to future climate shift impacts and spread of disease (Brondizio et al. 2019). Pollinators, which play a critical role in ecosystem resilience, are among the taxa experiencing declines (Biesmeijer 2006, Gordo and Sanz 2006, Willmer 2012, Kerr et al. 2015).

There is increasing evidence of declines in bumblebees (*Bombus*), a group of approximately 260 species which provide vital pollination services across North America and Europe (Arbetman et al. 2017). Rapid climate changes have exposed bumblebees to conditions that exceed their historically observed tolerances, including greater incidence of extreme weather and associated variance in environmental conditions. Recent evidence has shown striking regional declines in bumblebee populations. For example, *Bombus occidentalis* has experienced a 57% occupancy decline in the western U.S. since the late 1990s, largely attributed to rising temperatures, drought, and neonicotinoid pesticide use (Janousek et al., 2023). Similar large-scale losses have been reported across Europe (Blasi et al., 2023), with spring emergence of queens advancing by more than 10 days in intensively farmed regions, potentially disrupting floral synchrony. These shifts underscore the complex interplay between land use and climate in driving pollinator decline. Higher temperatures challenge the thermoregulatory capacity of certain *Bombus* individuals and decrease colony foraging and reproduction efficiency (Heinrich 2013). This is a leading hypothesis to explain the shrinking equatorial range boundaries over the past century in twenty North American *Bombus* species (Sirois-Delisle and Kerr 2018). As poikilotherms, whose internal temperatures vary considerably as individuals adjust to external conditions, *Bombus* species depend on suitable ambient air temperatures for efficient body function (Hegland et al. 2009). Beyond lethal thresholds, sublethal heat stresses impair foraging, development, and cognition in these and other bees (White and Dillon, 2023). In social species such as *Bombus*, these effects may accumulate over time and differ among castes. Recent physiological work indicates wide interspecific variation in heat tolerance, with queens showing lower thermal limits than workers, and limited acclimation capacity in many species (Feuerborn et al., 2023; Gamboa et al., 2023). Their cold-adapted nature (Hines, 2008; Heinrich, 1979), while advantageous in stable climates, renders them particularly vulnerable to rising temperatures (Woodard, 2017).

The predominant biotic responses to climate change that have been measured – phenological shifts and geographical range shifts – both permit species to remain within their realized climatic niches (Fitter and Fitter 2002; Walther et al. 2002; Parmesan and Yohe 2003; Visser 2008; Robinet and Roques 2010, Socolar et al. 2017, Sirois-Delisle et al. 2024). Range shifts are changes in a species' geographical distribution, usually due to modified availability of habitat, food, and suitable environmental conditions (Hannah et al. 2007). Traditionally, range shifts alone are considered in climate responses of fauna, without consideration of phenological changes. Species' capacities to colonize areas beyond their historical range limits, often toward the poles, may be insufficient relative to the pace of climate change (Bush and Lemmen 2019). If species expand their ranges slowly poleward but experience more rapid range losses in the hottest, or otherwise most extreme, parts of their ranges, then species' range sizes necessarily become smaller (Kerr et al. 2015). Extinction risks are likely to rise in such circumstances. The mechanisms for climate change impacts on bumblebees are linked to processes such as colony-level disruptions (e.g. inefficient thermoregulation (Gardner et al., 2006) reduced reproductive success (Archer et al., 2025) or brood developmental failures (White and Dillon, 2023) and reduced sperm viability (Martinet et al., 2021). In addition, extreme climatic conditions can impact the distribution and phenology of the plant resources found to be key in plant-pollinator mutualistic interacts (Hegland et al. 2009, Burkle et al. 2013).

Phenological shifts are changes in the seasonal timing of life history events, often in response to environmental cues (Willmer 2012). Pollinators also must keep pace with the phenology of their mutualistic partners: they require availability of floral resources, from the time that queens emerge from overwintering habitat in the spring until colony senescence in the autumn (Chuine 2010). An understanding of species' thermal tolerance and phenological timing as climate change responses can be supported through niche theory.

Species' niches encompass the conditions and resources required to enable persistence (Sax et al. 2013), and climate change can impose conditions that make such persistence less likely. There are many distinct niche concepts in widespread use (e.g. the Grinnellian niche (Grinnell 1917), Eltonian niche (Elton 1927), the Hutchinsonian niche from the n-dimensional hypervolume (Hutchinson 1957), and many refinements beyond (Janzen 1967; MacArthur 1967; Chase and

Leibold, 2003). The first chapter of this thesis is largely focused on broad geographical extents and relies on the realized climatic niche. The realized climatic niche is the geographical space occupied by a species after accounting for biotic interactions, in contrast to its fundamental niche, which encompasses the full extent of ecological space in which a species may potentially occur, irrespective of competition or other biotic interactions (Hutchinson 1957). Because our dataset is based on field occurrences, it reflects each species' realized climatic niche, not its full physiological (fundamental) limits (Araújo and Guisan 2006). Throughout this thesis, thermal position is the difference between a site's annual T_{max} and the species' historical upper thermal limit (Chapter 2 Methods, Eq. 1). Thermal tolerance refers to that upper limit itself. Consistent with this framing, bumblebee declines are greater where T_{max} values exceed those historical thermal tolerances (Soroye et al. 2020), taking species outside of their realized climatic niches. The proximity of environmental conditions to species' thermal tolerance limits can improve predictions of bumblebee species' range responses to warming (Soroye et al. 2020). Thermal tolerances are a consequence of the interplay between physiological mechanisms, such as neuromuscular function, and ecological factors, such as microclimatic variability and habitat structure (Oyen and Dillon, 2018). Climatic conditions that approach or exceed species' realized thermal niche limits are associated with a range response, either expansion (in the case of areas that were historically colder but have warmed) or loss (for areas that were among the warmest that a species occupied but that have warmed further). The discovery made by Soroye et al. (2020), that extreme weather outside of species' thresholds is now linked to species' extinction risk, catalyzed extensive research among other taxa, and evidence of this is now extensive for a variety of taxonomic groups (Harvey et al. 2020; Murali et al. 2023). Using species-specific information on species' thermal limits based on their geographical distributions, and if the macroecological trends are causal, I expect to observe differences in bumblebee species communities based on spatial differences in temperatures and associated exposure to temperature extremes related to land use. Chapters 3 and 4 of my thesis provide the first application of these concepts, which were derived using continent-wide analyses, to a series of intensively-sampled biological communities across southern Ontario. While thermal tolerance and extreme climatic events are key factors influencing bumblebee persistence, these pressures do not act in isolation, as land use changes compound their effects by altering habitat availability and ecosystem dynamics.

Land use change has been the single largest driver of species extinctions that shrinks suitable habitat for communities for several decades (Brambilla et al. 2010) and exacerbates the stressors already placed upon organisms by climate changes. To maintain healthy genetic diversity, a population of bumblebees requires 10km^2 of suitable habitat with several colonies within this area, each foraging approximately 3km^2 from their respective nests (Edwards 1999). Land use intensification, changing land from natural to urban or agricultural, is causing species losses through habitat fragmentation and loss. Land use intensity can alter bumblebee and other pollinator communities directly by limiting habitat availability (Millard et al. 2021, Birkenbach et al. 2024), and indirectly through interactions with changing availability of microclimates. Though pesticides are not a direct focus of my thesis, land use change is correlated with increased insecticide use and higher densities of managed bees (Meehan et al., 2011) and are included in the land use classification in Chapter 3 and 4. These factors introduce additional stressors to bumblebee populations. Neonicotinoids, for example, have been shown to impair navigation, foraging efficiency, and colony health, while pathogen spillover from managed bees, such as the spread of *Nosema bombi*, poses significant risks to wild populations (Chen et al., 2025). To understand the direct effects of land use change on biological communities, I examine data from Southern Ontario rather than relying solely on macro-scale models that may fail to capture local dynamics.

Analyses of well-sampled biological communities could reduce reliance on extrapolative models, like occupancy or species distribution models, that often perform very poorly when challenged with new observations (Jha et al., 2022). To test hypotheses related to how species respond to environmental changes, an alternative approach is simply to “scale down” analyses to those of individual biological communities that are directly measured. In an initial exploration that included biological community data, Williams et al. (2008) showed that bumblebee species declined in areas nearer their climatic limits and in areas where land uses were more intense, but data limitations prevented tests of these trends among bumblebee communities. These trends are widely observed among other groups also, and population declines for vertebrates are reported from areas with high intensity land use (e.g. high biomass crops) and extreme weather (Williams and Newbold 2021).

Microclimate availability interacts with land use (Braem et al. 2023); habitats can be more homogenous in agriculture settings compared to natural landscapes, which offer shelter in the form of shaded slopes, varied ground-level vegetation, rock faces, burrows beneath leaf litter, and canopy cover. Microclimatic heterogeneity is reduced at sites of intensive agriculture (Kuntzman et al., 2024), potentially contributing to population declines and local extinctions. Species near their thermal limits might be particularly affected if they depend on microclimatic refugia to persist through episodes of extreme weather. In contrast, diverse habitats can allow species in natural landscapes to take advantage of small cavities to escape thermal extremes or be shielded from the elements (Westrich 1996, Ednie and Kerr 2022). Conditions are more than 5℃

cooler in microclimate refugia than monthly maxima in certain semi-natural habitats (Suggitt et al. 2011). In areas of intense land use, such microclimate refugia are rarer, trapping species in a simplified environment with a lack of refugia to escape extreme conditions, compounding the effects of climate change (Cavender-Bares and Wilczek 2003). Detection and assessment of microclimate refugia improves prediction of climate change impacts on ectotherms (Pincebourde and Casas 2015), birds (Ramos et al. 2023), and butterflies and beetles (Suggitt et al. 2018).

To characterize these fine-scale environments, I used NicheMapR, a biophysical microclimate model that simulates near-ground conditions over space and time (Kearney and Porter 2017). The variation of the model I chose integrates inputs including terrain, vegetation, and climate data to estimate modelled outputs of hourly values of air temperature, humidity, solar radiation, and other key variables at a spatial resolution as fine as 1 m^2, measured at 2 meters above ground level. This is a practical solution to the logistical limitations of deploying environmental sensors across study sites, particularly over broad geographic areas. The accuracy of simulated microclimate conditions depends on the resolution and quality of the model's input layers, which vary by region. For example, terrain data from the *elevatr* R package range from 10 to 90 meters in resolution, while climate layers derived from NCEP Reanalysis data (NREP) have a coarser resolution of approximately 50 km at the equator. Since vegetation structure and land surface properties are drawn from datasets such as Landsat (10–30 m resolution) and the Global Aerosol Data Set (~5° x 5° grid), detail is highest in areas with high-resolution data availability and may decline in more data-sparse regions. Despite these limitations, NicheMapR offers a reproducible framework to estimate microclimatic conditions critical for understanding bumblebee ecology, especially when assessing species persistence in fragmented or thermally stressful landscapes.

Species traits, such as body size, may also influence how species interact with their environment, which affects distribution extent and how rapidly distributions may change through dispersal (Aguirre-Gutiérrez et al. 2016). Species traits reflect trade-offs between morphological, physiological, and biochemical capabilities of an organism to arrive at a cost-benefit strategy to respond to environmental pressure (Moor et al. 2017). Nesting location, body size, and phenology are all adaptations to environments in which species are found and can affect their environmental tolerances. Given this, rapid environmental changes may reduce a species' prospects for persistence, making it essential to understand how traits mediate species' vulnerability to decline.

In the three studies of this Ph.D. thesis, I test hypotheses that could explain bumblebee species persistence across North America and within particular biological communities. I aim to create a cohesive picture of climate and land use impacts on bumblebees and direct conservation initiatives towards the most impactful outcomes. In my first study (Chapter 2, published in *Biological Conservation*), I tested continent-wide processes that could affect bumblebee species' climate change vulnerabilities spatially and temporally, by considering shifts in species' emergence timing (or, phenologies). A limiting factor in testing phenological responses to environmental changes is availability of emergence records. I addressed that gap by estimating emergence timing using a new technique that can enable measurements of emergence timing even when that timing was imperfectly observed. I demonstrated the interaction between species' thermal niches, thermal position, and both bumblebee diversity and abundance, respectively.

In Chapter 3, I tested whether trends I discovered previously (Chapter 2), and that are now widely observed in other macroecological and global change research (e.g. Soroye et al., 2020, Outhwaite et al. 2022, Ghisbain et al. 2024) could be translated to individual bumblebee communities in agricultural and semi-natural landscapes across southern Ontario. I expected that bumblebee diversity within these systems would decline based on individual species' proximities to their upper thermal niche limits, which were assessed using microclimatic observations from each field site and from the surrounding landscape. This approach moves beyond the limitations imposed by reliance on extrapolative models, like occupancy or species distribution models, to assess bumblebee species diversity directly. This work demonstrates that continental-scale analyses of global change impacts on species can be extended directly to that of individual biological communities that can inform subsequent conservation efforts within habitats and landscapes.

In my final study (Chapter 4), I expanded this work to address both functional and phylogenetic diversity. I constructed a phylogenetic tree for *Bombus s*pecies that were detected in southern Ontario field sites to measure their phylogenetic relationships. I assembled trait data for bumblebee species. Then, I tested how both functional and phylogenetic diversity varied among sampled habitats and over time, finding pronounced declines in both over the study period. This work expands understanding of how diversity of these critical pollinator species can vary relative to both temperature and habitat conditions and shows that bumblebee diversity, in both functional and phylogenetic terms, can differ substantially even over short time periods.

These three studies examine interacting influences on bumblebee biodiversity, both at localized and broader scales, and may suggest new avenues for conservation and management of these species. This thesis also highlights how important thermal extremes are for predicting changes in bumblebee communities. While habitat factors like land use change have often been seen as the main drivers of population shifts, my results show that a joint consideration with temperature extremes can enable clearer predictions of bumblebee persistence at both broad and local scales.

The frequency and severity of extreme weather seems poised to alter where many bumblebee species can persist, and the analyses I develop in this thesis may help inform how other taxa will respond to both climate and land use changes.

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Chapter 2: Strong phenological shifts among bumblebee species in North America can help predict extinction risk

Note: This chapter is a slightly modified version of the following published article:

Koppel, O., Kerr, J. (2022). Strong phenological shifts among bumblebee species in North America can help predict extinction risk. *Biological Conservation.* https://doi.org/10.1016/j.biocon.2022.109675.

Abstract

Biological responses to climate change can affect species' survival prospects, and failures to track favourable climate conditions can increase extinction risk. Two predominant strategies to mitigate climate change are spatial and temporal shifts, however, the trade-offs between these responses for vital pollinator taxa are unknown. Also, the phylogenetic pattern of climate-driven phenology shifts is poorly understood. Here, I analyze emergence and peak phenology for 21 *Bombus* species across Canada and the United States during baseline (1954–1970) and modern (2004–2012) periods to assess whether *Bombus* phenology varies with spring onset. I find that bumblebee species which maintain phenological synchrony with spring onset demonstrated an improved persistence probability during the modern period compared to the baseline. Climate strongly explained variation in emergence and/or peak phenology in 15 of 21 species included in the study. Phenology shifts were not phylogenetically structured. This approach serves as a guide to analyzing spatiotemporal responses to climate change on a large scale across taxa.

Introduction

Recent climate change has exacerbated global biodiversity declines (Otto, 2018). Losses in bee pollination services has already had significant economic implications and cascading biodiversity consequences (Goulson et al., 2015; Kerr et al., 2015). Climate change imposes conditions that are outside of species' ecological tolerances, thereby directly increasing extinction risk and shrinking food and resource availability (Brondizio et al., 2019). There is mounting evidence of climate-driven declines in bumblebees (*Bombus*), a group of approximately 260 cold-adapted species that provide vital pollination services (Arbetman et al., 2017; Giannini et al., 2020). Hotter temperatures can lead to added energy expenditure for thermoregulation in bees, reducing efficiency in foraging and caring for the brood, and ultimately reducing colony size and success (Heinrich, 2013). This is a leading hypothesis to explain shrinking *Bombus* ranges over the past century in twenty North American species (Sirois-Delisle & Kerr, 2018).

While geographical range shifts area predominant response to climate change (Massimino et al., 2015; Parmesan & Yohe, 2003), species may also shift the timing of their biological activity to remain within their climatic niches (Parmesan & Yohe, 2003; Socolar et al., 2017; Visser, 2008). Bumblebees, like other pollinators, may also rely on phenological shifts to track floral resource availability (Kudo, 2014). Phenological synchrony between early-emerging *Bombus* and early flowering plants ensures *Bombus* will have access to floral resources. Therefore, it is reasonable to expect that environmental cues such as spring onset timing would be closely matched by early emerging species (Goulson, 2010). For both early- and later-emerging species, temperatures recorded at first emergence are associated with impaired colony development, such as reduced offspring production under heat stress (Vanderplanck et al., 2019). Earlier appearance and longer activity periods recorded in British butterflies were determined to have a strong relationship to temperature (Wood & Ripton, 2000).

The relative roles of phenology and range shifts in reducing climate-driven extinction risk remain highly uncertain and are likely to be context-dependent (Fig. 2.1). For example, geographical range shifts may allow species to escape potential negative impacts of rapid warming, particularly in landscapes where access to different elevations and microclimates is limited (Kerr et al., 2015). A variety of sites in proximity may allow species to move to conditions that are within their thermal limits. Alternatively, phenological shifts can enable critical life history activities to occur during more favourable periods of the year and represent another avenue to facilitate a population's persistence (Hereford et al., 2017; Singer, 2017). There is some evidence that *Andrena* and *Osmia* bee phenology might shift in response to warming conditions in the Northeastern United States (Bartomeus et al., 2011), paving the way for an analysis that considers where phenological shifts may mitigate the need for geographical range shifts, and vice versa.

Species' responses to climate change, whether in the form of shifts in the location of geographical ranges or seasonal timing, are also likely to depend on their evolutionary history. The outcome of both shifts is to cause species to track tolerable environmental conditions more successfully in space, time, or both. Species thermal limits are conserved across lineages among many groups, including bumblebees (Kerr et al., 2015), mammals (Jones et al., 2005), and plants (Patiño et al., 2017). Grab et al. (2019) demonstrate that pollinator species losses in commercial apple orchards are phylogenetically structured, leading to loss of pollinator functional diversity and impacts fruit yield and quality. Phylogenetic bias in declines has been demonstrated previously in tests of pathogen resistance in trees (Potts et al., 2016) as well as in bumblebees

(Arbetman et al., 2017). While range shifts and phenological change may be driven by different processes, if thermal tolerance is part of the cause of such changes, then there may be a phylogenetic signal in these climate responses. Conversely, species-environment interactions might more strongly affect such responses. Stemkovski et al. (2020) measured plant-pollinator mismatch on a local scale and identified traits specific to bees that may affect their rates of phenology change. Many other studies mentioned risks of homogenization of species with declines, for example the impact of decreased functional diversity on pollination services (Martins et al., 2015). However, they do not make explicit predictions for phylogenetic bias of extinction risk. Except for a recent publication examining phylogenetic structure of habitat breadth in German wild bee species(Hofmann et al., 2019), an explicit test of phylogenetic structure of large-scale extinction risk is lacking among vital pollinator taxa such as bumblebees. Understanding patterns of phenological change in *Bombus*' North American distribution, and why certain species are more susceptible to climate change-related extinction risks, is a critical knowledge gap. While *Bombus* provides crucial pollination services, many *Bombus* species face decline (Jackson et al., 2022). *Bombus* has exhibited large-scale range responses to climate, with population extinction risks rising in areas where species are near their upper thermal limits (Soroye et al., 2020). The assessment of spatiotemporal niche limitations of one plant species has illustrated that species could remain within tolerable environmental conditions by shifting either to new areas or by shifting phenologically (Hereford et al., 2017). This research identifies a framework for understanding the trade-off between range shifts and phenological responses. While studies have documented phenological shifts in response to climate (e.g., Blasi et al., 2023), few have linked the strength of phenology–climate relationships to species persistence at large scales. The extent to which these shifts follow phylogenetic patterns remains poorly understood for *Bombus*. This chapter fills this gap by examining whether phenology tracking leads to persistence advantages, and whether such responses are phylogenetically conserved. Here, I analyze a *Bombus* occurrence dataset of over 18 000 observations across Canada and the United States between 1954 and 2012. This data spans the baseline period of 1954-1970, prior to the increased rate of climate change, and a modern period of 2004-2012. I address three questions: (i) Is timing of spring onset a determinant of emergence and peak colony abundance of *Bombus*? (ii) Is species' probability of persistence directly related to the strength of the phenology-climate relationship? (iii) Is there a phylogenetic bias in climate-driven extinction risk? Describing the mechanisms that underlie climate-driven extinctions is a necessary step for effective biodiversity conservation.

Materials and Methods

All analyses were conducted in R v.4.0.5 (Team, 2017) and ArcGIS Pro v.2.7.3 (Environmental Systems Research Institute (ESRI), 2019).

Bee occurrence data

Occurrence data were taken from previously compiled museum collection records (Kerr et al., 2015). Baseline and modern periods consisted of 6505 and 6711 occurrence data points, respectively, after filtering for 21 bumblebee species for which sufficient data could be collected to construct tests (Fig. S2.2; Fig. S2.6).

I selected the durations of the modern and baseline periods to reduce the differences in number of records between them. I then categorized individual specimen collection locations into sites of 100 km by 100 km extent. This quadrat resolution was chosen given the density of available data points and considered to accurately estimate occupancy of species and characterize species richness (Hurlbert & Jetz, 2007) as well as to maintain climate data resolution. To address non-detection in an uncomplicated way, only sites with more than one recorded species per period were retained. This assumption was made to reduce the number of false absences of species due to non-detection, since sites with multiple detections are more likely to accurately reflect occupancy (Guillera-Arroita, 2019). Sampling intensity was also included in regression models, though was not found to be significant. Duplicate observations (i.e., multiple observations of the same species on the same day at the same site) were excluded.

I also only included observations in which a species was present in a site a minimum of five times in a period, as a minimum of five observations were necessary for the chosen emergence phenology estimation model (see below for emergence phenology estimation and model details, as well as peak phenology estimation methods). After emergence phenology was estimated for each species at each site per period, only sites where emergence confidence interval did not extend below zero were retained. Although the original dataset contained 25 species, only 21 species persisted across periods and could be included in the generalized linear mixed model (GLMM) analyses.

Climate data

To quantify the shift in spring onset, I compared the first day of the growing season between periods. Spring-onset date (hereafter "spring onset") served as my site-level climate variable. Natural Resources Canada defines spring onset as the first calendar day after five consecutive days with mean air temperature≥ 5ºC (NRCAN, 2019). Because it integrates daily temperature records across several days, this metric is a biologically meaningful proxy for local thermal climate (Schwartz et al. 2006) and is widely used to track warming trends in temperate regions. The first day of the growing period is a relevant indicator of shifts in climate patterns and captures a period where phenological mismatch between bees and appropriate temperatures can have consequences on colony abundance for the rest of the season (Kudo & Ida, 2013).Spring onset date was used from the year of each respective occurrence record, for the appropriate 100 x 100 km site.

Phenology estimation

To establish whether spring onset is a determinant of *Bombus* phenology, I estimated the annual emergence and peak colony abundance for each species at every site across their distributions. Since these analyses use museum collection data that were not explicitly collected to capture emergence timing, the date of absolute first appearance will have been recorded with a high error rate and is likely to be underestimated (i.e., species likely emerged earlier than the date on which they were first observed in a particular place; (Kharouba et al., 2018; Moussus et al., 2010). Also, colonies are started by a single queen bee each season, and so colony sizes are small at the start of the season and a species are less likely to be detected because bumblebees belonging to the species are simply less common then (Fig. S2.1; Fig. S2.5). Consequently, I estimated the first emergence of each species per site using a Weibull extinction curve method with code published in Pearse et al. (2017). The Weibull probability distribution estimates the theoretical distribution of a failure rate over time. For example, this distribution has been used to model the shrinking population size of the dodo over time to estimate the year of its extinction. This method was adapted in turn by Pearse et al. (2017) to model the distribution of the start of a process over time, rather than the end, and estimate the timing of a series of species' occurrences that may have been missed at the start of a sampling period. Here, the method can be helpful to estimate emergence timing in even a sparsely sampled site (Fig. S2.3).

The timing of the peak colony abundance is also a commonly implemented phenology metric that has the advantage of being robust to outliers at start of season (Taylor, 2019). Peak colony abundance was defined as the first day of the year by which 50% of reported observations were collected for each species at each site.

Modelling phenology drivers

All models were implemented in R (v4.0.5) using the *lme4*, *MuMIn*, and *phytools* packages.

I modelled the drivers of phenology across all study species with separate generalized linear mixed model (GLMM) analyses for emergence and for peak colony abundance timing, including spring onset, period, and sampling intensity as predictors and species ID as a random effect in both models. Only unique species, site, and period combinations were retained for models. Sampling intensity is represented by the number of species at each site and is included since sampling effort in museum collection data may vary across sites (Kharouba et al., 2014). In another set of models, site was included as a random effect to allow the relationship between phenology and climate to vary by site ID. I calculated marginal (i.e. fraction of variation explained by fixed effects only) and conditional (both fixed and random effects included) coefficients of determination (R^2) of a GLMM in package *MuMIn* (Barton & Barton, 2020; Nakagawa & Schielzeth, 2013). Residuals were visually assessed for normality and homoscedasticity, and variance inflation factors (VIFs) were checked to rule out multicollinearity among predictors.

I repeated regression model analyses predicting emergence and peak colony abundance timing for each individual species, with climate, period, and sampling intensity as predictors, and obtained species-level R^2 values as a measure of model goodness-of-fit. For each individual species I also calculated the correlation between the probability of persistence and the phenology-climate relationship.

Modelling persistence probability

Persistence probability was calculated as the ratio of the number of sites at which a species persisted in the recent period (2004–2012) to the number of sites it occupied in the baseline period (1954–1970). To explore the predictors of persistence probability, I tested whether this value was associated with the strength of the phenology-climate relationship for each species. Specifically, I used Kendall's rank correlation (τ) to test whether species with stronger correlations between spring onset timing and phenology (as measured by R^2 from species-level linear models) exhibited higher persistence probabilities. This approach does not involve a generalized model of persistence per site and instead examines persistence as a species-level summary metric associated with climate tracking ability.

Modelling extinction risk

I modelled extinction risk per species by quantifying the proportion of sites at which species were present in the baseline period but did not persist in the modern period.

Phylogenetic bias of extinction risk

I constructed a phylogeny using the most recent CO1 gene sequence data from GenBank. Sequences were manually trimmed, and alignments were created for this locus using MAFFT, an alignment method chosen for its relative speed and accuracy (Katoh et al., 2002). The best-fit model of nucleotide substitution with the lowest Bayesian information criterion score was estimated using ModelTest (Posada & Crandall, 1998) to be a General Time Reversible model with gamma distribution and invariant sites considered (GTR + G; BIC = 18028.7, AICc = 16833.1). The Bayesian inference method was used to construct a phylogeny with MCMC chain of 1 000 000 generations, and a burn-in of 100 000. The topology is congruent with previously published *Bombus* phylogenies (Cameron et al., 2007).

To determine whether there is phylogenetic bias in phenology shifts or climate-driven extinction risk, I tested for phylogenetic signal by estimating Pagel's lambda (λ;Pagel 1999) in R package *phytools* (Revell, 2012). Pagel's λ is a metric used to calculate whether species' traits are more similar in closely related species, i.e. whether traits display a 'phylogenetic signal'. Like Blomberg's K or Moran's I, this metric tests against the null hypothesis that more closely related species do not have more similar traits than expected by chance (Blomberg et al., 2003). Pagel's λ is an effective metric to test for phylogenetic signal under the Brownian motion model, a stochastic model of trait evolution that assumes random genetic drift (Munkemuller et al., 2012). If Pagel's λ is closer to 0, there is progressively less evidence of phylogenetic signal. Conversely, as the metric approaches 1, phylogenetic signal in the trait data is stronger.

Land use intensity

I calculated the mean land use intensity metric for each site using a global dataset of cumulative human modification of landscape; land use intensity is scaled between 0 and 1 and represents the proportion of land affected by thirteen metrics of human settlement, agriculture, transportation, and mining and energy production at a 1-km resolution (Kennedy et al., 2020). I constructed GLMMs of annual emergence and peak colony abundance for each species including land intensity as a predictor along with spring onset timing and compared these with models based on spring onset timing alone, by comparing marginal R^2 values. An R^2 value of greater than 0.2 was considered a high to moderate correlation. This threshold was chosen based on the nature of ecological and environmental data.

Results

Phenology changes

Spring onset shifted an average of 6.8 days earlier between baseline (1954-1970) and modern (2004-2012) periods across the study area (ranging from 35 days earlier to 6 days later), while emergence phenology shifted an average of 3.4 days earlier across all species, and peak colony abundance phenology shifted an average of 1 day earlier (Table S2.1). Of the 121 sites that were occupied in the baseline period, 99 remained occupied, suggesting that *Bombus* populations are struggling to persist in about 1/5th of sites examined.

Phenology-climate correlation

Spring onset timing did not account for variation in emergence and peak colony abundance across all species (marginal R^2 = 0.22 and 0.11, respectively). However, spring onset explained over 30% of variation in emergence phenology of six individual species; *B. mixtus*, *B. rufocinctus*, *B. melanopygus*, *B. huntii*, *B. fervidus*, *B. frigidus* (Fig. 2, Table S2), and over 30% of peak colony abundance of 11 species: *B. auricomus*, *B. melanopygus*, *B. borealis*, *B. morrisoni*, *B. vosnesenskii*, *B. occidentalis*, *B. terricola*, *B. mixtus*, *B. appositus*, *B. flavifrons*, *B.*

bimaculatus (all $p < 0.05$). R^2 is greater than 0.2 in 15 of 20 bumblebee species (Table S2), indicating that spring timing was a driver in emergence phenology for those species. There did not seem to be a bias between strength of emergence-climate correlation and whether a species was early- or late- emerging (Fig. S2.8).

The variation explained in emergence and in peak colony abundance by GLMMs was improved slightly by inclusion of a land use intensity metric as a predictor ($p = 0.01$ and $p = 0.002$ respectively; Table S2.3), indicating that anthropogenic land use contributes to variation in phenological timing alongside climatic factors.

Including site as a random factor in the GLMMs sharply increased the proportion of variation explained in emergence phenology (conditional $R^2 = 0.57$) and the phenology of peak colony abundance (conditional $R^2 = 0.52$).

Persistence probability and phenology

Persistence probability was positively related to the strength of the phenology-climate relationship across species (Kendall's $\tau = 0.26$, Fig. 4). Persistence probability was highest in sites where spring onset shifted no more than 10 days, while extinction rates were highest in sites with greater changes in spring climate, such as with advances in spring warming of more than 10 days (Fig. S7). Species' measured extinction probabilities were congruent with their statuses on the International Union of Conservation of Nature's (IUCN) Red List of threatened species, an international database of conservation status (IUCN, 2018); all bumblebee species with an endangered or vulnerable IUCN category were also found to have >80% extinction probability in my analyses (Table S4).

Phylogenetic signal in phenology

A phylogenetic signal was not detected in phenological shift or extinction risk ($\lambda < 0.01$), indicating higher divergence in these terms between species than would be expected under the Brownian motion model of evolution (Fig. S2.4) The strength of correlation between climate and phenology was also not phylogenetically biased (Fig. 2.3).

Discussion

Species' survival prospects are conditional on their biological responses to climate change. The decline or loss of pollinator taxa, like bumblebees, is likely to have ramifications for the stability of ecosystem service provision and vital aspects of human activity that depend on pollination. A failure to consider large scale phenology responses hinders reliable prediction and mitigation of ongoing bumblebee extirpations. This paper identifies large-scale, climate change-related bumblebee phenology shifts that have not previously been detected.

These models show large shifts towards earlier emergence timing across Canada and the United States for six of 21 *Bombus* species studied (Fig. 2.3) and peak colony abundance shifts in 11 species, with 15 species in total showing strong phenology shifts. This demonstrates that bumblebees exhibit large-scale, climate-driven phenology shifts, in addition to range changes previously demonstrated (Soroye et al., 2020) and highlights the need for exploring both phenology and range shifts when considering climate impacts across other taxa. This finding is consistent with single-species and local-scale studies showing that insect phenology is sensitive to climate change (Forrest, 2016; Gordo & Sanz, 2006; Schenk et al., 2017). My findings, including the broad distribution in species' phenology shifts (Table S1), also highlight that while climate change responses are widely site- and species- dependent, a central tendency towards earlier emergence and peak colony abundance is measurable.

Persistence probabilities for species that responded to climate with changes in emergence phenology were slightly higher than for those species that did not match phenology shifts to climate shifts in this way. This finding may demonstrate that phenology shifts are adaptive, allowing these *Bombus* species to respond to resource availability more effectively or avoid climatic conditions that hinder life history activities. The weak correlation between spring onset and phenologyfor most species' phenology shifts may indicate that other environmental changes, such as land use intensity, microclimatic variability, or resource availability also play a role in whether species respond with phenological shifts, rather than indicating an absence of phenological plasticity (Forrest, 2016). For example, species that have grown rarer over recent decades may respond less clearly to climate change in terms of their seasonal activities because other stressors constrain their activities already; alternatively, sparse records for such rare species can inflate the variance of our phenology estimates, adding statistical noise that partially masks a true climate signal. However, random effect analyses indicate that observation noise alone is not likely to generate the patterns reported. *B. pensylvanicus* faces threats from parasites, invasive pathogens and land use change and is classified as vulnerable in its North American distribution (Hatfield et al., 2014). Although *B. pensylvanicus* had moderate climate-driven emergence and peak colony abundance shifts ($R^2 = 0.21$ and 0.17, respectively), its persistence probability was low (7.7%). Including a predictor that represents a cumulative measure of anthropogenic stressor intensity, including land use intensity, marginally improved predictions of phenology (Table S2.2).

Phylogenetic bias was not observed in emergence phenology shifts or climate-driven extinction risk (Fig. 2.3). Closer evolutionary relationships between bumblebee species could give rise to similarities in relevant traits, such as climatic specialization (Williams et al., 2008) and, consequently, similar responses to environmental changes. Phylogenetic bias in phenology shifts was also expected, as this has been noted in plants (Davis et al., 2010; Willis et al., 2008). Phenology rates may diverge from expected Brownian motion evolution rates if species-environment interactions strongly affect phenology shifts (Felsenstein, 1985). This may be the case if abiotic conditions exert pressure on species to evolve more quickly. Further analyses into species-environment interactions that may impact phenology could explore why emergence phenology diverges from the expected Brownian motion rate of trait evolution.

The phenological responses of bumblebees to climate found in this study differ markedly from those observed previously using a much smaller version of this dataset (about 1/6 the size of the dataset used here; Bartomeus et al., 2011). Previous studies, such as Bartomeus et al. (2011), primarily used first appearance dates of queen bees to estimate emergence phenology. However, phenological responses to warming among bumblebees may have been underestimated, potentially due to a lack of power to detect trends. Reliance on observation timing of queens, which are relatively infrequently collected, likely also led to particularly conservative estimates of phenological responses to climate change. Further, observation of a queen bee does not guarantee that her colony is not already established, and workers are not already active, and in fact was not the case with these data (Fig. S2.1). In contrast, emerging statistical techniques like the application of the Weibull distribution to estimate emergence times (Pearse et al., 2017), developed subsequent to Bartomeus et al., (2011), can provide more powerful estimates of emergence phenology by retaining individuals of all castes in large-scale phenological analyses.

Such directional phenological shifts appear to be more common than would be expected among bumblebee species based on such previous studies, which may help explain why other forms of climate change response, such as geographical range shifts, occur relatively infrequently. Phenological shifts are important to consider in climate responses and should not be overlooked because of imperfect data availability.

Phenology shifts should be considered in tandem with range shifts for a comprehensive understanding of species responses under climate change. These results show that bumblebees are exhibiting phenological responses to climate change, and this affects persistence probability in some species. Large-scale, temporal climate responses are notable in *Bombus*. Future bumblebee climate response projections could be improved with the inclusion of phenology. This approach is a valuable tool to inform biodiversity conservation initiatives across taxa.

Figures 2.1 – 2.4

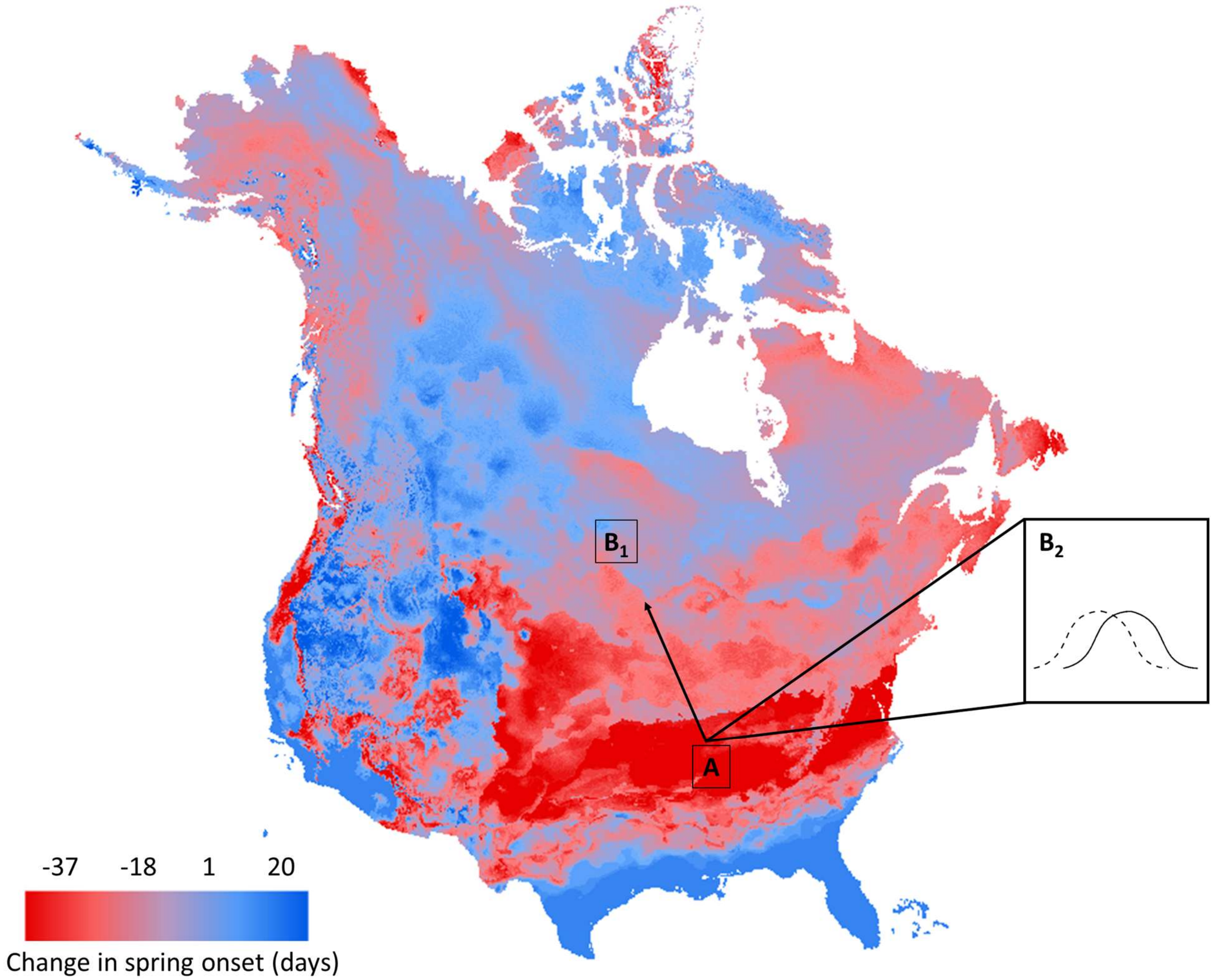

Figure 2.1. Conceptual representation of how climate change effects can be mitigated via a range shift (B1) or phenological shift (B2). Areas with earlier spring onset relative to the baseline period are represented by darker red areas of the map and as more negative values in the legend. Both range and phenology responses can help species remain within more similar climatic conditions to those in their historic distributions.

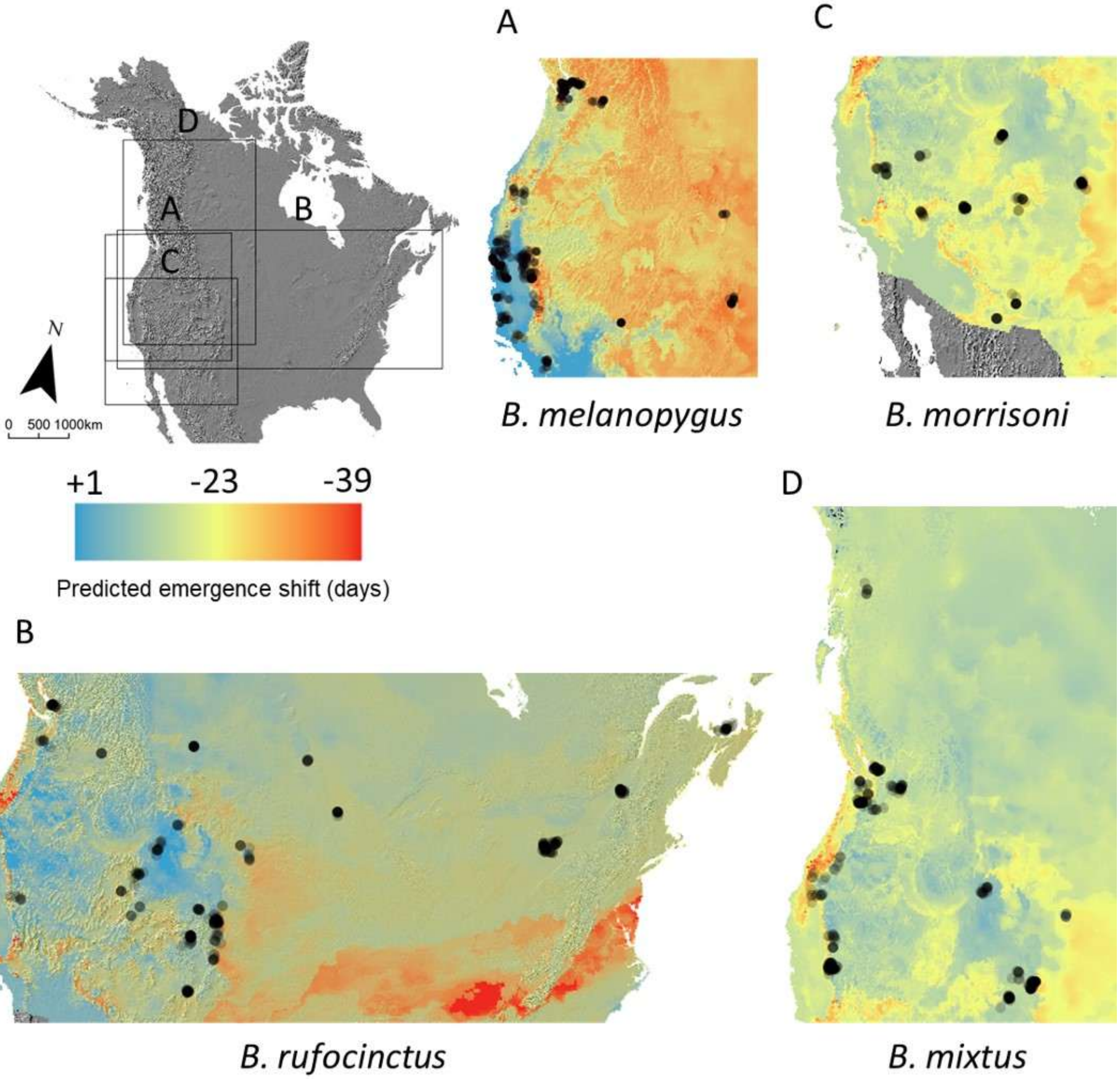

Figure 2.2. Model-predicted emergence phenology shift (days) between periods in four of seven species that had a strong ($R^2 > 0.25$) and statistically significant (p-value < 0.05) relationship with spring emergence onset: *Bombus melanopygus*, *B. morrisoni*, *B. rufocinctus*, *B. mixtus*. Predicted values were calculated by applying species-specific model coefficients to observed changes in spring onset. Negative values represent earlier spring onset. Black circles represent occurrence points.

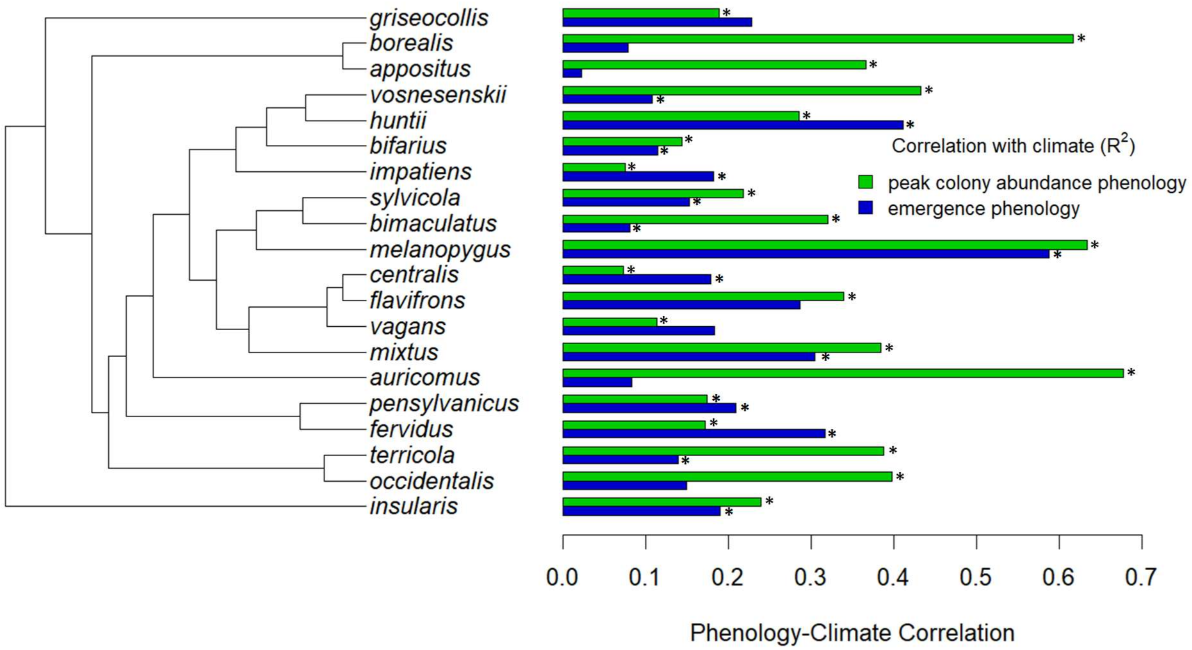

Figure 2.3. Phylogeny of 21 *Bombus* species and their relationships across species between first day of spring and phenology advance across species (Phenology-Climate Correlation). * denotes statistically significant correlation (p-value < 0.05). Note: *B. morrisoni* CO1 sequence was not available.

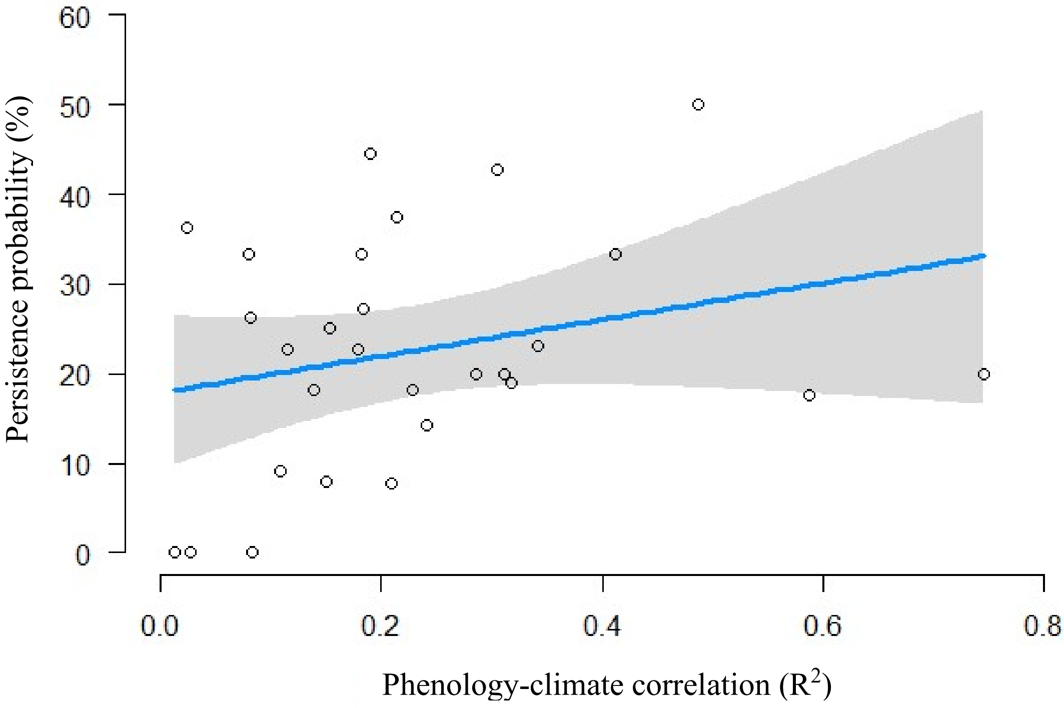

Figure 2.4. Change in persistence probability (%) with strength of phenology-climate correlation (R^2). Black dots represent individual species. Shaded area represents 95% confidence interval.

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Supplementary Figures S2.1 to S2.8

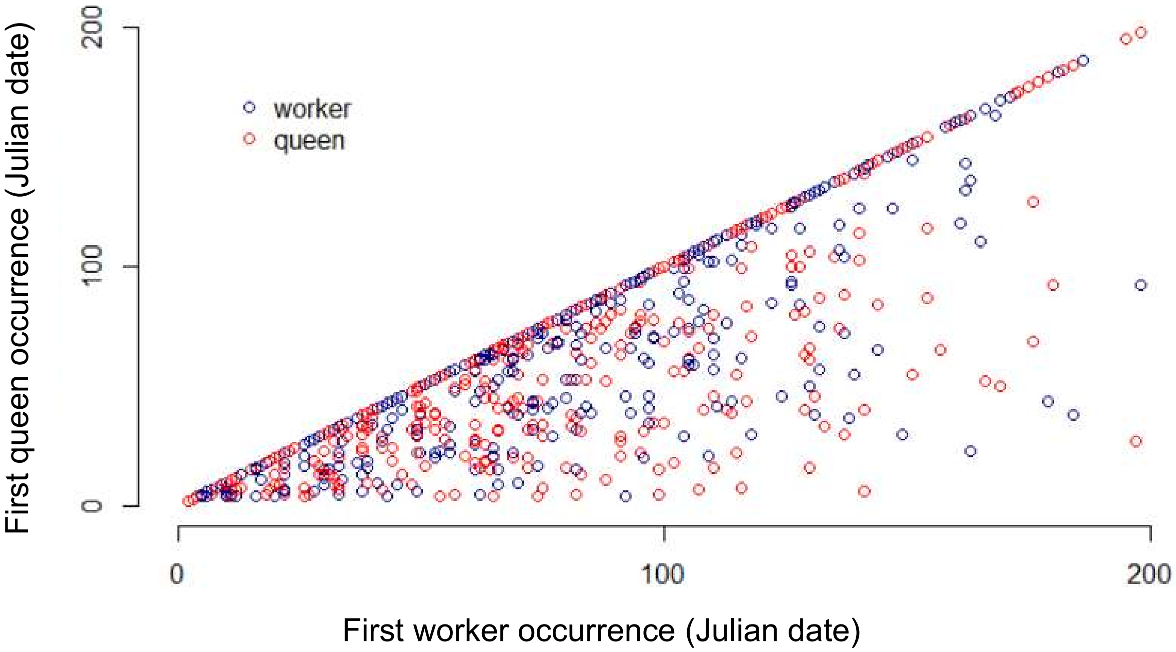

Figure S2.1. Julian day of earliest *Bombus* queen and worker observations in each site.

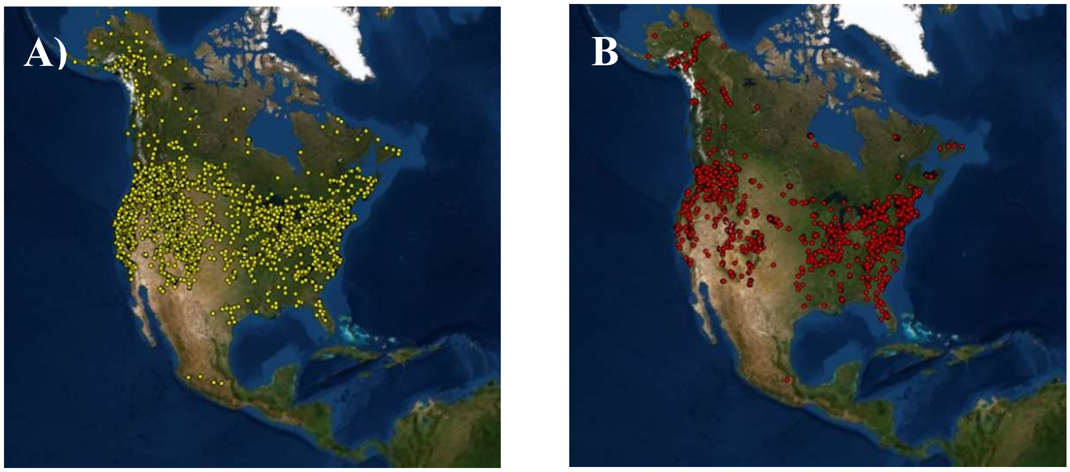

Figure S2.2. Distribution across North America of georeferenced records for the A) baseline period, 1954-1970 and B) recent period, 2004-2012.

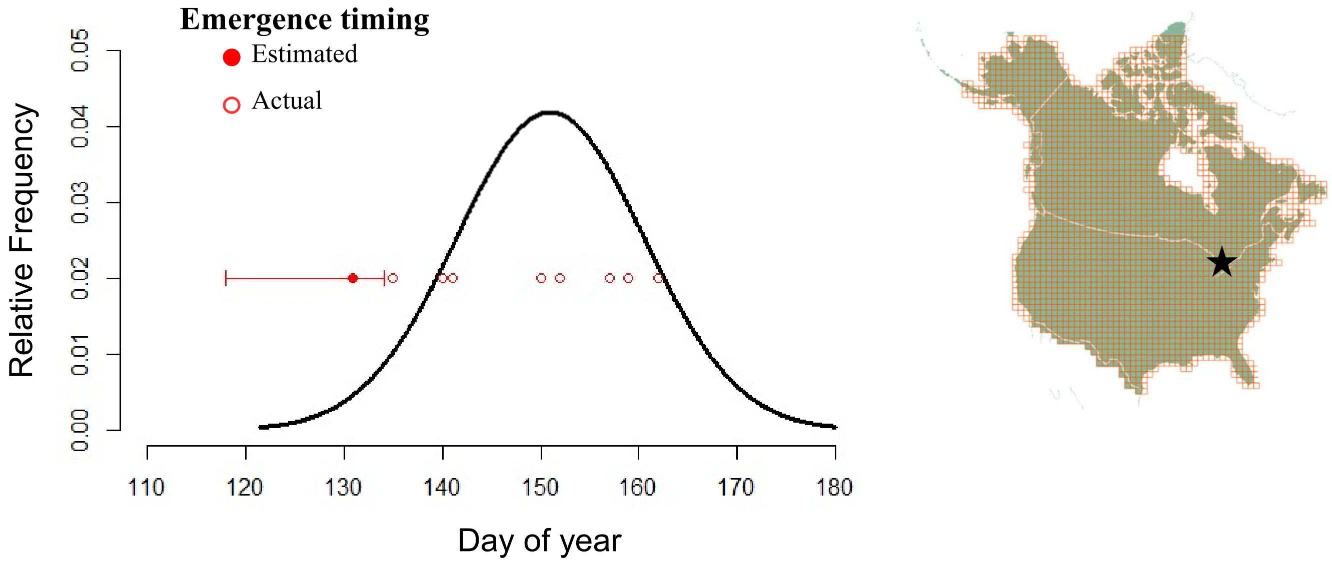

Figure S2.3. Illustration of the emergence timing estimation method at site #2322 in a sample year. The black curve shows the relative frequency of *B. bohemicus* occurrences over time throughout an active season. The stimated first emergence (Filled red dot (+/- 95% confidence interval) is compared with the actual earliest 10 occurences (empty red circles). The emergence estimation method adapted from Pearse et al. (2017) was used to arrive at first emergence dates per species.

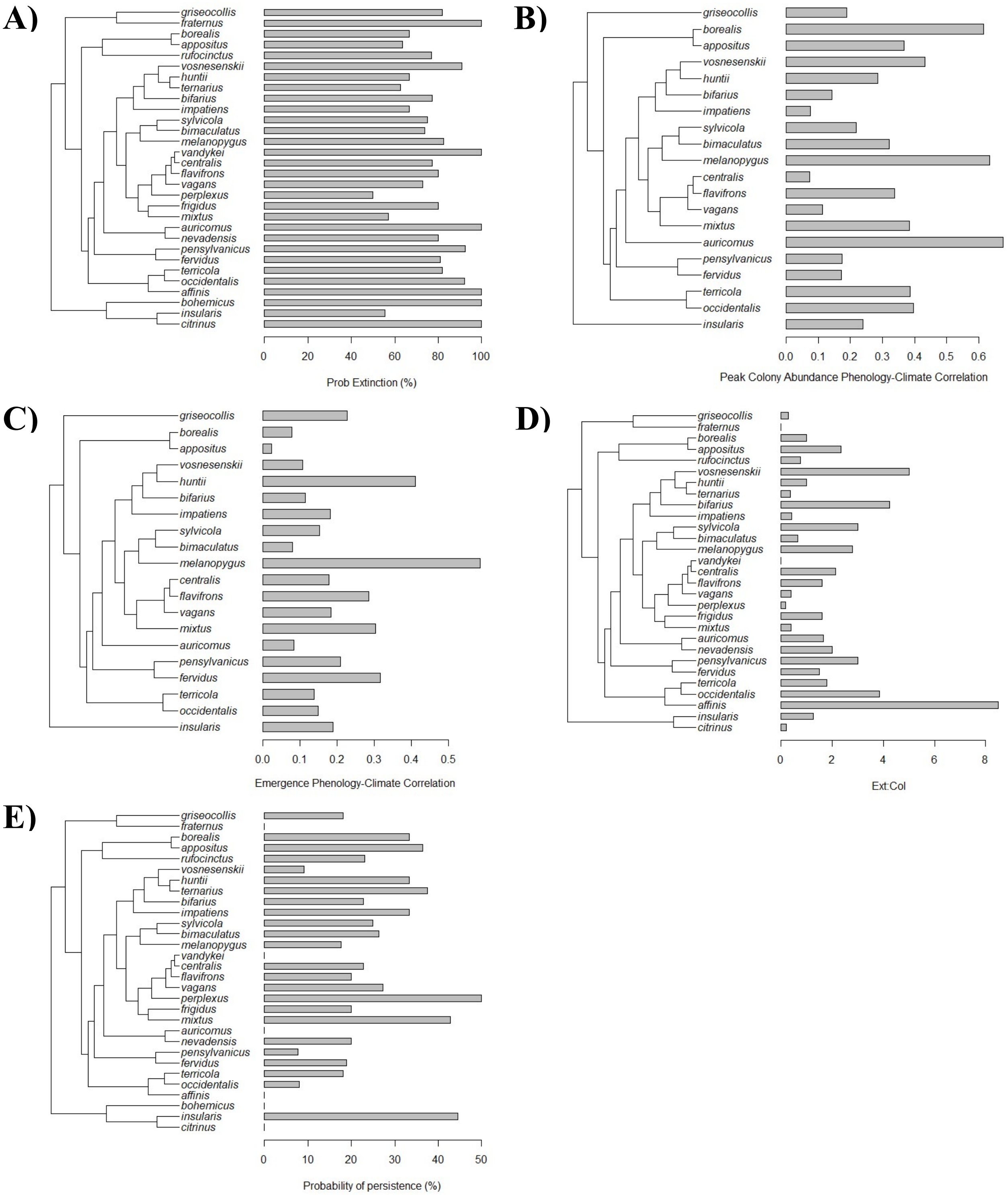

Figure S2.4. Phylogeny of bumblebee species included in studies alongside bar charts of: (A) probability of extinction (%), (B) species-level peak colony abundance phenology-climate correlations (%), (C) species-level emergence phenology-climate correlations (%), (D) extinction to colonization ratios, and (E) probability of persistence (%).

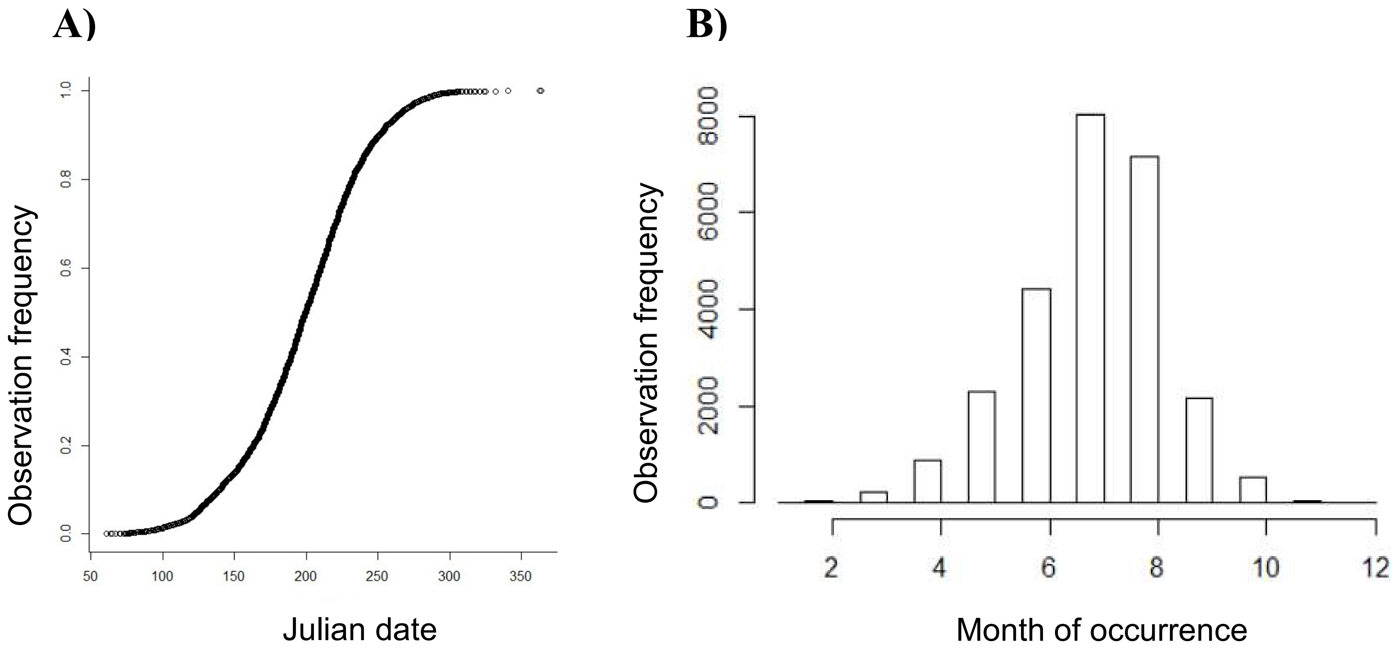

Figure S2.5. *Bombus* occurrence frequency collected throughout the calendar year. A) Cumulative frequency, B) Bar chart displaying observation frequency per month.

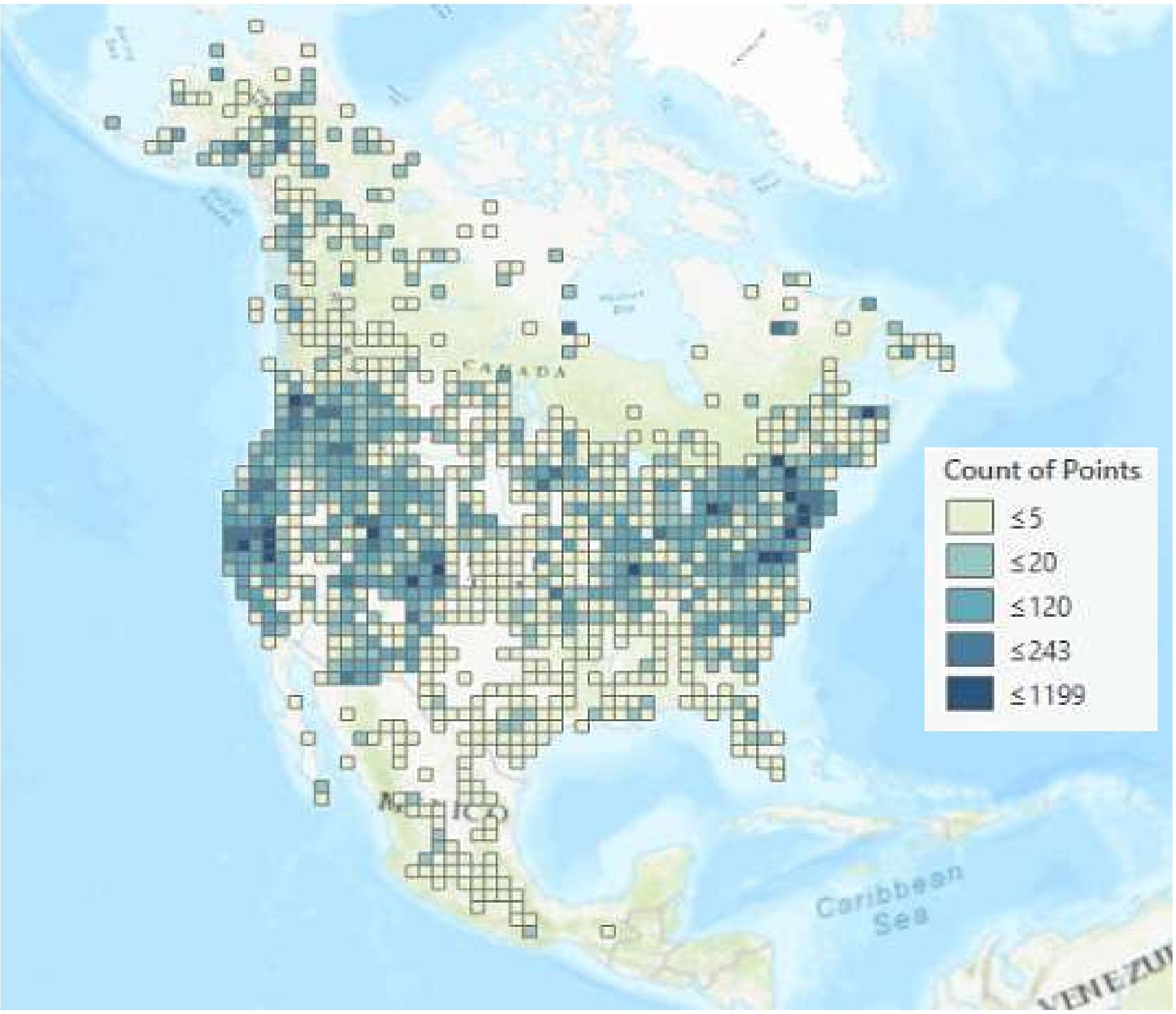

Figure S2.6. Sample frequency across sites in raw occurrence data. Poorly sampled sites were excluded from analyses.

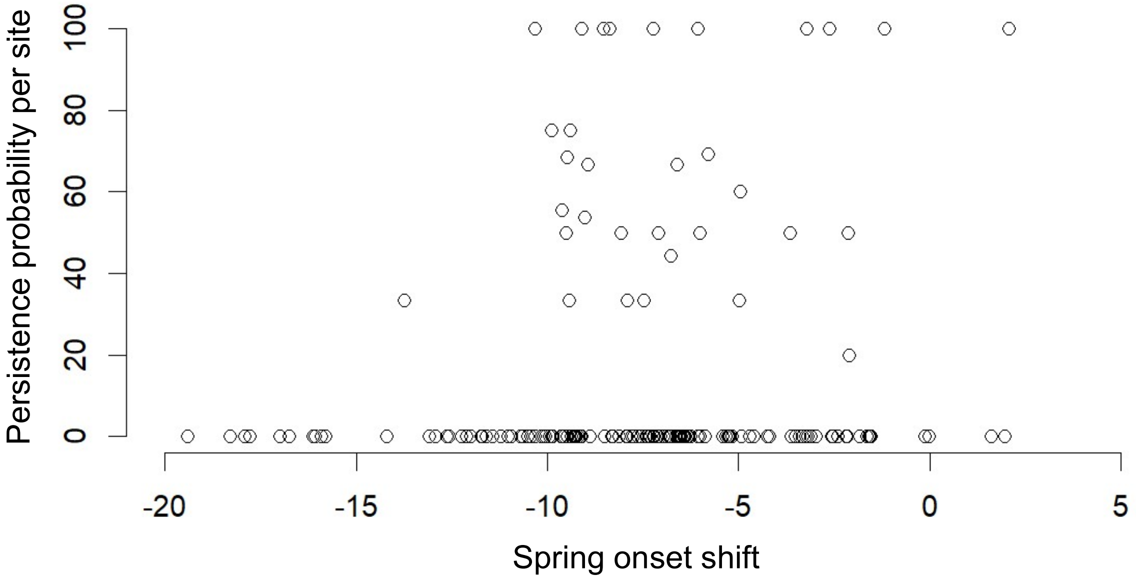

Figure S2.7. Probability of persistence (%) per site across varying spring onset shifts (days). Negative values represent earlier spring onset.

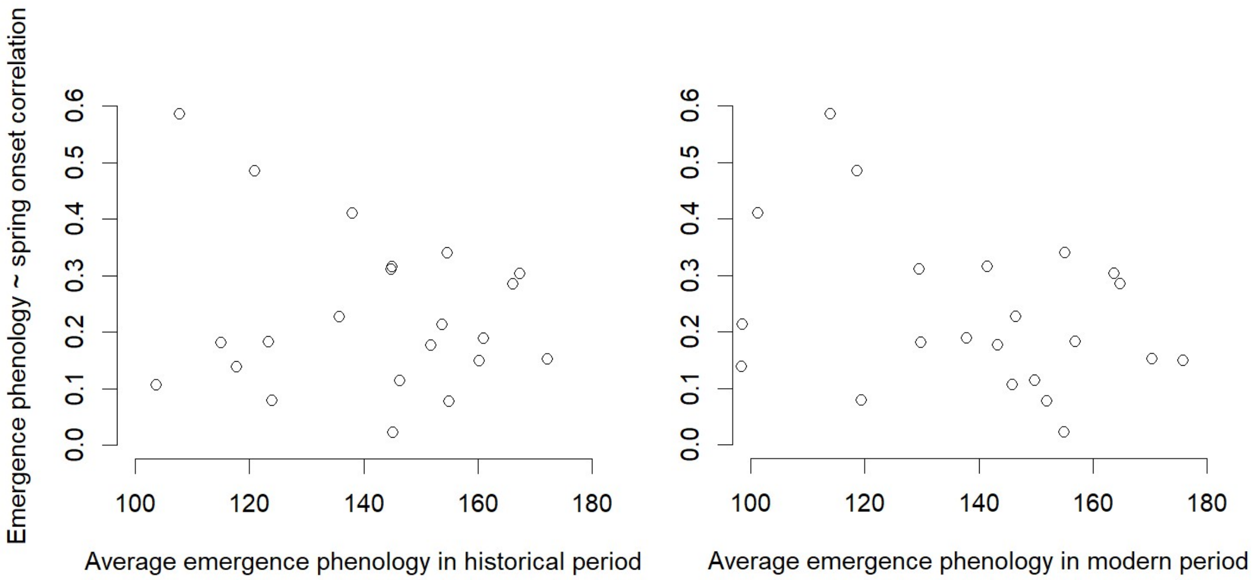

Figure S2.8. The correlation between emergence phenology and spring onset of *Bombus* species compared with their respective average emergence phenologies in the historical and modern periods.

Supplementary Tables S2.1 to S2.4

Table S2.1. Average Julian day of emergence and peak colony abundance phenologies with respective standard errors (SE) and phenology shifts between periods for 25 *Bombus* species in baseline and recent periods. Species that persisted in at least one site are included.

	Baseline period				Modern period				Shifts between periods	
Species	**Average emergence (Julian day)**	**SE**	**Average peak colony abundance (Julian day)**	**SE**	**Average emergence (Julian day)**	**SE**	**Average peak colony abundance (Julian day)**	**SE**	**Average emergence shift (days)**	**Average peak colony abundance shift (days)**
appositus	145.07	16.76	197.25	4.68	154.90	8.07	199.25	7.63	9.83	2.00
bifarius	146.25	10.62	190.80	7.33	149.75	11.49	192.40	7.62	3.50	1.60
bimaculatus	123.80	8.55	157.80	9.61	119.34	16.42	176.20	5.29	-4.47	18.40
borealis	154.95	13.01	185.00	3.00	151.90	0.11	196.50	6.50	-3.05	11.50
centralis	151.66	15.12	188.40	13.06	143.21	17.49	190.00	16.85	-8.46	1.60
fervidus	144.90	7.64	186.86	11.53	141.39	12.15	194.00	6.71	-3.51	7.14
flavifrons	166.07	7.03	198.75	8.18	164.71	15.28	203.50	9.42	-1.36	4.75
frigidus	144.70	13.65	191.50	27.50	129.50	11.56	170.00	25.00	-15.20	-21.50
griseocollis	135.68	21.46	173.00	8.00	146.38	11.86	191.50	5.50	10.70	18.50
huntii	137.97	18.24	186.75	10.80	101.13	9.65	165.50	18.04	-36.84	-21.25
impatiens	114.86	7.87	211.83	6.97	129.74	7.83	208.17	5.49	14.89	-3.67
insularis	160.93	3.55	192.50	9.74	137.81	14.64	176.75	15.97	-23.12	-15.75
melanopygus	107.71	41.99	147.00	18.25	113.85	37.06	152.00	21.96	6.14	5.00
mixtus	167.39	3.33	209.00	5.57	163.73	5.05	211.33	2.03	-3.66	2.33
morrisoni	167.26	NA	225.00	NA	180.38	NA	193.00	NA	13.12	-32.00
nevadensis	154.37	NA	186.00	NA	154.78	NA	195.00	NA	0.41	9.00
occidentalis	160.14	4.07	210.00	7.00	175.79	3.38	217.00	6.00	15.65	7.00
pensylvanicus	134.51	NA	213.00	NA	132.89	NA	190.00	NA	-1.62	-23.00
perplexus	120.86	2.71	143.50	7.50	118.62	13.24	187.50	1.50	-2.24	44.00
rufocinctus	154.64	6.45	196.00	9.07	155.04	3.42	202.00	10.41	0.40	6.00
sylvicola	172.18	5.90	211.67	3.38	170.30	1.50	207.00	4.93	-1.88	-4.67
ternarius	153.74	40.35	224.00	23.26	98.43	20.51	168.00	27.18	-55.31	-56.00
terricola	117.66	7.51	185.50	34.50	98.32	10.48	195.50	1.50	-19.34	10.00
vagans	123.22	3.00	187.67	16.25	156.80	11.90	199.33	5.46	33.59	11.67
vosnesenskii	103.59	16.31	178.50	31.50	145.77	44.02	173.50	19.50	42.18	-5.00

Table S2.2. Phenology-climate correlations from linear models for each species' emergence and Peak colony abundance phenologies (R^2) for 25 Bombus species. High to moderate correlations ($R^2 > 0.2$) and that are statistically significant (p-value > 0.05) are highlighted in yellow.

Species	**Emergence phenology-climate correlation (R^2)**	**p-value**	**Peak colony abundance phenology-climate correlation (R^2)**	**p-value**
affinis	0.012	0.198	0.184	0.078
appositus	0.023	0.047	0.366	0.002
auricomus	0.083	0.027	0.677	0.023
bifarius	0.114	<0.001	0.143	<0.001
bimaculatus	0.081	<0.001	0.320	<0.001
borealis	0.079	0.584	0.616	0.002
centralis	0.178	0.001	0.073	0.008
citrinus	0.027	0.049	0.191	0.625
fervidus	0.317	<0.001	0.172	<0.001
flavifrons	0.286	0.001	0.339	0.001
frigidus	0.311	0.711	0.731	0.058
griseocollis	0.227	0.001	0.189	<0.001
huntii	0.411	<0.001	0.285	<0.001
impatiens	0.182	<0.001	0.075	<0.001
insularis	0.189	<0.001	0.239	0.003
melanopygus	0.587	<0.001	0.634	<0.001
mixtus	0.304	0.002	0.384	0.001
morrisoni	0.241	0.002	0.454	0.002
nevadensis	0.745	0.414	0.695	0.820
occidentalis	0.150	0.003	0.398	<0.001
pensylvanicus	0.209	<0.001	0.175	<0.001
perplexus	0.486	0.535	0.378	0.194
rufocinctus	0.341	0.005	0.440	0.205
sylvicola	0.153	<0.001	0.218	<0.001
ternarius	0.214	0.843	0.035	0.658
terricola	0.139	0.158	0.387	0.012
vagans	0.183	0.004	0.114	0.042
vosnesenskii	0.108	<0.001	0.432	<0.001

Table S2.3. Generalized linear mixed models (GLMMs) used to analyze predictors of phenology. Each model included species as a random effect.

Response variable	Predictors	R^2	Significance (p-value)
Emergence phenology	Spring onset timing * Period + Sampling intensity	0.218	<0.001
Emergence phenology	Spring onset timing * Period + Sampling intensity + Land use	0.228	<0.001
Peak phenology	Spring onset timing * Period + Sampling intensity	0.111	<0.001
Peak phenology	spring onset timing * Period + Sampling intensity + Land use	0.113	<0.001

Table S2.4. Persistence and extinction probabilities for 31 *Bombus* species as calculated from the manuscript dataset, compared with IUCN Red List extinction risk category and status. In order of concern, from least to most: LC = Least Concern; VU = Vulnerable; EN = Endangered; CR = Critically Endangered.

Species	P(persistence)	P(Ext)	Ext:Col Ratio	IUCN Category	Status
bohemicus	0	100.00	Inf		-*
fraternus	0	100.00	Inf	EN	DECREASING
vandykei	0	100.00	Inf	LC	STABLE
affinis	0	100.00	8.50	CR	DECREASING
auricomus	0	100.00	1.67	LC	STABLE
citrinus	0	100.00	0.20	LC	STABLE
pensylvanicus	7.69	92.31	3.00	VU	DECREASING
occidentalis	8.00	92.00	3.83	VU	DECREASING
vosnesenskii	9.09	90.91	5.00	LC	STABLE
morrisoni	14.29	85.71	2.00	VU	DECREASING
melanopygus	17.65	82.35	2.80	LC	STABLE
terricola	18.18	81.82	1.80	VU	DECREASING
griseocollis	18.18	81.82	0.28	LC	STABLE
fervidus	18.92	81.08	1.50	VU	DECREASING
nevadensis	20.00	80.00	2.00	LC	STABLE
flavifrons	20.00	80.00	1.60	LC	STABLE
frigidus	20.00	80.00	1.60	LC	STABLE
bifarius	22.73	77.27	4.25	LC	STABLE
centralis	22.73	77.27	2.13	LC	STABLE
rufocinctus	23.08	76.92	0.77	LC	STABLE
sylvicola	25.00	75.00	3.00	LC	STABLE
bimaculatus	26.32	73.68	0.67	LC	STABLE
vagans	27.27	72.73	0.40	LC	STABLE
borealis	33.33	66.67	1.00	LC	STABLE
huntii	33.33	66.67	1.00	LC	STABLE
impatiens	33.33	66.67	0.41	LC	STABLE
appositus	36.36	63.64	2.33	LC	STABLE
ternarius	37.50	62.50	0.36	LC	STABLE
mixtus	42.86	57.14	0.40	LC	STABLE
insularis	44.44	55.56	1.25	LC	STABLE
perplexus	50.00	50.00	0.17	LC	STABLE

* Data deficient for North America

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Chapter 3: Linking Climate Change, Land Use, and Extinction Risk Across Taxa

Abstract

Climate change increases the frequency and severity of extreme weather. If conditions, such as temperature, exceed species' tolerances at any life stage, then population decline is expected. Land-use change and pesticide exposure, in combination with thermal extremes, act synergistically to drive species loss (Newbold, 2018; Soroye et al., 2020). Broad-scale studies have linked thermal extremes to reduced abundances across taxa, contributing to elevated extinction rates. However, such studies often rely on coarse-resolution data, leaving it uncertain whether similar effects are detectable at the scale of local biological communities. This study extends macroecological hypotheses to bumblebee species diversity, revealing a climate-driven mechanism linking land-use intensification to increased extinction risk across species, using *Bombus* pollinators as a model. I compared bumblebee species' thermal tolerances with temperatures experienced in28 communities using a high-resolution (1m^2) microclimate dataset. This fine-scale dataset allowed me to compare species' thermal limits to experienced temperatures at biologically-relevant, small scales.. I then investigated whether thermal tolerance, in addition to land-use change and pesticide application, could predict bumblebee species diversity. Diversity declined in communities where species conditions approached or exceed species' upper thermal limits, a trend that was also consistent across years ($p = 0.034$). Aboveground nesting species were more vulnerable to decline than underground nesters, whose abundance was higher in agricultural sites. Microclimatic diversity in surrounding landscapes positively influenced bumblebee diversity, particularly within predominantly agricultural areas,

where thermal conditions had a significant impact ($p < 0.01$). This study demonstrates strong links between species thermal limits and community-level dynamics within a critical pollinator assemblage, through direct observations of community and environmental dynamics.

Introduction

Climate change increases species' extinction risks and could overtake habitat loss-related impacts as the largest driver of extinction in the coming decades (Newbold 2018). Increasingly frequent and severe instances of extreme weather contribute to species' declines at broad spatial extents (Robinet and Roques 2010b, Sánchez-Bayo and Wyckhuys 2019). Climate change-driven trends in extreme weather contribute directly to the decline of species when conditions approach or exceed their upper thermal limits (Kearney et al. 2014a). Differences in community diversity and the relative abundances of species can have immediate consequences in natural and anthropogenic systems, particularly when species provide vital ecosystem services, like pollination. Bumblebees (genus *Bombus*) are globally important pollinators and are particularly vulnerable to the effects of climate change, reflecting their evolutionary origins in temperate-cool environments (Klein et al. 2007, Frei et al. 2018b).

How bumblebees respond to extreme weather at different scales remains highly uncertain: this presents challenges for local-scale conservation and management (De Palma et al. 2015). The availability of microclimates within particular habitats may cause broad-scale models to fail to detect species' vulnerabilities to temperature changes, leading to model predictions that either overestimate or underestimate species' vulnerabilities to the onset of novel environmental conditions. Microclimate availability has been shown to predict population changes in bumblebees and insects more broadly (Braem et al., 2023, De Palma et al. 2017, 2019, Słowińska et al., 2022), and the effects of habitat area within a site (Haddad et al. 2015, Gutiérrez-Chacón et al. 2020) are widely acknowledged as a determinant of diversity of pollinator and other communities. Similarly, land use changes and intensification can exert complex effects on species persistence within habitats and landscapes, with some species benefitting from land use changes and others declining

Land use intensity can alter bumblebee and other pollinator communities directly by limiting habitat availability (Birkenbach et al., 2024; Millard et al., 2021), exposing bees to potentially harmful pesticides (Schweitzer et al., 2012), and indirectly through interactions with changing availability of microclimates. Intensive agricultural land uses eliminate much of an area's microclimatic heterogeneity, a key factor in the harm to species diversity arising from intensive land uses. In the study region (Southern Ontario, Canada), where such land uses predominate, producers apply neonicotinoids extensively, especially imidacloprid, clothianidin, and thiamethoxam (Struger et al., 2017). Such pesticide applications are associated with increased extinction risk for many species in this area (Kerr & Cihlar, 2004). These substances, coupled with extensive habitat losses to agriculture and other human land uses, create an environment that poses significant challenges for bees. Recent meta-analyses confirm that increasing land-use intensity significantly reduces bee diversity and abundance (De Palma et al., 2021). In particular, agricultural intensification, including pesticide use and floral homogenization, amplifies the effects of warming on wild bee populations (Janousek et al., 2023). Yet few studies examine whether thermal stress measured via fine-scale microclimate sensors explains local *Bombus* diversity across land use types—a key gap this chapter addresses.

Bumblebee species populations show signs of decline when short-term thermal conditions exceed their upper realized thermal niche limits over broad areas (Soroye et al., 2020), and such effects should be more pronounced for species with aboveground nesting habits that expose colonies to greater temperature extremes (Pereira et al., 2021). Similarly, if cool microclimates exist within habitats or neighbouring areas, then abundances of bumblebee species should be higher than in areas where such microclimates are scarce or missing. Land use change and intensification can reduce or eliminate the availability of such microclimates by homogenizing habitat conditions, which can cause localized increases in temperature of 5°C or more and increase extirpation risk by 9% for insects (Suggitt et al., 2018). Models linking species' persistence trends at broad extents create testable predictions regarding population persistence within and among habitats that can only be directly evaluated with observations of bumblebee communities within those areas (Kearney et al., 2014a).

As central place foragers, bees rely heavily on the quality of their surrounding habitat to maintain healthy colonies (Osborne et al., 2008). A matrix characterized by agricultural landcover, which may provide fewer resources, or impose greater temperature extremes, can limit resource gathering or dispersal success of mated queens. This might reduce the number and size of colonies, potentially leading to local species loss, and therefore reduced bumblebee species diversity in landscapes with high agricultural land use intensities. Conversely, landscapes with more extensive semi-natural vegetation can include greater microclimatic heterogeneity and accessible resources, which enables bumblebee colony growth and increases the likelihood of dispersal success of mated queens (Papanikolaou et al., 2017). This is primarily because the altered landscape intensifies the difficulty of foraging nearby, threatening their ability to sustain healthy colonies.

Species' realized environmental niches – the conditions under which species persist – impact their response to changing climate conditions (Quintero & Wiens, 2013). To determine whether species diversity decreases in communities where climatic conditions approach species' upper thermal tolerance limits, I propose a series of hypotheses: First, I hypothesize that species diversity will decrease in communities nearing species' upper thermal tolerance limits. This is based on the expectation that thermal extremes might exceed species' physiological thresholds, reducing their ability to survive, and therefore diminishing community diversity. I use established models of bumblebee species' thermal limits, in conjunction with high-resolution microclimate data, to test whether bumblebee species diversity correlates with local thermal stress (Kearney et al., 2014a), predicting that sites with temperatures closer to the upper thermal tolerance of community members would host lower diversity than sites with more moderate temperatures.

My second hypothesis is that thermal stress has stronger negative effects on species in landscapes with higher land-use intensity. Land use intensification, through practices such as agriculture, not only reduces habitat complexity but can also eliminate microclimates that buffer extreme temperatures, amplifying the adverse effects of climate stress. If the first hypothesis is supported, linking thermal conditions with diversity, this second hypothesis then tests whether land use intensity is an interacting stressor on diversity alongside thermal conditions. I compare land use intensity – measured as a gradient of pesticide uses across semi-natural sites to predominantly agricultural sites –to test whether bumblebee species' thermal tolerance limits play a more important role in limiting diversity in more intensively managed landscapes.

My third hypothesis states that climate extremes in agricultural landscapes disproportionately affect certain species, particularly those with specific life history traits unable to seek refuge in more suitable microclimatic conditions. I compare abundance of species with various nesting locations (above ground, below ground, or parasitic) to land use intensity across sites. I expect that above-ground nesting bumblebees to have lower diversity in higher land use intensity sites, while underground nesting bumblebees, which make use of microrefugia, would fare better in agricultural sites than their above-ground nesting counterparts. I expect kleptoparasitic species, which rely on host species for reproduction, to fare the worst, as they rely not only on suitable habitat but also on the presence of host populations.

My fourth and final hypothesis is that the sampling sites with surrounding landscapes that have lower land use intensity and greater habitat heterogeneity will support higher species diversity within the site, particularly in areas where climatic conditions are less extreme. This is because less intensive land use tends to preserve microclimatic refuges and more diverse foraging resources, allowing species to persist more effectively despite rising temperatures.

Materials and Methods

Field surveys

Bumblebee species community data were collected from 28 sites across Southern Ontario, Canada, spanning a range of land cover types to include both high and low agricultural land use intensity. 12 sites were situated in agricultural areas and designated as high land use intensity, with less complex habitat structures and potentially lower levels of habitat heterogeneity (Fig. 3.5). The remaining 16 sites were designated as semi-natural, consisting predominantly of relatively undisturbed land cover, such as provincial parks, floodplains, and marshes. This distinction captured the characteristic differences between these environments, particularly in terms of structural complexity and habitat heterogeneity, which may be crucial for understanding the impact of land use intensity on pollinator populations.

Pollinator surveys were conducted across all sites by staff and students from the Ontario Ministry of the Environment and Climate Change (Ontario MECC) from May to September 2015 to 2017.

Sampling began once a bee was first sighted at the site. Nets were used to capture pollinators for sixty-minute periods at a time per one collector, 30 minutes per each of two people, and 20 minutes each for three people sampling. This adjustment ensured consistent sampling effort across varying team sizes. Abundances were recorded per site. Captured bees were immediately placed in glass or plastic vials and stored in a cooler at 4°C to preserve the specimens until further analysis. Specimens were identified to species at the microscopic level by bumblebee specialists at the Environmental Monitoring and Reporting Branch (EMRB) of the Ontario MECC.

Realized thermal niche limits

Realized thermal niche boundaries for each species were quantified using climate data from 20 000 North American occurrence records collected 1955-1965 from publicly available sources (published in Kerr et al., 2015). This period was chosen because it offers sufficient data resolution, with over 4000 data points per year and monthly climate records available, unlike earlier years with lower data resolution, and precedes the period of accelerated climate change. I identified the average of the five highest temperatures throughout species' realized niches, across all year-site combinations throughout 1955-1965. Maximum temperatures experienced were reported here (Figure S3.2), since my first hypothesis focuses on diversity in relation to conditions which meet or exceed species' upper thermal limits. I examined whether species' upper thermal niche limits varied with sample size (using the hottest 5, 10, 20 georeferenced occurrence records per species), and found little variation in measured thermal niche limits.

I used the thermal position index (TPI; Kerr, 2020) to estimate how close a species' environment is to its' thermal niche limit. This index has been demonstrated to improve predictions of species geospatial extinction-colonization dynamics (Kerr, 2020; Soroye et al., 2020) and to capture both the duration and extremity of conditions.

The species-level thermal position index is calculated as (Kerr, 2020) according to Equation 1 below:

$$P = \frac{1}{t}\sum_{i=1}^{t}\left(\frac{N_m - N_{Smin}}{N_{Smax} - N_{Smin}}\right)$$

Where N_m is the mean temperature at a sampling locale, N_{Smin} is the minimum temperature of the species realized environmental niche, and N_{Smax} is the maximum temperature of the species realized environmental niche.

To determine species' thermal limits in this chapter, N_{Smax} was calculated as the average maximum annual temperature at each site obtained through *microclima*, as described below, an average of the five highest yearly temperatures recorded during the sampling season, May to September (Fig S3.2).

Statistical analyses

All statistical and spatial analyses were completed in R (R, 2017) and ArcGIS Pro v.2.7.3 (ESRI, 2019), respectively.

Linear mixed models (LMMs) with Gaussian distributions were constructed to determine whether site-level TPI, year, land use category, and interactions of these terms affect site-level taxonomic diversity, measured as Hill number 1 (see below for details). Year was included as a fixed main effect in all models to account for temporal variation but was not modeled in interaction terms due to sample size constraints and risk of overfitting. Preliminary testing of interactions with year did not yield significant improvements in model fit and were excluded from final models. While I used random effects to account for site-level variation and tested for spatial autocorrelation, our models do not include all possible sources of environmental heterogeneity (e.g., pesticide exposure, nesting substrate availability). In the case of GLMMs, assumptions of normality and homoscedasticity of residuals were visually assessed. Models were fit using the lme4 package in R, with model performance evaluated via Akaike Information Criterion (AIC) and marginal and conditional R^2 values calculated using the *MuMIn* package.

Microclimate modeling

To test whether species diversity is lower in communities in which climatic conditions are closer to species' upper thermal tolerance limits, I first obtained extremely high-resolution microclimate estimates using the *microclima* package (Kearney et al., 2014b), which is based on the mechanistic modeling tool NicheMapR (Kearney and Porter, 2017). This approach downscales coarse macroclimate data into extremely high-resolution (1 m^2) hourly air temperature estimates at 2 meters above ground level by combining regional weather station data with detailed environmental inputs, including geographic coordinates, elevation, land cover type, and topography. The model applies principles of energy balance, accounting for solar radiation, wind speed, and latent heat fluxes to simulate near-surface air temperatures based on physical equations.

For each of the three sampling years (2015–2017), I modeled hourly air temperatures across the sampling season (May to September) for each site. These hourly outputs were then averaged across each season to characterize the thermal conditions of the sites, providing a more accurate reflection of local climate than using the weather conditions on any single sampling day. These model-derived microclimate estimates allowed me to quantify thermal environments at a biologically meaningful scale for small pollinators like bumblebees, providing the basis for the calculation of the Thermal Position metric.

Land use intensity and pesticides

To test my second hypothesis, that climate conditions that fall closer to species' thermal tolerance limits will more negatively impact species in higher-intensity landscapes, I collected Statistics Canada estimates of pesticide application across Ontario (Statistics Canada 2016). Land use intensity at a sampling locale was calculated from pesticide-use survey at the scale of groups of municipalities, known as census division units, as the proportion of area treated with insecticides, fungicides, and herbicides divided by the total area of farmland in that census division, following the methods of Malaj et al. (2020). Ultimately, my analysis focused on the application of insecticides as the most pertinent group of pesticides.

The number of pixels representing agricultural landcover were determined across sites and in surrounding landscapes (also referred to as buffer zones); although semi-natural sites were those with predominantly lower-intensity land cover, it was not assumed that semi-natural sites have a land use intensity of zero. Each of these pixels was then multiplied by the corresponding insecticide intensity for the region (Fig. S3.1). Subsequently, the average insecticide intensity across all pixels within the site's 1 km radius was calculated using this approach.

Nesting behaviour

I compiled known nesting behaviours for all species captured using published life history data (Williams et al., 2014, Rasmont et al., 2015) to test my third hypothesis that climate extremes in agricultural landscapes disproportionally affect species with certain life-history traits. I found underground, above-ground, and kleptoparasitic species across sites, although underground nesting was the predominant nesting choice across bumblebees.

Buffer zones

I modelled buffer zones around each site to test my fourth hypothesis: that sampling sites which are surrounded by lower intensity land use and greater habitat heterogeneity will support higher species diversity within the site than those sites surrounded by high intensity land uses. I measured land use in the surrounding landscapes of sites. Buffer zones were delineated as a 5 km radius around the 1 km radius study sites, and joined with spatial land use cover layers in ArcGIS Pro. I assumed that species within the sampling sites use the surrounding landscape for foraging and use the sampling site for nesting; therefore, semi-natural or natural landscapes that would not be foraging habitat, such as forests, were excluded. I focused on natural and semi-natural areas, including shrubland, wetland, peatland, and grassland, referred to throughout this study as the "suitable" foraging habitat.

To calculate thermal position within buffer zones, I randomly selected one hundred points for each of the three sampling years (300 points total) from suitable land cover within the buffer zones surrounding each site. Additionally, I randomly sampled one hundred points from within the buffer zone. Thermal position was then calculated using microclimate data collected over the entire study period at the buffer points, as well as the thermal tolerances of the species within the sites that the respective buffer zones surrounded. I calculated the Thermal Position Index (TPI) per buffer zone using Equation 1, presented above, and compared these values to the diversity of species within each respective site. To determine whether bee diversity was specifically associated with suitable foraging habitat rather than general landscape composition, I compared the diversity of species associated with buffer zones containing only "suitable" land cover to a null model. The null model was constructed by randomly generating 100 points from across the entire 5 km buffer zone surrounding each community, including all land cover types such as forests and agricultural areas. I quantified land use intensity at each buffer zone by calculating the proportion of agricultural area within the buffer zones and multiplying this proportion by the insecticide intensity in those areas. This information was then used to perform generalized linear models (GLMs) to assess whether land use intensity in the buffer zone affected the taxonomic diversity within the site.

Spatial autocorrelation

I tested whether spatial autocorrelation was present in community assemblage taxonomic diversity using Moran's I with the function *Moran.I* in the R library *ape*. I calculated a distance matrix based on the central coordinates of each sampling location and then compared the Observed Moran's I coefficient with the expected Moran's I (Gittleman and Kot, 1990). If Moran's I had been significant, I would have refit the models with a spatial error structure (for example, Gaussian correlation in a Matern spatial mixed model) and, if necessary, added Moran-eigenvector covariates until residual autocorrelation disappeared.

Community diversity

I quantified community alpha diversity with Hill Number transformations of Shannon indices (Hill, 1973), using the package *hillR* (Chao et al. 2014). Unlike other taxonomic diversity measurements that measure only species richness, this index weights each species by its relative abundance. The Hill number of order 1, based on Shannon Entropy, is calculated as:

$$P = \exp\left(-\sum_{i=1}^{R} p_i \ln(p_i)\right)$$

Where R is the species richness, and p_i is the proportional abundance of the *i*-th species. This transformation expresses diversity in terms of effective species, making it easier to interpret and compare across communities with varying abundances than other diversity indices, such as the original Shannon Entropy index (Jost, 2006; Dick, 2023).

Results

Field data collection

The diversity dataset reveals considerable variability in the abundance of different species, with a broad range of values observed across the species surveyed. Species such as *B. bimaculatus*, (range of abundance from maximum to minimum captured per site is 1-140) and *B. impatiens* (range = 2-98) exhibit the highest levels of variation, indicating a significant fluctuation in their population sizes across the sampled environments. In contrast, species like *B. ternarius* (range = 1-2), demonstrate minimal variation. In total, 4573 bumblebees were collected and identified across 15 species.

Spatial autocorrelation

I tested for spatial autocorrelation in the distribution of the Hill number transformation of Shannon Indices for using Moran's I. The expected value under the null hypothesis of no spatial autocorrelation was -0.0120. A small observed Moran's I statistic (0.0176, p = 0.27, SD = 0.026) indicates that spatial autocorrelation in taxonomic diversity was not detected across sites.

Land use and climate impacts on diversity

I find a strong negative relationship between site-level species diversity and thermal position, indicated by the site's mean thermal position index (mean TPI; Fig.3.1). Bumblebee diversity within habitats was predicted by the variables land use intensity (estimate = 0.002, SE = 0.020), site type (semi-natural or agricultural; estimate = –0.259, SE = 0.449), and the average thermal position of the community (estimate = –0.647, SE = 0.184), along with the interaction between land use intensity and thermal position, (estimate = 0.016, SE = 0.028; Table 3.1; $R^2 = 0.34$). A baseline model, which excluded the TPI term and accounted only for land use intensity, had a reduced explanatory power for diversity (F-value of 7.55, $p = 0.01$). Model comparison based on AIC (Table 3.3) confirmed that the full model outperformed simpler models, supporting the inclusion of both land use and climate variables.

Only underground nesting species were found to be robust to increased land use intensity (Fig. 3.5). The relative abundance of underground nesting species was higher in agricultural sites than semi-natural sites. The relative abundance of kleptoparasitic and aboveground nesting species was higher in semi-natural sites; there were twice as many above-ground nesting species in the semi-natural sites than in agricultural sites.

Temporal pattern in bumblebee diversity decline

There were temporal shifts in diversity, with the years 2016 and 2017 showing marked differences from the baseline year, suggesting declines in diversity patterns over time (coefficients -1.02 and -1.28 respectively, $p < 0.01$; Fig. 3.1). Diversity declined in agricultural areas across sampling years, from 2015 to 2017 ($p = 0.034$). Conversely, diversity in semi-natural sites did not change significantly under the same climatic pressures (Fig. 3.3).

The average TPI within the sampled habitat was observed to be a strong predictor of bumblebee diversity, declining in areas with higher TPI values. This trend is more pronounced in agricultural settings, where diversity falls more sharply with increasing TPI compared to semi-natural areas.

Thermal position in landscapes surrounding sampling sites had a significant impact on diversity only among agricultural sites. Thermal position did not predict bumblebee diversity among semi-natural areas (Table 3.2). Biologically, a higher thermal position index means that bumblebee communities at these warmer, urban sites are experiencing temperatures nearer to their species' upper thermal limits. This can result in increased thermal stress, potentially reducing foraging efficiency, impairing reproduction, and increasing mortality. Over time, these pressures may lead to the exclusion of thermally sensitive species and a shift toward communities dominated by more heat-tolerant taxa.

Discussion

Extreme weather events, driven by climate change, pose significant challenges to species survival, potentially surpassing habitat loss as the primary driver of extinction in the future (Newbold et al., 2013). Bumblebees, as globally important pollinators, are particularly vulnerable to these changes due to their evolutionary origins in temperate-cool environments (Frei, Bennett, et al., 2018; Klein et al., 2007). Understanding how bumblebees respond to extreme weather at different scales is crucial for local-scale conservation efforts (De Palma et al., 2015). Microclimate availability within habitats plays a critical role in predicting species' vulnerabilities to temperature changes (De Palma et al., 2015, 2019; Newbold et al., 2015), yet broad-scale models often overlook these nuances, potentially leading to overestimation or underestimation of species' vulnerabilities to novel environmental conditions.

My study aimed to address these complexities by testing a series of hypotheses regarding the relationship between climatic conditions, land use intensity, and bumblebee diversity. Accounting for species' realized thermal niche limits improves modelled predictions of diversity differences across landscapes where the presence of those pollinators is intrinsic to the provision of ecosystem services.

The interaction effect between thermal position and land use intensity suggests that the effects of thermal position are mediated by the surrounding landscape (Table 3.1; Fig. 3.3). In high-intensity land use areas, where shelter from extreme weather is scarce, bumblebee species appear more vulnerable to the stressors associated with their thermal limits. Conversely, more complex landscapes with extensive natural areas may buffer bumblebees from these stressors, providing refuges that mitigate the combined impacts of land use and thermal extremes. Species at semi-natural sites may be more robust to climatic extremes than those at agricultural sites due to increased availability of microclimate refugia. I demonstrate that the trends observed at a macroecological scale for bumblebee occurrence and climate response (Koppel & Kerr, 2022) hold at a local scale. Community-level dynamics of a critical pollinator community align closely with individual species' proximity to their upper thermal niche limits, indicating that temperature extremes are a more robust predictor of species diversity than broader land use patterns alone. In addition to the interaction between thermal position and land use intensity, I found a significant interaction between land use intensity and site type (estimate = 0.138, p = 0.006), suggesting that the effects of land use differ between agricultural and semi-natural habitats. While habitat loss and fragmentation undoubtedly impact biodiversity, these factors, when considered independently, provide weak predictions of species diversity within specific habitats. For instance, broad-scale land use models may miss local variability, particularly microclimatic refugia, which can offer critical protection against temperature extremes, especially for temperature-sensitive species. This aligns with findings for other taxa. For example, Atlantic Forest endemic birds suggested that landscape-scale climate suitability is predicted to vary little from current to future conditions, despite the projected effects of climate change (Tourinho et al., 2022). Although land use change remains a significant driver of species loss, temperature thresholds relative to species' thermal tolerance capacities offer greater explanatory power in predicting diversity differences among bumblebee species in this region. Incorporating microclimatic data into models predicting diversity change is essential for understanding and forecasting pollinator vulnerabilities (Buckner et al., 2024).

Climatic suitability of sites appears to be an important determinant of diversity. Climatic suitability of sites is a determinant of diversity in this study. That bumblebee diversity declined in areas nearest species' upper thermal limits is consistent with Soroye et al. (2020), who showed that species near their upper thermal limits were more likely to become regionally extinct. This analysis relied on high resolution microclimate measurements and direct observations of bumblebee communities. However, species found in semi-natural sites appear more resilient to climatic extremes, possibly due to greater accessibility of microclimate refugia. This is consistent with the other studies suggesting that microclimate conditions, rather than broader macroclimate models, play a significant role in buffering species from temperature extremes, enabling them to persist in areas where macroclimatic conditions would otherwise be unsuitable (Maclean & Early, 2023).

Semi-natural landscapes, with higher microclimatic heterogeneity, may provide a buffer against climate extremes. This is consistent with studies from forest systems showing that intact vegetation buffers microclimatic extremes (Ewers & Banks-Leite, 2013; Hardwick et al., 2015). My results extend this concept to open terrestrial habitats, where fine-scale vegetation complexity may similarly mediate thermal exposure. Protecting these sites while managing other habitats to enhance microclimatic diversity in agricultural areas could be key strategies for mitigating pollinator declines. Significant temporal shifts in diversity were observed, with the years 2016 and 2017 showcasing marked departures from the baseline year (Fig. 3.1). This highlights the importance of considering both landscape-scale and fine-scale microclimatic factors when assessing species diversity. Integrating these scales can help conservationists better target areas where species are most at risk due to climate change and land use intensification (Maclean & Early, 2023; Suggitt et al., 2018).

Although climate and land use intensity are often correlated, particularly as intensive land use can alter microclimatic conditions, the inclusion of both variables in the same models improved explanatory power (Table 3.2), supporting their independent contributions to diversity patterns. While some shared variance is likely, the consistency of effects across habitat types and scales suggests that both thermal extremes and land use changes are necessary components to understand local *Bombus* diversity. Given the modest sample size ($n = 28$), the number of predictors in the full model raises the possibility of overfitting. While key predictors were significant and consistent with hypotheses, these results should be interpreted with caution and verified in larger or independent datasets.

The higher proportion of underground nesting species compared to other nesting locations in agricultural landscapes supports my prediction that underground cavities may provide refuge in heat waves, as well as potentially protect species from above-ground disturbance of many agricultural activities. Kleptoparasites, which are mostly host-specific and predominantly take advantage of above-ground nesting host bees and their collected resources, declined at a similar proportion to the above-ground nesting species (*B. citrinus* and *B. flavidus*), such as *B. rufocinctus*, *B. pensylvanicus*, and *B. auricomus*. This finding, resulting from direct field observations rather than model-based extrapolations of species' presences or community diversity (for example, from occupancy models and species distribution models), suggests that bumblebee responses to climate have been underestimated. My investigation is missing species known to inhabit Southern Ontario and recognized as declining: *B. ashtoni*, *B. insularis* and *B. sandersoni*. Their absence may be due to their declining populations, making them harder to detect. Increasing sampling resolution could help target these vulnerable species more effectively.

I found a positive relationship between species diversity in agricultural sites and the extent of natural and semi-natural habitat in the surrounding landscape (Table 3.2). This suggests that species diversity within survey sites is influenced by the quality of foraging opportunities in the surrounding landscape, particularly in agricultural areas where land use is more homogenized. Specifically, in agricultural sites, the diversity of bumblebee species was influenced by the climatic and land cover suitability of buffer zones. This is in line with the findings of Rivers-Moore et al. (2020), which demonstrated that the loss of semi-natural habitats in agricultural landscapes negatively impacts wild bee populations, but that maintaining a diversity of these habitats—such as wooded and herbaceous areas—increases diversity of wild bees. These habitats complement each other and play a critical role in ensuring the pollination of both crops and wild plants. Diversity of bumblebee species in semi-natural areas did not increase if surrounding areas also had greater semi-natural habitat extent. Within those areas, I suspect that floral resources and microclimatic conditions are sufficient for bumblebee species to maintain populations, reducing reliance on surrounding areas.

I demonstrated that temperature extremes predict bumblebee species diversity within individual biological communities. This result provides the first evidence that continent-wide models of bumblebee species' responses to warming (Soroye et al. 2020) can be adapted to predict bumblebee diversity across spatial gradients and through time. This test required the use of microclimatic data at spatial resolutions that are biologically relevant to the movements and activities of individual bees. Thermal conditions have rarely been assessed in landscape studies, with few exceptions (e.g. Nowakowski et al. 2018, Gu et al. 2024). Species' responses to environmental changes at local spatial extents may reflect a larger role for climatic conditions than has commonly been appreciated.

Figures 3.1 – 3.4

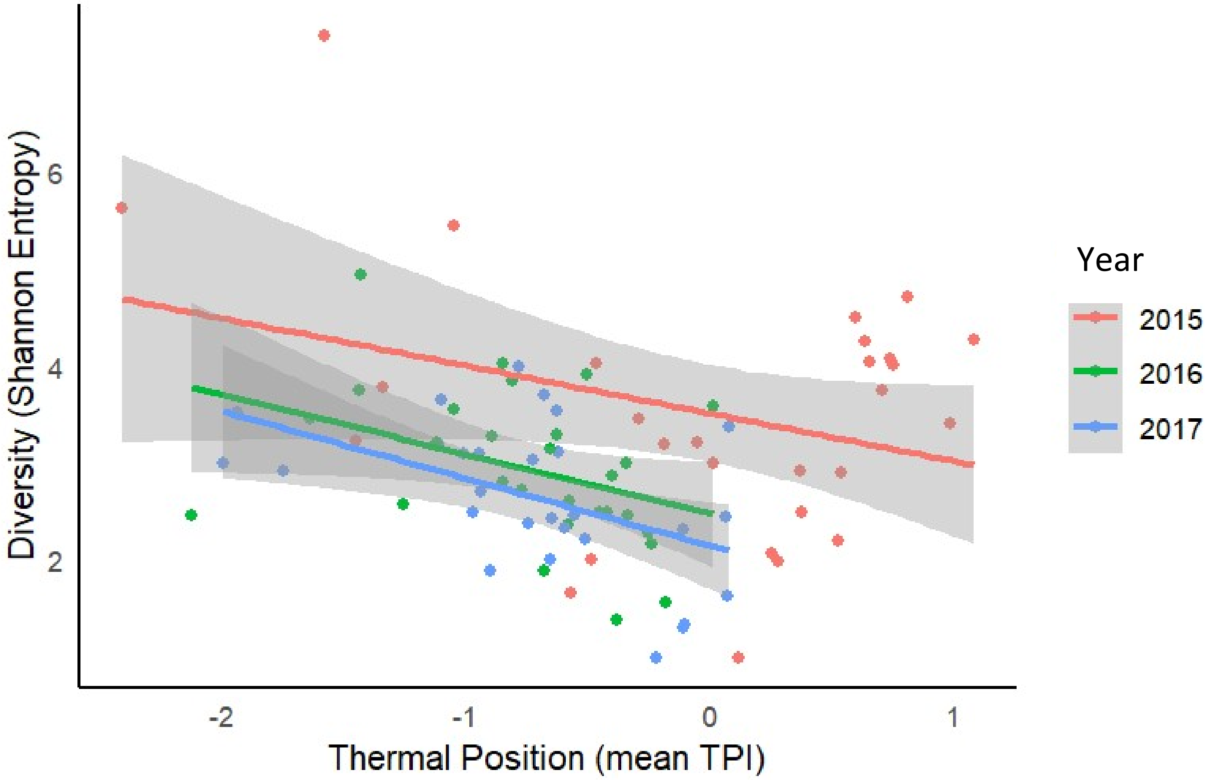

Figure 3.1. The relationship between taxonomic diversity and thermal position across sampling years 2015-2017. Diversity is plotted as Shannon Entropy (Hill number 1).

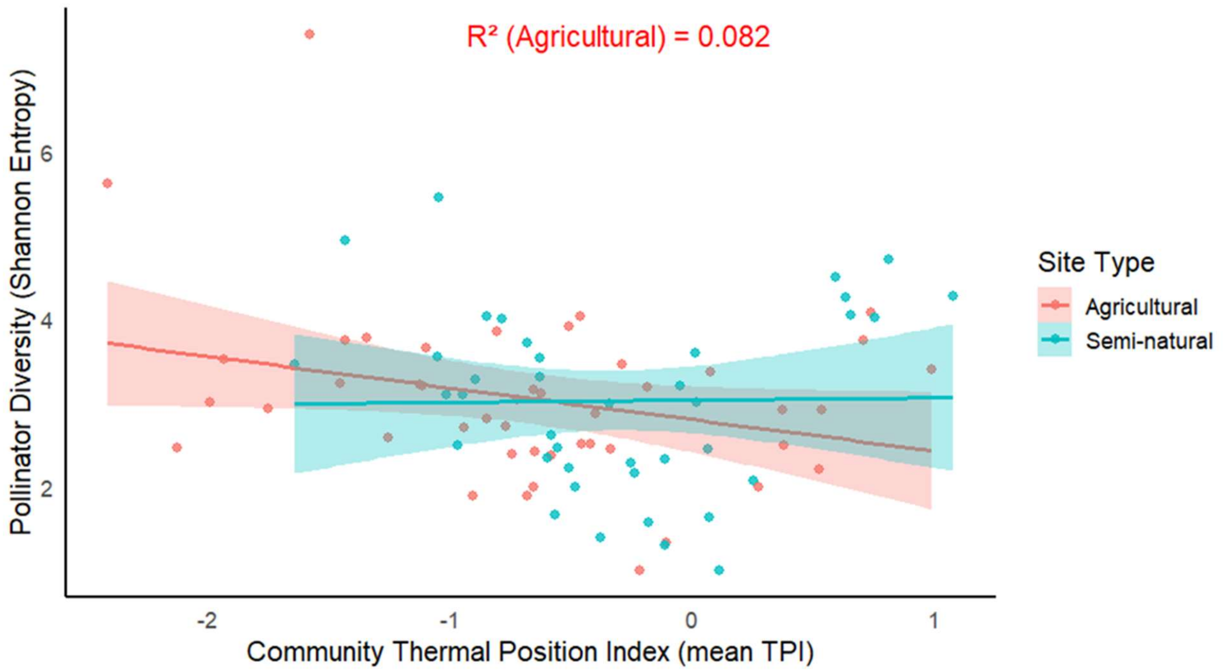

Figure 3.2. The best-fit linear regression (+/- 95% confidence intervals) between community thermal position (mean TPI) and diversity (Hill number 1, Shannon Entropy) across agricultural (R^2 = 0.082) and semi-natural (habitats.

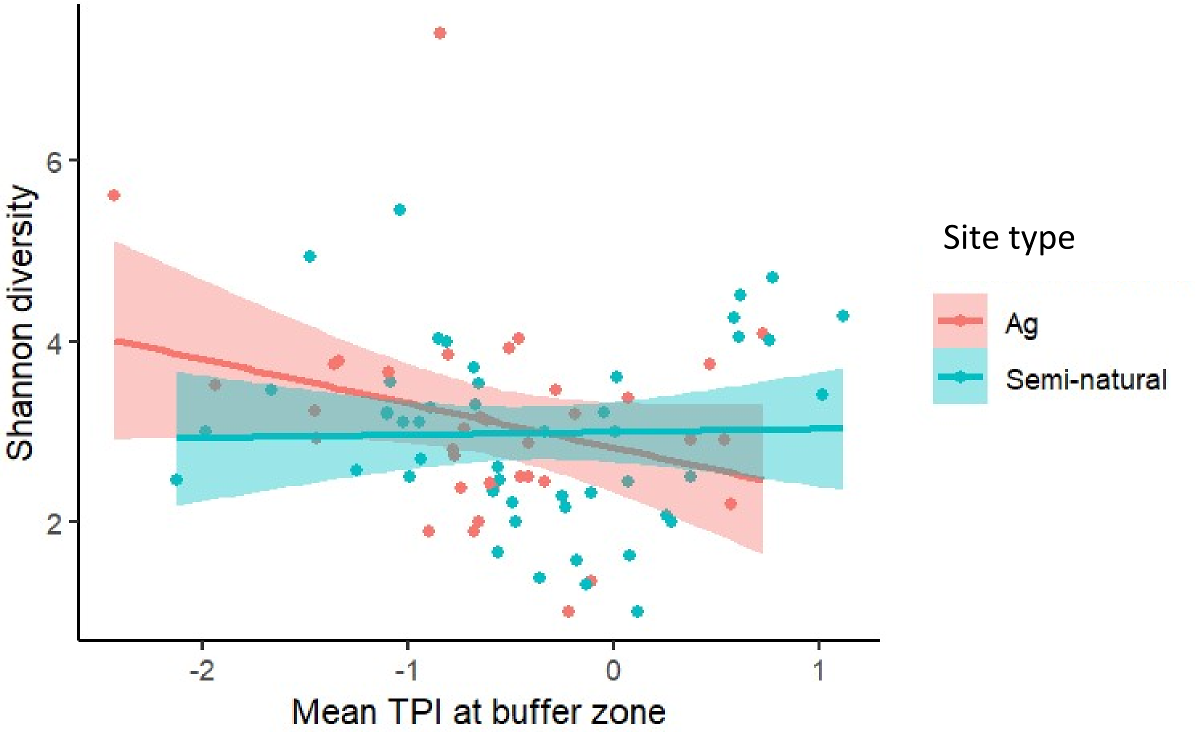

Figure 3.3. The impact of the thermal position (mean TPI) in surrounding landscapes on taxonomic diversity (Shannon Entropy) of agricultural ($R^2 = 0.49$) and semi-natural ($R^2 = 0.03$) habitats. Mean TPI of surrounding landscapes is based on measured microclimate temperature measurements in each of three years from the landscape surrounding the sampled habitat.

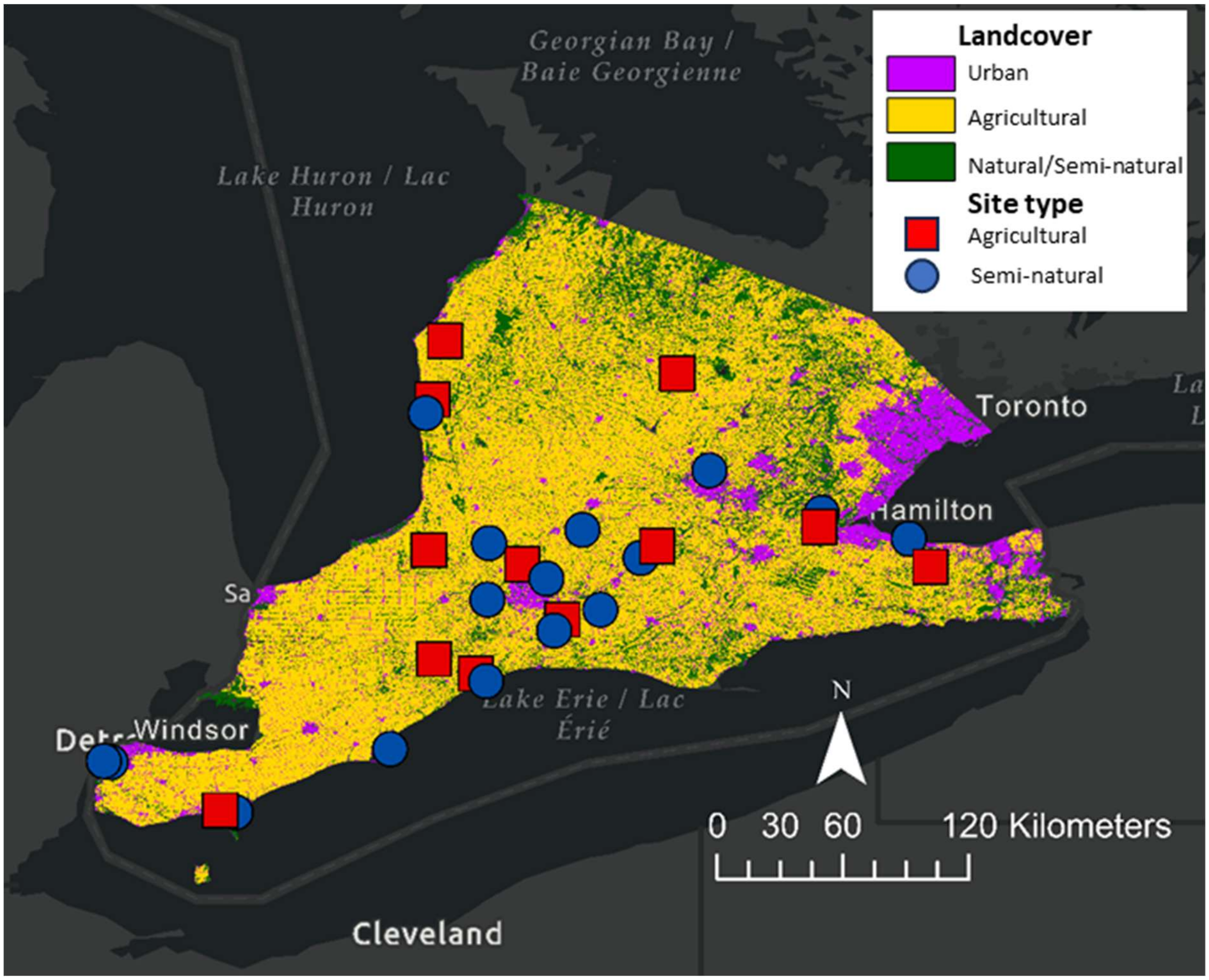

Figure 3.4. Map of 31 agricultural (red square) and 25 semi-natural (blue circle) sites for bumblebee sampling across Southern Ontario, 2015-2017.

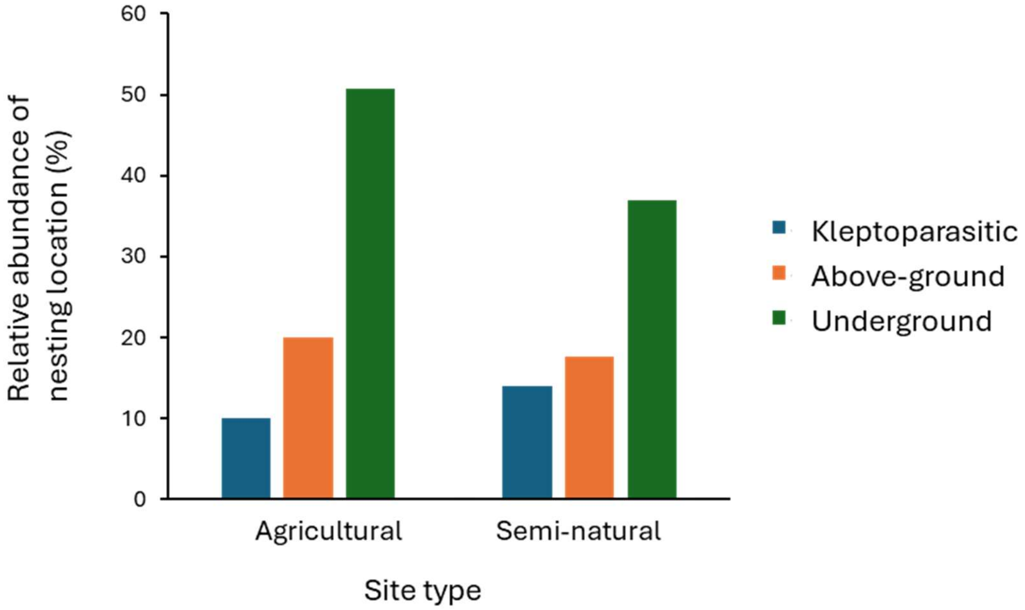

Figure 3.5. Relative abundance adjusted for sampling effort nesting location (%) of kleptoparasitic, above-ground, and underground nesting species across agricultural and semi-natural sites.

Tables 3.1 – 3.3

Table 3.1. Results of linear mixed model testing the impacts of land use intensity, site type, year, and their interactions on bumblebee community diversity. Model $R^2 = 0.34$.

Effect	**Estimate**	**SE**	**t value**	***p***
Intercept	3.337	0.394	8.472	0.001
Land use intensity	0.002	0.020	0.123	0.903
Site type	-0.259	0.449	-0.576	0.566
Year	**-0.977**	**0.272**	**-3.588**	**0.001**
Mean TPI	**-0.647**	**0.184**	**-3.511**	**0.001**
Land use intensity:Mean TPI	**0.016**	**0.028**	**0.598**	**0.005**
Land use intensity:Site type	**0.138**	**0.049**	**2.809**	**0.006**

Table 3.2. Results of a linear mixed model testing the impacts of land use intensity at buffer, site type, Mean TPI at buffer, mean TPI within the site, and their interactions on site diversity. Model $R^2 = 0.55$.

Effect	**Estimate**	**SE**	**t value**	***p***
Intercept	5.419	6.2348	0.869	0.389
Land use intensity at buffer	26.87	28.08	-0.957	0.345
Site type	**39.63**	**9.673**	**4.097**	**0.001**
Mean TPI at buffer	**97.56**	**18.49**	**5.278**	**0.001**
Mean TPI at site	**-2.031**	**35.80**	**-5.675**	**0.001**
Mean TPI at buffer:Total agricultural area at buffer	**0.001**	**0.001**	**5.250**	**0.001**
Mean TPI at buffer:Site type	**-39.65**	**9.654**	**-4.107**	**0.001**
Mean TPI at buffer:Total suitable area at buffer	**-0.001**	**-0.001**	**-5.256**	**0.001**

Table 3.3. Comparison of linear mixed-effects models predicting bumblebee community diversity across 28 sites in Southern Ontario. Models differ in the inclusion of climate (thermal position index), land use, site type, and year. The full model includes all fixed effects and significant interaction terms reported in Table 3.1. AIC = Akaike Information Criterion; ΔAIC = difference from best-performing model. R^2 values reflect marginal R^2 (fixed effects only).

Model	Predictors Included	AIC	ΔAIC	R^2
Null	Intercept only	133.2	+12.7	0.00
Land use only	Land use intensity	128.1	+7.6	0.10
Site only	Site type	127.5	+7.0	0.12
Full model	Land use × TPI, Site type, Year	120.5	0.0	0.34

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Supplementary Materials

Thermal position

Species thermal niche limits were determined from 1600 records of species between 1955-1965, a period before an increase in rate of climate change in North America. Data were compiled by (Kerr, 2020). The average of the five highest monthly maximum and five lowest monthly minimum temperatures from among the values for all location and year combinations within the baseline period across their North American range. These maximum and minimum temperatures were assumed to represent the thermal limits for the species, and previous studies have found that this measure is robust to both variation in the number of records used to calculate this and variation in species sampling effort (Kerr and Cihlar 2004, Soroye et al., 2020).

Buffer zones

To delineate spatial regions of interest around specific geographic points, buffer zones with a radius of 4 kilometers were generated in ArcGIS Pro. 100 random point features were generated within the 4-kilometer buffer zones per sampling year. The aim was to distribute random points uniformly within the specified buffer zones. Two separate extraction processes were carried out in ArcGIS Pro: extraction of land cover data within the buffer zones and extraction of suitable land cover data within the same buffer zones.

Supplementary References

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Supplementary Figures S3.1 – S3.3

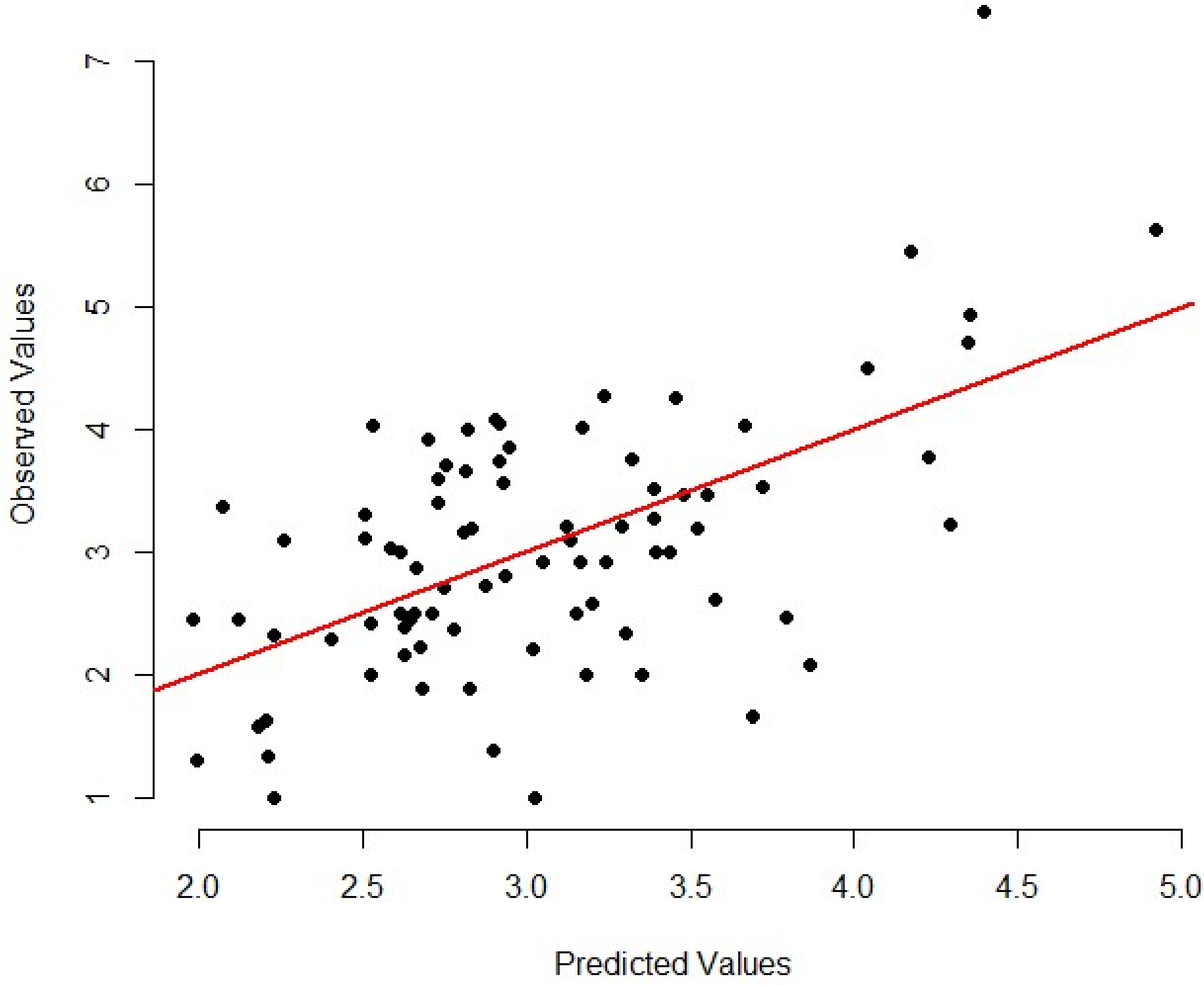

Figure S3.1. Observed versus predicted diversity values based on coefficient of linear mixed model predicting site-level diversity.

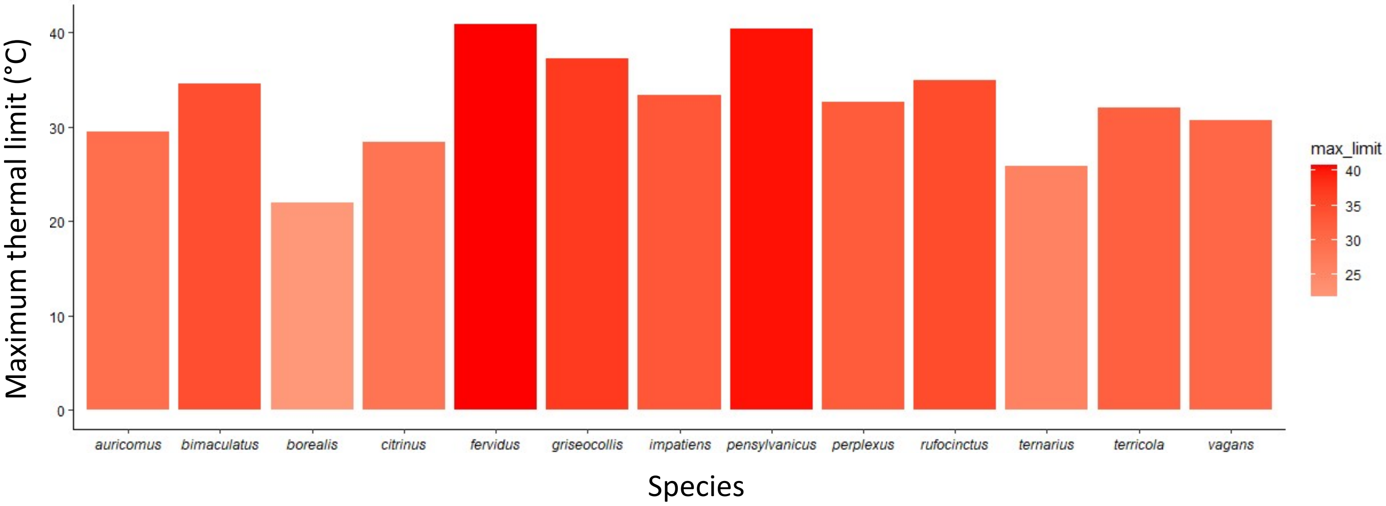

Figure S3.2. Maximum thermal limits of thirteen *Bombus* species calculated from over 1600 observations per species across North America.

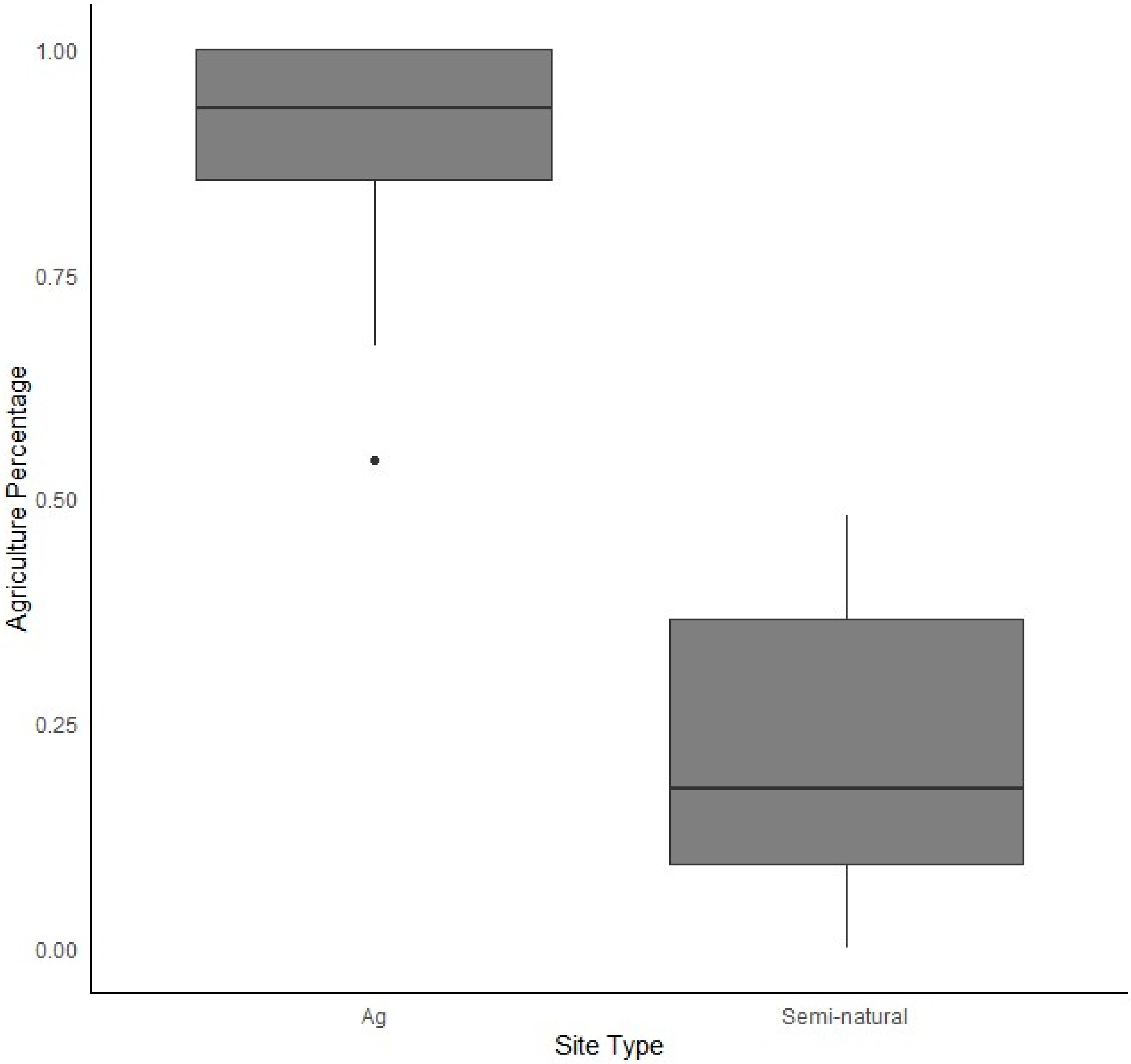

Figure S3.3. Percentage of agricultural landcover across agricultural and semi-natural sampling sites.

Supplementary Table S3.1

Table S3.1. Observed and predicted diversity (Shannon diversity) across study sites and sampling years with 95% confidence intervals.

Site	Year	Actual diversity	Predicted diversity	Lower CI	Upper CI
1	2017	3.034	2.575	2.187	2.963
1	2016	2.367	2.763	2.367	3.160
1	2015	3.744	3.026	2.556	3.497
4	2017	3.521	3.287	2.641	3.933
4	2016	2.500	2.698	2.182	3.215
4	2015	2.910	3.133	2.598	3.669
7	2017	2.497	2.703	2.266	3.140
7	2016	3.557	3.022	2.579	3.465
7	2015	3.000	3.413	2.995	3.831
9	2017	3.538	3.751	2.967	4.535
9	2016	4.937	4.491	3.667	5.315
9	2015	4.711	4.197	3.381	5.013
10	2017	3.197	2.798	2.405	3.192
10	2016	3.216	3.076	2.683	3.469
10	2015	3.405	2.862	2.323	3.400
11	2017	3.115	2.511	2.056	2.966
11	2016	2.500	2.663	2.185	3.142
11	2015	3.464	3.601	3.161	4.041
12	2017	3.096	3.214	2.746	3.683
12	2016	3.272	3.453	2.990	3.916
12	2015	2.075	3.799	3.344	4.253
13	2017	3.709	2.800	2.396	3.204
13	2016	3.596	2.670	2.228	3.112
13	2015	5.457	4.297	3.745	4.849
14	2017	3.374	2.110	1.624	2.596
14	2016	2.876	2.661	2.241	3.080
14	2015	4.087	3.011	2.533	3.489
16	2017	2.702	2.709	2.193	3.225
16	2016	2.461	3.670	2.991	4.348
16	2015	2.492	3.227	2.705	3.748
17	2017	2.383	2.599	2.009	3.188
17	2016	3.849	2.905	2.315	3.495
17	2015	2.914	3.233	2.638	3.827
18	2017	2.217	2.698	2.297	3.099
18	2016	1.383	2.894	2.488	3.300
18	2015	4.274	3.057	2.561	3.554
19	2017	2.457	2.155	1.650	2.660
19	2016	4.037	2.597	2.083	3.112
19	2015	2.000	3.398	2.851	3.946
20	2017	2.337	3.333	2.753	3.912
20	2016	2.609	3.593	3.014	4.173
20	2015	4.503	3.923	3.324	4.521
21	2017	1.336	2.227	1.602	2.852
21	2016	2.455	2.633	2.022	3.245
21	2015	3.190	3.556	2.946	4.167
22	2017	4.000	2.879	2.469	3.289
22	2016	3.464	3.648	3.124	4.173
22	2015	4.256	3.337	2.905	3.768
23	2017	2.926	3.169	2.698	3.641
23	2016	3.750	3.258	2.839	3.677
23	2015	7.407	4.354	3.769	4.938
24	2017	1.305	1.965	1.468	2.462

24	2016	3.301	2.539	2.058	3.019
24	2015	4.045	2.803	2.300	3.306
25	2017	2.000	2.529	2.047	3.010
25	2016	2.726	2.865	2.389	3.340
25	2015	5.624	4.832	4.023	5.642
26	2017	1.890	2.672	2.220	3.125
26	2016	1.890	2.816	2.352	3.280
26	2015	3.780	4.212	3.654	4.771
27	2017	3.000	3.308	2.780	3.836
27	2016	2.579	3.151	2.727	3.576
27	2015	1.994	3.273	2.824	3.721
29	2017	2.320	2.198	1.761	2.635
29	2016	2.998	2.605	2.183	3.026
29	2015	1.666	3.747	3.271	4.224
30	2017	2.448	1.925	1.429	2.420
30	2016	2.281	2.380	1.912	2.849
30	2015	3.210	3.275	2.810	3.739
32	2017	3.654	2.787	2.362	3.212
32	2016	3.155	2.800	2.363	3.236
32	2015	4.034	3.702	3.274	4.129
39	2017	1.633	2.150	1.700	2.600
39	2016	2.166	2.600	2.181	3.020
39	2015	4.020	3.036	2.589	3.484
42	2017	1.000	2.270	1.660	2.880
42	2016	3.920	2.709	2.132	3.286
42	2015	3.226	4.273	3.632	4.913
44	2017	3.101	2.362	1.809	2.915
44	2016	1.569	2.149	1.607	2.691
44	2015	1.000	2.990	2.459	3.520
46	2017	2.421	2.527	2.089	2.964
46	2016	2.808	2.913	2.485	3.341
46	2015	2.203	3.126	2.632	3.621

Chapter 4: Functional, phylogenetic, and phenological diversity in Southern Ontario landscapes

Abstract

Pollinators such as bumblebees are needed for 35% of the world's fruit, vegetable, and seed crops (Klein et al. 2007) but face many stressors associated with agricultural land use development, including habitat loss, pesticide exposure, monoculture farming, and landscape simplification, that led to extirpation of numerous species. Warming climates may further exacerbate these stressors, imposing conditions outside of species' thermal tolerances in landscapes where microclimatic refuge from extreme temperatures is already less available. Identifying traits that affect species' sensitivity to environmental change can point to trends in species loss and subsequent shifts in community composition. Taxonomic diversity, or the number of species lost under such stressors, was correlated with land use intensity in Chapter 3 and set the stage for this further investigation into functional and phylogenetic diversity which will provide insight into the ecosystem resilience and potential long-term effects of those losses. A phylogenetic approach to analysis of patterns of decline can supplement trait-based analyses, especially if it is not clear which traits can be most strongly affected by thermal and land use stressors. The main objective of this study was to model responses in bumblebee trait diversity (body size, nesting location, and activity timing) and phylogenetic diversity across land use and climates using generalized linear mixed models (GLMMs). I assembled a database of 3115 bumblebee observations from 14 species in southern Ontario, which were collected at 28 field sites. A database of body size, nesting location, and activity timing traits was assembled from a literature source (Williams et al. 2014). After constructing a phylogenetic tree for bumblebee species identified from field sites, I tested for a phylogenetic signal in individual species traits, which was detected in nesting location and emergence phenology. Bumblebee phylogenetic diversity was significantly lower in agricultural landscapes compared to semi-natural areas ($t = 2.10$, $p = 0.03$), with a marginal trend toward reduced functional diversity ($p = 0.05$). Both functional (adjusted $R^2 = 0.21$) and phylogenetic diversity (adjusted $R^2 = 0.18$) declined with increasing thermal position across agricultural sites, while trait composition varied by temperature and site type, with smaller-bodied species and above-ground nesters more common in warmer, agricultural areas. Despite expectations, emergence phenology did not differ between land use types, suggesting that floral resource availability in surrounding landscapes may buffer temporal mismatches. These findings highlight the need for conservation strategies that increase habitat heterogeneity and provide climate refuge, informing policies to balance agriculture with biodiversity conservation.

Introduction

Pollinators, particularly bumblebees, play a pivotal role in ecosystem service provision and are particularly vital to the productivity of fruit, vegetable, and seed agriculture essential for global food security (Klein et al. 2007). The intensification of agricultural practices has led to loss of natural habitat and simplification of landscapes in terms of plant diversity. These changes disrupt the intricate ecological networks upon which bumblebees and other pollinators depend, leading to a decline in their populations and the ecosystem services they provide. Frei et al. (2018b) refer to agricultural landscapes as a “dichotomy of promise and peril”; while croplands require pollinators for productivity and are necessary to support human populations, they have also drastically altered over a third of landscapes globally and negatively impacted pollinator diversity overall (De Palma et al. 2015). Many crops are monocultures, which likely flower simultaneously, leaving gaps in floral resource availability throughout the spring and summer and altogether excluding bees whose activity timing does not match that of the flowering crop (Hemberger and Gratton 2023). Agricultural tilling also disrupts nesting, foraging, and overwintering habitats. The resulting bumblebee population declines have already had significant economic implications and cascading biodiversity consequences; the absence of bumblebees, even in the presence of other bees, reduced farmer profit in orchards by 2.4x and ripe fruit set by almost half (Pérez-Méndez et al. 2020).

Climate change poses distinct threats to bumblebee persistence and can amplify effects of other stressors (Goulson et al. 2015, Nebauer et al. 2024). Since the 1970s, climate change has imposed conditions outside of species environmental tolerances through rapid warming and extreme weather events that make species persistence less likely (Robinet and Roques 2010, Sánchez-Bayo and Wyckhuys 2019). Species exposed to climatic conditions closer to upper thermal niche limits are expected to be at higher risk of extirpation in the case that the local environment warms and pushes species outside of their tolerable climate conditions (Kerr 2020). Across North America and Europe, bumblebee declines are greater where warming temperatures exceed species' upper thermal niche limits (Soroye et al. 2020).

Body size, emergence phenology, and nesting location contribute to overall functional diversity (FD), which reflects the range of ecological roles or traits that species express in an assemblage, and which can inform understanding of the effects of changing community composition (Williams et al. 2010). The overall functional diversity of a community has been found to predict ecosystem changes (Suding and Goldstein 2008) and drive ecosystem processes (Laliberté and Legendre 2010). Functional traits represent measurable trade-offs in morphology, physiology, and biochemistry which shape an organism's cost-benefit strategy in adapting to environmental pressures (Moor et al. 2017). These traits determine species' contributions to ecosystem functioning and the degree of niche differentiation within a community (Srivastava and Vellend 2005, Violle et al. 2007, Laliberté et al. 2014). As Rodrigues (2025) proposes, integrating functional diversity and species' ecological traits into conservation planning can help identify species and ecosystems that are particularly important for maintaining ecosystem services like pollination under changing environmental conditions.

While recent work has highlighted the importance of functional diversity in maintaining pollination stability under climate stress (Katumo et al., 2022), there is limited empirical evidence linking thermal stress or land use intensity to variation in *Bombus* functional or phylogenetic diversity in temperate systems. This chapter fills this gap by evaluating how diversity dimensions vary across agricultural gradients and thermal contexts using real-world community data.

Traits such as body size, nesting location, and phenology may help determine bumblebee species' vulnerabilities to climate change and land use changes. Body size may affect species' interactions with the environment through its relationship with species' dispersal capacities and consequent distribution across landscapes (Aguirre-Gutiérrez et al. 2016). De Palma et al. (2019) find that smaller bee species are less prevalent in European agricultural landscapes, while Pardee et al. find that larger, cavity-nesting bees fare worse than smaller, soil-nesting bees with increasing summer temperatures in Colorado mountain landscapes (Pardee et al. 2022). Most declining bumblebees in the UK have long or medium tongues, which are correlated with larger body size (Cariveau et al. 2016)but bumblebees that persist in agricultural land are more frequently short-tongued (including *Bombus terrestris* and *B. lapidarius*). Regular plowing means that mid-successional perennials, which are favoured by longer-tongued bees, are not available (Steinert et al. 2021). Nesting location is also correlated with species vulnerabilities under land use intensification; when considering agricultural practices that remove above-ground biomass, disruption of above-ground habitats may disproportionately affect surface and above-ground nesting bees in those habitats (Williams et al. 2010). Foraging activity timing, or foraging phenology, ranges between May and July for bumblebee colonies in Ontario and can influence species' climate vulnerabilities (Koppel and Kerr 2022). In monoculture crops, which flower synchronously, a narrower range of phenologies may be supported than in natural landscapes with varied flora (Ollerton et al. 2014). Understanding the spatial variation in decline is crucial to protection of bumblebees and their habitats (Liczner and Colla 2019). As nesting location, body size, and phenology are all adaptations to species' environmental conditions, I expect that certain trait values may affect species' survival as climatic conditions change, as described below (see also Table 4.1, Materials and Methods).

Early vs late emergence and activity period

Incidence of extreme temperature events at the start of the annual activity period can be potentially more damaging to *Bombus* colonies than later in the season, as drops in temperatures can push species past their environmental tolerances. As larvae lack the thermoregulatory abilities of adults, worker bees must expend additional energy to fan and cool larvae during extreme temperature events (Baudier and O'Donnell 2017). The climate in the month preceding spring worker bee emergence is a sensitive period in *Bombus* life history: in this time, larvae emerge and feed for two weeks, followed by a two-week incubation before emerging as adults (Williams et al. 2014). Brood temperature above 32°C in colonies of *B. impatiens* and *B. affinis* require workers to turn to thermoregulation at the expense of caring for larvae or foraging (Vogt

1987). Inability to adequately cool larvae results in fewer offspring maturing to adulthood in the colony (Goulson 2010).

Later emerging species may face increased nest and food resource competition, emerging at a time when total pollinator abundance is high. Susceptibility to decline in late-emerging species has been observed in British and Irish bumblebees including *B. jonellus* and *B. hortorum* (Edwards and Williams 2004, Fitzpatrick et al. 2007) and in *B. ternarius* in Canada (Williams et al. 2008). Later emergence could also be disadvantageous if species have a shorter remaining available season length in which new queens can mate, due to depletion of food resources (Williams 1991).

Earlier emerging *Bombus* species appear to be advancing their phenology more quickly than later emerging species (Willmer 2012). These species may also more successfully shift poleward than later emerging species, having more time in the season to rear offspring than their counterparts (Williams et al. 2008). I expect that late emergence will be a trait associated with decline, while earlier emerging species will be more successful in expanding or maintaining range under climate shifts.

In agricultural landscapes dominated by monocultures, the availability of floral resources is often restricted to a brief, synchronized flowering period (Saunders 2016). This creates strong selective pressures on pollinator populations to align their emergence timing with peak floral resource availability. I expect that bumblebees in these agricultural environments will exhibit narrower emergence timings than bumblebees in semi-natural environments to align with the single flowering period of monocultures

Nesting type

Queen bees emerging from overwintering require a nest site with access to floral resources for nest building and food throughout the season (Williams et al. 2014). Most of the queens nest underground in existing cavities or abandoned nests, however some find aboveground or surface level sites. Cuckoo bees are kleptoparasitic *Bombus* species which rely on existing nest structures built by another species' queen bee to lay their eggs. Nesting preference can influence the degree of species' exposure to climate extremes; underground cavity nest sites may be sheltered in a microclimate that allows species to escape sudden temperature shifts and prolonged thermal extremes, as in *Apis* species (Stone et al. 1999). I expect that underground nesting species will be the least sensitive to climate changes.

Body size

Larger body size may be an adaptation to retain heat in cooler climates, which might appear maladaptive for species trying to avoid overheating in areas that have warmed substantially (Woodard 2017). However, body size relates positively to foraging range and dispersal ability (Greenleaf et al. 2007, Ogilvie and Forrest 2017). As climate change leads to changing resource availability, access to suitable foraging habitat may become limited, making increased dispersal ability to more suitable foraging areas an important factor in species survival.

In addition to functional traits, a species' evolutionary history—reflected in its phylogenetic relationships— can also impact a species' susceptibility to climate and land use stressors (Mazel et al. 2018). Phylogenetic diversity reflects taxon-wide genetic differentiation, which means that areas with low phylogenetic diversity are more likely to have less capacity to continue to provide pollination services after the onset of novel environmental conditions (Cadotte et al., 2012). For this reason, understanding of how phylogenetic diversity has changed may also provide insights into future resilience of both biological communities and the provision of ecosystem services

(Cadotte et al., 2008). Arbetman et al. (2017) demonstrate that *Bombus* decline in range size is phylogenetically structured, biased towards *Alpinobombus* and *Thoracobombus* subgenera. The phylogenetic diversity (PD) of an assemblage captures the evolutionary history shared between species, measured by the overall distance between branch lengths (Tucker et al. 2018, Faith 1992a). In an assemblage of closely related species, phylogenetic diversity is low, which might indicate that traits shared among them are necessary to tolerate that environment (Munkemuller et al. 2012). Of the approximately 250 extant *Bombus* species across 15 subgenera, 46 *Bombus* species are historically present in North America, representing each of those 15 subgenera (Williams et al. 2014c). In other words, the North American bumblebee species assemblage is broadly representative of the entire clade, so patterns in response to climate and land use stressors across the subgenera here are likely to be broadly applicable, offering insights into potential species of interest across other geographical areas. In the past, bumblebee decline studies have focused on extrinsic drivers of decline, ignoring potential genetic vulnerabilities within declining species (Arbetman et al. 2017). These vulnerabilities could be reflected in lower phylogenetic diversity in regions with high-intensity land cover, as species with limited evolutionary adaptations are more likely to decline. I expect that areas with high intensity land uses will effectively filter out some species that will lead to reduced phylogenetic diversity. Phylogenetic and functional diversity each provide a unique attribute of biodiversity that the other does not offer (Le Bagousse-Pinguet et al. 2019). Despite both reflecting underlying ecological and evolutionary relationships among species, PD and FD show contrasting patterns in some contexts; in assemblages with high functional redundancy, the loss of a single species may have little impact on functional composition if its ecological role is shared by other species. For instance, in post-fire bee communities within Mediterranean regions, taxonomic changes did not correspond to functional replacements (Moretti et al. 2009). When species face competition or resource scarcity, traits that enhance ecosystem function may be favored through selective pressures, potentially overriding expected patterns of phylogenetic trait evolution and resulting in a shift in trait values. In this case, this shift in trait values may occur independently of phylogenetic structure. For example, more closely related mammal species were less similar in size than would be expected at random (Fritz and Purvis 2010). This was also the case for a solitary bee population's response to clear cutting; while removal of woody debris paired with forb removal altered community functional composition, forb removal altered only the phylogenetic relationships of bee species assemblages (Sydenham et al. 2016). While previous studies have separately examined the impacts of agricultural intensification and climate change on bumblebee populations, investigating the synergistic effects of these stressors from the perspective of both functional and phylogenetic diversities is a needed next step.

This chapter furthers the investigation undertaken in Chapter 3, which focused on the impact of these stressors on species diversity alone. This work furthers knowledge by testing how environmental variation alters the functional and phylogenetic diversity of bumblebee assemblages, providing implications for the interaction of ecosystem function and evolutionary history interact under the dual pressures of agricultural intensification and climate change.

Materials and Methods

Field surveys

This chapter draws from the same dataset and field sampling protocol described in Chapter 3. In brief, specimens were collected at 28 sites across Southern Ontario, Canada from May to September 2015-2017 by staff and students from the Ontario Ministry of the Environment and Climate Change (Ontario MECC). Specimen identifications were confirmed in the laboratory by bumblebee specialists at the Environmental Monitoring and Reporting Branch (EMRB) of the Ontario MECC.

The study sites spanned a broad geographical area that varies considerably in dominant land uses (Fig. 4.1). Some study sites are amid high intensity agriculture, including high biomass crops, like corn and soybeans. Habitat remnants in these areas are few and relatively isolated. Conversely, other study sites are within or adjacent to protected areas, floodplains, grasslands, and marshes where habitats are largely undisturbed. This assemblage of sites allowed me to evaluate the impact on biodiversity of a range of land use intensities.

Life-history trait measurement

I compiled species-level life-history trait information for all 14 species on three traits that are likely to impact persistence under land use intensity and climate stressor (Table 4.1): nesting location (above- vs under-ground, or kleptoparasite), phenology (species-level emergence timing), and body size (small, medium, or large). Table 4.3 lists traits used in analyses and their source.

Emergence phenology for all 14 species was estimated following the approach described by (Koppel and Kerr 2022), as adapted from (Stemkovski et al. 2020) using an extensive occurrence dataset compiled by (Kerr et al. 2015). This method calculates emergence dates over 34 years of observations (1975–2010) across Canada and the USA within predefined 100 × 100 km quadrats. For each species, the first emergence day is averaged from quadrats where it was observed across North America. This approach was chosen because it leverages a large dataset not specifically designed to capture first emergence, using a distribution curve to estimate actual emergence dates. These estimates align with the coarse monthly observations reported by Colla and Dumesh (2010).

Species were assigned to three nesting types: aboveground, underground, and kleptoparasites, which rely on existing host nests and are often, but not always, specialized to specific above- or below- ground hosts (Williams et al. 2014, Rasmont et al. 2015b).

Species were categorized as small (queens approximately 15–20 mm in length, workers ~9–14 mm), medium (queens ~18–22mm, workers ~10–16 mm), or large (queens ~21–26 mm, workers ~9–19 mm) with data compiled from (Williams et al. 2014) and (Rasmont et al. 2015). Grouping body sizes into distinct categories avoided errors due to uncertainty in individual measurements and provides more power to detect differences between each category.

Phylogenetic distance measurement

To measure phylogenetic distances within assemblages at each site, a molecular phylogeny was created for all species using CO1 gene sequence data from Genbank (Sayers et al. 2022). Like other mitochondrial genes, the CO1 locus is conserved across individuals of the same species in animals but is distinct between species, making it an ideal marker for a single-locus phylogeny (Rach et al. 2017). Nucleotide sequences were manually trimmed, and alignments were created for this locus using the multiple sequence alignment program MAFFT (Multiple Alignment using Fast Fourier Transform), a method chosen for its relative speed and accuracy (Katoh et al. 2002). A phylogenetic tree was produced in MEGA (Kumar et al. 2016) and cross-referenced to the subgenera level with Hines et al. (2008) for accuracy. Creating a phylogenetic tree using CO1 data allowed for direct inclusion of species sampled in this study, many of which were not covered in the Hines et al. (2008) tree.

Climate measurements

For small pollinators like bumblebees, which are no larger than 3cm in length, fine-scale climatic patterns influence species' persistence (Pincebourde and Woods 2020). The package *microclima* (Kearney et al. 2014) was used to obtain high-resolution ($1m^2$) estimates of air temperature at two metres above surface level from a gridded hourly dataset. From this dataset, species' upper historical thermal niche limits were calculated as the mean of the five highest daily mean temperatures recorded at locations where each species has been observed, during the baseline period 1979–1985. Similar approaches have been applied in birds and butterflies to characterize species' thermal niches and their responses to climatic variation (Devictor et al. 2012). Maximum annual temperatures were also obtained through *microclima*, calculated as the average of the five highest yearly temperatures recorded at each site during the sampling season, May to September. I then measured the mean of the thermal position of each individual species at a site each year as the average of all differences between species' historical, upper thermal limits and the maximum annual temperatures at each site. This approach uses each species' known thermal tolerance range to assess how close local microclimate conditions are to their upper limits. For each species detected at a site, I substituted microclimate-modeled maximum temperatures (N_m) into the species-specific TPI equation using that species' historical thermal limits. This yields an estimate of thermal position for each species at a given location. Community-level TPI values were then calculated by averaging the species-level TPIs across all Bombus species present at that site and time point.

Taxonomic, functional and phylogenetic diversity

Taxonomic diversity was measured using the first Hill number, Shannon Entropy (Hill 1973). This is a common diversity index that estimates taxonomic evenness based on the number of species at a site. It is widely considered an appropriate metric to quantify abundance-based diversity when considering landscape management questions, especially as it is sensitive to rare species, a facet that is key to overall biodiversity conservation strategies but often missed with abundance-based metrics (Nagendra 2002; Jost 2006; Chao et al., 2014).

Functional diversity for each site was measured using the multidimensional functional dispersion metric, FDis (Laliberté and Legendre 2010), in the R package *FD* (Laliberté et al. 2014). FDis quantifies how traits of individual species are distributed in a multidimensional trait space, where each axis represents a different trait. The metric calculates the average distance of each species from the center of this trait space, and accounts for species abundance by shifting the center point closer to more abundant species, effectively giving more weight to traits of common species while still including rare species in the calculation. This weighting allows FDis to reflect both the diversity of traits present in a community and the dominance of certain traits.

Phylogenetic diversity was measured with the mean nearest taxon distance (MNTD; Webb et al. 2002) method using function *ses.MNTD* in the package *picante* (Kembel et al. 2010). This metric standardizes the average distance between species and their closest relative in the community, by comparing community MNTD to randomly generated null communities. MNTD is considered a more accurate diversity metric than the original phylogenetic diversity metric, Faith's phylogenetic diversity metric, PD (Faith 1992), which is measured as the sum of the branch lengths that span the species of interest but is highly correlated with species richness (Cadotte et al. 2009).

Statistical analysis

I used multiple linear regression models to predict variation in taxonomic, functional, and phylogenetic diversity as a function of site thermal position, sampling year, and site type. Trait data were incorporated to explore their influence on diversity metrics, and model assumptions were checked for normality and homoscedasticity, and all analyses were conducted in R. I estimated phylogenetic signal of body size, nest type, and month of species' emergence using *fitDiscrete* (Yang 2006, Fitzjohn et al. 2009), a transformation of Pagel's lambda (λ, Pagel 1999) to calculate the phylogenetic signal of discrete characters. This likelihood model function in the R package *Geiger* reflects the degree of phylogenetic conservatism in the trait across the phylogenetic tree, independent of site type, year, or other external variables. Generalized linear models were constructed with the *lm* function to estimate the effects of land use, climate, year and their interactions on each of taxonomic, functional, and phylogenetic diversities at each site. I used the function *stepAIC* from the R package *MASS* (Venables and Ripley 2002) to select the model with the fewest predictors based on the Akaike information criterion (AIC). Multinomial logistic regressions were used to estimate the effects of land use, climate, year and their interactions on each of the three individual, discrete functional traits (body size, nesting location, emergence timing). A logistic regression analysis was chosen here because a linear model would not be appropriate for nominal dependent variables with multiple categories. Multinomial logistic regression assumes independence of irrelevant alternatives (IIA), which may not fully apply here if traits covary in ways not captured by the model structure. Future analyses using mixed-effects multinomial models may offer more nuanced insight into nested trait patterns.

Results

Functional and phylogenetic diversity

A total of 3115 bumblebee individuals from 14 species, collected across 28 sites, were included in this study. This total is lower than the 4573 individuals mentioned in Chapter 3 because species without complete trait data were excluded from trait-based analyses. To reduce bias and ensure accurate functional and phylogenetic metrics, only species for which all trait categories were available (body size, nesting type, emergence timing) were retained.

Phylogenetic diversity was significantly lower in agricultural sites than in semi-natural areas (t-statistic = 2.10, p = 0.03; Fig. 4.2A). In contrast, functional diversity also showed a decline in agricultural sites, but this relationship was marginal (t-statistic = 0.23, p = 0.05; Fig. 4.2B) and should be interpreted cautiously. When analyzed in relation to thermal position, both diversity types declined in warmer agricultural sites (adjusted $R^2 = 0.18$ for phylogenetic, $R^2 = 0.21$ for functional), but the ecological mechanisms underlying these patterns may differ, and that effect was not detected among semi-natural areas (Fig. 4.3). While phylogenetic diversity reflects shared evolutionary history and potential genetic vulnerabilities, functional diversity captures ecological roles, which may show higher redundancy in disturbed landscapes. These differences suggest that climate and land use may jointly reduce overall community diversity but through partly independent pathways. Year had a slight negative effect in all models – all metrics of diversity decreased over the three sample years (Table 4.3).

Trait composition

Emergence timing showed little variation between agricultural and semi-natural sites (Fig. 4.2), contrary to the expectation that bees at agricultural sites would exhibit a narrower range of emergence timings compared to those at semi-natural habitats. The positive coefficient (0.0002) in the multinomial regression indicates that increases in thermal position are associated with increase in number species emerging in June ($p = 0.001$). Lower thermal position values were associated with increased numbers of species emerging in May ($p = 0.001$). The intercepts and year predictors, or interaction terms, do not significantly contribute to the model.

Thermal position impacted nesting trait distribution across sites as well. The negative coefficient (-0.0002, SE = 0.0001) indicates that as site thermal position increases, the odds of encountering bees in the underground nesting type decreased relative to the odds of above-ground bees. Presence in a semi-natural site was associated with increased odds of being in the underground nesting category compared to above-ground ($p = 0.001$). The effects of year and interaction with semi-natural sites did not contribute significantly to the model.

These findings indicate that both thermal position and site type are important predictors for all three dependent variables that I modelled. Fig. 4.3 shows how these predictors interact, highlighting significant differences in the effect of site type on thermal position (or, proximately to upper thermal niche limits).

Thermal position was a significant predictor of emergence timing, nesting location, and body size. Smaller species were found closer to their thermal limits. Thermal position negatively impacted the likelihood of observing medium-sized bees ($p = 0.001$). In terms of body size, both thermal position and site type had significant effects. Small-sized bees were more likely to be found in areas with higher mean thermal position, while large bees were more likely to be found in semi-natural sites.

Phylogenetic diversity declined in agricultural land cover

Species represented seven subgenera, about half of those present in North America. Body size did not exhibit phylogenetic signal ($\lambda = 0$; Fig. 4.4A), demonstrating that body sizes are not significantly clustered phylogenetically and appear instead to be distributed independently across species. There was a moderate-to-strong phylogenetic signal of nesting location ($\lambda = 0.706$; Fig. 4.4B), indicating that more closely related species tend to share similar nesting location preferences. For emergence phenology, I detected a moderate phylogenetic signal ($\lambda = 0.572$; Fig. 4.4C), so there is some tendency for species' emergence timing to be more similar among more closely related species.

Discussion

In my study, temperature and land use acted as compounding stressors, exerting negative effects on the taxonomic, functional, and phylogenetic diversity of the measured bumblebee assemblages in Southern Ontario. Biodiversity in all three metrics was compromised in environmental conditions which exceed the bumblebee assemblage's thermal tolerances. This finding highlights the importance of climate interacting with other stressors across land use types and life history traits.

Functional diversity was significantly reduced in agricultural compared to semi-natural habitats. This pattern aligns with global analyses showing erosion of trait diversity under high land-use intensity (De Palma et al., 2021). My results contribute finer-scale evidence from a temperate pollinator system, highlighting specific community-level functional losses tied to local land use. Given that both thermal position and land use intensity can influence habitat conditions, some degree of correlation between these variables is expected. However, models that included both predictors explained more variance in functional and phylogenetic diversity than models with either alone (Table 4.3), indicating they capture distinct environmental stressors. This supports the interpretation that land use and climate act both independently and interactively to shape bumblebee community structure.

The loss of one-third of species from agricultural landscapes over three years is a large loss of pollinator diversity, but one that is comparable to those that have been previously observed. Aldercotte et al. (2022) found similar interannual trends, and noted their findings were one of less than ten time-series studies of changes in bee abundance conducted in agricultural settings, so more studies were needed to support their findings. Whether results reported here represent a permanent loss or striking interannual variability remains to be seen, but long-term monitoring of pollinator assemblages seems necessary to distinguish between such possibilities;bumblebee community responses may be nonlinear, exhibit thresholds, or involve lagged effects not captured in this short-term dataset. Future studies should consider longer time series or flexible modeling frameworks to better capture complex temporal dynamics.

Contrary to expectations, emergence phenologies did not vary significantly between agricultural and semi-natural sites. This was surprising given prior evidence that land use affects microclimatic buffering (Frey et al., 2016; Katumo et al., 2002). This also contrasts with recent findings by Blasi et al. (2023), who documented earlier queen emergence in agricultural landscapes in northern Europe. One possible explanation is that dominant species in our system show greater phenological plasticity or that microclimatic differences between land use types were less pronounced. Resource availability in surrounding landscapes may suffice to permit bumblebee species to persist similarly well regardless of their emergence timing, even if habitats are intensively used for agriculture. This may be because species use adjacent areas as food sources in periods that fall between monoculture flowering times; many agricultural sites were surrounded in part by semi-natural landscapes (Ollerton et al. 2014). A study considering timing and diversity of resources available in the immediate surrounding landscapes could provide a better understanding of how surrounding landscapes influence species' phenologies in agricultural settings. While no result reported here suggests that agricultural land uses in this region benefit bumblebee species, negative effects do not appear to be a reflection of seasonal timing. One possibility is that emergence timing in this region is more tightly constrained by photoperiod than by microclimate, or that generalist *Bombus* species dominate both habitats and show less phenological variation.

Kleptoparasitic bees showed the lowest diversity across landscapes. Kleptoparasites that do not collect their own pollen or nectar and rely on nests of host bees, and often rely on a single host species, have been found to have the lowest diversity across landscapes (Sheffield et al., 2013). This might reflect natural rarity, the effects of habitat loss and fragmentation of unsuitable temperature, or a combination of the effects of multiple stressors.

Another unexpected result was that trait divergence was not consistently lower in agricultural landscapes. While I predicted that land use filtering would lead to functional homogenization, the persistence of several ecologically distinct species suggests that trait-based responses may be mediated by factors not captured in my models, such as nesting substrate or behavioral plasticity. Conservation strategies based solely on taxonomic diversity may overlook critical aspects of ecosystem function and evolutionary potential (Miatta et al. 2021). This study reveals that both climate change and land use intensification are significant stressors that act in concert, exacerbating declines in taxonomic, functional, and phylogenetic diversity. This finding underscores the urgency of addressing multiple environmental pressures simultaneously to effectively conserve pollinator populations. Climate and land use change are demonstrated to be compounding stressors on bumblebee biodiversity, often likened to the aphorism 'death by a thousand cuts' (Laurance, 2010; Wagner et al., 2021). Understanding how these stressors may be mediated by species traits is crucial for the conservation of native bumblebee species, both in the current landscape and in a predictive capacity for other species predisposed to declines based on their traits.

There is no apparent negative response of PD or FD to within-habitat microclimates that may approach or exceed species' upper thermal limits. Bumblebee species present in those areas may minimize use of subsections of habitat that are most thermally challenging, or that those thermal challenges are present in very limited parts of the summer activity periods. Reduced phylogenetic diversity may signal the selective loss of evolutionarily distinct lineages. Similar patterns have been observed in tropical systems under land use change (Brosi & Briggs, 2013), though few studies have tested this in temperate *Bombus* communities. However, after considering land use context, a different result emerges: PD and FD both declined in areas situated within agricultural landscapes. These are the areas in which human dependence on pollination services are most conspicuous, so there may be practical implications of such declines that should be explored (Flynn et al. 2011). Beyond that, however, is the direct evidence presented here that natural or semi-natural landscapes appear to mitigate otherwise negative effects of hot summer temperatures that are known to reduce species diversity under some circumstances. While this result has been reported before (Newbold 2018, Millard et al. 2021), those results were at very broad scales and relied on coarse environmental observations. This study reinforces that land use type interacts with warming temperatures to harm these critical pollinator species. Conversely, maintaining natural areas may buffer species, at least for a time, from some negative effects of extreme summer heat.

Increasing habitat heterogeneity and providing climate refuge emerge as crucial approaches to mitigate the adverse effects on bumblebee populations. Moreover, protecting habitats that support a wide variety of phylogenetically diverse species can help safeguard genetic diversity and enhance ecosystem resilience in the face of environmental perturbations. My findings emphasize the importance of implementing conservation strategies that consider both species-specific traits and broader ecosystem dynamics to effectively address the threats facing pollinator populations.

High resolution environmental observations, such as for microclimates and land use/land cover improve understanding species responses to environmental change. Microclimate data with high spatial resolution offer more biologically relevant insights into insect occurrences, emphasizing the importance of preserving microclimatic buffering capacity to sustain populations within their current geographic range (Lembrechts 2023). Pincebourde and Woods (2020) call for the downscaling of ecological processes to understand the thermal and landscape conditions, choosing 1m^2 as the relevant microclimate scale at which to understand environmental conditions impacting organisms about 20mm long. This coincides with the resolution of *microclima* data used in this study (Kearney et al. 2014). Different land cover types create distinct microclimates, and this study aims to demonstrate how these variations in microclimates influence the traits of species across land cover types. However, it is important to note that while the final microclimate output is provided at 1 m^2 resolution, it is derived from input layers (e.g., solar radiation, soil texture, vegetation cover) that vary widely in spatial detail. Some inputs are modeled at coarser regional scales and may not fully capture fine-scale heterogeneity in land surface conditions, introducing potential mismatches between ecological inference and underlying data granularity. How precise microrefugia available at different agricultural landcovers, and how this interacts with a species' potential to escape thermal extremes remains to be investigated.

Phylogenetic diversity of species assemblages can reflect the role of environmental filtering and shape how biological communities contribute to ecosystem function (Pearse et al. 2019). Furthermore, protecting existing populations for species will surely be an easier task than attempting to protect them ex situ or through introducing them to new areas. I found evidence that phylogenetic diversity can change substantially in these habitats in the midst of land uses that require pollination services, both from one area to another and through time. Using phylogenetic diversity to prioritize areas for conservation has a long history (Faith, 1992; Vane-Wright et al. 1992; Hennig, 1999; Rodrigues et al. 2009). The measurements made here could inform such practices, but setting conservation priorities is outside the focus of this work.

The study sets the stage for future research directions, including investigating additional trait-based responses across diverse taxa and expanding the geographic scope to other regions. Longitudinal studies tracking bumblebee populations over extended periods can provide further insights into the dynamics of environmental change on pollinator communities. Future research efforts should also focus on elucidating the mechanisms driving trait-mediated responses to environmental stressors and exploring novel conservation interventions that promote resilience and adaptation in bumblebee populations.

Figures 4.1 – 4.4

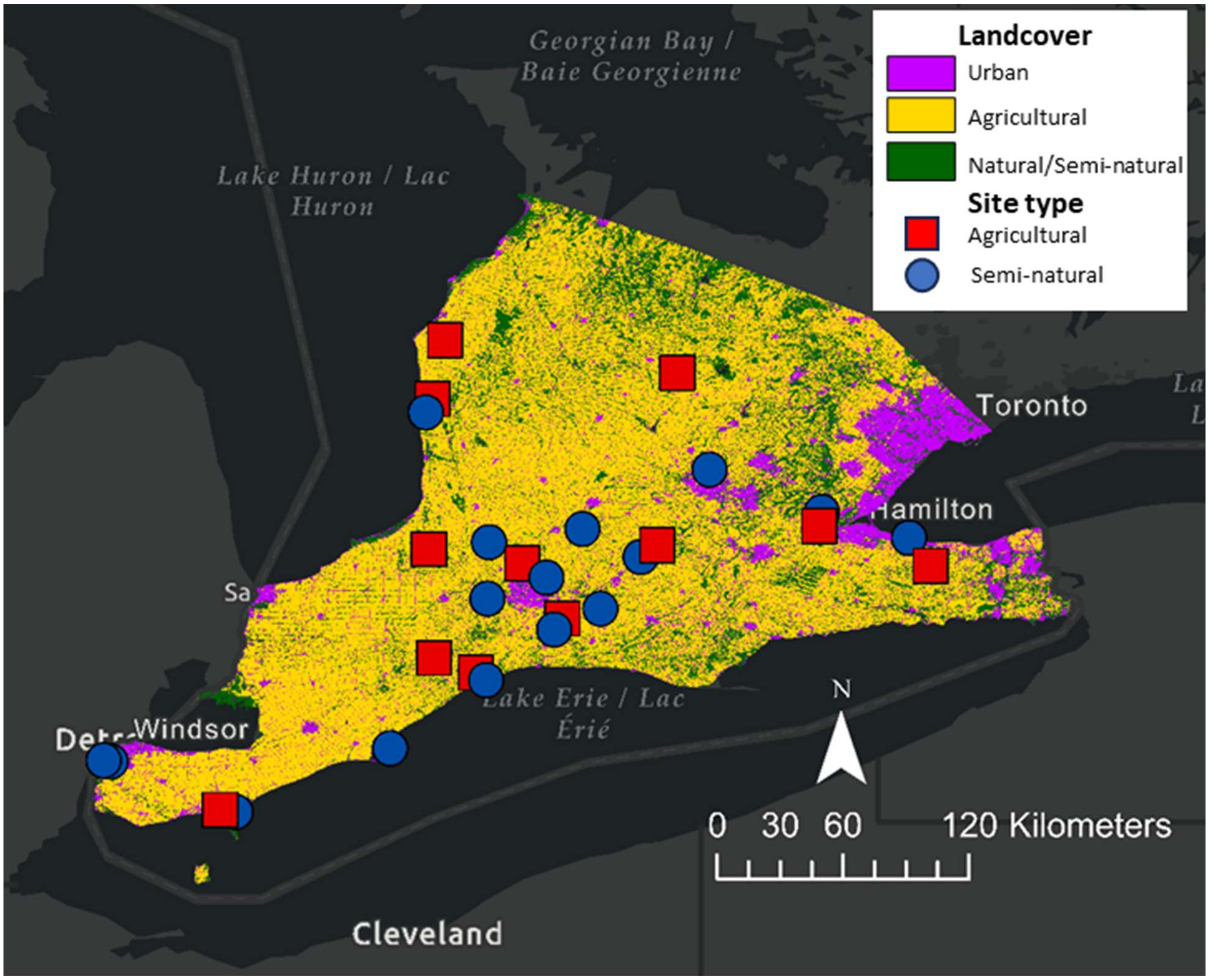

Figure 4.1. Map of 12 agricultural sites and 16 semi-natural sites for bumblebee sampling across Southern Ontario, 2015-2017.

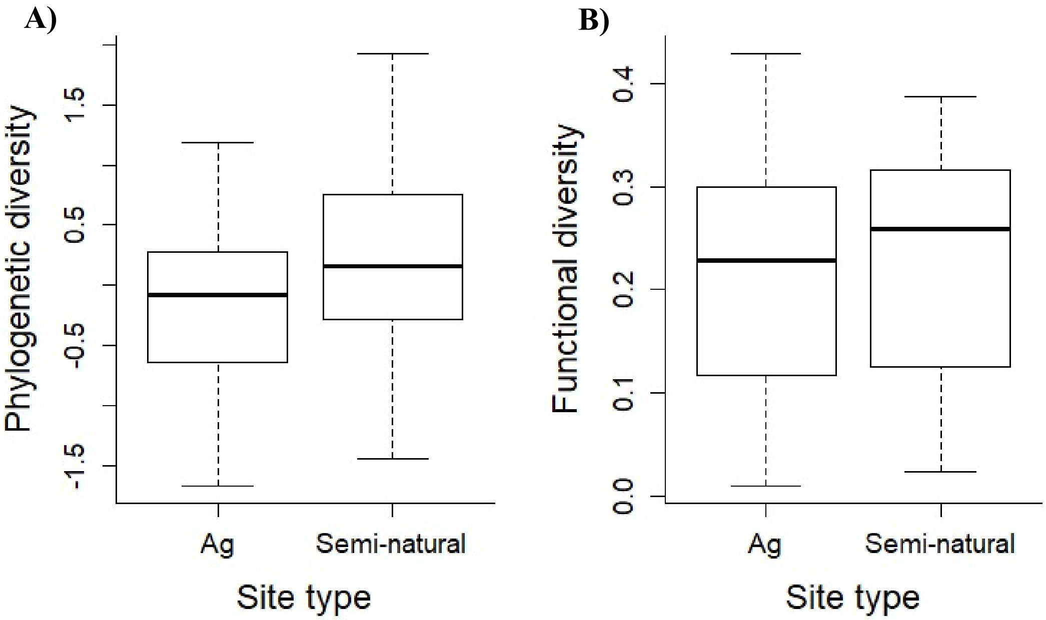

Figure 4.2 Box plots of A) Phylogenetic diversity (Purvis' D) and B) Functional diversity (Fdis) across agricultural and semi-natural sites. Boxes show median lines and interquartile ranges, whiskers show 1.5*interquartile ranges. Phylogenetic diversity is lower in agricultural than in semi-natural sites ($p = 0.03$; panel A); functional diversity shows a marginal reduction ($p = 0.05$; panel B).

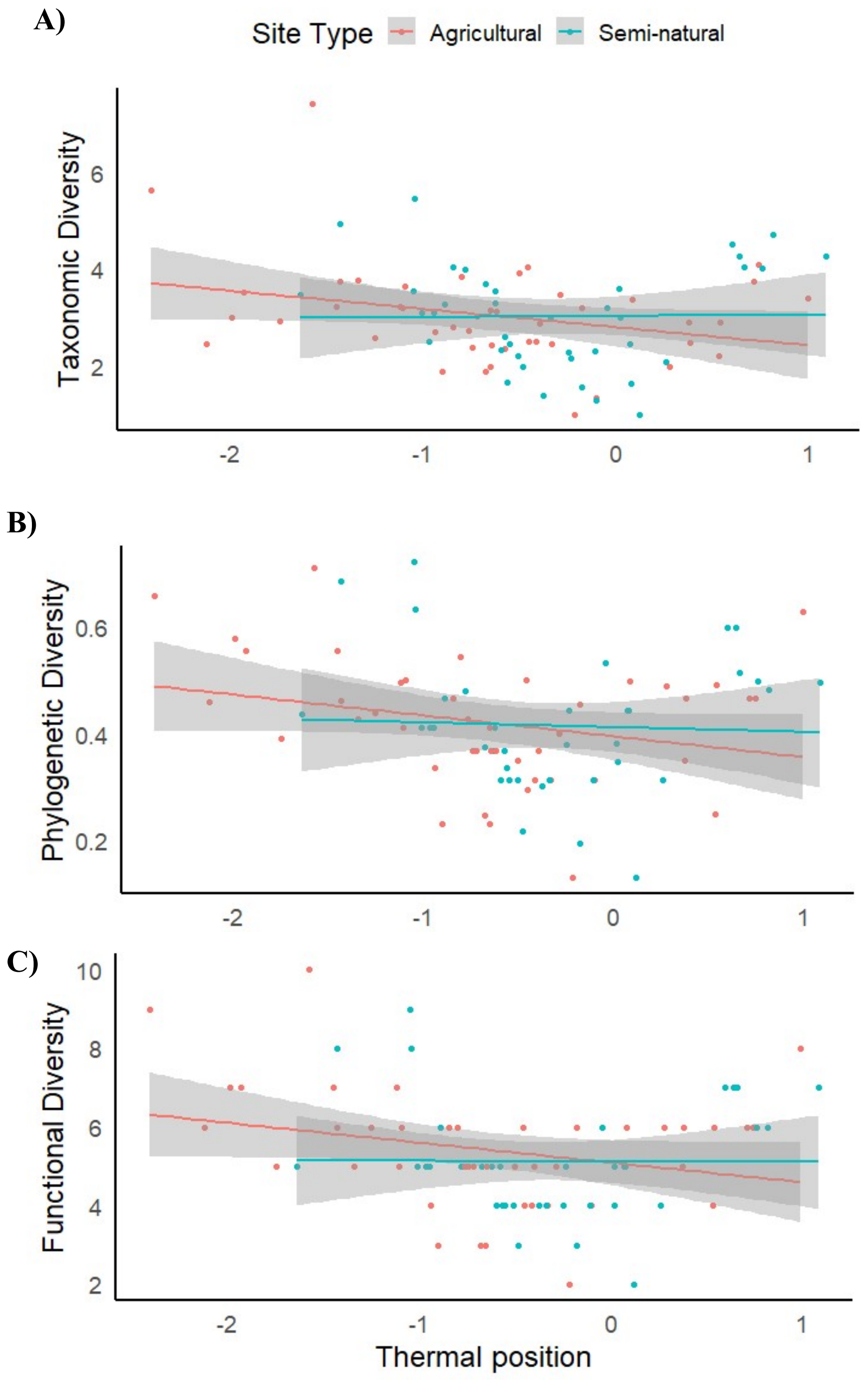

Figure 4.3. Relationship between site-level thermal position and A) Taxonomic diversity (Shannon Entropy), B) Phylogenetic diversity (Purvis' D), and C) Functional diversity (Fdis) at agricultural (orange) and semi-natural (blue) sites. Panel A repeats the Chapter 3 result for comparison. Lines are slopes from the linear mixed effects models (Table S4.2); bands are 95% confidence intervals.

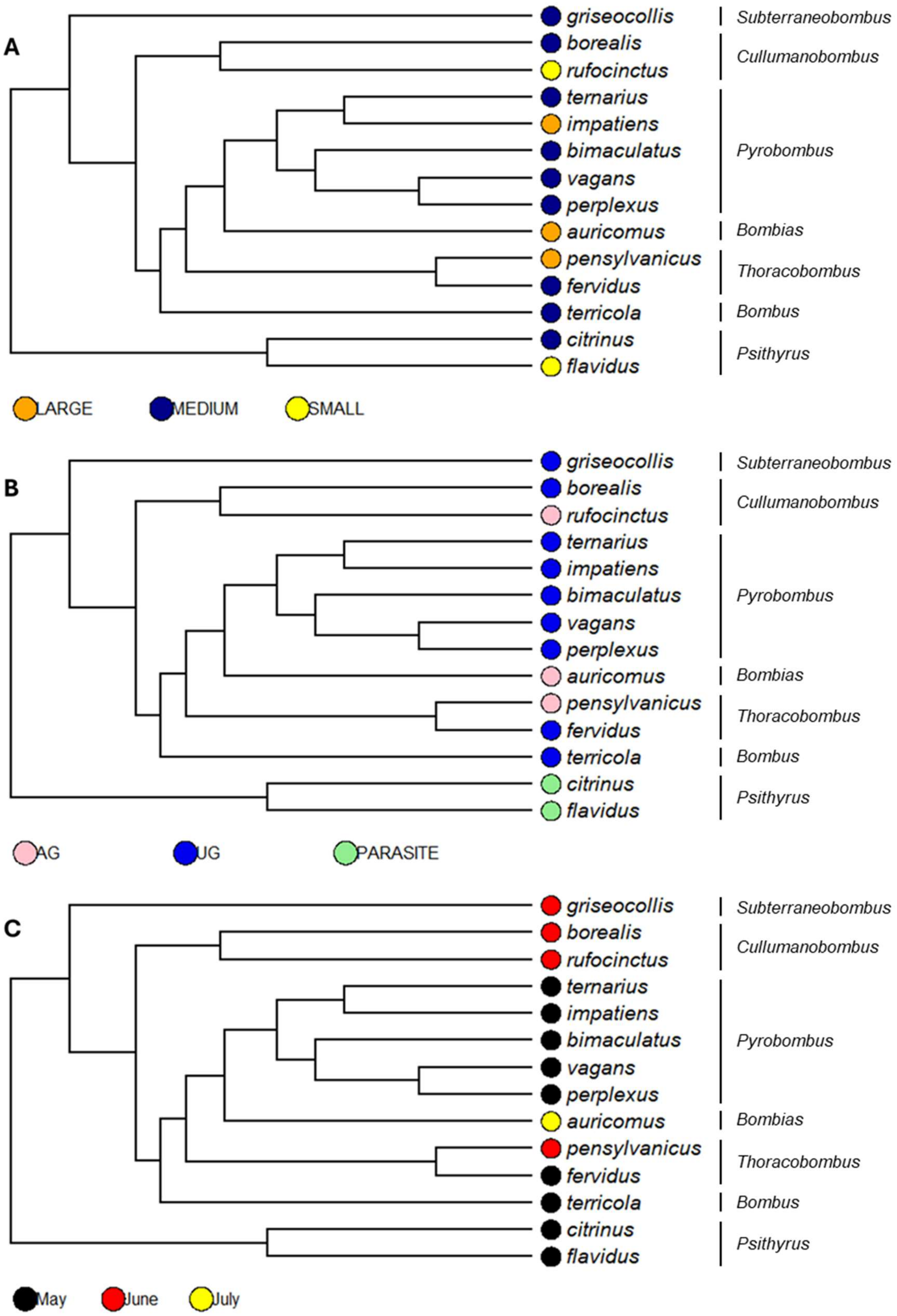

Figure 4.4. Phylogenetic distribution of A) Body size, B) Nesting location, C) Emergence phenology among 14 Bombus species. Subgenera are indicated.

Tables 4.1 – 4.3

Table 4.1. Species-level emergence, body size, and nesting traits for 14 bumblebee species included in analyses.

Species	Emergence month	Size	Nesting
B. impatiens	May	Large	Underground
B. bimaculatus	May	Medium	Underground
B. griseocollis	June	Medium	Underground
B. rufocinctus	June	Small	Above-ground
B. vagans	May	Medium	Underground
B. perplexus	May	Medium	Underground
B. ternarius	May	Medium	Underground
B. fervidus	May	Medium	Underground
B. borealis	June	Medium	Underground
B. pensylvanicus	June	Large	Above-ground
B. citrinus	May	Medium	Kleptoparasite
B. auricomus	July	Large	Above-ground
B. terricola	May	Medium	Underground
B. flavidus	May	Small	Kleptoparasite

Table 4.2. Expected associations of traits with climate change sensitivity. Kleptoparasitic was included as a level for nesting type.

Trait of interest	Related Function	Categories	Data source	Expected association
Annual emergence timing	Phenology, ability to find nest, maximum possible colony size	May, June, July	(Koppel and Kerr 2022)	Earlier peak emergence more robust to environmental changes (Pawlikowski et al. 2020); bees in agricultural monocultures exhibit narrower emergence timings to align with the single flowering period
Nesting type	Resource niche breadth, habitat use	aboveground, underground, surface, kleptoparasites	(Williams et al. 2014)	Underground nesting more robust to environmental changes, while ground-nesting bees facing losses (Pereira et al. 2021)
Body size	Dispersal ability, foraging range	small, medium, large	(Williams et al. 2014)	Larger size leads to lower sensitivity to environmental changes (Williams et al. 2010)

Table 4.3. Summary of linear regression model estimates predicting taxonomic, functional, and phylogenetic diversity from thermal position, sampling year, and site type (agricultural or semi-natural). The table shows the estimated coefficient, standard error, t-statistic, and p-value for each predictor in the models. Significant p-values bolded and represented with an asterisk (*).

Response	Term	Estimate	Std. error	t-statistic	p-value
Taxonomic Diversity (Shannon's Entropy)	**(Intercept)**	**1093.01**	**478.56**	**2.28**	**0.03***
	meanTPI	-335.66	438.52	-0.77	0.45
	Site type	699.89	658.16	1.06	0.29
	Year	**-0.54**	**0.24**	**-2.28**	**0.03***
	Thermal position:Site type	**2592.50**	**845.43**	**3.07**	**0.00***
	Thermal position:Year	0.17	0.22	0.76	0.45
	Site type:Year	-0.35	0.33	-1.06	0.29
	Thermal position:Site type:Year	**-1.29**	**0.42**	**-3.07**	**0.00***
Phylogenetic Diversity (MNTD)	**(Intercept)**	**179.9**	**57.1**	**3.149**	**0.00***
	Thermal position	51.7	52.3	0.989	0.32
	Site type	-32.7	78.5	-0.417	0.67
	Year	**-0.08**	**0.02**	**-3.141**	**0.00***
	Thermal position: Site type	100.2	100.9	0.993	0.32
	Site type: Year	0.016	0.039	0.417	0.67
	Thermal position: Site type (Ag):Year	-0.02	0.02	-0.99	0.32
	Thermal position: Site type (Semi-natural): Year	-0.07	0.04	-1.76	0.08
Functional Diversity (Fdis)	**(Intercept)**	**1720.19**	**374.53**	**4.59**	**0.00***
	meanTPI	**-0.67**	**0.20**	**-3.27**	**0.00***
	Year	**-0.85**	**0.19**	**-4.58**	**0.00***

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Chapter 5: Synthesis and Conclusion

Bumblebee declines are poignant reminders of the fragility of ecosystems. Managing bumblebee species losses requires an understanding of the mechanisms by which species interact with their changing habitat and climatic conditions (Soroye et al., 2020). This thesis used both macroecological and community scale research to better understand the mechanism by which thermal extremes and land use intensity drive biodiversity shifts usingfine-scale climate resources, intensive field sampling, and large assemblies of museum collection data. This thesis advances our understanding of the relationship between climate change, land use, and bumblebee biodiversity by examining species' thermal tolerances, emergence timing, nesting behaviors, and the role of comparative phylogenetics in quantifying biodiversity alongside functional and taxonomic diversity. These findings build on Chapter 3, which identified stronger associations between species loss and thermal extremes, and Chapter 4, which demonstrated that climate stress also erodes phylogenetic and functional diversity, particularly in already disturbed landscapes. This research adopts a multi-scale approach that eliminates the need to rely on extrapolative, and often unreliable, models of diversity to infer how species respond to environmental changes.

Phenological shifts to escape extreme climates

In my first data chapter, Chapter 2, I ask whether species that shift seasonal activity timing to align more closely with shifts in spring onset timing improve persistence compared to species that do not. This question aims to explore the potential for phenological shifts as a mechanism for bumblebees to cope with climate change and improve their long-term persistence.

To address this question, I examine the direct and indirect impacts of climate change on bumblebee communities across North America. I compare data from two time periods: 2004-

2012, when climate shifts were accelerating, and a baseline period from 1954-1970, when climate shifts were less pronounced. By examining how bumblebee activity timing has changed over time, I assess the role of phenological synchrony with climate in species persistence.

I find that maintaining phenological synchrony with climate significantly improves the likelihood of a population being recorded in the same area decades later. In 15 of 21 species studied, populations that had aligned their seasonal activity timing with shifts in spring onset timing were more likely to persist. This suggests that phenological shifts are a significant climate response in bumblebees, like what has been observed in plant species (Inouye, 2022; Singer, 2017). Notably, the magnitude of phenological shifts over time was not phylogenetically structured, meaning that the ability to escape unfavorable climatic conditions by altering activity timing was not confined to specific subgenera of bumblebees. The temporal shifts observed in bumblebee activity timing reveal the dynamic nature of their response to changing climatic conditions, with implications for their long-term persistence (Hemberger & Williams, 2024). Further research could explore whether there is a physiological underpinning to certain species' abilities to shift activity timing more readily than others, in the ways that are better understood in plant communities (Woodard 2017). There is some evidence to suggest variation in adaptive capability between species in terms of environmental conditions they are found in; *Bombus terrestris*, for example, may have more physiological flexibility since it has been widely introduced globally outside of its native range, to Chile and Argentina, while other species have not demonstrated this ability to acclimate to environments so different from the cool alpine conditions in Sichuan, China where they evolved (Hines, 2008). However, this hypothesis remains untested in a comprehensive, species-wide study and warrants further investigation.

Such studies would help deepen our understanding of how phenological shifts might be leveraged to improve bumblebee conservation strategies in the face of ongoing climate change.

Bumblebee vulnerability to climate and land use stressors at local scales

In Chapter 2, I focused on the role of phenological shifts in enhancing bumblebee persistence by aligning seasonal activity timing with changes in climate. However, while phenology plays a key role in species' ability to cope with climate change, local-scale factors, such as land use intensity, can further complicate species' ability to persist. In Chapter 3, I examine the role of land use intensity in exacerbating the effects of climate change on bumblebee populations at the community level. Given that bumblebees experience their environments at scales of millimetres and prefer to forage less than 5km from their nests given the resource availability to do so (Osborne et al., 2008), I aimed to understand how species' thermal position, previously explored at macroecological scales (Soroye et al., 2020), influences species persistence in different land use types.

To address this question, I used fine-scale, spatially explicit thermal data to model species' interannual tolerances to extreme temperatures. I integrate these models with high-resolution microclimate data and measures of land use intensification for agricultural areas. Using linear models, I test whether thermal conditions at a microclimate level can explain variation in species persistence across agricultural and semi-natural landscapes.

I find in Chapter 3 that agricultural intensification and habitat fragmentation drive the loss of bumblebee taxonomic diversity. Species were closer to their thermal limits at the agricultural sites, despite all 28 sites being in the Southern Ontario region. This indicates the availability of more microclimates in the lower-intensity, semi-natural sites. Following the finding of greater taxonomic decline at agricultural sites compared to semi-natural sites, I then investigate whether there is a pattern in species persistence at agricultural sites. I find that agricultural sites have a higher proportion of below-ground nesting species than semi-natural sites.

This chapter highlights the critical role of thermal suitability in shaping species diversity, in addition to land cover and fragmentation. The observed patterns of species persistence suggest that agricultural landscapes may act as barriers to species that are sensitive to thermal extremes, particularly above-ground nesting species. The availability of microclimatic refugia in semi-natural sites is key to maintaining bumblebee biodiversity. This chapter integrates species' thermal tolerances into the broader context of landscape ecology, recognizing that while habitat fragmentation and loss have long dominated discussions of habitat availability (Fahrig, 2003), thermal suitability - especially at fine scales - adds a dimension that helps to explain distribution. Future studies could consider these thermal dynamics to provide a more comprehensive view of challenges faced by bumblebees, particularly in fragmented landscapes (Nowakowski et al., 2018). Landscape studies could further explore the effect of landscape intensification on microclimate refugia availability, and the impact on species' thermal positions and persistence.

Community diversity on three axes offers added biodiversity insight

In Chapter 4, I ask how functional and phylogenetic diversity in bumblebee communities are influenced by thermal position and land use, particularly in agricultural versus semi-natural areas. I aim to assess whether climate change and land use interact to shape biodiversity in more nuanced ways beyond taxonomic diversity, as discussed in Chapter 3.

To answer this question, I analyze the impacts of thermal position on functional and phylogenetic diversity across three years in agricultural and semi-natural habitats. I use thermal position, which reflects the thermal conditions of a site relative to species' tolerances, to understand how climate affects biodiversity. I also explore how thermal position, land use type, and community-level diversity metrics (functional, phylogenetic, and taxonomic) interact and contribute to species' persistence in these habitats.

Functional and phylogenetic diversity decreased with increasing thermal position in agricultural sites - but not in semi-natural areas. This finding underscores the interactive effects of climate change and land use on biodiversity that were observed for taxonomic diversity in Chapter 3. Thermal position, which reflects site-specific thermal conditions relative to species tolerances, provides a nuanced understanding of how climate impacts biodiversity (Oyen and Dillon, 2018). This result aligns with prior work demonstrating that agricultural intensification amplifies climate-driven biodiversity loss by reducing habitat complexity and resource availability (Outhwaite et al., 2022). The absence of this pattern in semi-natural areas suggests that these habitats buffer against thermal stress, potentially due to higher structural and microclimatic heterogeneity, reinforcing their importance in conservation planning. To my knowledge, this work provides the first demonstration that broad-scale measurements of thermal position can be effectively applied to assess biodiversity responses at local scales.

The slight decline in all metrics of diversity over the study's three years, as indicated by negative year estimates, underscores the potential impacts of environmental stressors. A much longer time series of observations from study sites would be necessary to infer that this trend was part of the broader decline among pollinators that has been reported elsewhere, and interannual variation is large relative to the declines observed over the three years of data collection here. Nevertheless, this trend does point to the possibility that these pollinator species are in decline in the study region, perhaps because of the climate-related effects described here in detail, or other factors, such as pesticide use or land use/land cover changes (Brunet & Fragoso, 2024).

The predictive power of thermal position and site type for emergence timing, nesting location, and body size illustrates the intertwined effects of climate and land use on functional traits. Nesting traits and emergence phenology exhibited moderate-to-strong phylogenetic signals, suggesting that closely related species share vulnerabilities tied to shared evolutionary histories. These findings align with research showing that phylogenetic signals can influence community responses to environmental change, with implications for ecosystem services provided by bumblebees (Leclercq et al., 2023).

Agricultural land cover was associated with significant declines in phylogenetic diversity and trait variability, reinforcing the role of intensified land use as a key driver of biodiversity loss (Birkenbach et al., 2024; Williams & Hemberger, 2023). The disproportionate impacts of climate and land use changes on smaller species and above-ground nesters highlight their heightened sensitivity to environmental stressors, consistent with studies linking these traits to reduced adaptive capacity and habitat availability (Williams et al., 2010). This research suggests that conservation strategies could prioritize creating thermal refugia and enhancing habitat quality to mitigate these effects.

These findings show the compounded effects of climate change and land use on bumblebee communities. The decline in functional and phylogenetic diversity in agricultural sites highlights the significance of habitat quality, with more intense land use exacerbating biodiversity loss. The vulnerability of smaller species to thermal extremes underscores the need for conservation actions specifically targeting these species. The phylogenetic signals in nesting and emergence traits suggest that evolutionary relationships play a crucial role in determining species' responses to environmental stressors, with implications for ecosystem services provided by bumblebees.

This reinforces the importance of considering both functional and evolutionary diversity in conservation planning.

These results serve as an early warning and call for longitudinal studies to better quantify the persistence of these patterns. However, additional research with a longer study period could better capture long-term trends. Further research could explore the role of microclimatic refugia in mitigating the negative impacts of thermal extremes on smaller species, especially in agricultural landscapes. Additionally, investigating the relationship between phylogenetic diversity and ecosystem services could provide insights into how evolutionary history influences bumblebee contributions to pollination and other ecosystem functions. This research can support the growing body of work that indicates the need to protect and restore habitats, create thermal refugia, and improve habitat quality to support bumblebee diversity in increasingly modified landscapes (Gaiarsa and Bascompte, 2022; Ulrich and Sargent, 2025).

Chapters 3 and 4 together provide complementary insights into how climate and land use shape bumblebee biodiversity in Southern Ontario, highlighting patterns that would be missed if examined in isolation. Chapter 3 demonstrated that community-level taxonomic diversity declined in agricultural landscapes, particularly in areas where thermal stress was greatest. This suggested that proximity to upper thermal limits is a key driver of local diversity loss. However, Chapter 4 expanded this by revealing that even in cases where taxonomic diversity appeared stable, both functional and phylogenetic diversity showed significant reductions. These declines suggest that land use intensification may be selecting for a narrower suite of traits and evolutionary lineages, which may be a signal of ecological filtering and potential functional redundancy. Functional trait convergence in agricultural sites (e.g., similar body size and nesting strategies) may mask early warning signs of ecosystem degradation that are invisible to taxonomic metrics alone. The convergence observed in Chapter 4 also contextualizes the thermal sensitivity trends from Chapter 3: species surviving in these thermally stressful environments may be those with traits conferring greater heat tolerance or nesting flexibility. When integrated, these two chapters suggest that climate and land use not only reduce diversity but also erode ecological and evolutionary distinctiveness. This strengthens the case for using trait-based and phylogenetic metrics alongside traditional diversity measures to detect biodiversity loss under global change and to inform more nuanced conservation planning.

Looking ahead for pollinator conservation

The availability of new tools and analyses can enable researchers to explore existing occurrence datasets in new ways. Chapter 2 takes advantage of a 13000-occurrence dataset from museum collections across North America, and, while many such compendia exist, adapting these to fill in gaps in spatial resolution and time-series implementations remains a challenge. An estimated 40%-80% of current biological records are currently discarded from use, a part of which is due to data deficiencies (Vargas et al., 2024). In Chapter 2, I employed a novel method of estimation of annual colony emergence timing, validated by published life histories of these species. This creates the opportunity to leverage large occurrence datasets, which were not specifically collected for phenological data, to inform predictive models of species persistence under climate change. By applying this method to bumblebees and other taxa, researchers can gain critical insights into how shifting phenology may impact pollinator populations and support more effective conservation strategies. Integrating phenological shifts into conservation models could also help mitigate climate change impacts, improving species persistence by preserving habitats that support these shifts in activity timing.

The findings in this thesis highlight the need for conservation strategies that increase access to microclimates, reducing species' exposure to thermal extremes. For example, semi-natural habitats, as shown in Chapter 4, buffer pollinators from thermal stress, suggesting that protecting and restoring such habitats could be a key strategy for resilience. While studies have demonstrated the large local variation in temperature is related to local variation in land cover, the availability of such tools has been a limiting factor in understanding habitat-scale dynamics (Suggitt et al., 2011). The 1 m^2-resolution microclimate data I used in Chapters 3 and 4 (Kearney & Porter, 2017) enabled more precise tests of how such conditions affected habitat use at biologically relevant scales. Bumblebee community diversity tracked thermal extremes closely in Chapter 3; in conditions that were hot relative to species' upper thermal niche limits, bumblebee community-level diversity declined, a trend that remained highly consistent between years. Through this microclimatic lens, the finding that agricultural sites have a higher proportion of below-ground nesting species than semi-natural sites may reflect the heightened exposure of above-ground nesting sites to disturbance and climatic extremes in agricultural sites compared to semi-natural sites. Without the microclimatic data, predictions about the relationship between the species distribution and its climate response may be misleading (Somero, 2005). The disproportionate decline of above-ground nesting bumblebee species in intensively managed agricultural landscapes suggests the importance of preserving suitable nesting habitats and microclimatic refugia.

Microclimates can serve as stepping stones for movement, aiding in genetic connectivity across fragmented landscapes to reduce the risk of extirpation (Heller & Zavaleta, 2009). For example, if there are microclimates that act as temperature refugia from extreme heat events, this can explain why species can exist in areas that are on a larger-scale seemingly outside of their thermal tolerances, better linking their thermal tolerance to habitat (Lembrechts, 2023; Pincebourde & Casas, 2015). Including these insights into predictive ecological models improves the accuracy of our predictions of bumblebee distributions and population dynamics under novel climate scenarios (Barahona et al., 2024; Mola et al., 2021).

My research has demonstrated that considering thermal tolerances can provide additional explanatory power to landscape ecological patterns and processes that have long been focused on habitat availability, due to either fragmentation or loss. The findings from Chapter 4, where thermal position was shown to influence biodiversity, particularly in agricultural areas, highlight how climate impacts species differently based on their thermal tolerances. My research points to the vulnerability of smaller-bodied species, which are disproportionately affected by thermal extremes. Targeted conservation actions, such as creating thermal refugia and improving habitat quality, should prioritize these species in thermally stressed agricultural landscapes.

Implementation of foresight science tools such as the recently developed Thermal Position Index (TPI; Soroye et al, 2020) in habitat suitability models also offers promising avenues for predicting and mitigating the impacts of climate change on biodiversity. These tools can predict areas where species are more likely to thrive based on their thermal limits, offering valuable insight for conservation planning. The compounded effects of climate change and land use on bumblebee communities call for integrative conservation approaches that address both environmental stressors and land management practices.

Future research should explore the degree to which thermal limit interactions with climate and land use vary spatially. Southern Ontario, where field work for Chapters 3 and 4 was conducted, has a continental climate where bumblebees experience temperatures varying between 5 – 25°C during their active period (Environment and Climate Change Canada, n.d.). Meanwhile, bumblebees in tropical landscapes experience a comparatively narrow range of temperatures and likely persist closer to their upper thermal limits. The interaction between land use intensification and warming temperatures may be more lethal in other, warmer climates (Outhwaite et al., 2022). Conversely, winter activity reported in bumblebees in the UK in response to climate change (Owen et al., 2013) could be an opportunity to test the interaction between climate and land use at a species' lower thermal limit. Lower thermal limits in terrestrial ectotherms are less constrained, meaning there is generally more variation in their ability to survive extreme cold compared to heat (Hoffmann et al., 2013). Bumblebees' evolutionary origins in cold climates may have shaped their exceptional capacity to tolerate cold, as well as their inability to cope with extreme heat. This cold-adapted history likely influences their capacity to persist in conditions exceeding their lower thermal limits but leaves them vulnerable to conditions exceeding their upper thermal limits.

In addition to these habitat-focused strategies, future research should explore whether the phenological shifts observed in Chapter 2 are consistent across other taxa and regions. As well, understanding the physiological basis for some species' ability to adapt to changing conditions – such as the increased flexibility observed in *Bombus terrestris* – could offer valuable insights into species' capacity to cope with climate change. Research into these physiological traits could reveal which species are more adaptable and provide a better understanding of how we can support vulnerable species (Leroy et al., 2023).

The phylogenetic diversity discussed in Chapter 4 also highlights the importance of evolutionary relationships in shaping species' responses to environmental change. Conservation strategies should explicitly account for the evolutionary history of species, not only to supplement gaps in trait data but also as an additional axis of diversity that can highlight patterns contributing to extinction risk (Vereecken, 2015). Recognizing that closely related taxa often share similar vulnerabilities to extinction, and understanding how species' shared evolutionary histories relate to the ecosystem services they provide, can help inform conservation priorities (Cadotte and Davies, 2010). This approach ensures the preservation of not only biodiversity but also the critical ecosystem services these species support.

Policy implications of conservation work

This thesis has examined the intricate relationship between climate change, land use, and bumblebee biodiversity, shedding light on the complex challenges these pollinators face. The insights provided here underscore the importance of aligning conservation efforts with robust policy frameworks. Rapid urbanization presents the need to link climate biology with landscape modifications (Gu et al. 2024), and develop conservation strategies to reflect the findings. Urban expansion often leads to habitat loss and fragmentation, exacerbating the effects of climate change on pollinator populations. Understanding these compounded stressors is critical to developing effective conservation strategies.

In 2002, The Government of Canada allocated approximately $84 million over 10 years to support pollinator health initiatives as part of the National Pollinator Health Initiative (Government of Canada, 2022). This initiative focuses on addressing the main stressors affecting pollinator health, including habitat loss, pesticide exposure, diseases, and the impacts of climate change. The Canadian Agricultural Partnership (CAP) has also provided $3 billion over five years for projects that include pollinator conservation efforts (Agriculture and Agri-Food Canada, 2021). These investments are critical when considering the substantial economic benefits that pollinators bring. Agricultural pollination services contribute over $2 billion annually to the Canadian economy and support broader ecosystem services, including biodiversity conservation, carbon sequestration, and soil fertility (Government of Canada, 2021). The findings in this thesis emphasize that such investments will only reach their full potential if they are guided by data-driven policymaking. Research like mine provides the evidence base needed to develop and refine conservation strategies. Policymakers must prioritize actions to protect habitats, reduce pesticide use, and address climate change impacts, informed by the nuanced relationships between these factors and bumblebee health. Integrating research findings into land management practices and conservation policies will help safeguard bumblebee populations and the essential ecosystem services they provide.

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