The Mite-y Bee: Factors Affecting the Mite Community of Bumble Bees (*Bombus* spp., Hymenoptera: Apidae)

By

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Abstract

Parasites and other associates can play an important role in shaping the communities of their hosts; and their hosts, in turn, shape the community of host-associated organisms. This makes the study of associates vital to understanding the communities of their hosts. Mites associated with bees have a range of lifestyles on their hosts, acting as anything from parasitic disease vectors to harmless scavengers to mutualistic hive cleaners. For instance, in *Apis mellifera* (the European honey bee) the parasitic mite *Varroa destructor* has had a dramatic impact as one of the causes of colony-collapse disorder. However, little is known about mites associated with bees outside the genus *Apis* or about factors influencing the makeup of bee-associated mite communities. In this thesis, I explore the mite community of bees of the genus *Bombus* and how it is shaped by extrinsic and intrinsic aspects of the bees' environment at the individual bee, bee species, and bee community levels. *Bombus* were collected from 15 sites in the Ottawa area along a land-use gradient and examined for mites. The number of individual mites and number of mite species hosted by particular bee species increased significantly with bee species abundance. In addition, several bee species differed in terms of mite abundance, mite species richness, mite prevalence, and mite diversity at the level of individual bees and at the species level. In particular, individuals of rare bee species tended to have particularly high mite abundance in comparison to other bees. However, geography, site quality, and bee diversity were never significant predictors of mite community attributes at any level of analysis. Overall, the best predictor of bee-mite community attributes is the bee species themselves. Thus, these mite communities were not shaped by the factors that are known to shape the parasite communities of other species (i.e., geographic distance, host diversity), perhaps because of the commensalistic nature of most of the mite species investigated here. These findings have implications for conservation of bumble bees, given that commensals may become cleptoparasitic at high densities and may act as disease vectors.

Résumé

Les parasites et les autres organismes associés à des espèces-hôtes influencent l'environnement de leurs hôtes, et ceux-ci, à leurs tours, façonnent l'environnement des parasites. Cela rend l'étude des associés essentielle pour comprendre la communauté écologique de leurs hôtes. Les acariens associés aux abeilles ont un éventail de différentes interactions avec leurs hôtes. Il y a des espèces agissant en tant que vecteurs de maladies, des charognards inoffensifs et des mutualistes qui nettoient la ruche. Par exemple, l'acarien parasite *Varroa destructor* est un des facteurs pouvant expliquer le déclin des abeilles à miel (*Apis mellifera*). Cependant, on sait peu de choses sur les acariens associés aux abeilles en dehors du genre *Apis,* ni sur les facteurs qui influencent la composition d'acariens associés aux abeilles. Dans cette thèse, j'explore les communautés d'acariens de bourdons (*Bombus*) et comment elles sont façonnées par les facteurs extrinsèques et intrinsèques de l'environnement aux niveaux de l'abeille individuelle, de l'espèce et de la communauté d'abeilles. Les abeilles ont été prélevées dans 15 sites de la région d'Ottawa le long d'un gradient d'utilisation des terres et ont été examinées pour la présence d'acariens. Le nombre d'acariens et le nombre d'espèces d'acariens hébergés par une espèce d'abeille particulière ont augmenté avec l'abondance des espèces d'abeilles. De plus, plusieurs espèces d'abeilles différaient en relation à l'abondance d'acariens, le nombre d'espèces d'acariens, la prévalence d'acariens et la diversité d'acariens au niveau de l'abeille et de l'espèce. En particulier, les espèces d'abeilles rares ont tendance à avoir une abondance d'acariens particulièrement élevée par rapport aux espèces plus communes. Cependant, la géographie, la qualité du site et la diversité d'abeilles n'ont jamais été des prédicteurs significatifs des caractéristiques des communautés d'acariens à tous les niveaux d'analyse. Dans l'ensemble, les meilleurs prédicteurs des caractéristiques de la communauté d'acariens associés aux abeilles sont les abeilles elles-mêmes. Ainsi, les communautés d'acariens n'étaient pas régies par les facteurs habituels qui régissent les communautés de parasites d'autres organismes (la distance géographique, la diversité des hôtes), peut-être en raison du fait que la plupart des interactions entre les acariens et les abeilles étaient commensales. Ces résultats ont des implications pour la conservation des bourdons, étant donné que les acariens peuvent agir comme vecteurs de maladies et que leur comportement peut passer de commensaliste à cleptoparasites lorsqu'ils se retrouvent à des densités de population élevées.

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Introduction

Host–Associate Interactions

Almost all organisms play host to a variety of associates including parasites, mutualists, and commensals, with the identity of the hosts generally determining the identities of the specific associates (Hechinger and Lafferty 2005). For the purpose of this thesis, an associate is defined as an organism with a close relationship to another organism, a host, on which it relies heavily for resources, such as nutrients and dispersal; the effect of the organism on its host (positive, negative, or neutral) is unspecified. Parasites, and to a lesser extent mutualistic symbionts, are normally closely associated with one or a few host species (Poulin and Mouillot 2003, Thrall et al. 2007). While less is known of commensals, the same level of specialization is often assumed. This host specialization would mean that the makeup of the community of hosts is likely to shape the community of associates. Conversely, parasites and other associates can act as important, but frequently neglected, drivers of the community composition of their hosts (Hudson et al. 2006, Krkošek et al. 2011, Vergara et al. 2011). In particular, multi-host organisms that either affect different hosts unequally or prefer certain hosts over others, can contribute to which individuals and species fail or thrive (Krkošek et al. 2011). For parasites and mutualists, the potential fitness costs and benefits to their hosts are relatively apparent. However, all associates, including commensals, have the potential to act as disease vectors as well, thereby indirectly influencing host fitness. In addition, a loss of hosts or preferred hosts could trigger a decline in the associate, while increased host fitness can provide increased resources for those same associates. Thus, a reciprocal relationship occurs between hosts and associates, with each potentially driving the population dynamics and community composition of the other.

From the perspective of the host, the rationale for studying the communities of its parasites and mutualists is relatively obvious compared to that of its commensals. However, the effect of an associate can also be context dependent, with associates ranging from mutualistic to parasitic depending on factors such as host development stage and environment (Brown et al. 2012). For instance, branchiobdellid worms provide an ostensibly beneficial cleaning service to crayfish, but the relationship shifts to parasitic according to the level of sediment accumulation (Thomas et al. 2013), branchiobdellid density (Brown et al. 2012), and host age (Skelton et al. 2014). This shift in the effect of branchiobdellids on their hosts in turn affects how these

associates interact with other associates (Skelton et al. 2016). These context-dependent interactions add complexity to the relationship of hosts and their associates, with the line between mutualist and parasite a fuzzy one. Therefore, a firm understanding of the communities of all types of associates is important for the sake of understanding the host community.

Drivers of Parasite Diversity

The availability and heterogeneity of resources are often thought to shape communities of free-living organisms, with more diverse and abundant resources providing increased niche availability and decreased extinction probability (Hutchinson 1959, MacArthur 1970, Siemann 1998, Tews et al. 2004, Messmer et al. 2011, Wang et al. 2015). These theories are frequently referenced in parasite community ecology as well (Hechinger and Lafferty 2005, Anderson and Sukhdeo 2013, Johnson et al. 2016), a field that is well developed in comparison to the community ecology of other host-associated organisms (Poulin and Morand 1999, Holt et al. 2003, Hechinger and Lafferty 2005, Anderson and Sukhdeo 2013, Scordato and Kardish 2014, Johnson et al. 2016). The main distinction is that, for parasites, the major source of resources and habitat is their hosts. This leads to the frequently cited 'host-diversity-begets-parasite-diversity' hypothesis (Hechinger and Lafferty 2005, Dunn et al. 2010, Kamiya et al. 2014, Johnson et al. 2016). Host diversity is one of the more consistent predictors of parasite diversity (Hechinger and Lafferty 2005, Kamiya et al. 2014, Johnson et al. 2016), while host abundance is frequently found to be an important secondary predictor (Hechinger and Lafferty 2005, Fredensborg et al. 2006, Johnson et al. 2016). Increases in host diversity are intuitively linked to increases in parasite diversity since parasites are generally specialized on a few hosts (Poulin 2014), so increases in available host species should increase niche availability. Similarly, increases in host abundance should lead to increases in parasite abundance and diversity due to increased resource availability.

Environment and Associates

For host-associated organisms, the main source of resources is the host, but the quality of the environment of the host should also affect the associates. For one thing, associates may have a free-living stage during which they are found independently of their host and could be affected directly by the quality of the environment. In addition, the quality of the environment affects the health of the host, and this in turn affects the success of associates. However, the impact of

environment on the associate can vary depending on the nature of the associate. For instance, more parasitic symbionts have been shown to be favoured in situations of higher environmental quality, while mutualists, or less aggressive parasites, have the advantage in situations where environmental quality is lower (Hochberg et al. 2000). For example, areas of high host density—which are likely to be in higher-quality environments (Öckinger and Smith 2007)—tend to favour horizontal transmission and therefore more antagonistic (virulent) associates (Hochberg et al. 2000), while in areas with low nutrients, and low-quality environments, mutualists that increase host nutrient-uptake are favoured (Thrall et al. 2007). Despite the potential for direct and indirect impacts of environment quality on the community of associates, effects of the external environment may often be indistinguishable from the direct effect of the host community, which itself is likely to vary with environmental conditions.

Geography is also an important factor in structuring communities of both free-living (Nekola and White 1999) and parasitic organisms (Poulin and Morand 1999, Locke et al. 2012). Physical location in space affects isolation, with increasing distances reducing probabilities of colonization from neighbouring communities (MacArthur and Wilson 1967). Thus close, inter-connected communities should be more similar than those further apart and with reduced likelihood of dispersal. The same should hold true for parasites and anything else that travels host to host, such as pathogens. (For the purpose of this thesis, the term pathogen is used specifically to refer to harmful bacteria, fungi, and viruses, while organisms that extract nutrients at the expense of their hosts are grouped as parasites.) The dispersal of pathogens among hosts is often at least initially dependent on the dispersal of the hosts (White et al. 2000). System-specific transmission modes, such as wind dispersal or intermediate hosts, can result in transmission rates that exceed the dispersal of the primary host (Dwyer 1992). Nonetheless, hosts that are physically distant should generally harbour more distinct parasite communities.

From Parasite Communities to Communities of Associates

While geography, environment quality, host abundance and host diversity have been tested as predictors of parasite communities in many parasite–host systems (Poulin and Morand 1999, Hochberg et al. 2000, Hechinger and Lafferty 2005, Pérez-del-Olmo et al. 2009, Locke et al. 2012, Anderson and Sukhdeo 2013, Kamiya et al. 2014), little is known about how these factors shape communities of other associates. Parasites differ from other associates in several

aspects of their ecology that could result in some differences in how they respond to environmental variables. For instance, parasites generally have higher transmissibility (Hochberg et al. 2000), so the effect of geography could be weaker for parasites than for other associates. Similarly, increased transmissibility can give parasites an advantage in higher-quality environments (Hochberg et al. 2000). Therefore, one could expect opposite trends in the effect of environmental quality for mutualists. Furthermore, parasites are often more specialised than either mutualists or commensals since hosts tend to resist parasite infection, resulting in a coevolutionary arms race that leaves only a few well-adapted and specialized parasites (Ulrich et al. 2011). This means that non-parasites and their hosts may not be as closely linked, and thus host abundance and diversity may not have as strong an effect on a general associate community as on a parasite community. Therefore, geography, environment quality, host abundance and host diversity may or may not be important to all associates.

Mites and their Associations with Bees

Mites are a diphyletic group including families within the superorders Acariformes and Parasitiformes (Arthropoda: Chelicerata: Acari). They have colonized almost every known habitat, both as free-living organisms and in association with hosts ranging from plants to insects and vertebrates (Lindquist et al. 1979). Mites are most frequently parasitic, but there are also fungivorous, saprophagous, and predatory species (Lindquist et al. 1979). In number, biomass, and niche breadth, mites rival the class Insecta; in Canada alone, there are an estimated 10,000 species representing 800 genera and 265 families (Lindquist et al. 1979). Mites also have great economic importance as pests of both plants and animals (Krantz and Lindquist 1979, Sastre et al. 2016), and as vectors of pathogens (Rodrigues and Childers 2013). They also act as predators of pests (Schausberger and Walzer 2001) and as important decomposers (Erdmann et al. 2012). However, the amount of research conducted on mites is not proportional to their diversity or economic impact, and the ecology of many mite guilds has not been studied at all.

In this thesis, I examine the mite community associated with bumble bees (*Bombus* spp.). Mites associated with bees have a broad range of interactions with their hosts (Eickwort 1994). One of the best-studied examples of mite–bee association is the parasitic relationship between the mite *Varroa destructor* Anderson and Trueman and its host, *Apis mellifera* Linnaeus (Akimov et al. 1988, Sammataro et al. 2000, Akimov and Kiryushyn 2010, Le Conte et al. 2010,

Di Prisco et al. 2011, Guzman-Novoa et al. 2012). *Varroa destructor* is thought to be a contributor to colony collapse disorder (Akimov et al. 1988, Le Conte et al. 2010, Di Prisco et al. 2011), a phenomenon wreaking havoc across the managed and wild colonies of *A. mellifera*. The mite's effect is two-fold: as a parasite that devastates the drone population of colonies (Akimov et al. 1988) and as a disease vector for two viruses, the deformed wing virus and the Israeli acute paralysis virus (Williams et al. 2009, Di Prisco et al. 2011). However, the majority of mites associated with bees are not parasitic (Eickwort 1994). Several are known mutualists, such as *Laelaspoides* mites that clean the nests of halictid bees such as *Megalopta genalis* Meade-Waldo and *M. ecuadoria* Friese (Eickwort 1994, Biani et al. 2009); still more are considered to be commensalistic, like the fungivorous *Imparipes apicola* (Banks) on the alkali bee *Nomia melanderi* (Cockerell) (Cross and Bohart 1992, Eickwort 1994).

Bumble bees are important pollinators of wildflowers and crops around the world. However, populations and range sizes of several bumble bee species are declining (Cameron et al. 2011, Kerr et al. 2015). Despite growing conservation concern around bumble bees, little is known about the associates of bumble bees. A large number of these are mites, the effects of which are largely unknown. Few of these mite species are thought to be true parasites; however, several are potentially cleptoparasitic, feeding from the pollen and nectar reserves within the hive (Richards and Richards 1976, Eickwort 1994; see Appendix A). To date, most research on bumble-bee-associated mites has been taxonomic (e.g. Hunter 1966, Karg 1971, Delfinado et al. 1976, Richards 1976), with little emphasis on either physiology or ecology. For this reason, the feeding strategies of many of these mites are inferred only based on genus, and the effects of the mites on their hosts can only be guessed at (Delfinado and Baker 1976b, Eickwort 1994, Okabe 2013). Mite species associated with bees often specialize on individual host genera or even single host species, and rarely have broader host ranges; however, little is known about which (if any) bee species are preferred by different mite taxa and what other forces shape the mite communities of bees.

Mite and Bumble Bee Lifecycles

Most mites associated with bumble bees are specialists on the genus *Bombus* (Klimov et al. 2016), and the life cycles of host and associate appear to be deeply intertwined (Richards and Richards 1976). The following life-cycle information about bumble bees comes from Michener

(2007). Bumble bees are primitively eusocial, meaning they typically live in annual colonies of closely related individuals. Bumble bee colonies consist of three castes: a single breeding female (the queen), with several smaller non-breeding females (workers), and eventually, breeding males. Mated queens start new colonies at the beginning of each year. Their first offspring are workers that forage and care for their queen and siblings. At the end of the season, the colony will produce several new queens and males. These reproductive offspring disperse and breed before the new queens overwinter alone, while the males and the remainder of the old colony die by winter. Most mites associated with bumble bees feed and breed within the nest of their hosts throughout the summer (Eickwort 1994). Depending on the species of mite, they will feed there on pollen, nectar, fungi and other detritus, other microorganisms (such as other mites and nematodes), or the bees themselves (Richards and Richards 1976, Eickwort 1994, Klimov et al. 2016). To disperse, most mites will attach to bees in a non-feeding phoretic stage (Richards and Richards 1976, Houck and Oconnor 1991, Eickwort 1994). Some mites disperse throughout the summer, attaching to workers and transferring to bees from other colonies via flowers; however, at the end of the season, mites must attach to a bee to survive the winter (Richards and Richards 1976, Zamec 2014). Since only new queens overwinter, this means mites either attach to new queens within the nest, or to males with the purpose of transferring to queens during copulation. Mites then remain dormant on the queen bees until spring when new colonies are initiated. Thus, within a single year, bumble bees complete one generation, while their mites might have achieved several generations.

Objectives of this Study

Herein, I examine how the mite community of bumble bees is impacted by the local bee community and by the environment beyond the host bee. I expect that the drivers of mite community characteristics will be similar to those that often shape parasite communities. In particular, I expect host species diversity and abundance, host identity, and spatial factors to influence the bee-associated mite community. However, as these mites are not necessarily reliant on their hosts for their entire life cycles, I also expect that habitat factors outside of the bee could affect the mite community. Habitat quality (i.e., availability of floral resources and potential nesting sites) can influence bee communities (Potts et al. 2003), so I expect at least an indirect impact of habitat quality on the mite community. I investigate the effect of these environmental

factors by examining trends in the mite communities of bumble bees both at the level of individual bees and at the level of bee species. I also use multivariate statistics to compare bee-mite communities among locations differing in site quality and bee community.

Methods

Sampling

Fifteen sites (Figure 1) were chosen as a subset from a broader bee-health study consisting of 28 sites within a 50 km radius in the Ottawa area (PIs Cardinal, S., Javorek, S., and Wonneck, M. of Agriculture and Agri-Food Canada (AAFC)). The original 28 sites were chosen to represent a range of soil types. Within each soil type, 2 sites next to an agricultural field and 2 sites next to a woodland were chosen. This created a habitat gradient both locally within a soil type and across all sites. The 15 sites used in my study were selected from these 28 as the most likely to yield a sufficient sample size of bumble bees (based on sampling conducted in 2014) while also encompassing a range of habitat. Each week from 05 May to 02 October 2015, I sweep-netted at each site for 15 minutes, collecting all bumble bees seen in that period of time. Sweep-netting was done along roadsides within 1 km of the coordinates reported in Appendix B, focusing on areas with high floral density. Surveys were conducted between 08:30 and 17:30 when temperatures were 15°C or higher and it was not raining. The order in which sites were visited was frequently reversed so that sites would be visited at different times of the day. Captured bees were individually transferred into 20 mL vials containing roughly 10 mL of 90% ethanol. This was important to ensure mites were not lost and could be associated with individual bees. The time it took to transfer bees from the net to vials was considered negligible and was included in the 15 min total per site.

Bees were dried and pinned, while the ethanol they were stored in was set aside. Bees were dried either within individual sealed mesh bags in a clothes dryer or pat-dried with a paper towel. The former method restores the specimen to a more natural state to aid in identification, while the latter is quicker. The mesh bag ensured no mites were lost in the process. After pinning, I identified all bumble bees to species under the supervision of Sophie Cardinal of AAFC (using Williams et al. 2014). All specimens are deposited in the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC).

After processing of the bees, the bees themselves, the ethanol from the corresponding vials, and the mesh bags used for drying were examined for mites. Under a dissecting microscope, most mites identified previously can be identified to genus level. Therefore, at least 10% of the individual mites of each genus, from each bee or location on the bee, was slide-mounted in polyvinyl alcohol (PVA) to be identified to species under the supervision of Fred Beaulieu of AAFC (using various sources; see Appendix A). Other mites of the same genus from the same location on an individual bee (e.g. posterior mesosoma) or in alcohol were then assumed to belong to the same species. All slide-mounted mites and those in alcohol are deposited in the CNC. Those mites that could be identified without removal remain on their host specimen. To assess whether the mite community had been adequately sampled, I fit a rarefaction curve of all mite species against the number of bees collected (Figure 2).

Habitat Quality

Sites were chosen across a range of habitat. For each site, different habitat and crop types within a 4 km^2 square quadrat centred on the sampling area were identified remotely by Steve Javorek of AAFC using the 2011 AAFC Annual Crop Inventory land-cover maps at a resolution of 30 m (AAFC 2011). A radius of about 1 km is conventional for bumble bee studies; 1 km is the maximum foraging distance documented for most bumble bee species (Darvill et al. 2004, Knight et al. 2005), and effects of surrounding habitat are not often seen at scales greater than 1 km (Knight et al. 2009, Bartomeus et al. 2014). Each land-cover type was assigned a "quality index" based on floral availability and ranging from 0 to 1, where 1 represents excellent habitat (large quantities of flowers), and 0 no habitat (no flowers; Appendix C). Quality of each habitat type was estimated based on expert opinions from the literature (Kennedy et al. 2013, Zulian et al. 2013; Appendix C). The overall quality of a given site was calculated based on weighting the proportion of each habitat type making up the surroundings by its quality, irrespective of distance from the central point. A second measure of habitat quality in the form of percent woodland within the 4 km^2 quadrat was also used. Site quality is based on floral availability and so should give a measure of resource availability for bumble bees, while percent woodland should give a measure of the type of habitat. Habitat type may better reflect nesting habitat of bumble bees and overall community structure.

Statistics

The mite communities of the 15 sites were analyzed in three successively higher units: diversity measures on (1) individual bees, (2) species of bee, and (3) the entire bumble bee community at the site. The first two units allow for examining how environment and host bee species affect mite assemblages, while the third compares how bees within a site differ from those at other sites in their aggregate mite community.

Analyses at the individual and species levels were done in similar ways, using the same predictor and response variables. They differed only in the unit of measurement. Four response variables were calculated to describe mite communities at the individual and species levels: mite prevalence, abundance, richness, and diversity. For an individual bee, prevalence was the presence or absence of any mites on that bee, regardless of mite species; at the species level, prevalence was defined as the proportion of bees having at least one mite of any species. In both cases, data were fit to a binomial distribution. Mite abundance was the number of any type of mite (regardless of species) found either on each bee or on all bees of a species at a site. Both models fit a negative binomial distribution. Mite richness was represented as either the number of mite species found on a bee or on all bees of a species at a site and were both fit to an over-dispersed Poisson model. Mite diversity was calculated as Simpson's Index (1 – D). For both individual and species levels, these data were fit to a binomial distribution. For mite diversity, bees without any mites were excluded (mite diversity for these bees would have been undefined), leaving a total of 669 bees with at least one mite.

As predictor variables, all individual- and species-level models included habitat quality, percent woodland, bee abundance (of that species at that site), bee diversity (Simpson's Index) of the site, and bee species identity as fixed factors, and site identity as a random factor. Bee diversity represents habitat heterogeneity for the mites. For most models, all 11 *Bombus* species were included as levels. For three analyses, however (mite abundance at the individual level and mite diversity at the individual and species level), models including all 11 species failed to converge. For mite abundance at the individual level and mite diversity at the species level, the three species with the lowest sample size in terms of site representation (*B. terricola* Kirby, *B. perplexus* Cresson, and *B. fervidus* (Fabricius), each present at < 4 sites) were excluded. For mite diversity at the individual level, the five species with the lowest sample size in terms of site

representation (the previous three, as well as *B. bimaculatus* Cresson and *B. citrinus*, each present at < 11 sites) were excluded. Multiple comparisons were also performed to determine which bee species pairs differed significantly. All p-values were (and are presented as) FDR (False-Discovery Rate) corrected (transformation according to Benjamini and Hochberg 1995). Marginal R^2 values (giving the proportion of variance explained by only the fixed factors) and conditional R^2 values (giving the proportion of variance explained by both fixed and random factors) were calculated for models containing only significant ($p<0.05$) or marginally significant ($p<0.1$) terms (before FDR correction) according to Nakagawa and Schielzeth (2012) and Johnson (2014).

Since the sample size of most bees was small within sites, only bee species that had at least 10 individuals at a site were included in site-level analyses. (At the individual and species level, this restriction was not necessary since bee abundance was accounted for by using the number of bees of each species as an independent variable.) The only species to meet this criterion at all 15 sites was *B. impatiens* Cresson, so inter-site differences could only be assessed for all sites when examining *B. impatiens* alone or all bumble bees together, regardless of species. However, *B. rufocinctus* Cresson and *B. vagans* Smith met the $N \geq 10$ criterion at 10 and 7 of the sites, respectively. Therefore, mite communities of these two species were compared among subsets of sites as opposed to among all 15.

In order to visualize similarities between mite communities, one master canonical correlation analysis (CCA) was performed that included every bee species separately at every site at which that species had any mites. Thus, χ^2 distances were calculated between sites for a bee species, but also between bee species at all sites. Since the objects in this type of ordination lack independence, no statistical tests were done on this ordination; however, the visual ordination plot is informative for examining patterns in similarity between bee species and associations with individual mite species. This ordination was constrained by only site quality and percent woodland. To properly analyze mite community composition in relation to a more complete set of environmental factors, I conducted CCAs with forward stepwise ordination (Sokal and Rohlf 1995, Legendre and Legendre 2012). Four separate ordinations were performed, one each for the mite communities of *B. impatiens*, *B. rufocinctus*, and *B. vagans*, and one for all bee species summed. By completing a single ordination for each bee species,

these ordinations did not suffer from lack of independence and so statistical tests could be performed. The factors used for constraint in the stepwise ordinations included habitat quality, percent woodland, and the abundance of each bee species at each site. In addition, the distances among sites were modeled using distance-based Moran's Eigenvector Maps (dbMEM). This method generates several independent eigenvectors that model the distances among sites at different scales; it has replaced the Mantel test in evaluating spatial autocorrelation due to its increased power (Legendre and Fortin 2010). In my dataset, dbMEM generated 11 eigenvectors with positive eigenvalues to be included in the ordination.

For the sake of comparing mite community similarities to those among bee communities, a sixth CCA was conducted with the χ^2 distance between sites of the bee community as a response variable. Again, a forward stepwise ordination was used, using the 11 dbMEM eigenvectors, as well as site quality and percent woodland as potential constraining factors. This also allowed for confirmation of whether these factors, as measured, were meaningful for the bees.

Results

Sampling Results

A total of 1,857 bumble bees were caught, representing 11 species and six subgenera (Table 1; Figure 1), with more than half the species belonging to the subgenus *Pyrobombus* (Table 1). Due to the unevenness among subgenera in species numbers, subgenus identity could not be included as a factor in any analyses. Associated with these bees, I found 10,300 mites in total, representing at least 29 species and 12 families, including acarids, scutacarids, and parasitids (Table 2). Of the 29 species, 15 were identified to a unique species, 5 were identified to the level of genus, 3 to the level of family, and the remaining 6 to order. Based on visual inspection of the rarefaction curve comparing mite species richness to number of bees collected (Figure 2), sufficient bees were sampled to adequately represent the mite community in the study region. However, it should be noted that individual castes of bees, considered independently, did not sufficiently sample the mite community (i.e., rarefaction curves for individual castes do not appear to be approaching asymptotes).

Mite Prevalence

Bee species identity and bee abundance were marginally significant predictors of mite prevalence at the individual level (i.e. all mite species pooled); however, no environmental factors (diversity, site quality, or percent woodland) were significant predictors of mite prevalence (Table 3). Bee abundance had a marginally negative effect on mite prevalence. Despite a lack of a significant effect of bee identity on mite prevalence at either the individual or species levels, a single bee species did differ from the others in mite prevalence based on pairwise comparisons (Table 4; Figures 3 & 4): mite prevalence was significantly lower in *B. rufocinctus* than in *B. vagans* or *B. impatiens* at both the individual and species levels. In addition, *B. vagans* had marginally higher mite prevalence than *B. ternarius* Say at the individual level.

Mite Abundance

Bee abundance was a significant predictor of mite abundance at the bee-species level, although not at the individual level (Table 3)—that is, bee species that were more numerous in my sample hosted more mites in total, but not on a per-bee basis. Bee diversity, site quality, and percent woodland were not significant predictors of mite abundance at either the individual or species level; however, bee species identity was a significant predictor of mite abundance at both the individual and species levels. Mite abundance differed significantly between several bee species pairs (Table 4; Figure 5a). At the species level, *B. citrinus*, *B. perplexus* and *B. terricola* all had significantly higher mite abundance than *B. bimaculatus*, *B. borealis* Kirby, *B. griseocollis* (DeGeer), *B. impatiens*, *B. rufocinctus*, and *B. ternarius*. Of the species included in the individual-level analysis for mite abundance, *B. vagans* had significantly greater mite abundance (per bee) than *B. borealis*, *B. rufocinctus*, and *B. ternarius*. *B. borealis* also had significantly lower mite abundance than *B. citrinus*, *B. griseocollis*, and *B. impatiens*. Mite abundance at the bee species level increased with bee abundance for all bee species, although the rate of increase differed among bee species (Figure 5a).

Mite Richness

Bee diversity, site quality, and percent woodland were not significant predictors of mite richness at the individual or species level. Mite richness increased significantly with bee

abundance at the bee-species level, but not at the individual level (Table 3). There were no differences among bee species in the strength of this relationship at the species level (i.e., slopes in Figure 4b are similar). However, at the individual level, *B. rufocinctus* had significantly lower mite richness than either *B. impatiens* or *B. vagans* (Figure 4a).

Mite Diversity

At both the individual and species levels, no environmental factors (bee abundance, diversity, site quality, or percent woodland) were significant predictors of mite diversity (Table 3). Bee species identity was a significant predictor of mite diversity at the species level but not at the individual level (Table 3). At the species level, only a single bee species differed meaningfully from the others in mite diversity (Table 4; Figure 3): mite diversity was significantly higher in *B. borealis* than in *B. vagans*, and marginally higher than in *B. ternarius* and *B. bimaculatus* at the species level. There were no interspecies differences at the individual level (Figure 4b).

Site-Level Analyses

Based on the stepwise forward regression using canonical correlation analysis (CCA), among-site variation in the mite community (across all bee species) could not be explained by distances among sites, site quality, percent woodland, or local abundance of any bee species. The same result was found in species-specific ordinations of the mite communities of *B. impatiens, B. rufocinctus,* and *B. vagans*. The visual results of the master ordination including all bee species separately and all sites are presented in Figure 6. Based on the CCA with bee community as a response variable, 2 of the 11 eigenvectors modelling distance, as well as percent woodland (but not site quality) were significant predictors of bee community similarity between sites (dbMEM1: F=7.2, p=0.005; dbMEM4: F=58, p=0.005; percent woodland: F=60, p=0.005, R^2=0.64).

Discussion

Mites and their Association with Bumble Bees

This is the first study to be conducted on the mites associated with bumble bees in Southern Ontario. Due to this novelty, associations between certain mite and bee species have

been recorded here for the first time. For instance, the mite genus *Sancassania* has not been previously reported on the bee genus *Bombus*, but it occurred in large numbers in this survey. Previously, *Sancassania* species had been found on a variety of insects, including other bees (Eickwort 1994, Klimov et al. 2016). No well-sampled mite species in my dataset (i.e., represented by more than 5 individuals) was associated with only a single host. That is, these mites were not host-specific within the genus *Bombus*. Approximately half of the mite species or genera found associated with bees in this study have been found only or primarily on bumble bees (i.e. other associations are singular and likely to be due to contamination), and are thought to be restricted to the genus (Klimov et al. 2016). Of the remainder, there is a mix of genera or families that are specialists on bees in general (Apoidea) and genera or families that are generalists on several orders of animals and plants. Some of the mites of which only a few individuals were found are possibly contamination from other insects or plants caught with the bumble bees (e.g. mites of the family Eriophyidae, of which only one individual was caught, are exclusively parasites of plants (Krantz and Walter 2009)).

The effect the mites in this study have on their hosts is largely unknown. For several mite species, such as *Vulgarogamasus pollinerus* El-Banhawy and Nasr, *Cerophagus nearcticus* OConnor, and species of the genus *Proctolaelaps* that are associated with bumble bees, both the diet and effect on their hosts is entirely unknown. Other mites have been better studied, such as mites of the genus *Parasitellus* and *Kuzinia*, the diets of which are known from laboratory studies (Richards and Richards 1976, Zamec 2014); however, their fitness effects on their hosts are uncertain. Both of these genera are known to feed on pollen in the nest; however, whether the quantities consumed are enough to negatively impact their host is unknown. Finally, a few of the mites found in this study are known cleptoparasites (e.g. *Pneumolaelaps* spp. (Klimov et al. 2016)) and commensals (e.g. *Scutacarus acarorum* Goeze complex and *Sancassania* spp. (Klimov et al. 2016)).

Effects of Bee Abundance on Mite Communities

My results suggest that, overall, the major factors shaping attributes of the mite community of bumble bees are bee abundance per site and bee species identity. However, these factors are dependent on the level at which the bee community is examined—in particular, the individual bee or bee species level. Bee abundance was a strong driver of both mite abundance

and mite richness at the bee species level. This is an intuitive correlation, in that increasing the number of bees should increase the number of mites found, as well as the probability of finding more mite species. However, this correlation was not found at the individual level. Thus, increasing the total number of bees does not increase the number of mites or mite species that are carried by an individual bee; rather, the average number of mites and mite species per bee remain constant for a given bee species.

Host abundance or density is frequently examined as a factor likely to affect parasite community attributes. The general expectation is that increased host abundance will increase parasite abundance and diversity at the species level. Indeed, in most epidemiological studies there is some positive effect of host abundance on either parasite or pathogen abundance or diversity (Arneberg et al. 1998, Dobson 2004, Hechinger and Lafferty 2005). In my study this was seen through increases of mite abundance and species richness (although not diversity) with host abundance at the species level. However, it is also generally expected that there will be an increase in the proportion of hosts carrying parasites—that is, parasite prevalence—as host density or abundance increases. My results run contrary to this expectation, at both the species and individual levels: mite prevalence was uncorrelated with bumble-bee abundance. Increasing host abundance and density is typically expected to increase parasite prevalence by increasing the probability of transmission; however, it is possible that host densities did not reach high enough levels in this study for this relationship to be observed. One might expect total *Bombus* abundance to be more important to mites than abundances of individual *Bombus* species, given the apparently generalist nature of most of these mites (i.e., all mite species represented by more than 50 individuals were found on most bee species represented by more than 50 individuals). Nevertheless, when total *Bombus* abundance was included as an explanatory variable in my analyses, it was never a significant predictor of any mite community attribute (results not shown). My study is not alone in finding no association between associate prevalence and host abundance: Stanko et al. (2006) found that flea abundance and prevalence were either negatively correlated or uncorrelated with host abundance, depending on the flea and host species.

Effects of Bee Identity on Mite Communities

For almost every mite community attribute, I found differences in mite communities among bee species. The most striking example of this involves mite abundance. Three of the

rarest bee species in my study (*B. terricola*, *B. perplexus*, and *B. citrinus*) had significantly higher mite loads at the species level (Figure 5a) than most other bee species (Table 1). While three bee species could not be analyzed at the individual level for this metric, the individual-level results were qualitatively similar—that is, *B. terricola*, *B. perplexus*, and *B. citrinus* appeared to have higher mite loads per bee than other bee species. Inevitably, my sample size of rare bees was small, and it is possible that a survey encompassing larger numbers would cause the observed association between rare bee species and mite abundance to disappear. Still, the finding of high mite loads on locally rare bee species corresponds to what has been seen with pathogens of bumble bees. In particular, a study by Cameron et al. (2011) found that bumble bees with declining or unstable populations tended to have higher loads of *Nosema bombi* Fantham and Porter, an obligate gut pathogen of bumble bees. This finding is especially relevant for *B. terricola*, since it is the only bee species in my study listed under the Species at Risk Act of Canada (SARA) due to its decline across much of its range (COSEWIC 2015). *Nosema bombi* is thought to be a potential cause of the decline of some bumble bees, and the high levels of *N. bombi* on declining species are consistent with this hypothesis. Mites could also play a role in bee declines, particularly if normally commensalistic mites reach densities high enough to act as cleptoparasites. When I ran a general linear mixed model that included mite abundance per bee, mite prevalence per bee, and bee identity as predictors of bee abundance, mite prevalence was a significant predictor (bee species with lower mite prevalence being more abundant), although mite abundance was not (marginal R^2=0.701, conditional R^2=0.975; mite prevalence: χ^2=15.6, $p<0.001$; mite abundance: χ^2=3.18, p=0.39). High mite prevalence could therefore be a cause of low bee abundance. Alternatively, bee rarity may be contributing to high mite loads per bee, rather than the converse. Allen et al. (2007) found high mite loads on bumble bees (*B. terrestris*) in Tasmania, and suggested that the low genetic diversity in this bee population might be responsible. Rare species generally have low genetic diversity due to genetic drift (Reed and Frankham 2003, Darvill et al. 2006). This low genetic diversity can result in reduced resistance to pathogens and parasites (Ellstrand and Elam 1993, Spielman et al. 2004, Hawley et al. 2005). However, it is not possible to determine the direction of causation from the data presented here.

The biology of *B. citrinus*, one of the three rare bee species with many mites, suggests another possible mechanism for high mite loads. *B. citrinus* is a social parasite (Fisher 1983)—the only one in my study. Socially parasitic bumble bees (subgenus *Psithyrus*) are naturally rarer

than their hosts (other bumble bees), so low sample numbers do not necessarily indicate a declining population, as they do with *B. terricola* (COSEWIC 2015). Social parasites like *B. citrinus* act by displacing the queens of existing bumble bee nests (Fisher 1983). The invading queen then lays her own eggs within the nest and uses the existing workers as her own. This means that the mite load of social parasites could be more representative of whatever host they supplanted. All of the mites found on *B. citrinus* were also found on two of its host species, *B. impatiens* and *B. vagans* (although not on *B. bimaculatus*, its third host) (Fisher 1983, Williams et al. 2014), so this idea cannot be discounted; however, the sample size of *B. citrinus* was not great enough (N=5) for the comparison to be robust. Alternatively, since social parasites tend to visit multiple nests repeatedly before finally parasitizing one, they can act as important dispersal agents for mites (Richards and Richards 1976). Therefore, these bees could be particularly attractive to mites, perhaps explaining their high mite loads in my study. In contrast, other studies have found that *Psithyrus* bees frequently have few or no mites (Hunter and Husband 1973, Schwarz et al. 1996, Otterstatter and Whidden 2004, Kissinger et al. 2011). However, the sample size of *Psithyrus* is almost always too low to properly compare it to other species. It would be interesting to test if socially parasitic bee-mite communities match those of their hosts, and whether they have consistently higher mite loads than non-parasitic species, in a system with more numerous *Psithyrus* species and individuals.

Aside from population decline and social parasitism, another reason for rarity in bee species is simply proximity to a range limit. At the poleward range limit, it is hypothesized that abiotic factors—such as temperature—limit range expansion, while at the equatorward limit biotic interactions—such as competition and parasites—limit the ranges of species (MacArthur 1972). It is possible that the interaction with mites could be one of these biotic limiting factors, particularly for rare bee species with high mite loads. However, of the rare bee species in my study, two are near their northern range limits—as are most of the bumble bee species in this study—while *B. terricola* is actually near the centre of its range (Williams et al. 2014). It is possible that interactions with mites are contributing to limiting range expansion for these species, although this would be inconsistent with the usual expectation that abiotic factors are the main force limiting poleward range expansion.

My results imply that differences among bee-mite communities are not primarily due to external factors, but rather to the intrinsic characteristics of the bees themselves. Different aspects of the mite community vary among bee species. For instance, *B. borealis* tended to have low mite abundance, but high mite diversity at the species level and no particular difference from other species in mite richness or prevalence. Similarly, *B. rufocinctus* tended to have lower mite species richness and prevalence than other bee species at both the individual and species level, but no particular difference in diversity at either level. This discrepancy can be explained by higher mite species evenness both within and across bees for *B. rufocinctus* and across bees for *B. borealis*.

Bee life-history traits or nesting habit may explain differences in mite community attributes between bee species. Among bumble bees, there is little variation in life-history traits, but there are a few differences that could be relevant to mites (Colla 2016). One trait that seems likely to be relevant to mite communities in the Ottawa area is the emergence time of bumble bees; an earlier emergence could be advantageous for mites since it would allow a longer breeding season. While I do not have a direct measure of bumble bee emergence times in the Ottawa area, *B. rufocinctus* is generally the latest to emerge among the bumble bees found in my study (Colla 2016). Interestingly, *B. rufocinctus* also tended to have lower mite richness and prevalence. Other factors could also be important in determining differences in mite communities between bumble bee species, although I had no direct evidence supporting them for this study. For instance, while most bumble bees will nest both below ground in soil and above ground in wood, species differ in their nesting-substrate preferences (Colla 2016). This could alter which hosts are preferred by mites if they, in turn, prefer a certain habitat. In particular, mites of the genus *Scutacarus* have been known to move through soil to disperse (Eickwort 1994) and therefore might be expected to occur predominantly in association with soil-nesting bees. In addition, bumble bees vary in size (Williams et al. 2014), which might impact the number of mites that can be carried as well as dispersal distances. Size is also correlated with other physiological attributes that may be important to mites, such as host body temperature (Stone and Willmer 1989). However, the variability in nesting preference and size among the bumble bee species found here does not appear to predict variation in mite community attributes. Bee species such as *B. rufocinctus* and *B. borealis* that had somewhat distinctive mite communities are not particularly small or large, nor do they prefer one nesting habitat to another

(Colla 2016). All else being equal, the later emergence time of *B. rufocinctus* could make it a less desirable host for mites. A future study could quantitatively investigate the relationship between bee phenology and mite loads.

Despite some differences in mite community aspects for some outstanding bee species, most bumble bees tended to have fairly homogeneous mite communities. Almost all bee species tended to host the same dominant mite species (in particular *Kuzinia* sp., *Sancassania* spp., and to a lesser extent *Scutacarus acarorum* complex and *Histiostoma* spp.; see Appendix D for the full distribution), although certain mite species tended to be more closely associated with individual bee species. For instance, *Kuzinia* sp. is almost always the numerically dominant mite species, with *Sancassania* spp. second or third most abundant. However, on *B. rufocinctus*, *Sancassania* spp. is most abundant, with *Kuzinia* sp. second most abundant. Despite these few differences in mite community, my results suggest that mite communities of different bee species are largely independent of one another. For my site-level analysis, I constructed ordinations that constrained the difference among mite communities by the abundance of each bee species. Based on this ordination, despite differences in the mite community attributes among certain bee species, no one bee species significantly changes the mite community of other bee species; that is, the abundances of different bee species were never significant predictors of mite community similarity. The mite community is primarily determined by the host bee species and no other factor that I could detect.

Influences of Other Factors on Mite Communities

Host Diversity

Host diversity, like host abundance, is frequently a predictor of parasite diversity at the species level, as outlined in the host-diversity-begets-parasite-diversity hypothesis (Hechinger and Lafferty 2005, Johnson et al. 2016). However, I found no effect of host diversity on mite diversity or richness, nor was there an impact of host diversity on mite abundance or prevalence. Other researchers have also found no effect of host diversity on associate communities. As Anderson and Sukhdeo (2013) suggested with their work on the parasites of marsh killifish (*Fundulus heteroclitus* (Linnaeus)), a lack of effect of host diversity could be attributed to the coarseness of the independent variable—in the case of my study, Simpson's Index of local bee communities. An increased sampling effort at a different spatial or temporal scale might better

reflect habitat heterogeneity (i.e., host diversity) as experienced by mites. Alternatively, the lack of an effect of bee diversity could be explained by the generalist nature of most of the mites I collected (Appendix D). The diversity of bee species may be less important than total *Bombus* host abundance for generalist mites—although I did not detect an effect of total *Bombus* abundance on mite diversity, either. For some mite species, the abundance of other bees or insects might also be important.

Habitat

Site quality and percent woodland were not significant predictors of mite community attributes at any level of analysis. For each of my analyses, I also tested whether site quality and percent woodland alone (independent of bee community characteristics) were predictors of mite community attributes. However, this did not change my results, suggesting that there were neither direct nor indirect effects of percent woodland or site quality (as measured here) on bee-mite communities. Theoretically, it is possible that site quality could impact the mite community directly; high floral density could facilitate mite transfer between bees via flowers (Schwarz and Huck 1997) if increases in floral availability attract a disproportionately high number of bees to the area. Site quality could also indirectly affect the mite community by impacting the bee community and thus, potentially, the mite community. However, my data do not support this idea. Site quality may not be as important to mites as are the bees themselves. Furthermore, since the overall bee community in terms of species abundance and diversity do not detectably affect the mite community, it seems likely that any effect of site quality or percent woodland on bee community structure would likewise be irrelevant to the mites.

It is possible that habitat measures were not found to have an indirect effect on mite communities because the measures used were not relevant to the bees themselves. While I did find that percent woodland was a significant predictor of bee community composition, neither site quality nor percent woodland were significant predictors of bee abundance or diversity, nor was site quality a predictor of bee community similarity between sites. Therefore, my measure of site quality is likely not measuring anything of importance to either the bees or the mites, or was not measuring it on the right scale. Since site quality has previously been shown to be an important determinant of bee abundance and diversity (Hatfield and LeBuhn 2007, Rundlöf et al. 2008), a different metric, or scale, of site quality might have been a better explanatory variable.

Neither percent woodland nor site quality as I measured it were able to capture the overall quality of a site (since neither correlated with bee abundance or diversity). However, percent woodland at the 4 km^2 scale appears to have captured aspects of habitat composition that are relevant for bees, perhaps including availability of certain types of nesting sites. In particular, *B. borealis*, *B. griseocollis*, *B. ternarius*, and *B. terricola* tended to be more associated with woodland habitats than other *Bombus* species. The problem with site quality may be with the expert opinions referenced by Zulian et al. (2013) and Kennedy et al. (2013). These expert opinions of floral availability were based on insect pollinators and flowers across the world, so they may not be accurate for bumble bees in the Ottawa region. A more direct measure of floral availability could act as a better predictor of both bee and mite communities. This is particularly relevant as there was little variation among sites in the metric I used (Appendix B). The lack of variation may also be due to measuring floral availability at too broad a scale; a smaller scale would result in more heterogeneity within the metric, and perhaps a better predictive power. Much of the mites' lifecycle takes place inside the nest of their hosts, so nesting habitat quality might be a better predictor of mite community attributes; unfortunately, data on bee nesting habitat were not available for my study area, nor could they be reliably inferred from the land-cover types on which I did have data. Finally, Ewers et al. (2013) found that, while bumble bee abundance decreased towards the interior of forests, mite loads increased. Therefore, forest edges might be a better predictor of mite communities than percent woodland. These variables were not readily available for my sites, and so could not be incorporated into my analyses.

For the site-level analyses, percent woodland was not a significant predictor of mite community similarities; however, in the visual 'master' ordination (Figure 6), the mite communities are well spread across the second component of the CCA, which is comprised of both percent woodland and site quality. This implies that habitat does play a role in shaping the similarities between mite communities. For percent woodland, this may be explained by its effect on bee community similarities (Figure 7); however, this is not true for site quality.

Geography

Using an ordination, I found no significant predictors of differences in mite community composition among sites. The lack of effect of geographic distance is contrary to what is normally found with parasites and pathogens. The most likely explanation for this lack of trend is

uniformity of the geographical distribution of mites over the relatively small scale of my study. Similarly, Allen et al. (2007) found the mite *Kuzinia laevis* to be extremely abundant and widespread in Tasmania, infecting every colony of bumble bees investigated. They did not find an effect of geography on mite abundance, likely because *K. laevis* is simply everywhere in Tasmania. At the level of about 50 km, the scale of my study, distance between sites may not influence mite assemblage similarity; but perhaps at a much larger scale, an effect would be seen. A study by Vignon and Sasal (2010) of parasite communities of coral reef fishes found that at a local scale, geographical effects were indistinguishable from those of other environmental variables, while at scales of 1500 km or more, geography was the most important factor. To distinguish the relevant spatial grain for bee-mite communities, larger-scale surveys may be required.

Regardless, within the Ottawa area, bumble-bee-associated mite assemblages have a relatively uniform distribution, with no clear differences in mite community between sites. This suggests a large dispersal distance for mites in the Ottawa area. However, the bee community is not uniform across the Ottawa area. Based on the CCA with bee community similarity as a response factor, two eigenvectors associated with my dbMEM were significant predictors of the similarity of the bee community between sites. This means that the bee community is not uniform, and that closer sites do have more similar bee communities, but not mite communities. This implies that mites have a greater dispersal distance than their hosts. On the face of it, mites exceeding the dispersal of bumble bees seems unlikely since the dispersal of bee-associated mites is almost wholly a function of the dispersal of their hosts. While some bee-associated mites move through the soil as a form of dispersal, almost all transfer from bee to bee, whether directly during bee copulation, or indirectly via flowers (Eickwort 1994, Schwarz and Huck 1997). However, mites also have multiple generations within a single year, and for some species, each generation has a dispersal phase (Richards and Richards 1976, Eickwort 1994). While little is known about actual dispersal distances for mites, multiple dispersals within a single year could easily exceed the dispersal distance of bumble bees, and thus show a much more uniform community than what is seen with their hosts. Effective dispersal by mites associated with bumble bees could have serious consequences for bumble bee populations if a mite were to become a severe threat to its hosts as either a parasite or a disease vector (as with *Apis mellifera* and *Varroa destructor*).

It is nevertheless possible that an existing spatial structure in these bumble bee mite communities went undetected. A pattern in the spatial structure could be hidden by other patterns in the bee community. In particular, mites have different affinities for different bee castes. Proportions of males, workers and queens varied among bee species and sites in my dataset. However, when analyzing my data, I pooled queens, workers, and males since sample sizes were not sufficiently large for any one caste; the entire mite community could only be represented using all castes pooled together. Figure 2 shows that, despite much lower sample sizes, queens had comparable numbers of mite species to workers, and more than males. In general, queens had higher mite loads than either workers or males, and males had higher mite loads than workers—a finding supported by studies that have found mites to prefer queens and males over workers (Richards and Richards 1976, Klimov et al. 2016). With a disparity in proportion of castes sampled across sites, spatial pattern in mite communities could be hidden. For example, if two sites have similar mite communities, but in one I collected predominantly queens and the other predominantly workers, any species-level similarity could be hidden. This type of shrouding of the geographic effect on associate communities was also seen by Locke et al. (2012) with their work on the parasites of ring-billed gulls: in ring-billed gulls, younger gulls tended to have higher parasite abundances, so the effect of distance between sites on parasite abundance was not observed until age was taken into account. The same could be true for bee castes.

Conclusion

In conclusion, the primary factor affecting the mite community of bumble bees is the bees themselves. While the environment has been shown to have an impact on bee communities (Hatfield and LeBuhn 2007, Rundlöf et al. 2008) and thus likely an indirect effect on bee-associated mites, an effect of the external environment was not detectable here. The mite community of bumble bees does not appear to be shaped by the same factors as most parasite communities, in particular host diversity and geographic proximity. The majority of the mites collected in this study are thought to be commensals; however, it would be interesting to see if mites that are primarily parasitic follow distribution patterns more similarly to those of other parasites, with increases in prevalence, abundance, richness and diversity with host abundance and diversity, and site proximity predicting similarities in mite community composition. This

might be expected since parasitic mites may be more specialized than commensal mites to individual host species or even local populations. Host identity is the most important factor in determining several aspects of the mite community associated with bumble bees, with the high abundance of mites on rare bee species as well as socially parasitic bees being of particular interest for future work.

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Tables and Figures

Table 1. Total number of bees, mites, and mite species, as well as the number and standard error per bee and standard error of the number of mites per individual bee for each *Bombus* species.

Subgenus	Species	No. of Bees	Total Mites	Mite Species	No. Mites per Bee	Standard Error
Pyrobombus	*impatiens* Cresson	1090	6238	29	5.73	0.75
	vagans Smith	201	1753	18	8.72	1.96
	ternarius Say	106	280	13	2.64	0.80
	bimaculatus Cresson	29	74	9	2.55	1.72
	perplexus Cresson	5	283	1	56.6	56.60
	rufocinctus Cresson	232	697	18	3.00	0.88
Cullumanobombus	*griseocollis* (DeGeer)	99	426	16	4.30	1.42
Subterraneobombus	*borealis* Kirby	76	86	12	1.13	0.33
Bombus	*terricola* Kirby	9	227	1	25.2	16.92
Psithyrus	*citrinus* (Smith)	8	350	3	43.8	25.48
Thoracobombus	*fervidus* (Fabricius)	2	9	1	4.50	4.50
Total		1857	10423	34	5.61	0.55

Table 2. Total number of individuals for each mite species, as well as the number of individual bees and number of *Bombus* species on which each mite species occurred.

Family	Species	No. of Mites	No. of Bees	No. of Bee Species
Parasitidae	*Parasitellus perthecatus* (Richards)	135	113	7
	P. talparum (Oudemans)	96	76	7
	Vulgarogamasus pollinerus El-Banhawy and Nasr	35	29	5
Laelapidae	*Pneumolaelaps longanalis* Hunter and Husband	49	29	4
	Pn. costai Hunter and Husband	5	5	2
	Pn. connieae Hunter and Husband	18	16	6
Ascidae	*Proctolaelaps longanalis* (Westerboer)	8	7	4
	Pr. longisetosus (Westerboer)	34	25	8
	Pr. bombophilus (Westerboer)	2	2	2
	Pr. ornatus (Westerboer)	10	10	5
Acaridae	*Kuzinia* sp. (Dujardin)	7379	319	10
	Sancassania spp.	1013	114	7
Gaudiellidae	*Cerophagus nearcticus* OConnor	588	112	5
Histiostomatidae	*Histiostoma* spp.	116	46	6
Scutacaridae	*Scutacarus acarorum* complex (Goeze)	728	116	7
	Imparipes spp.	2	2	2
Trochometridiidae	*Trochometridium* spp.	40	6	2
Tarsonemidae	*Tarsonemus* spp.	22	14	4
	Unknown	4	4	3
Tydeidae	Unknown	3	3	1
Eriophyidae	Unknown	1	1	1
Winterschmidtiidae	*Saproglyphus* sp.	1	1	1
Podapolipidae	*Locustacarus buchneri* (Stammer)	1	1	1
Unknown3	Unknown sp.	1	1	1
Unknown4	Unknown sp.	2	2	2
Unknown6	Unknown sp.	3	3	1
Unknown7	Unknown sp.	1	1	1
Unknown9	Unknown sp.	2	2	2
Unknown10	Unknown sp.	1	1	1

Table 3. Chi-squared values from general linear mixed models and associated p-values for mite community variables at the individual bee and bee species levels. Response variables are: total number of mites found on each bee and bee species ("mite abundance"); the presence or absence of mites at the individual level, or the proportion of bees with mites at the species level ("mite prevalence"); the total number of mite species found on each bee and bee species ("mite richness"), and the Simpson's Index of mites on each bee and all bees of a species ("mite diversity"; 1 − D). Model-level marginal R^2 (mR^2) and conditional R^2 (cR^2) are reported. P-values have been FDR corrected.

	Mite Abundance		**Mite Prevalence**		**Mite Richness**		**Mite Diversity**	
	χ^2	**p**	**χ^2**	**p**	**χ^2**	**p**	**χ^2**	**p**
Individual Level	mR^2=0.42		mR^2=0.021		mR^2=0.020		mR^2=0.042	
	cR^2=0.57		cR^2=0.029		cR^2=0.020		cR^2=0.042	
Bee Abundance	0.17	0.91	7.4	0.063†	0.036	0.96	0.67	0.81
Bee Diversity	0.87	0.77	0.0059	0.99	0.87	0.78	0.0092	0.98
Site Quality	0.40	0.85	0.53	0.84	3.0	0.44	2.1	0.59
Percent Woodland	0.14	0.91	3.0	0.45	0.46	0.85	2.8	0.47
Bee Identity	38	<0.001*	24	0.063†	21	0.15	2.7	0.91
Species Level	mR^2=1.0		mR^2=0.046		mR^2=0.72		mR^2=0.58	
	cR^2=1.0		cR^2=0.059		cR^2=0.72		cR^2=0.58	
Bee Abundance	62	<0.001*	4.3	0.23	75.70	<0.001*	1.7	0.63
Bee Diversity	0.94	0.76	1.49	0.67	0.063	0.95	6.4	0.096†
Site Quality	2.0	0.60	0.0	1.0	0.094	0.92	0.43	0.86
Percent Woodland	0.0	1.0	0.80	0.78	0.17	0.91	0.0	1.0
Bee Identity	54	<0.001*	22	0.14	8.9	0.86	24	0.014*

*****Statistically significant ($p<0.05$) †Marginally significant ($p<0.1$)

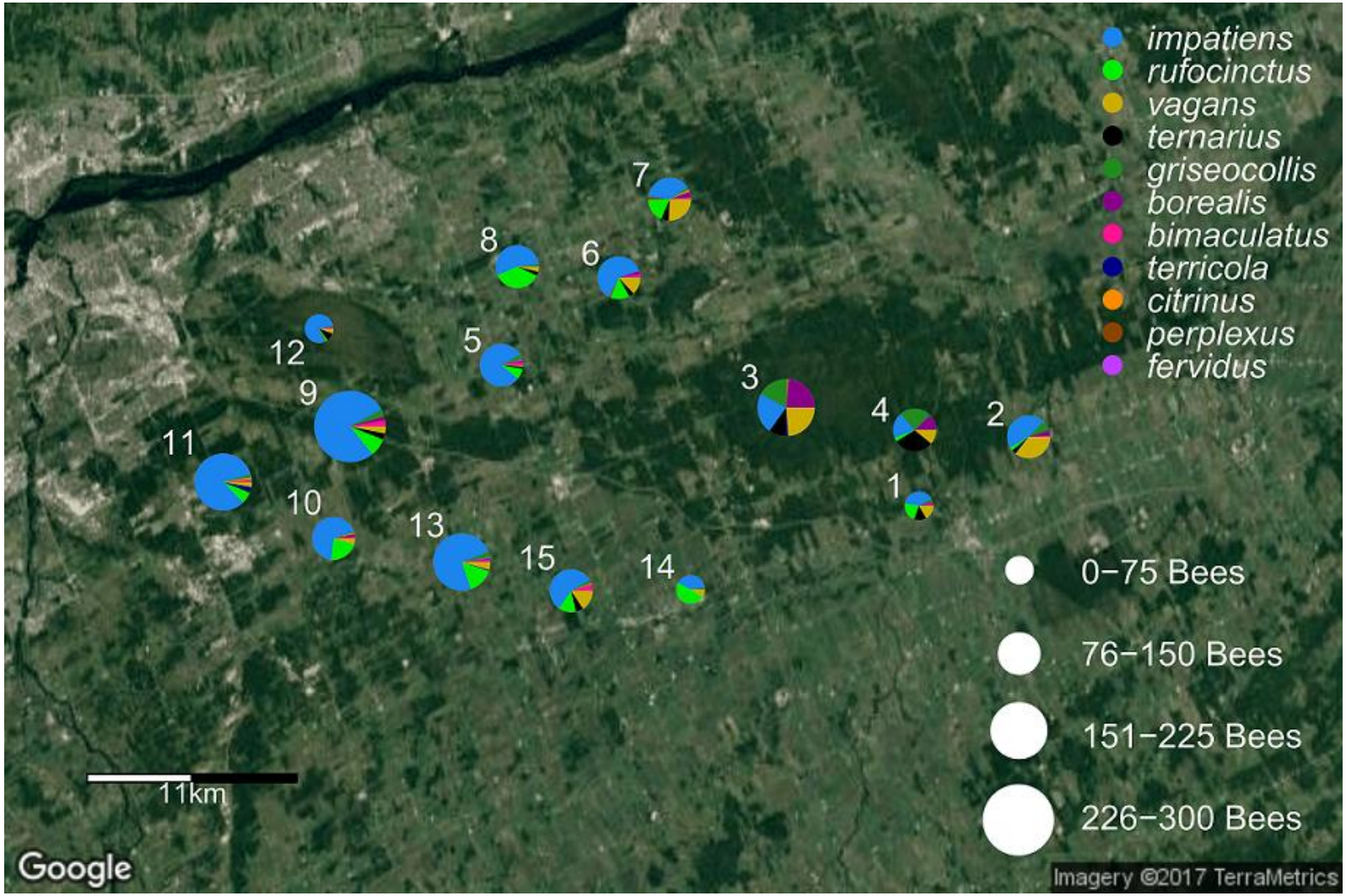
Table 4. FDR-corrected p-values for pairwise comparisons between *Bombus* species for various mite community metrics at the individual and species levels. In cases of significant differences, the species with the greater value is indicated in parentheses by the first few letters of its name.

		Mite Abundance		Mite Prevalence		Mite Richness		Mite Diversity	
Species 1	**Species 2**	**Individual**	**Species**	**Individual**	**Species**	**Individual**	**Species**	**Individual**	**Species**
bimaculatus	*Borealis*	0.62	0.38	0.95	0.95	0.86	0.99	NA	$0.056^{\dagger(bor)}$
bimaculatus	*Citrinus*	0.22	$<0.001^{*(cit)}$	0.76	0.75	0.67	0.85	NA	0.95
bimaculatus	*Fervidus*	NA	0.83	0.99	0.99	0.88	0.89	NA	NA
bimaculatus	*griseocollis*	0.85	0.63	0.99	1.0	0.90	0.91	NA	0.86
bimaculatus	*impatiens*	0.77	0.71	0.84	0.84	0.95	0.95	NA	0.52
bimaculatus	*perplexus*	NA	$0.0092^{*(per)}$	0.78	0.78	0.90	0.69	NA	NA
bimaculatus	*rufocinctus*	0.98	0.65	0.84	0.85	0.70	0.90	NA	0.78
bimaculatus	*ternarius*	0.95	0.87	0.89	0.96	0.69	0.99	NA	0.99
bimaculatus	*terricola*	NA	$0.031^{*(terr)}$	0.89	0.89	0.82	0.67	NA	NA
bimaculatus	*Vagans*	0.47	0.82	0.69	0.70	0.89	0.84	NA	0.95
borealis	*Citrinus*	$0.021^{*(cit)}$	$<0.001^{*(cit)}$	0.79	0.79	0.56	0.86	NA	0.48
borealis	*Fervidus*	NA	0.38	1.0	1.0	0.95	0.88	NA	NA
borealis	*griseocollis*	$0.037^{*(gri)}$	0.89	0.91	0.91	0.95	0.90	0.85	0.21
borealis	*impatiens*	$0.0030^{*(imp)}$	0.92	0.85	0.84	0.58	0.96	0.85	0.48
borealis	*perplexus*	NA	$<0.001^{*(per)}$	0.73	0.73	0.86	0.68	NA	NA
borealis	*rufocinctus*	0.26	0.89	0.58	0.56	0.84	0.85	1.0	0.21
borealis	*ternarius*	0.46	0.63	0.71	0.85	0.97	0.98	0.91	$0.073^{\dagger(bor)}$
borealis	*terricola*	NA	$<0.001^{*(terr)}$	0.85	0.85	0.99	0.66	NA	NA
borealis	*vagans*	$<0.001^{*(vag)}$	$0.064^{\dagger(vag)}$	0.64	0.67	0.46	0.82	0.90	$0.047^{*(bor)}$
citrinus	*fervidus*	NA	0.27	0.90	0.91	0.89	0.84	NA	NA
citrinus	*griseocollis*	0.32	$<0.001^{*(cit)}$	0.73	0.74	0.65	0.91	NA	0.89
citrinus	*impatiens*	0.34	$<0.001^{*(cit)}$	0.86	0.86	0.79	0.89	NA	0.85
citrinus	*perplexus*	NA	0.96	0.61	0.61	0.64	0.62	NA	NA
citrinus	*rufocinctus*	0.12	$<0.001^{*(cit)}$	0.58	0.57	0.47	0.76	NA	0.88
citrinus	*ternarius*	0.11	$<0.001^{*(cit)}$	0.64	0.69	0.55	0.85	NA	0.91
citrinus	*terricola*	NA	0.78	0.68	0.68	0.73	0.58	NA	NA
citrinus	*vagans*	0.61	1.00	0.91	0.90	0.85	0.96	NA	0.91

		Mite Abundance		Mite Prevalence		Mite Richness		Mite Diversity	
Species 1	**Species 2**	**Individual**	**Species**	**Individual**	**Species**	**Individual**	**Species**	**Individual**	**Species**
fervidus	*griseocollis*	NA	0.51	0.98	0.98	1.00	0.86	NA	NA
fervidus	*impatiens*	NA	0.59	0.99	0.98	0.98	0.88	NA	NA
fervidus	*perplexus*	NA	0.46	0.85	0.85	0.90	0.89	NA	NA
fervidus	*rufocinctus*	NA	0.57	0.91	0.91	0.95	0.91	NA	NA
fervidus	*ternarius*	NA	0.69	0.93	0.96	0.96	0.90	NA	NA
fervidus	*terricola*	NA	0.63	0.91	0.91	0.89	0.91	NA	NA
fervidus	*vagans*	NA	0.91	0.95	0.95	0.95	0.85	NA	NA
griseocollis	*impatiens*	0.91	0.9956	0.68	0.69	0.61	0.95	0.97	0.71
griseocollis	*perplexus*	NA	$<0.001^{*(per)}$	0.77	0.78	0.85	0.65	NA	NA
griseocollis	*rufocinctus*	0.64	0.99	0.67	0.66	0.76	0.69	0.82	0.95
griseocollis	*ternarius*	0.63	0.78	0.82	0.91	0.88	0.87	0.91	0.85
griseocollis	*terricola*	NA	$0.0013^{*(terr)}$	0.89	0.88	0.99	0.61	NA	NA
griseocollis	*vagans*	0.48	$0.072^{\dagger(vag)}$	0.41	0.45	0.46	0.91	0.91	0.78
impatiens	*perplexus*	NA	$0.0031^{*(per)}$	0.67	0.66	0.77	0.66	NA	NA
impatiens	*rufocinctus*	$0.064^{\dagger(imp)}$	0.99	$0.010^{*(imp)}$	$0.010^{*(imp)}$	$0.010^{*(imp)}$	0.70	0.65	1.0
impatiens	*ternarius*	0.19	0.81	0.24	0.51	0.22	0.91	0.88	0.88
impatiens	*terricola*	NA	$0.0094^{*(terr)}$	0.76	0.78	0.85	0.63	NA	NA
impatiens	*vagans*	0.23	0.12	0.84	0.84	0.79	0.85	0.79	0.82
perplexus	*rufocinctus*	NA	$<0.001^{*(per)}$	0.85	0.85	0.85	0.73	NA	NA
perplexus	*ternarius*	NA	$0.0029^{*(per)}$	0.84	0.80	0.86	0.70	NA	NA
perplexus	*terricola*	NA	0.88	0.89	0.89	0.89	0.95	NA	NA
perplexus	*vagans*	NA	$0.055^{\dagger(per)}$	0.62	0.63	0.70	0.62	NA	NA
rufocinctus	*ternarius*	0.95	0.79	0.91	0.78	0.85	0.89	0.91	0.77
rufocinctus	*terricola*	NA	$0.0031^{*(terr)}$	0.99	1.0	1.0	0.72	NA	NA
rufocinctus	*vagans*	$0.0030^{*(vag)}$	$0.063^{\dagger(vag)}$	$0.0030^{*(vag)}$	$0.0032^{*(vag)}$	$0.0057^{*(vag)}$	0.40	0.88	0.70
ternarius	*terricola*	NA	$0.0076^{*(terr)}$	0.95	0.91	0.99	0.66	NA	NA
ternarius	*vagans*	$0.013^{*(vag)}$	0.48	$0.063^{\dagger(vag)}$	0.21	0.18	0.73	1.0	0.98
terricola	*vagans*	NA	0.14	0.68	0.69	0.77	0.54	NA	NA

*Statistically significant ($p<0.05$) †Marginally significant ($p<0.1$)

Figure 1. Map of the 15 study sites. Site numbers corresponding to the latitude and longitude found in Appendix A are presented with adjacent pie charts that represent the proportion of each bee species found at each site. Pie size reflects total bee abundance at each site.



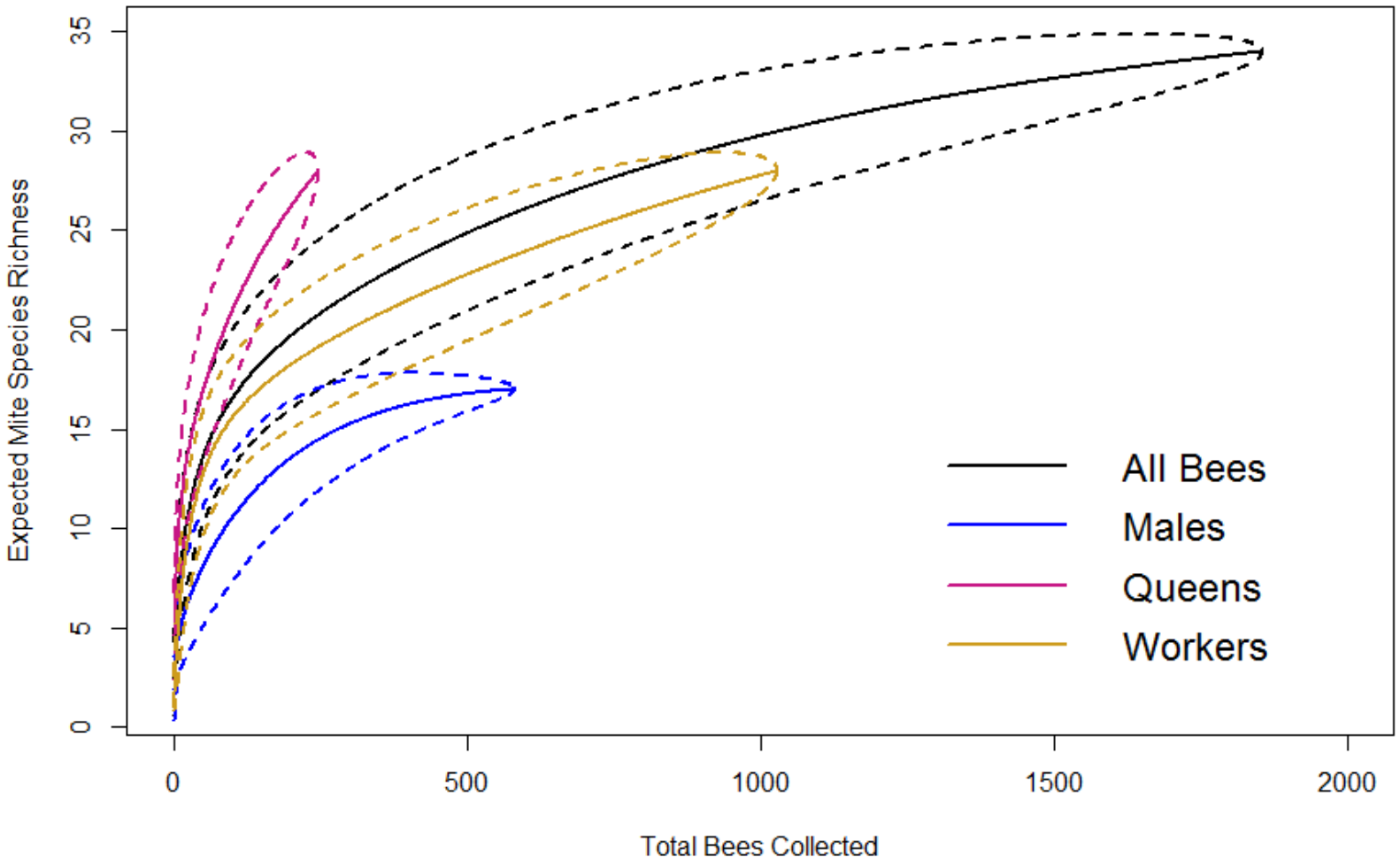


Figure 2. Rarefaction curves of the number of mite species given the number of *Bombus* individuals collected for all bees (N=1856), male (N=580), queen (N=246; including female *B. citrinus*), and worker bees (N=1030). Standard deviation at each point is represented with dotted lines.

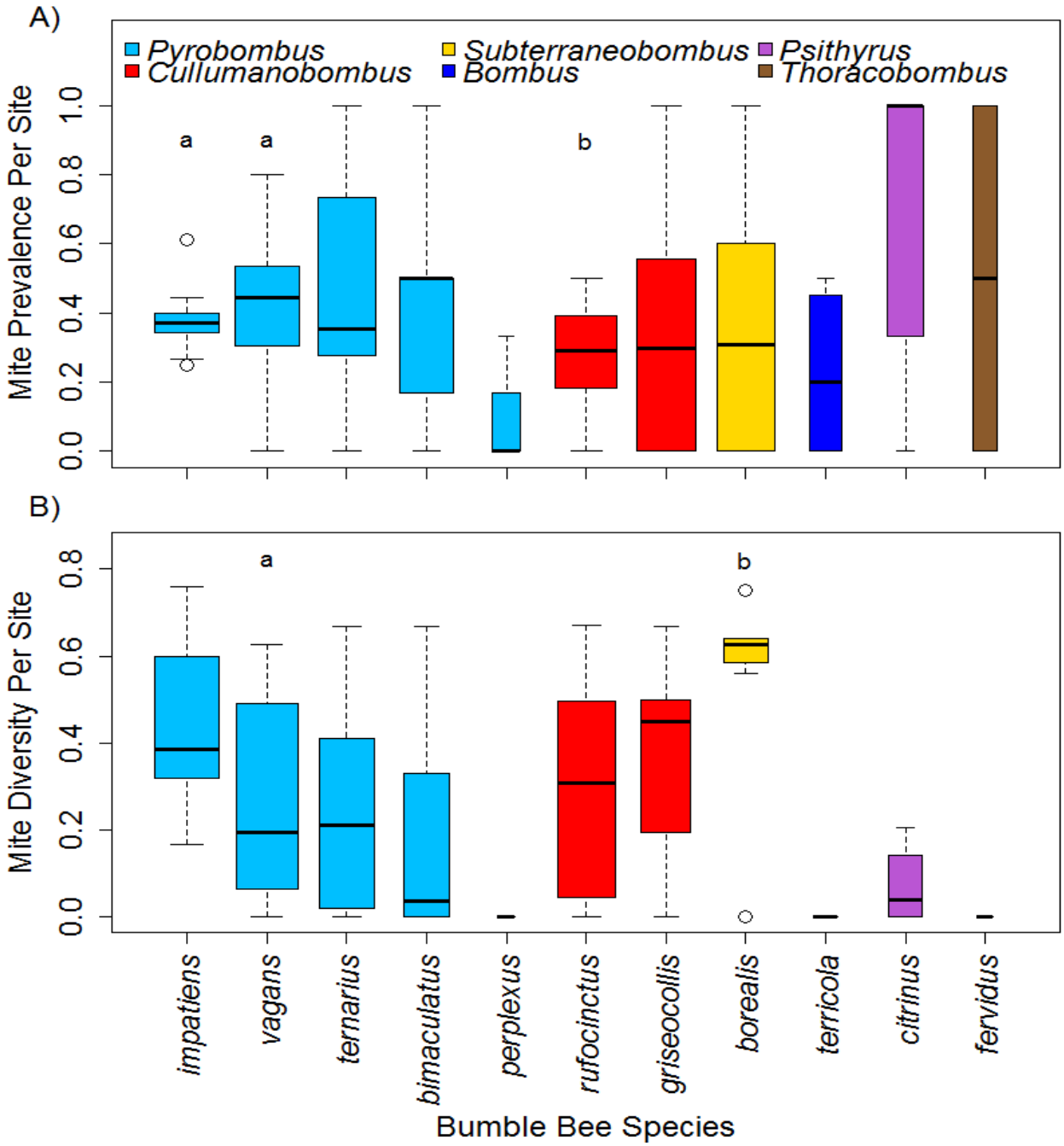


Figure 3. Mite prevalence (A), and Simpson's Index (1−D) (B) at the bee-species level for each of 11 *Bombus* species. Number of sites per species ranges from 2 to 15, with box width proportional to sample size (number of sites), and bee species ordered by subgenus and then from most to least abundant within subgenera. Box ends represent the first and third quartiles, with the midline representing the median. Whiskers extend to 1.5 times the interquartile range from the box or the most extreme point. Bee species with letters that differ are significantly different in a model including bee abundance, bee diversity, site quality, percent woodland, and bee host identity. All species without a letter are not significantly different from any other.

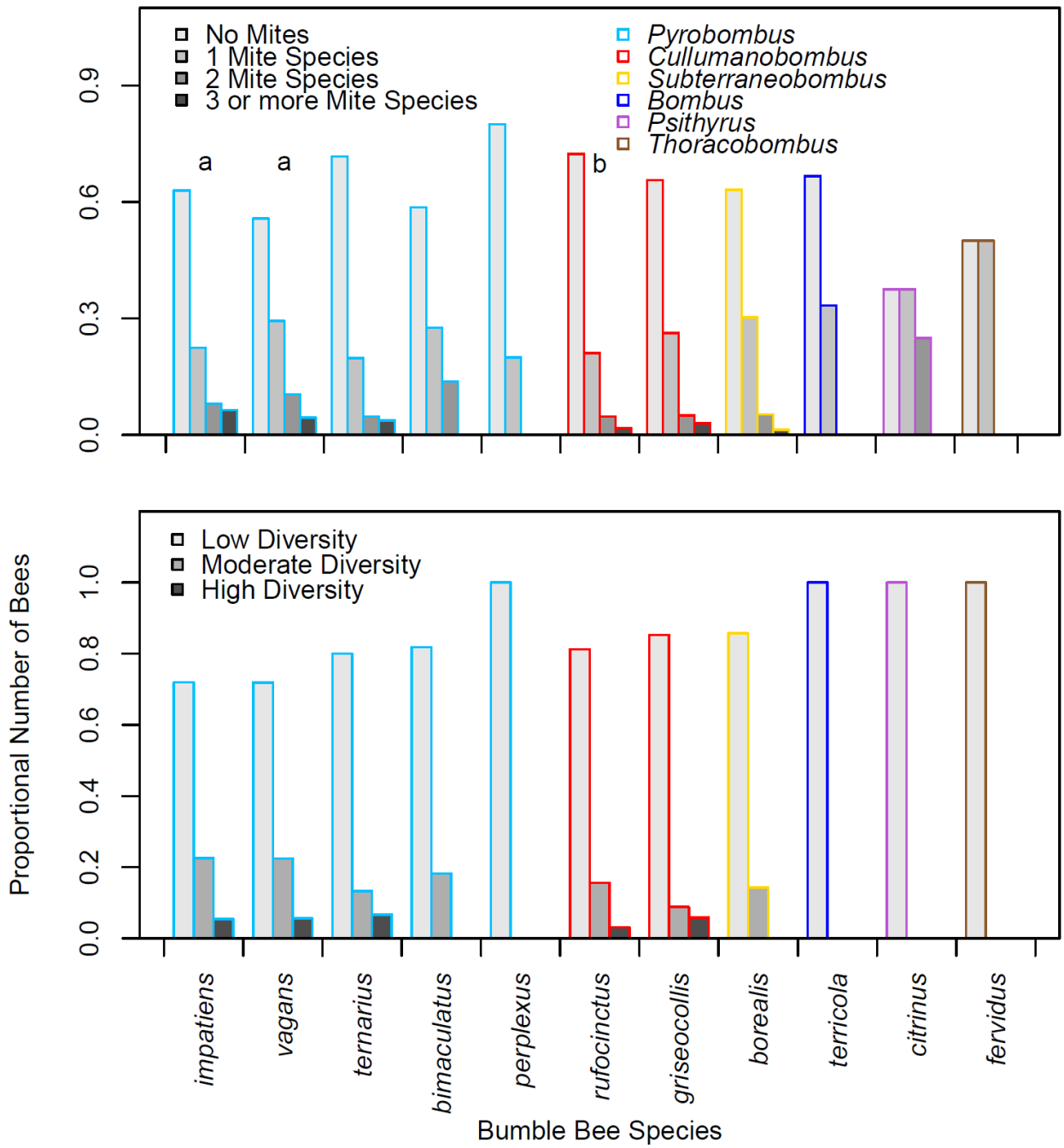


Figure 4. Proportions of individual bees with a given species richness (A) and Simpson's Index (1−D) (B) of mites for 11 *Bombus* species. Bee species are ordered by decreasing sample size within subgenera (N=2–1090). Bars in plot A represent the proportion of bees of a given species that have either 0, 1, 2, or 3 or more mite species on an individual. Diversity in plot B is represented by Simpson's Index. Bars represent the proportion of bees of a given species that have very low diversity (1−D<0.3), moderate diversity (0.3<1−D<0.6), and very high diversity (0.6<1−D<1). Bee species with letters that differ are significantly different at the individual level in a model including bee abundance, bee diversity, site quality, percent woodland, and bee host identity. All species without a letter are not significantly different from any other.

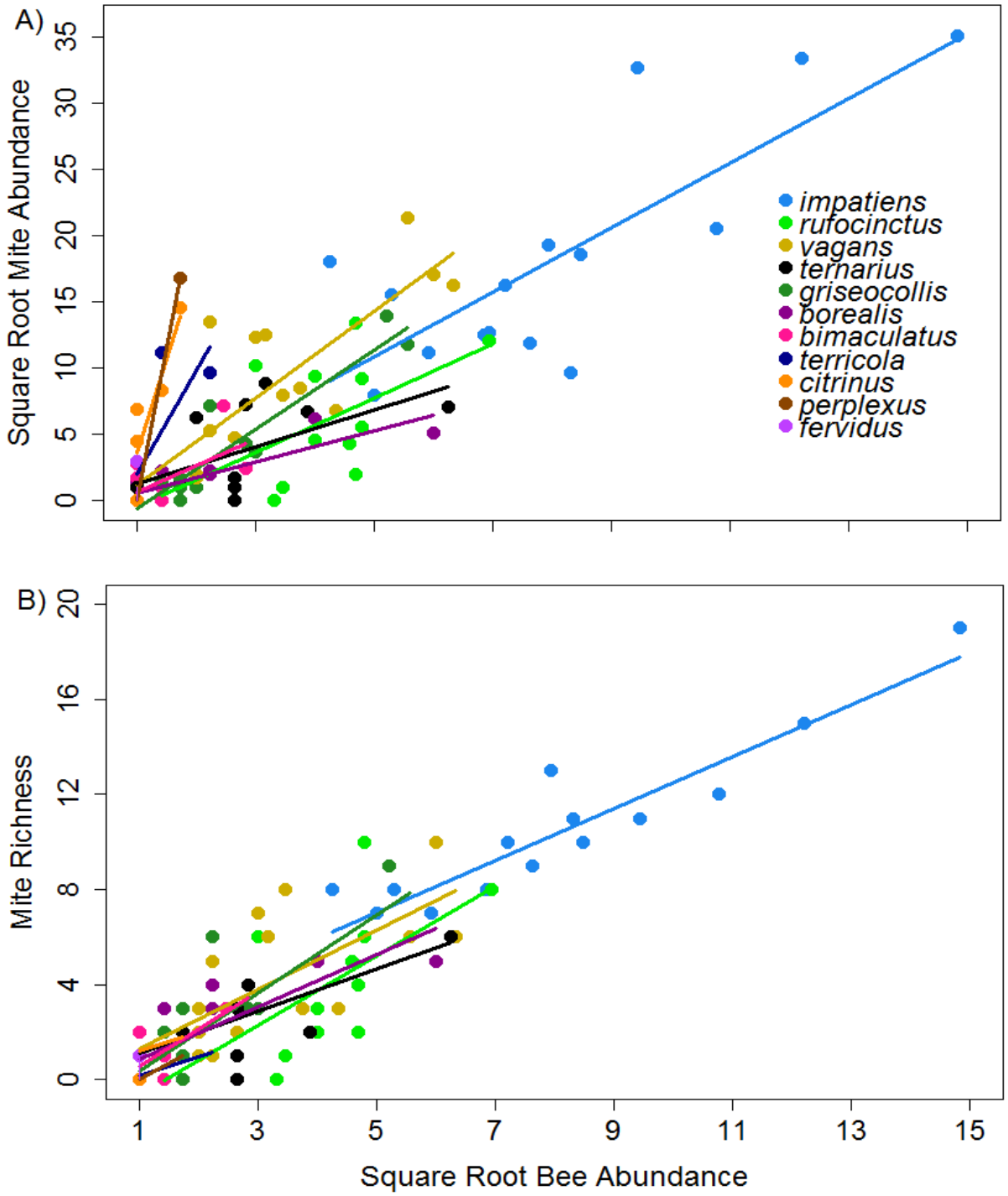


Figure 5. Square-root transformed mite abundance (A) and mite richness (B) at the species level as a function of square root-transformed bee abundance for each of 11 *Bombus* species at a maximum of 15 sites. Lines of best fit are fitted to each set of sites for a given bee species. Species in the legend are ordered from most to least abundant.

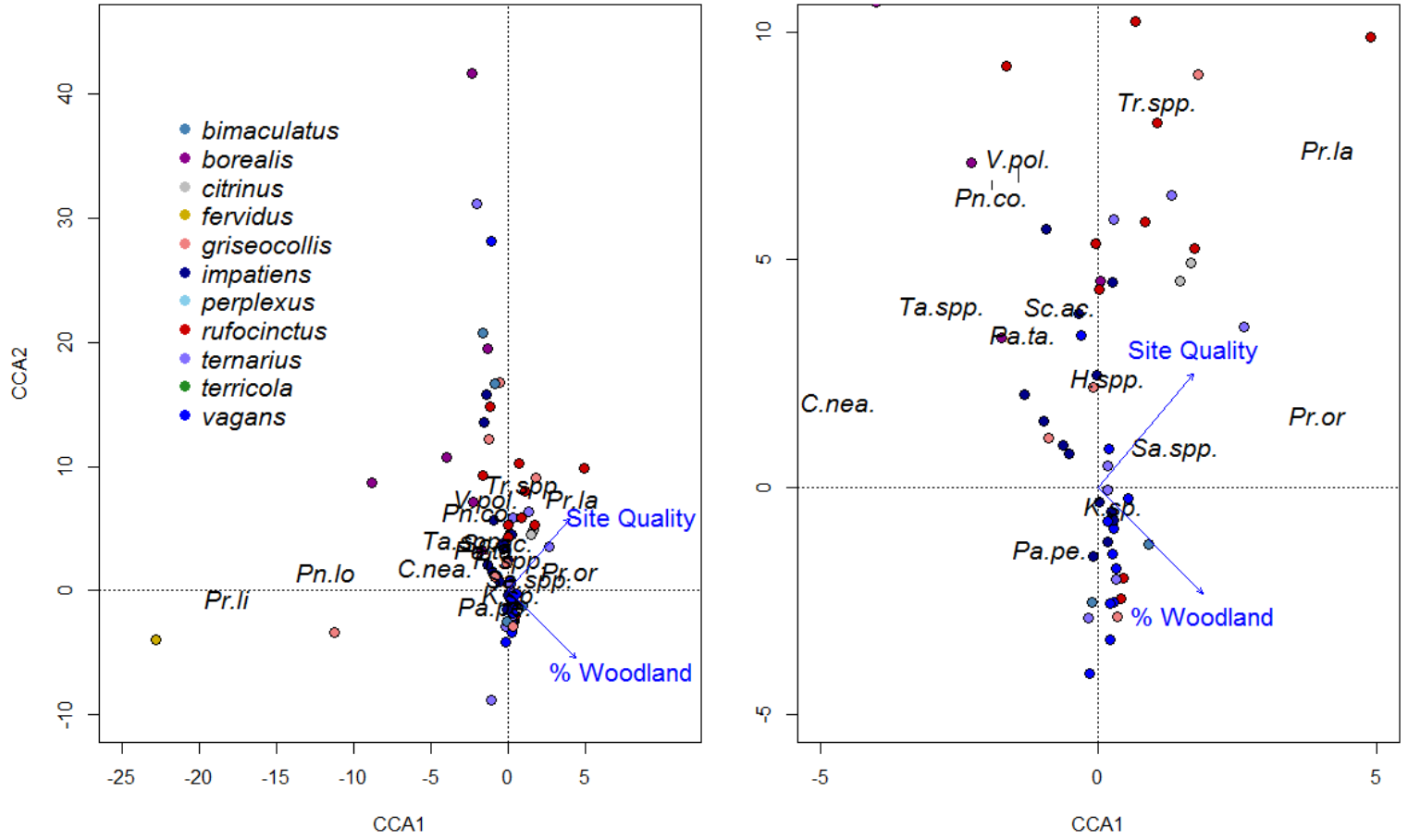


Figure 6. Canonical correspondence analysis (CCA) of the χ^2 distance between the mite community per bee of each bee species at each site. Panel B represents an expanded view of the central cluster of points in Panel A. Distances were constrained by the percent woodland and site quality at each site. While distances were not constrained by bee species identity, points are colour-coded by bee species. Only bee–site pairings that had mites could be included, and only mite species with >5 individuals were included (N=15 mite species used). Mite vectors are presented using abbreviations for species names; see Appendix A for full names. Note these points have been scaled to minimize overlap, so mite species' contributions to principal axes cannot be directly compared to those of the environmental vectors.

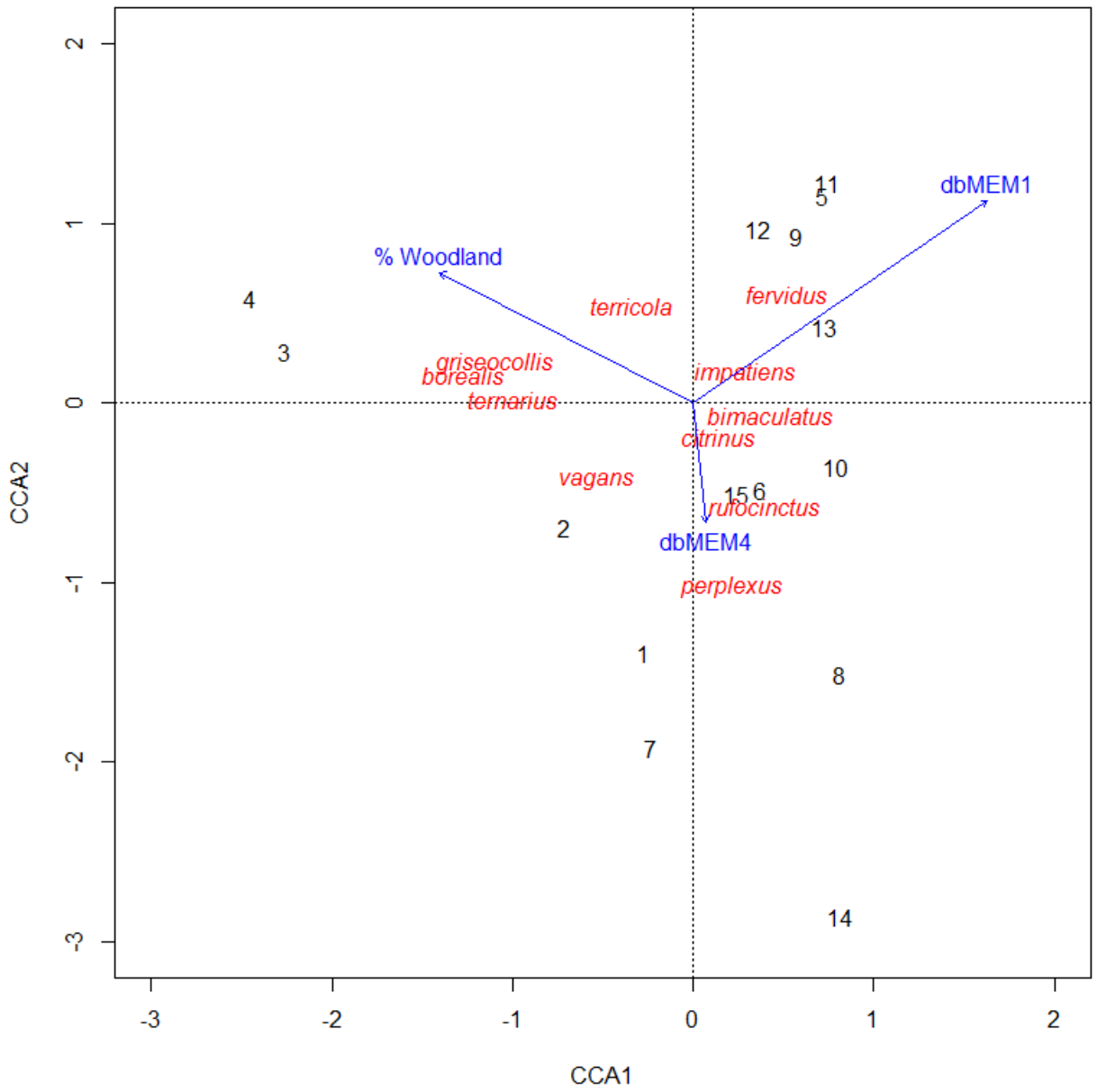


Figure 7. Canonical correspondence analysis (CCA) of the χ^2 distances between the bee communities of different sites. The CCA is constrained by the only three significant predictors of bee community similarity – two distance-based Moran's Eigenvector Maps that model distance between sites at different scales, and the percentage of woodland surrounding each site. Both eigenvectors model distance at a large scale, with dbMEM1 representing a larger scale than dbMEM4. Sites are represented by numbers corresponding to those in Fig. 1 and Appendix B.

Appendix A

Feeding class for each mite species, as well as the host relationship according the reference cited under Biology Source, and the reference(s) used to identify each mite species.

Family	Species	Abbreviation	Feeding Class[2]	Host Relationship	Biology Source	Identification Source[1]
Parasitidae	*Parasitellus perthecatus* (Richards)	*Pa.pe.*	p,c	commensal-cleptoparasite	Richards and Richards 1976, Klimov et al. 2016	Richards 1976, OConnor and Klimov 2016
	P. talparum (Oudemans)	*Pa.ta*	p,c	commensal-cleptoparasite	Richards and Richards 1976, Klimov et al. 2016	Richards 1976, OConnor and Klimov 2016
	Vulgarogamasus pollinerus El-Banhawy and Nasr	*V.pol.*	unknown	unknown		El-Banhawy and Nasr 1984, OConnor and Klimov 2016
Laelapidae	*Pneumolaelaps longanalis* Hunter and Husband	*Pn.lo.*	p,c	cleptoparasite	Hunter and Husband 1973, Klimov et al. 2016	Hunter and Husband 1973, OConnor and Klimov 2016
	Pn. costai Hunter and Husband		p,c	cleptoparasite	Eickwort 1994, Hunter and Husband 1973, Klimov et al. 2016	Hunter 1966, Hunter and Husband 1973, OConnor

						and Klimov 2016
	Pn. connieae Hunter and Husband	*Pn.co.*	p,c	cleptoparasite	Eickwort 1994,Hunter and Husband 1973, Klimov et al. 2016	Hunter and Husband 1973, OConnor and Klimov 2016
Ascidae	*Proctolaelaps longanalis* (Westerboer)	*Pr.la.*	c?	unknown	Krantz and Lindquist 1979, Klimov et al. 2016	Karg 1971, OConnor and Klimov 2016
	Pr. longisetosus (Westerboer)	*Pr.li.*	c?	unknown	Krantz and Lindquist 1979, Klimov et al. 2016	OConnor and Klimov 2016
	Pr. bombophilus (Westerboer)		c?	unknown	Krantz and Lindquist 1979, Klimov et al. 2016	OConnor and Klimov 2016
	Pr. ornatus (Westerboer)	*Pr.or.*	c?	unknown	Krantz and Lindquist 1979, Klimov et al. 2016	OConnor and Klimov 2016
Acaridae	*Kuzinia* sp. (Dujardin)	*K.sp.*	c,s	commensal-cleptoparasite	Zamec 2014, Delfinado and Baker 1976b, Eickwort 1994,	Zamec 2014, Delfinado and Baker 1976b, OConnor and Klimov 2016

					Klimov et al. 2016	
	Sancassania spp.	*Sa.spp.*	c,s	commensal	Eickwort 1994	Klimov 1997, OConnor and Klimov 2016
Gaudiellidae	*Cerophagus nearcticus* OConnor	*C.nea.*	unknown	unknown	Klimov et al. 2016	OConnor 1992, OConnor and Klimov 2016
Histiostomatidae	*Histiostoma* spp.	*H.spp.*	s	mutualist-commensal	Okabe 2013, Eickwort 1994	OConnor and Klimov 2016
Scutacaridae	*Scutacarus acarorum* complex (Goeze)	*Sc.ac*	s	commensal	Eickwort 1994, Delfinado and Baker 1978, Schousboe 1986, Klimov et al. 2016	Delfinado and Baker 1978, Delfinado and Baker 1976a Delfinado et al. 1976, OConnor and Klimov 2016
	Imparipes spp.		s	commensal-parasitic	Eickwort 1994	Delfinado and Baker 1978, OConnor and Klimov 2016, Hajiqanbar et al. 2009
Trochometridiidae	*Trochometridium* spp.	*Tr.spp.*	c	cleptoparasite		OConnor and Klimov 2016

Tarsonemidae	*Tarsonemus* spp.	*Ta.spp.*	s	unknown	Okabe 2013, Eickwort 1994, Klimov et al. 2016	OConnor and Klimov 2016
	Unknown		s?			OConnor and Klimov 2016
Tydeidae	Unknown		s		Eickwort 1994	OConnor and Klimov 2016
Eriophyidae	Unknown					
Winterschmidtiidae	*Saproglyphus* sp.		s	commensal	Klimov et al. 2016	OConnor and Klimov 2016
Podapolipidae	*Locustacarus buchneri* (Stammer)		h	parasite	Klimov et al. 2016	OConnor and Klimov 2016
Unknown3	Unknown					
Unknown4	Unknown					
Unknown6	Unknown					
Unknown7	Unknown					
Unknown9	Unknown					

[1]Identification aided by comparing specimens to identified specimens in the Canadian National Collection of Insects, Arachnids, and Nematodes

[2]p=predator of other associates within the nest, c=provisions, s=fungi and detritus, h=haemolymph

Appendix B

The latitude and longitude of the central point of each site. Site quality is based on floral availability from Appendix C. Overall site quality was calculated for 4 km^2 square quadrats centred on the latitude and longitude given. Floral availability was weighted by percent makeup of each land class type to give an overall site quality.

Site	Latitude	Longitude	Site Quality	Percent Woodland
1	45.33228	-75.13078	0.399	42.8
2	45.36536	-75.06447	0.348	65.1
3	45.38217	-75.22547	0.307	91.8
4	45.36728	-75.13967	0.275	97.6
5	45.39897	-75.40719	0.385	11.1
6	45.43914	-75.32967	0.415	15.1
7	45.47519	-75.29669	0.393	39.9
8	45.44536	-75.39631	0.247	24.8
9	45.37500	-75.51461	0.438	34.7
10	45.32439	-75.51783	0.394	36.1
11	45.35222	-75.59933	0.276	91.6
12	45.39356	-75.52889	0.343	81.5
13	45.31403	-75.43756	0.202	8.50
14	45.29500	-75.28639	0.104	5.50
15	45.29900	-75.36497	0.463	18.0

Appendix C

Floral availability for each of 14 land classes found in the study area. Floral availability is a metric based on expert opinion, ranging from 0.00 to 1.00, with 0.00 representing no floral availability and 1.00 excellent floral availability.

Land Cover Type	Floral Availability	Source
Corn	0.00	Zulian et al. 2013
Barley	0.05	Zulian et al. 2013
Oats	0.05	Zulian et al. 2013
Cereals	0.05	Zulian et al. 2013
Soybeans	0.50	Zulian et al. 2013
Urban and Developed	0.31	Kennedy et al. 2013
Exposed Land and Barren	0.12	Kennedy et al. 2013
Water	0.00	Kennedy et al. 2013
Wetland	0.35	Kennedy et al. 2013
Shrubland	0.69	Kennedy et al. 2013
Pasture and Forages	0.42	Kennedy et al. 2013
Mixedwood Forest	0.25	Kennedy et al. 2013
Coniferous Forest	0.06	Kennedy et al. 2013
Broadleaf Forest	0.53	Kennedy et al. 2013

Appendix D

Total number of mites of each species found on each bee species across all individuals and sites.

Family	Species	*bimaculatus*	*borealis*	*citrinus*	*fervidus*	*griseocollis*	*impatiens*	*perplexus*	*rufocinctus*	*ternarius*	*terricola*	*vagans*
Parasitidae	*P. perthecatus*	4	7	0	0	14	73	0	13	3	0	17
	P. talparum	2	8	0	0	3	64	0	5	4	0	9
	Parasitellus spp.	0	0	0	0	0	2	0	0	2	0	0
	Vulgarogamasus pollinerus	0	1	0	0	1	26	0	1	0	0	6
Laelapidae	*Pneumolaelaps longanalis*	0	0	0	0	6	31	0	7	0	0	1
	Pn. costai	0	0	0	0	0	4	0	0	0	0	1
	Pn. connieae	0	3	0	0	1	8	0	1	2	0	3
	Pneumolaelaps spp.	0	0	0	0	1	1	0	1	0	0	0
Ascidae	*Proctolaelaps longanalis*	0	0	0	0	3	3	0	1	0	0	1
	Pr. longisetosus	1	6	0	9	3	7	0	5	1	0	1
	Pr. bombophilus	0	0	0	0	0	1	0	0	1	0	0
	Pr. ornatus	1	1	0	0	0	3	0	2	1	0	0
	Proctolaelaps spp.	0	1	0	0	0	0	0	0	0	0	0
Acaridae	*Kuzinia* sp.	59	25	241	0	193	3978	283	220	140	219	1595
	Sancassania spp.	0	7	108	0	42	398	0	340	42	0	32
Gaudiellidae	*Cerophagus nearcticus*	0	1	1	0	0	556	0	7	0	0	4
Histiostomatidae	*Histiostoma* spp.	2	11	0	0	0	69	0	2	6	0	25
Scutacaridae	*Scutacarus acarorum* complex	3	1	0	0	126	468	0	48	9	0	23
	Imparipes spp.	1	0	0	0	0	1	0	0	0	0	0

Trochometridiidae	*Trochometridium* spp.	0	0	0	0	0	39	0	1	0	0	0
Tarsonemidae	*Tarsonemus* spp.	0	0	0	0	1	9	0	0	1	0	11
	Unknown	0	0	0	0	1	2	0	0	0	0	1
Tydeidae	Unknown	0	0	0	0	0	3	0	0	0	0	0
Eriophyidae	Unknown	0	0	0	0	1	0	0	0	0	0	0
Winterschmidtiidae	*Saproglyphus* sp.	0	0	0	0	0	1	0	0	0	0	0
Podapolipidae	*Locustacarus buchneri*	1	0	0	0	0	0	0	0	0	0	0
Unknown3	Unknown	0	0	0	0	0	1	0	0	0	0	0
Unknown4	Unknown	0	0	0	0	1	0	0	0	0	0	1
Unknown6	Unknown	0	0	0	0	0	3	0	0	0	0	0
Unknown7	Unknown	0	0	0	0	0	0	0	1	0	0	0
Unknown9	Unknown	0	0	0	0	0	1	0	0	0	0	0
Unknown10	Unknown	0	0	0	0	0	1	0	0	0	0	0