

Do bees show response diversity to environmental variables in a montane ecosystem?

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Abstract

With climate change threatening a wide variety of organisms and ecosystems, expanding our knowledge of how they will respond is vital for making predictions and conservation decisions. One important group of organisms impacted by climate change is the wild bees, which provide an essential ecosystem service through their role as plant pollinators. Therefore, in an effort to understand better how bees are responding to changing weather patterns, we examined how the abundances of different species changed with response to environmental variables. Additionally, we looked at the relationship between response diversity and environmental variables and bee traits. We sampled bees at three groups of sites at the Rocky Mountain Biological Lab in Gothic, CO, using pan traps and netting, and collected environmental data on yearly wind, precipitation, and temperature from nearby weather stations. Using generalized linear models we found that different species exhibited significant responses to different environmental variables. Additionally, most of the species that responded to a variable responded in the same direction. We employed a fourth corner analysis to find a correlation between traits and responses, but it produced no significant results.

Introduction

Anthropogenic climate change is a major issue that impacts organisms all around the world (Parmesan 2006). Climate change is evident in altered precipitation levels, more extreme temperature variation, increasingly frequent tropical storms, and changes in the length of growing seasons (Easterling et al. 2000, Parmesan 2006). Additionally, organisms are responding in unknown ways and to unspecified variables (Schneider & Root 1996). Unfortunately, changes in various aspects of certain wildlife populations may threaten the delicate balance of ecosystems by compromising important ecosystem functions (Easterling et al. 2000).

One such relationship that is threatened by climate change is the interaction between plants and pollinators (Van der Putten et al. 2010). Almost 90% of the world's total plants and 75% of crops are pollinated by animals, meaning that pollinators are very important to both natural ecosystems and agriculture (Winfree 2010). Bees are the main animal pollinators, and although honey bees may be the most well-known, especially for agriculture, wild native bees also play a significant role in pollinating crops (Winfree 2010; Motzke et al; 2016, Danforth 2007). Bees may be impacted by climate change, but we do not know specifically if or how they

will respond. Since bees play such an important role in terrestrial ecosystems worldwide, it is essential to develop a better understanding of how bee populations will shift in the face of ongoing environmental changes.

A potential factor in maintaining certain ecosystem functions is response diversity, in which different species of organisms respond differently to disturbance or environmental changes (Mori et al. 2013). Given that climate change is associated with altered weather patterns, these deviations from the norm could act as disturbances to established ecosystems (Easterling et al. 2000, other citation needed). Different bee species have unique characteristics and life history traits that may cause them to respond to environmental variables in distinctive ways. For example, bee species that nest above ground and in previously established nests are more prone to disturbances than species that nest in the ground or excavate their own nests (Williams et al. 2010). Different bee species also show different responses to overwintering temperatures in terms of weight and phenology (Frund et al. 2013). Additionally, bees that are pollen specialists could be impacted more by climate change than generalist bee species, because they feed on fewer plants and thus have a higher chance of losing vital plant species (Winfree 2010). However, in general there have been few studies examining response diversity of bees to environmental changes. Response diversity may be important to the functioning of ecosystems because if species did not respond differently, a small disturbance could harm many functionally similar species. Therefore, response diversity acts as a buffer against environmental variation and protects ecosystem functions (Mori et al. 2013). Response diversity has been shown to be important in sustaining phenological synchrony between plants and pollinator communities, because different pollinators change phenology at different rates compared to plants, resulting in more stable phenological synchrony (Bartomeus et al. 2013). If climate change does negatively impact bees, it could affect vital plant-pollinator interactions, rendering our understanding of bee response diversity especially important.

With the issue of climate change looming over important ecosystem functions such as plant-pollinator interactions, we examined response diversity in different bee species. Specifically, we were curious as to whether different bee species respond differently to climate change related environmental variables such as temperature, precipitation, and snow melt timing. Additionally, we investigated whether their responses are correlated to certain shared traits,

which would allow us to make predictions about responses by other bee species not included in this study.

Methods

We conducted this study at the Rocky Mountain Biological Laboratory (38°57.5 N, 106°59.3 W), in the Colorado Rocky Mountains, USA. We sampled for bees at nine previously established sites which were divided into three blocks with three sites each (Figures 1 - 4). All sites were within walking distance of the Gothic town site. We approximately followed the procedure outlined in Gezon, 2015. We used pan trapping to collect small native bees and hand netting for bumblebees (*Bombus* spp.). We sampled each block of sites every two weeks throughout the summer from 2009 to 2016. Throughout each summer, we worked in the field about three days each week and the remaining days we spent in the lab pinning, labelling, sorting, and identifying the bee specimens we caught.

On each sampling day, we first set out the pan traps, or “bee bowls” at each site. The bee bowls were bright white, blue, or yellow shallow hexagonal containers filled with soapy water, specifically tap water with a small amount of Dawn Ultra Dishwashing soap, original scent. The fluorescent colors attracted bees and other insects which then flew into the soapy water and got stuck. Fifteen bowls of alternating colors were set up along each previously established transect at each site, resulting in 30 bowls per site. Then we netted at each site for an hour, evenly divided among the samplers. When netting, *Bombus* species were identified with the help of a bee plunger which allowed us to view the bee more easily, marked with a small dab of paint using a paint pen, and released, so as to reduce the impact on the population. We then recorded the species of *Bombus* and the plant species on which it was found. We netted twice a day: once in the morning and again in the afternoon. Following afternoon netting, we picked up the pan traps, collected bee specimens from the bowls, and tossed the bycatch and remaining soapy water. We stored the bees from the pan traps in vials of ethanol labelled with the date, site, and color of the pan traps.

Pinning the bees entailed rinsing them, drying them, and finally pinning them into boxes. For each vial, we transferred the bees to a vial of water and shook it for ten to thirty seconds to rinse the bees. We then placed the bees on a paper towel to dry except for the larger bees, which were placed in a glass jar with a mesh lid and dried with a hair dryer. Usually we rinsed several

vials of bees at a time to give them time to dry. We then made labels for each group of bees from each vial, pinned those into a box with a foam layer on the bottom, and then pinned the corresponding bees in rows following the label. Later, we made more detailed labels for the bees which included information about the habitat and location of the site where the bees were caught along with the information on the original labels on the vials, and pinned those to each bee.

We gathered our data about environmental variables from the National Oceanic and Atmospheric Administration past weather data for Crested Butte and Billy Barr's personal weather data that he has been collecting in Gothic since 1974. Specifically, we got monthly precipitation and temperature data from the NOAA weather station and monthly wind data from Billy Barr. We averaged all of our environmental data for June through July, during which we conducted our sampling. The precipitation data was measured in inches; the temperature data was measured in degree days, which are the difference in degrees from the daily average temperature; the wind data was measured on a scale from zero to four where zero represented no wind and four represented strong wind. We selected these variables based on inferred relevance to bee and flower populations. For example, when sampling, we observed fewer bees on windy days. Additionally, flower abundances, and therefore bee populations, tend to be larger when the amount of precipitation is greater. Although we initially intended to look at snowmelt timing as well, we found that it was collinear with the other variables, and thus decided to remove it from our analysis.

We collected data about bee traits for each species using information from scientific literature or by measuring some of our specimens. The traits we examined included sociality, lecticity (whether the species was a generalist or specialist), nest substrate, whether the species excavated its own nest or simply inhabited a previously made cavity, nest location, and body size. We gathered most of the trait data from Packer et al. 2007, though for the body sizes of all of the *Bombus* species except *Bombus fervidus*, we measured the average intertegular distance of five worker specimens and used the average (Gezon et al. 2015, Cariveau et al. 2016).

For our analysis, we used the abundances of 17 groups of bees: *Bombus bifarius*, *Bombus fervidus*, *Bombus appositus*, *Bombus flavifrons*, *Bombus insularis*, *Halictus rubicundus*, *Halictus virgatellus*, *Sphecodes* sp., *Panurginus ineptus*, *Panurginus cressoniellus*, *Pseudopanurgus bakeri*, *Pseudopanurgus didirupa*, *Dufourea maura*, *Hoplitis fulgida*, *Hoplitis robusta*, *Hylaeus basilis*, and *Hylaeus annulatus*. Since this study was part of a long-term project, we used data

from the past seven years (2009-2015), specifically the abundance of each species per year per site standardized by sampling effort. We chose these particular species because they had the most data, and therefore produced the most accurate results. We analyzed how the abundance within years related to our predictor variables – precipitation, temperature, and wind - using a generalized linear model for each species. *Bombus* species respond to environmental variations during the current year whereas solitary bee species respond to environmental variations of the previous year (Crone 2013). Therefore we used weather data from the current year when analyzing the abundance of *Bombus* species by year and weather data from the previous year when analyzing the abundance of solitary bee species by year. Then, we examined whether their responses correlate to the previously mentioned traits by using a fourth corner analysis. The linear mixed model analyzes several sets of data and identifies relationships between those data sets and the significance levels of those relationships (Winter 2013). We used the negative binomial distribution for all models, and conducted all GLM analyses using the R package glmmADMB (Skaug et al. 2013).

In order to examine the relationship between bee traits and the response of bee species to environmental variables, we used a statistical method known as fourth corner analysis. The fourth corner analysis combines three matrices – in this case the abundance of each bee species, trait data, and environmental variable data – and identifies significant associations between abundance of individuals with certain traits and environmental variables while ignoring the species attached to the abundance data (Dray et al. 2014). The fourth corner analysis was performed using the R package ade4 (Dray and Dufour 2007). We executed both analyses using the programming software R (R Development Core Team 2008).

Results

Using data from 2009 to 2015, we found a variety of responses among bee species. Seven species exhibited no significant response to any of the environmental variables, seven species showed significant responses to one environmental variable, and three species demonstrated significant responses to two or more variables (Table 1). Wind and temperature both elicited significant responses from five species while precipitation produced significant responses from four species. All but one of the species that responded to wind showed decreased abundance with increased wind. *Panurginus cressoniellus*, however, responded positively to increased wind.

Similarly, all but one of the species that responded significantly to temperature were negatively impacted by increased temperature, but again *Panurginus cressoniellus* exhibited increased abundance with increased temperature. Two of the species with significant responses to precipitation showed increased abundance with increased precipitation while the other two species responded negatively to increased precipitation (Table 1).

The fourth corner analysis produced no significant correlation between environmental variables and traits.

Discussion

According to our results, bees exhibit response diversity with different species responding most strongly to different environmental variables. This display of response diversity may help protect the ecosystem from being altered by environmental variation by acting as a buffer, and thus play an important role in preserving ecosystem function.

Most of the bee species that responded significantly to wind and temperature did so in the same direction. Increased wind generally resulted in reduced abundance of the bee species that were affected. While sampling, on windier days we tended to see fewer bees, possibly because the wind made foraging more energetically expensive since the bees might have to fly against the wind. Therefore, bees may forage less on windier days, resulting in the collection of fewer resources and thus weaker or disadvantaged bees with lower fitness.

Increased temperature negatively impacted the abundance of the majority of bee species that exhibited significant responses. These results suggest that the affected bee species are close to their upper thermal limit and if the temperature continues to increase, they may respond with more dramatic decreases in population size (Oyen et al. 2016, Pyke et al. 2016). This negative affect on bee populations could be due to decreased foraging ability or increased mortality due to higher temperatures. Alternatively, the increased temperature could be increasing asynchronicity between bees and the flowers they feed on (Pyke et al. 2016). Higher temperatures may cause flowers to bloom earlier, but bees have yet to alter their phenology and are not emerging until the flowers have already blossomed (Pyke et al. 2016). Therefore, there are fewer floral resources available to the bees, thus giving them a disadvantage in terms of collecting necessary resources.

The responses to precipitation were split evenly between positively and negatively impacting the relevant bee species, thus implying both positive and negative consequences of

precipitation for bees. Increased precipitation, up to a point, may result in a greater abundance of flowers by providing plants with greater water resources. The abundance of bees may then increase due to the availability of more floral resources (Goulson et al. 2015, Hegland and Boeke 2006). Conversely, as with wind, rain may inhibit bees' ability to forage and thus negatively impact them.

Though the fourth corner analysis produced no significant results, this lack of significance implies several things. Firstly, we may simply have had too little diversity in the trait data to find any significant patterns. For example, only four of the bee species were social and only two were parasitic. Thus, we may not have had enough individuals with the same traits for that trait to show a significant response to any environmental variables. One way to remedy this potential problem would be to include more species and select them based on their traits to ensure a more even spread of traits. Secondly, the various responses may have been linked to traits that were not included in this study, such as phenology. A solution for this would be to include more trait data for each species, which would require additional research. Lastly, the responses may not correlate to traits at all and may be determined by other factors such as individual habits and tendencies, interactions with predators and other animals, and the ability to compete. Future studies on other factors that may relate to bee response diversity to environmental variables could provide additional information about the drivers behind changes in bee population abundance.

Given that response diversity helps maintain ecosystem stability and acts as a buffer against change, the lack of response diversity in the bees we studied could indicate that the ecosystem is more prone to alterations by environmental factors. Additionally, the lack of trait diversity suggests that many of the bee species play functionally similar roles in the ecosystem, because they share many characteristics. If the bee species included in this study play similar roles in ecosystem functions and they generally respond in the same direction, they may be more likely to be impacted by changes in environmental variables, thus rendering the ecosystem less stable and less able to successfully cope with a changing environment.

Although the null results from the fourth corner analysis mean that we may not accurately extrapolate about the responses of species beyond this study, the analysis of the species at least offers suggestions about what we may expect to see in terms of responses for the bees included in this study. With climate change and the increasing frequency of extreme and unpredictable

weather events, conservationists may use our results to predict how bee abundances will respond to various weather patterns and how we may counteract those responses if they are deemed dangerously unhealthy for the bee populations.

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Tables and Figures

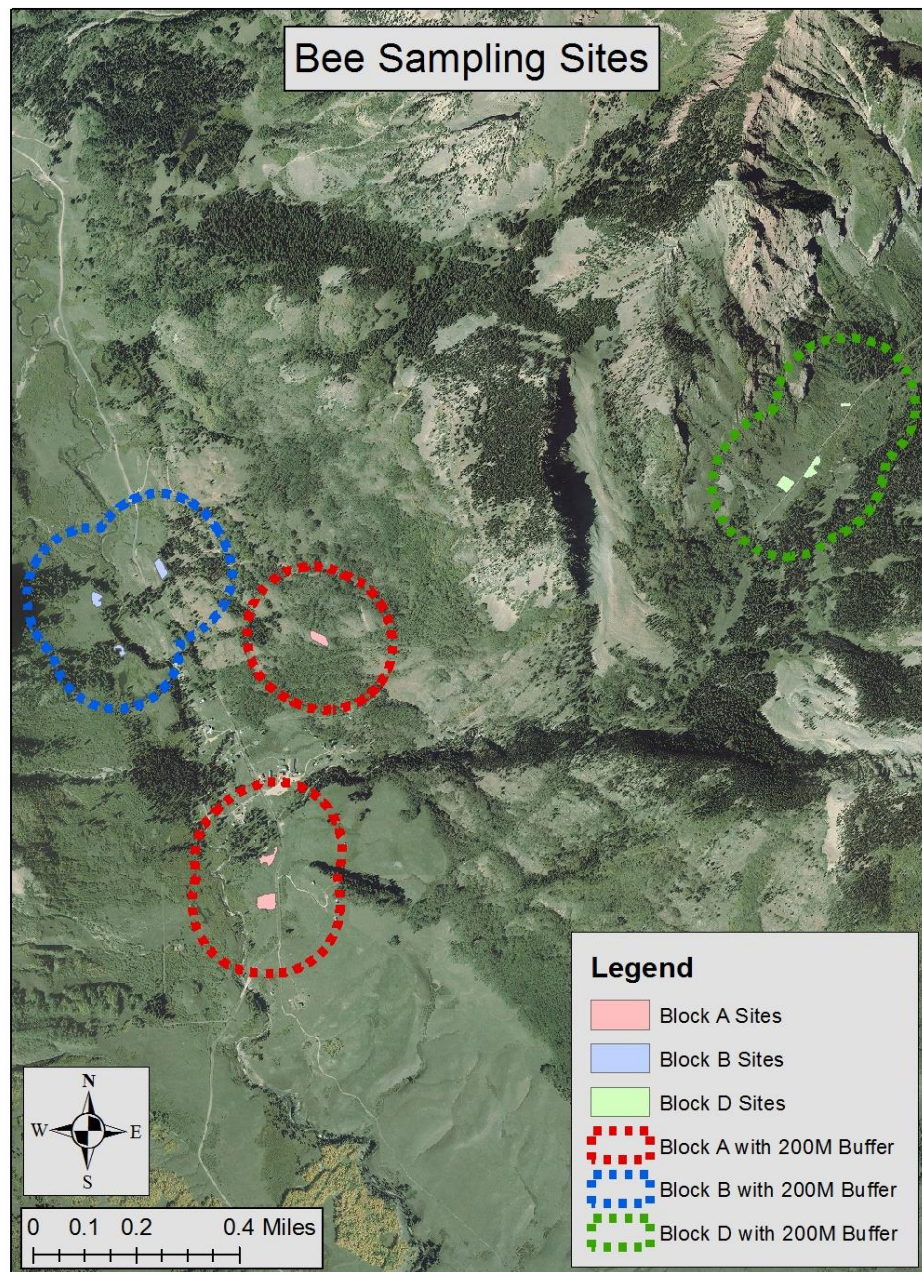


Figure 1. A map of all of the groups of sites where we sampled.

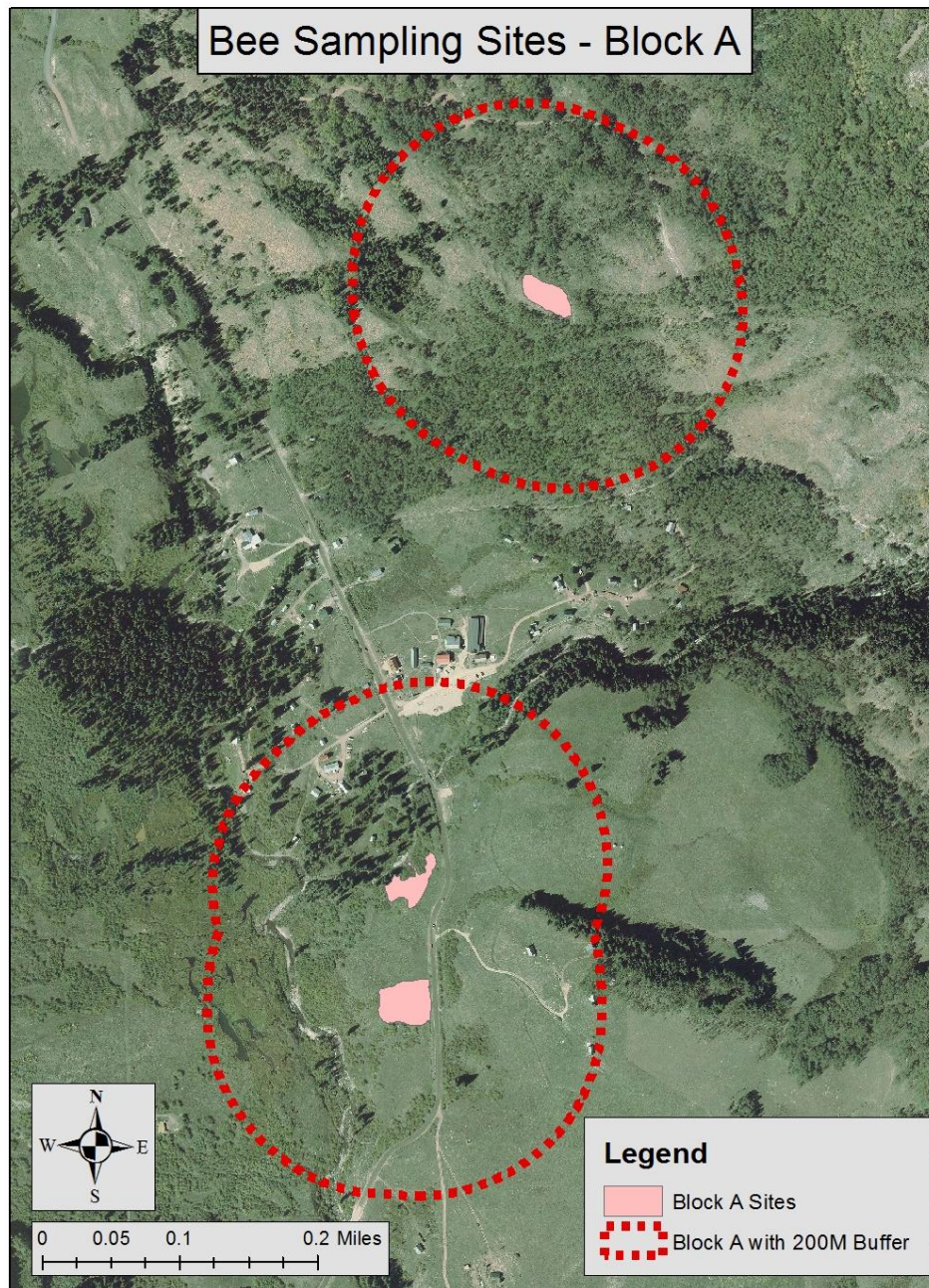


Figure 2. A map of the sites in Block A.

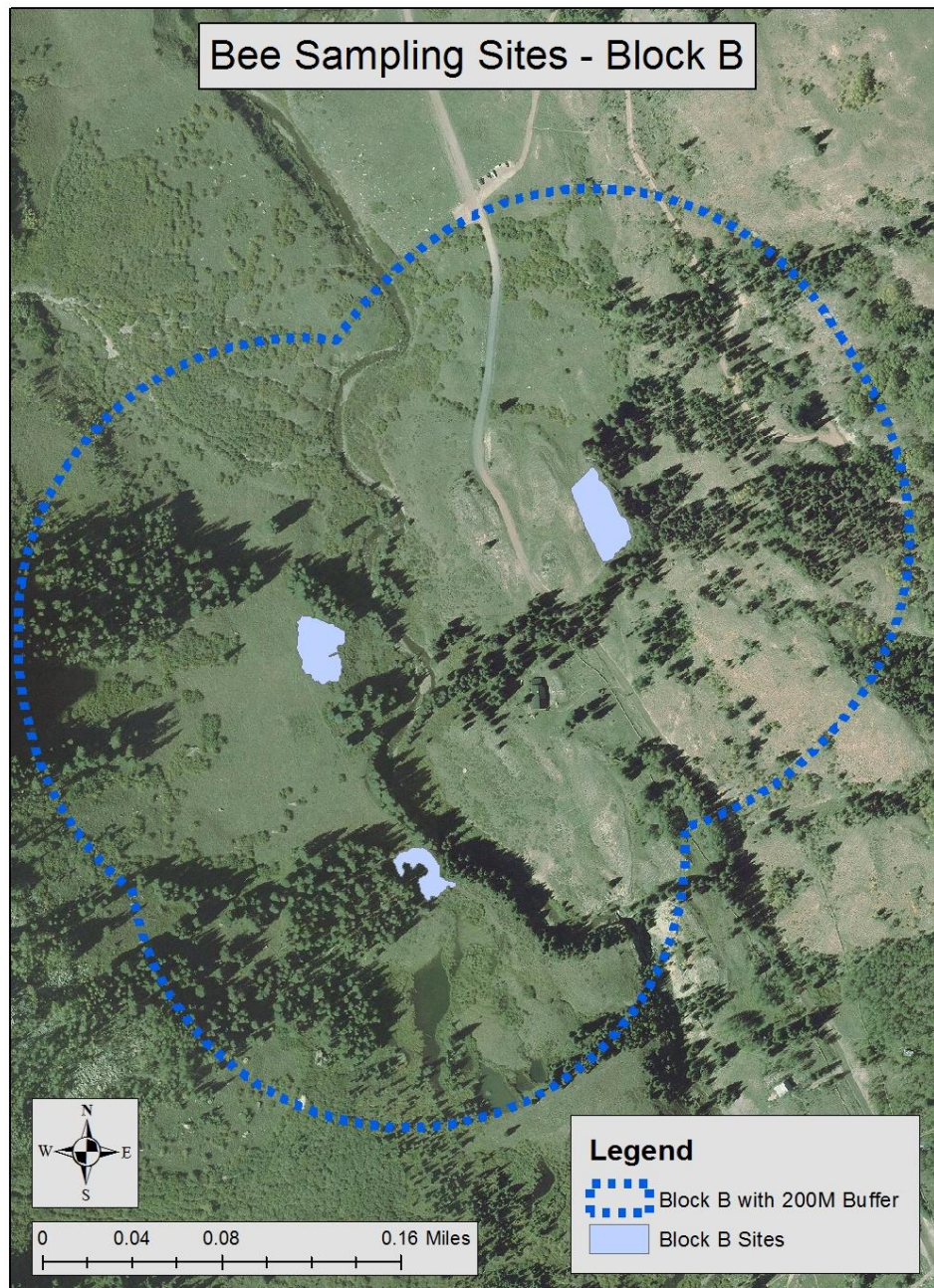


Figure 3. A map of the sites in Block B.

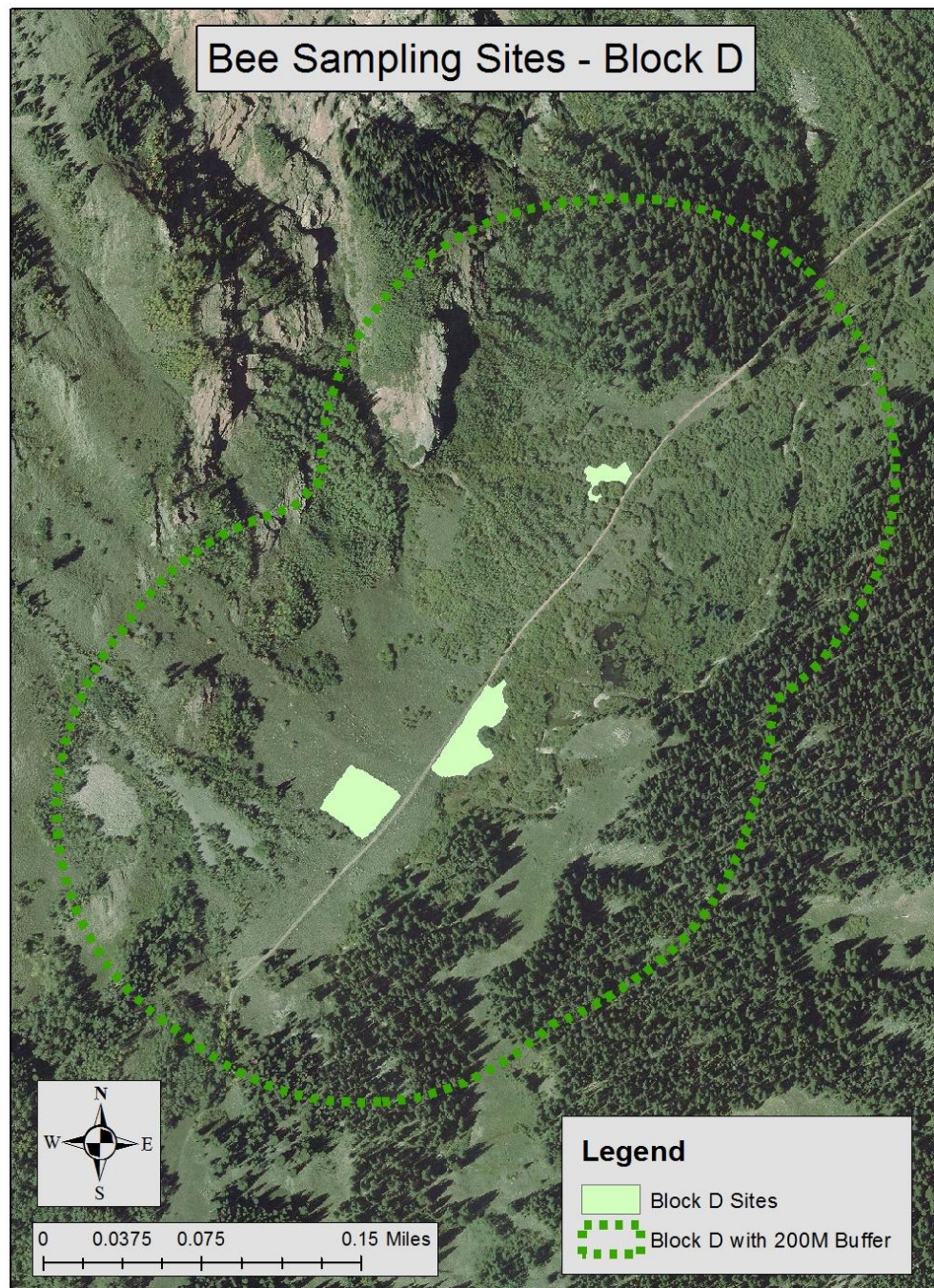


Figure 4. A map of the sites in Block D.

Table 1. A table of the results from the linear mixed model analysis which states which years' worth of environmental data the population of each species is responding to and how they are responding. Bolded entries are significant and the number of asterisks indicates the level of significance.

Species	Year (current or previous)	Wind		Degree Days		Precipitation	
		Test Statistic	P-value	Test Statistic	P-value	Test Statistic	P-value
<i>Bombus bifarius</i>	Current	0.20	0.652	-0.01	0.122	0.18	0.051
<i>Bombus fervidus</i>	Current	0.71	0.271	-0.01	0.157	0.23	0.078
<i>Bombus appositus</i>	Current	0.77	0.118	-0.01	0.029*	0.13	0.219
<i>Bombus flavifrons</i>	Current	0.35	0.470	-0.01	0.245	0.22	0.036*
<i>Bombus insularis</i>	Current	0.28	0.6455	-0.02	0.0057**	0.43	0.0011**
<i>Halictus rubicundus</i>	Previous	0.53	0.189	-0.04	5.0e-7***	0.18	0.160
<i>Halictus virgatellus</i>	Previous	-0.29	0.32	-0.002	0.77	-0.09	0.35
<i>Sphecodes sp.</i>	Previous	0.03	0.9332	-0.02	0.0005***	0.16	0.1346
<i>Panurginus ineptus</i>	Previous	-0.22	0.606	0.01	0.315	-0.20	0.179
<i>Panurginus cressoniellus</i>	Previous	0.66	0.0032**	0.02	4.5e-6	-0.27	3.5e-5***
<i>Pseudopanurgus bakeri</i>	Previous	-0.34	0.398	0.004	0.521	-0.22	0.066
<i>Pseudopanurgus didirupa</i>	Previous	0.44	0.5055	-0.02	0.0859	-0.07	0.7787
<i>Dufourea maura</i>	Previous	-0.14	0.788	-0.03	0.105	0.05	0.875
<i>Hoplitis fulgida</i>	Previous	-1.64	9.5e-8***	-0.005	0.595	-0.31	0.081
<i>Hoplitis robusta</i>	Previous	-1.17	0.0007***	-0.01	0.3790	-0.17	0.2446
<i>Hylaeus basilis</i>	Previous	-2.29	8.9e-8***	0.01	0.37	-0.36	0.09
<i>Hylaeus annulatus</i>	Previous	-1.14	0.0192*	0.01	0.3133	-0.40	0.0017**