Vaccinium membranaceum and its bumble bee pollinators: how climate change may affect their joint survival

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To the little girl who wanted to pet a bumble bee

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ABSTRACT

Vaccinium membranaceum (thinleaf huckleberry) berries are an important food source for humans and wild animals. It relies on pollinators to produce its berries and bumble bee pollinators may be particularly important because of their ability to use vibration to extract hard-to-reach pollen. In this study, I assessed the impact of climate change on the location of the suitable niche of *V. membranaceum* and three of its bumble bee pollinators: *Bombus mixtus, Bombus insularis,* and *Bombus melanopygus.* Through generating environmental niche models, I assess the predicted gains and losses of the suitable niche of each species in future climate scenarios and the predicted gains and losses of suitable niche overlap between the plant and pollinator species in future climate scenarios. Each species had predicted shifts in suitable niche in each climate scenario and the amount of predicted suitable niche overlap between species decreased across time in some scenarios. The results of this study indicate that these species may be negatively impacted by climate change. Future studies that assess suitable niche using additional environmental variables and studies that assess dispersal ability and factors that influence geographic range limits will continue to illuminate the extent of climate change impact on these species.

INTRODUCTION

Overview of the Study

In this study, I looked at the effects of climate change on the location and overlap of the suitable niches of thinleaf huckleberry, *Vaccinium membranaceum* Douglas ex Torr., and three of its bumble bee pollinators: *Bombus mixtus* Cresson 1879*, Bombus insularis* Smith 1861*,* and *Bombus melanopygus* Nylander 1848. Pollinators are essential for the reproduction of many flowering plants, which are a major food source for numerous organisms on earth (Nabhan and Buchman, 1997; Abrol, 2011). Wild bee populations are critical for the pollination of flowering plants around the globe (Garibaldi et al., 2013; MacInnis and Forrest, 2019). Bumble bees (*Bombus*) are particularly important because they can pollinate using sonication, also known as buzz pollination (King and Buchmann, 2003). This makes them highly efficient pollinators of certain flower types, including many in the blueberry (*Vaccinium*) genus (Javorek et al., 2002; Ratti et al., 2012; Cortés-Rivas et al., 2023). As climate change continues and global surface temperatures rise, bumble bee populations are predicted to decline due to their potential habitat loss, limited dispersal ability, and their adaptations for cold weather (Lepais et al., 2010; Hagen et al., 2011; Kerr et al., 2015; Carvell et al., 2017; Mola et al., 2020; Maebe et al., 2021). In addition, the symbiotic relationship between bumble bees and the plants they pollinate requires range overlap between species. As climate change continues, the ecological role of this symbiotic relationship makes focusing on the mutual survival of plants and their pollinators especially important. Understanding how climate change may impact plant and pollinator range overlap is an important piece in determining whether or not their mutualistic relationship will persist in the future.

Pollinator and Plant Interactions

Many flowering plants and their pollinating animal counterparts have developed a mutualistic relationship so intertwined that they cannot exist without the other. In this relationship, the pollinator transfers pollen from the anther of one plant to the stigma of another, facilitating sexual reproduction (Abrol, 2011). Some plants are able to reproduce through asexual reproduction without pollination, however they are unable to undergo genetic recombination without pollination. The transfer of pollen is a side effect of the foraging done by the pollinator. Some pollinators forage for pollen, a protein source, and nectar, a carbohydrate source, from flowering plants (Nicolson, 2011). Pollinator-plant interactions were some of the first described examples of coevolution, which is the process of two species interacting in a way that impacts the survival of the other and influences their evolution (Thompson, 1994, 24). Advantageous floral traits that attract pollinators have evolved in plants as a response to pollinator preference (Parachnowitsch and Kessler, 2010; Waser and Price, 1983). Concurrently, pollinators have evolved mechanisms to effectively forage in response to floral traits (Cardinal et al., 2018). In the mutualistic pollinator-plant dynamic, each organism is serving its own purpose, but it is undeniable that each also relies on the other to survive or reproduce.

Approximately 90% of the estimated flowering plants in the world rely on pollination from animals to undergo sexual reproduction (Nabhan and Buchman, 1997). Many different animals carry out pollination, including various insect, bird, and mammal species (Abrol, 2011). The pollinator-plant mutualistic relationship is important for the ecosystem, as well as human survival. Bees are a particularly important pollinator for crop pollination (Nabhan and Buchman, 1997). They are responsible for 95% of the pollination of the approximate 100 most important agricultural crops and up to 72% in more comprehensive studies (Nabhan and Buchman, 1997; Abrol, 2011). Many pollinators are keystone species in their ecosystem, and their absence could cause an ecosystem collapse (Abrol, 2011). If pollinator populations are lost or decline within an ecosystem, many plants in that ecosystem would be unable to reproduce. This would lead to a decrease in the biomass of plants, resulting in a lower abundance of food for many herbivores in the ecosystem. The downstream effects of pollinator loss would have large impacts on the survival of organisms in the food chain they are a part of. Due to their mutualistic relationship, the loss of flowering plants would have similar effects on an ecosystem, as it would result in a decrease of pollinators due to a reduction of food availability. The pollinators and plants in an ecosystem are equally important, and it is the maintenance of their mutualistic relationship that provides the foundation for biodiversity in many terrestrial ecosystems. Climate change poses a threat to this mutualistic relationship because of its impacts on pollinators and plants.

Climate Change

The global surface temperature has increased by approximately 1.0 degree Celsius since pre-industrial times due to human activity (IPCC, 2018). Human activity is the largest contributor to global warming, and activity causing greenhouse gas emissions is particularly impactful (IPCC 2023). The Intergovernmental Panel on Climate Change (IPCC) is the leading source of information regarding climate change and its effects on the world. The IPCC is responsible for assessing the current and future global impacts of climate change and reporting on their findings.

In their sixth assessment, which reported data up to 2021, the IPCC stated that the average global surface temperature has increased by 1.1 degrees Celsius since 1850 (IPCC 2023). The reports from the IPCC are on a 5 to 10 year cycle, which leads to information gaps between reports (Forster et al., 2024). To combat this, the Indicators of Global Climate Change, IGCC, was created. The IGCC provides annual assessments of the climate and impacts on climate by humans, using methods derived from the IPCC. Their annual updates help fill the gaps of information between IPCC reports. In the 2023 update, the IGCC data showed that the average global surface temperature in 2014-2023 was 1.19 degrees Celsius higher than the average global surface temperature in 1850-1900 (Forster et al., 2024). When comparing the 2014-2023 IGCC average global temperature to the 2010-2020 IPCC average global temperature, there was a difference of 0.10 degrees Celsius, with the IGCC average being higher than the IPCC average (Forster et al., 2024). Even in short time frames, average global surface temperatures are noticeably rising (Forster et al., 2024). Unless greenhouse gas emissions are decreased, it is expected that the global surface temperature will continue to rise (IPCC 2023).

High temperatures associated with global warming have caused large-scale mortality events, local species loss, ecosystem structure changes, species range shifts, and seasonal timing shifts (IPCC 2023). A meta-analysis assessing the range boundary shift of 99 species found that on average the range boundary of species has shifted northward or to higher elevations with a rate of 6.1 km per decade (Parmesan and Yohe, 2003). With global warming reaching 1.5 degrees Celsius, 4% of vertebrates, 6% of insects, and 8% of plants out of 105,000 species studied are expected to experience a loss of half or more of their geographic range (IPCC 2018). With global warming reaching 2.0 degrees Celsius, this increases to 8% of vertebrates, 18% of insects, 16% of plants (IPCC 2018). The risk of species loss is also predicted to increase as the global surface temperature increases (IPCC 2018; IPCC 2023).

Climate change is not the only factor that can impact the long-term survival of species. There are many other anthropogenic impacts on the environment that amplify current global biodiversity losses. Jaureguiberry et al.

(2022), looked at the factors contributing to biodiversity loss globally. They outlined the direct drivers of climate change as: land/sea use change, invasive alien species, direct exploitation, and pollution (Jaureguiberry et al., 2022). When comparing the direct drivers of biodiversity loss globally, they found that land/sea use change is the dominant driver, followed by direct exploitation, pollution, climate change, and invasive alien species (Jaureguiberry et al., 2022). Despite this, climate change is considered to be the driver that is increasing in intensity most quickly (Jaureguiberry et al., 2022).

Impacts of Climate Change on Pollinator-Plant Relationships

Climate change is predicted to impact each organism in different ways, but its impact on pollinator-plant relationships may be particularly consequential because they are so interdependent. Plants, pollinators, and their relationship will be affected by seasonal shifts, erratic weather patterns, and distribution changes caused by climate change.

Seasonal shifts impact pollinator migration, pollinator emergence, and plant flowering times. A meta-analysis by Parmesan and Yohe (2003) found that across 172 species there was a shift towards an earlier spring with a mean of 2.3 days per decade. Additionally, across 677 species, 62% displayed trends of spring advancement, including earlier first flowerings and butterfly migration (Parmesan and Yohe, 2003). Of the measured shifts in phenologies, 81% were following the trend predicted due to climate change (Parmesan and Yohe, 2003). Multiple studies have found a response of earlier flowering in plants due to increasing temperatures, however not every species follows this trend (Bradley et al., 1999; Menzel and Fabian, 1999; Fitter and Fitter, 2002). Additionally, studies have found that the dates of emergence of bees in the spring are becoming earlier due to climate change (Bartomeusa et al., 2011; Stemkovski et al., 2020). Currently, the phenology of wild bee emergence and blooming times are not consistently shifting at the same rate and direction; however, as temperatures rise, these changes may become more dramatic, which may lead to a risk of phenological mismatch in the future (Bartomeusa et al., 2011; Stemkovski et al., 2020). If the emergence time and flowering time between interacting species do not match, the success of the species may decrease.

Climate change has also caused an increase in erratic weather patterns including heat waves, flood, and harsh storms (Cook et al., 2018; Clarke et al., 2022). Heat waves and increased temperatures can impact both plant reproductive function and pollinator foraging ability (Chaturvedi et al., 2021; Russell and McFrederick 2022; Hemberger et al., 2023). Plants exposed to heat stress can experience reduced pollen viability, reduced fertility, and reduced pollen production (Chaturvedi et al., 2021). Extreme heat events might also impact the microbial communities in nectar that are responsible for altering the composition of sugars in the nectar; however, the impact of this is unclear (Russell and McFrederick 2022). Additionally, extreme conditions of heat can inhibit bumble bee pollinators from foraging (Hemberger et al., 2023). Harsh storms and floods can damage plants through water exposure and inhibit pollination in various ways (Jacquemart, 1996; Burke, 2002; Huang et al., 2002; Sun et al., 2008; Sanderson et al., 2015). Exposure to water has been shown to degrade pollen in multiple plants, preventing those grains from successfully entering the stigma and/or reproducing (Jacquemart, 1996; Burke, 2002; Huang et al., 2002; Sun et al., 2008). However, some plants that experience degradation when exposed to water have mechanisms that protect the anthers from water exposure during rainfall (Huang et al., 2002; Sun et al., 2008). The increase of harsh storms due to climate change may increase the exposure of pollen to water. The negative impacts of these erratic weather events on pollen could impact not only the successful pollination of flowering plants but the availability of pollen for foraging pollinators. These storms may lower the amount of suitable foraging time as high rain and wind conditions are negatively correlated with colony activity (Sanderson et al., 2015).

Climate change will not only directly impact the plant and pollinator function but may also constrict their ranges. Pollinators and flowering plants are experiencing, and are predicted to experience, shifts in their distribution and suitable niche due to climate change (Parmesan et al., 1999; Breed et al., 2013; Prevéy et al., 2020; Pélissié et al., 2022). If pollinators and plants that rely on each other experience a shift or constriction in their range that results in a lack of overlap in their distribution, they will no longer be able to fulfill their mutualistic relationship.

The Importance of Wild Bees

Managed honey bees are the bees most associated with agricultural pollination. However, studies have shown that wild bees are equally, if not sometimes more, effective for agricultural pollination (Garibaldi et al., 2013; MacInnis and Forrest, 2019). A comprehensive study across every continent, excluding Antarctica, compared the effectiveness of pollination done by wild bees versus managed honey bees in 41 different crops (Garibaldi et al., 2013). They found that the quality of pollination done by honey bees was low in comparison to that of wild bees (Garibaldi et al., 2013). Additionally, they found that fruit set in plants pollinated by wild bees increased twice as much as those pollinated by honeybees (Garibaldi et al., 2013). The scale of this study provides clear evidence for the importance of wild bee pollination for crop yields around the globe.

These findings have been corroborated by smaller scale studies. MacInnis and Forrest (2019) compared pollen deposits and strawberry mass between flowers pollinated by honey bees versus wild bees. They found that while the amount of pollen did not differ with bee type, the flowers pollinated by wild bees produced strawberries that were heavier than those pollinated by honey bees (MacInnis and Forrest, 2019). Additionally, when flowers were pollinated by both wild bees and honey bees, those that were first pollinated by honey bees produced fruit that was 48% lighter than those first pollinated by wild bees (MacInnis and Forrest, 2019). They believe that these results are due to wild bees delivering more outcrossed pollen than honey bees (MacInnis and Forrest, 2019).

Wild bees may also contribute to pollination by enhancing the efficiency of honey bee pollination (Greenleaf and Kremen, 2006). A study by Greenleaf and Kremen (2006) looked at the pollination effectiveness of honey bees and wild bees on a hybrid sunflower. They found that both wild bee species abundance and richness increased the seed set of sunflowers pollinated by honey bees (Greenleaf and Kremen, 2006). Flowers pollinated by wild bees had a seed set that ranged from <1 to 19, and on average flowers pollinated by honey bees produced a seed set of 3 (Greenleaf and Kremen, 2006). However, in the presence of wild bees, the honey bee seed set increased to an average of 15 seeds per visit (Greenleaf and Kremen, 2006). They found that the honey bees were more likely to move from a male flower to a female flower after coming into contact with a wild bee (Greenleaf and Kremen, 2006). Even if wild bees are not more consistently effective than honey bees at pollinating certain plants, it is possible that their presence still positively impacts pollination.

Humans rely on pollination of their crops for a majority of their food, and many organisms, including humans, also rely on pollination of wild flowering plants to provide food sources. Statistics regarding the effectiveness of wild pollinators on agricultural crops do not fully account for the impact they have on wild flowering plants. However, their facilitation of successful pollination in agricultural settings where managed bees are present, and their tendency to be more effective than managed bees in these settings, indicates that their impact in settings where managed pollinators are absent may be particularly important.

An Overview of *Bombus*: Bumble bees

There are approximately 20,000 species of bees found around the world, only 250 are of the genus *Bombus*, and only 46 out of those 250 are found in North America (Williams et al., 2014, 10-11). Species in the genus *Bombus* are particularly important pollinators because of their pollination strategy: sonication. However, their life cycle and foraging needs make them vulnerable to changes in the environment.

Bumble bees are social insects functioning in a colony with a queen, workers, and males, each with distinct roles (Williams et al., 2014, 12). The queen is responsible for egg production and establishing a new colony after overwintering (Williams et al., 2014, 13). The workers are responsible for a majority of the foraging for hive resources, as well as various hive maintenance roles (Williams et al., 2014, 13). The males leave the hive to be a reproductive partner for other queens (Williams et al., 2014, 14).

Bumble bees have many adaptations to cold weather that are particularly important for the survival of overwintering queens. During each winter, the males and workers of the colony die, causing the continuation of the colony to depend on the queen staying alive through underground hibernation during the cold season (Goulson, 2010; Williams et al., 2014). Prior to her hibernation, the queen mates with a male so she will be fertilized when emerging in the spring (Williams et al., 2014). This overwintering is a strategy to avoid the consequences of cold weather. Bumble bees are endotherms and have physical adaptations to cold temperatures, including setae (hair) length and color (Peat et al., 2005; Williams, 2007). The queens shiver their flight muscles to thermoregulate during cold weather and this process may be supplemented with additional thermoregulation through substrate cycling (Heinrich and Kammer, 1973; Staples et al., 2004). They need to be able to undergo these mechanisms when exposed to cold weather because they cannot fly if their flight muscles drop below 30 degrees Celsius (Heinrich, 2004). Additionally, during diapause the base metabolic rate of bumble bee queens lowers in order to conserve energy reserves (Rondot and Darveau, 2024). If the queen survives hibernation, she will emerge in the spring, find a nesting site, and begin the new colony (Williams et al., 2014, 12-13).

Bumble bees nest underground, but instead of digging their own cavities, they take over spaces like small abandoned dens, hollow logs, tufts of tall grass, and even some man-made structures (Williams et al., 2014, 13). Once a nesting site has been established, the queen can begin laying the first round of eggs, collecting nectar, and building up the colony (Williams et al., 2014, 13). This is a very vulnerable stage of the colony cycle, as weather, food availability, and even other queens can put the colony at risk of death (Williams et al., 2014, 13).

Bumble bee colonies do not have large food stores and must be able to constantly forage to maintain the hive population throughout the growing season (Heinrich, 2004). There is no need to store large amounts of food for the cold season because the entire colony, save the queen, dies before winter. Without these stores, bumble bee colonies can be vulnerable to death during periods of low flower abundance. This leads bumble bees to occupy habitats where flowers continue to bloom throughout the growing season (Williams et al., 2014, 11-12). However, they can be found anywhere where flowers are available to pollinate (Williams et al., 2014, 11-12).

Bumble bees have an especially important relationship with flowering plants that have poricidal anthers because their sonication ability makes them more efficient at pollinating those flowers than non-sonicating pollinators. When foraging, bumble bees are able to access pollen from plants through sonication; this trait is not exhibited by honey bees and is exhibited by some, but not many, wild bee species (King and Buchmann, 2003). Sonication, also known as buzz pollination, is a mechanism that allows pollinators to access pollen from poricidal anthers (Fig. 1). Poricidal anthers store their pollen internally and the pollen is accessed through a pore that allows the pollen to fall out. During sonication, the bee bites the anther with their mandible and then uses their wings to generate vibration (King and Buchmann, 1996; King and Buchmann, 2003). This encourages the release of pollen from poricidal anthers in the flower.

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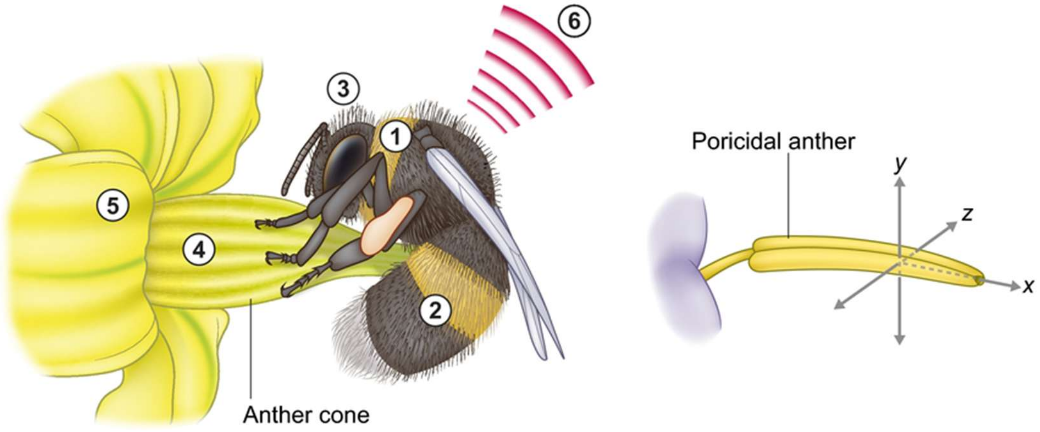


Figure 1. Diagram depicting sonication (Vallejo-Marín, 2019). The image on the left shows the bee thorax (1), bee abdomen (2), bee head (3), flower anther cone, or cluster of anthers that contain pollen (4), flower petals and sepals (5), and vibration from the bee (6). The bee transmits vibration through the head, thorax, and abdomen. The vibrations are transmitted to the anther cone, the sepals and petals, and the air. The image on the right shows a single poricidal anther with the axes of vibration depicted on the poricidal anther (x, y, z) (Vallejo-Marín, 2019). When vibrations occur, the pollen exits the anther through a pore at the top of the anther.

Sonication is documented to be important for the pollination of some species in the genus *Vaccinium* (Javorek et al., 2002; Ratti et al., 2012; Cortés-Rivas et al., 2023). *Vaccinium membranaceum* (thinleaf huckleberry), *V. corymbosum* (highbush blueberry) and *V. macrocarpon* (cranberry) have poricidal anthers (Ratti et al., 2012; Wallace, 2017). It has been shown that pollination from bumble bees compared to other bee species significantly increases the berry mass of both highbush blueberries and cranberries, which is correlated with the number of mature seeds produced (Ratti et al., 2012). In a study comparing pollination of *Vaccinium angustifolium* (lowbush blueberry), bumble bees were found to deposit more pollen, have faster floral visitation rates, and pollinate more flowers per minute than other bee species (Javorek et al., 2002). When directly compared to honey bees, it was found that in order to deposit the same amount of pollen as a bumble bee queen, a honey bee would need to visit the flower 4.3 times (Javorek et al., 2002). While there are no studies looking at the effectiveness of bumble bees on *V. membranaceum* pollination when compared to other pollinators, it can be inferred that bumble bees may have a significant positive impact on the success of *V. membranaceum* pollination.

Impacts of Climate Change on Bumble Bees

Despite having evolved mechanisms to maximize foraging and avoid cold weather, bumble bees' foraging requirements and overwinter hibernation make them vulnerable. This vulnerability makes them less resilient to the impacts of climate change on the regions they inhabit. Larger storms, more variable weather, and temperature shifts can impact both the growing season of flowers and the ability of the bumble bee to forage.

As with other pollinators, bumble bees will experience the effects of climate change through shifts in flowering time, impacts to nectar and pollen, and disruption of pollination due to erratic weather events. Shifts in flowering times are particularly concerning for bumble bees because the queen emerges from hibernation alone. As climate change continues to cause more variation in weather and flowering times, the queen's emergence from hibernation and establishment of a colony may become less consistently successful. It is reasonable to think that if the queen emerges and the flowers are not blooming, it is unlikely that she will be able to survive and restart the colony. If many queens in the same region experience this in the same season, it may lead to a decrease in bumble bee populations in that area. Additionally, bumble bees store very little of their foraged food in the nest and require a near constant stream of foraging to survive (Heinrich, 2004). As flowering times shift, it may become more difficult for bumble bees to forage consistently throughout the season, potentially impacting colony health.

As the average global temperature continues to warm, the ranges of various terrestrial species have been documented to be shifting and many more are expected to follow this pattern (Bergamini et al., 2009; Chen et al., 2011; Forero-Medina et al., 2011; Breed et al., 2013). In general, species ranges are shifting away from the equator and to higher elevations with a weighted mean of 16.6 kilometers per decade and 11.1 meters per decade respectively (Chen et al., 2011). Insect species, especially those that are cold adapted, are generally experiencing range shifts to higher latitudes in response to increasing temperatures (Parmesan et al., 1999; Pélissié et al., 2022). The species following the cold edge of their range in the northern hemisphere are shifting further north.

Bumble bees, as a whole, are experiencing a range constriction at their warmer edge (Kerr et al., 2015). Their situation is particularly distressing as they are unable to track with the cooler northern edge, so their overall range is shrinking (Kerr et al., 2015; Sirois-Delisle and Kerr, 2018). Kerr et al. (2015)

performed a comprehensive study documenting the shifting range of 67 bumble bee species across North America and Europe, measuring the shift in range across historical and current data. They found that on both continents bumble bees have failed to track the warming edge of their range and experienced range loss in their southern limits, leading to overall range constriction.

Range shifts and shifting flowering times are only part of the impact of changing temperatures on bumble bees. The hibernation of the queen is also a point of concern. The expected increase of average temperature due to climate change will likely increase the average temperature of winters. As average winter temperatures increase, the queens may be exposed to warmer conditions during hibernation, which would disrupt their mechanisms for cold survival (Vesterlund et al., 2014). This may make queens with lower energy reserves and smaller body sizes less likely to emerge with sufficient energy stores, as their mechanisms to maintain energy stores could be disrupted (Vesterlund et al., 2014). Additionally, the pathogen defenses of queens, particularly the lowering of phenoloxidase activity, may be inhibited through exposure to warmer winters (Vesterlund et al., 2014). This may leave bumble bee queens vulnerable to pathogens when emerging in the spring (Vesterlund et al., 2014).

The Species of This Study

As climate change makes pollination more vulnerable, it is important to take a multispecies approach to conservation that addresses concerns for both plants and pollinators. In this study, I looked at the relationship between *Vaccinium membranaceum* and three of its bumble bee pollinators, *Bombus mixtus, Bombus insularis,* and *Bombus melanopygus* (Fig. 2).

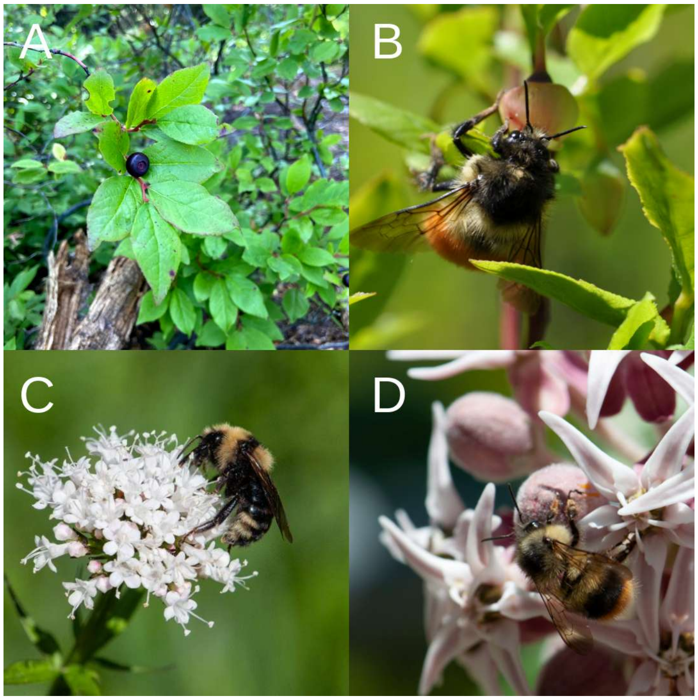


Figure 2. Images of the study species. A: *Vaccinium membranaceum* in fruit (Drummond 2021). B: *Bombus melanopygus* (Hatfield 2024). C: *B. insularis* (Hatfield 2024). D: *B. mixtus* (Hatfield 2024).

Vaccinium membranaceum Douglas ex Torr. (thinleaf huckleberry) is a plant native to North America. It has a disjunct, or discontinuous, geographic distribution with a large number of populations in the Pacific Northwest and fewer, isolated populations in the Great Lakes region (Fig. 3) (Drummond et al., 2022). It is typically found in subalpine habitats, particularly fir and hemlock forests (Simonin, 2000). It is considered to be a keystone species, both ecologically and culturally, in the Pacific Northwest. Ecologically, it is a keystone species because it is a food source for many animals and insects, as well as a source of cover and nesting habitat (Lichtenberg and Graves, 2023). The berry is also culturally significant for Native American people who practice traditions surrounding the plant's cultivation, collection, consumption, and storage.

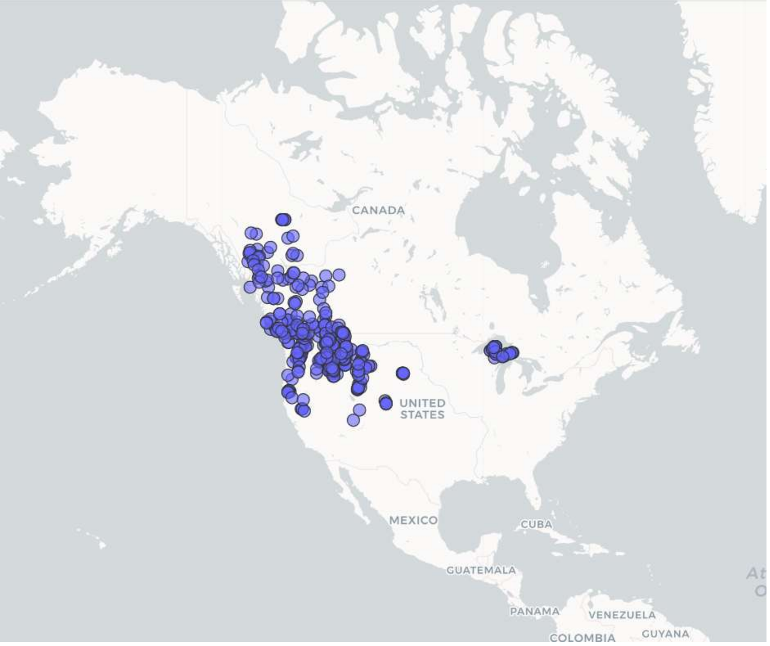


Figure 3. ***Vaccinium membranaceum*** **occurrence in North America.** Each blue dot represents a GPS locality derived from an individual preserved specimen. Locality data were obtained from the Global Biodiversity Information Facility (GBIF) on September 20, 2024 and were cleaned by removing duplicate records, NA or blank values, and improbable or errant data points based on manual inspection of the preserved specimen record. The map was generated using the packages *sf* (Pebesma and Bivand, 2023), *mapview* (Appelhans et al., 2024), and *ggplot2* (Wickham, 2016) in RStudio.

Vaccinium membranaceum is a plant that is capable of both sexual and asexual reproduction. It is a rhizomatous shrub, so it is capable of cloning itself by sending its stem horizontally underground and then sending a shoot back up through the ground (Simonin, 2000). This process can allow the plant to persist while maintaining the genetic diversity of the population, but it does not allow for genetic recombination, which prevents the plant from adapting through evolution. In order for genetic recombination to occur, *V. membranaceum* must undergo sexual reproduction through pollination. The genetic variation of the plant may be lower in the Great Lakes region's populations because of their isolation that results in reduced gene flow and their small population sizes. Small populations are generally prone to low genetic diversity, which leads to a less adaptable population (Booy et al., 2000).

Various species of bees, wasps, flies, ants, moths, butterflies, and beetles were seen visiting *V. membranaceum* during an observational study conducted in Montana (Lichtenberg and Graves, 2023). While any of these visitors may have facilitated pollination, bees had the highest percentage of observations (50.4%) followed by wasps (18.3%) (Lichtenberg and Graves, 2023). With the visits from bees being so much higher than any other insect category, it is likely that they are the main pollinator of the plant (Lichtenberg and Graves, 2023). Bumble bees made up 43.1% of all pollinators that visited the plants. So, while bees may be the main pollinator, bees of the genus *Bombus* are particularly important for the sexual reproduction of *V. membranaceum*.

Lichtenberg and Graves (2023) identified the species of *Bombus* visiting *V. membranaceum* in their study and laid out the percent of each species visiting:

Bombus mixtus (28.6%)*, Bombus vancouverensis* (25.5%)*, Bombus melanopygus* (22.9%), *Bombus sitkensis* (9.4%)*, Bombus flavifrons* (6.8%)*, Bombus insularis* (3.6%), *Bombus rufocinctus* (1%)*, Bombus flavidus* (1%)*, Bombus centralis* (0.5%)*,* and *Bombus occidentalis* (0.5%). Since this study was only conducted in a small region of Montana, it is likely that this data does not equate to the percentages of pollinators in other regions or throughout the entire population in North America. However, this is some of the only available information regarding specific species and their abundance of pollination for *V. membranaceum*.

The bumble bee species selected for this study were chosen because their geographic ranges across North America are all relatively similar to that of *V. membranaceum* (Fig. 4, Fig. 5, Fig. 6). In addition, *B. mixtus* and *B. melanopygus* were two of the three species with the highest percentage of visitations in Montana. *Bombus mixtus* (Cresson, 1878), commonly known as the Fuzzy-horned Bumble bee, is generally found in a variety of habitats including open grassy spaces, shrub and chaparral regions, and mountain meadows (Williams et al., 2014). *Bombus melanopygus* (Nylander, 1848) is commonly known as the Black Tail Bumble bee (Williams et al., 2014). They start nesting earlier than most other species and will occupy areas both above and below ground, typically in birdhouses or building insulation (Williams et al., 2014). They are found in a variety of habitats including open grassy spaces, shrub and chaparral regions, urban green spaces, and mountain meadows (Williams et al., 2014).

Figure 4. ***Bombus mixtus*** **occurrence in North America.** Each blue dot represents a GPS locality derived from an individual preserved specimen. Locality data were obtained from the Global Biodiversity Information Facility (GBIF) on September 20, 2024 and were cleaned by removing duplicate records, NA or blank values, and improbable or errant data points based on manual inspection of the preserved specimen record. The map was generated using the packages *sf* (Pebesma and Bivand, 2023)*, mapview* (Appelhans et al., 2024)*,* and *ggplot2* (Wickham, 2016) in RStudio.

Figure 5. *Bombus melanopygus* occurrence in North America. Each blue dot represents a GPS locality derived from an individual preserved specimen. Locality data were obtained from the Global Biodiversity Information Facility (GBIF) on September 20, 2024 and were cleaned by removing duplicate records, NA or blank values, and improbable or errant data points based on manual inspection of the preserved specimen record. The map was generated using the packages *sf* (Pebesma and Bivand, 2023), *mapview* (Appelhans et al., 2024), and *ggplot2* (Wickham, 2016) in RStudio.

Figure 6. *Bombus insularis* occurrence in North America. Each blue dot represents a GPS locality derived from an individual preserved specimen. Locality data were obtained from the Global Biodiversity Information Facility (GBIF) on September 20, 2024 and were cleaned by removing duplicate records, NA or blank values, and improbable or errant data points based on manual inspection of the preserved specimen record. The map was generated using the packages *sf* (Pebesma and Bivand, 2023), *mapview* (Appelhans et al., 2024), and *ggplot2* (Wickham, 2016) in RStudio.

Bombus insularis was included even though it has a much lower total percentage of pollination because it has interesting life cycle requirements and its distribution in the Great Lakes region is more similar to *V. membranaceum* than the other two bumble bee species chosen. It is commonly known as the Indiscriminate Cuckoo Bumble bee, and is a social parasite (Williams et al., 2014). There are multiple species of Cuckoo Bumble bees in North America, and they all are social parasites. A social parasite attacks colonies during their early development and raises their young using the resources that the host colony collects (Williams et al., 2014). These bees must attack at the time where the host colony is large enough to support them, but not so large that the workers will kill them (Williams et al., 2014). This reliance on other bee colonies surviving will make the impact climate change has on the survival of *B. insularis* potentially more intense. If one or all of its host species collapses, the collapse of *B. insularis* will likely follow. *Bombus insularis* is known to be a parasite for three of the other bumble bee species found pollinating *V. membranaceum*: *B. flavifrons, B. occidentalis,* and *B. rufocinctus*. None of these species were included in the study either because of extremely low pollination visit percentage or a distribution that did not match *V. membranaceum* upon visual inspection.

Environmental Niche Modeling

Assessing species niches, as well as the species niche overlap between interacting species, has been a longstanding point of research in biology (Grinnell, 1924; Vandermeer, 1972; Pianka, 1974; VanDerWal et al., 2009). Initially, this research has been focused on determining the resources used by species, range limitations due to abiotic and biotic factors, competition between species, and resource use overlap between species. However, as the climate continues to change at an unprecedented rate, the need for quantifying or modeling a species' environmental niche and predicting potential shifts in the location of that niche has emerged. An environmental niche is the precise sector of an environment where a certain species can survive and reproduce.

As the climate changes, the location of suitable habitats, or environmental niches, for species will change alongside it (Parmesan et al., 1999; Bergamini et al., 2009; Chen et al., 2011; Forero-Medina et al., 2011; Breed et al., 2013; Kerr et al., 2015; Sirois-Delisle and Kerr, 2018; Pélissié et al., 2022). While some species' environmental niche may encompass a wide variety of environmental conditions, allowing them to exist in many different environments, other species have a smaller range of conditions they can survive in, leaving them more vulnerable to change in their environment if they are unable to adapt through evolution at the same rate. Predicting the potential geographic changes in suitable niche through modeling is one way to get ahead of the impacts of climate change. Environmental niche models are very useful because they can provide a glimpse into the potential future of a species. This can help inform conservation strategies for species either already of concern, or for species that are hypothesized to experience large amounts of niche loss.

There are different approaches for environmental niche modeling. The software MaxEnt (Philips et al., 2006) is one of the most common and well-studied approaches. By analyzing species occurrence data and environmental variables, MaxEnt is able to generate a model of the current suitable niche of the species (Philips et al., 2006). Once a model has been generated, the software can project the model onto future environmental scenarios and predict where the suitable niche may be in the future (Philips et al., 2006).

Importantly, an environmental niche model projection is not a prediction of a species' range, only the potential location of its suitable niche. When a future niche prediction is mapped, for example, it is not a guarantee that the species will be found there. Instead, it is a prediction of where its suitable niche might occur. The species would need to overcome the obstacles of dispersing and establishing in order to colonize any new suitable niche space. Through looking at a combination of future niche space predictions and dispersal potential, it is possible to begin to determine if a species might be capable of tracking environmental changes.

The Goals of This Study and Hypotheses

Under the Fifth Assessment from the IPCC, *Vaccinium membranaceum* and all three of these bumble bee species are predicted to experience range loss in future climate scenarios (Sirois-Delisle and Kerr, 2018; Prevéy et al., 2020). However, with the release of the Sixth Assessment, the climate scenarios used in these studies are now outdated making remodeling with the updated climate scenarios crucial (Hausfather & Peters, 2020). In addition, since all of the bumble bee species interact with *V. membranaceum* through pollination, looking at the overlap in potential suitable niche between the pollinators and the plant could help predict future ability to interact.

There are two overarching aims of my study: 1) compare the current and future potential suitable niche space for each species to assess the shift in niche space location and size and 2) compare the current potential suitable niche overlap between *V. membranaceum* and its pollinators to their future potential suitable niche overlap to assess shifts in interacting potential.

Aim 1 will measure the amount of overlap between current and future suitable niche using a D-statistic (Warren et al. 2009). A D-statistic value of 1 indicates exact overlap between the suitable niche data while a value of 0 indicates no overlap. When comparing the future and current suitable niches, any D-statistic less than 1 represents a shift in suitable niche space with larger shifts being closer to 0. I hypothesize that there will be a shift in suitable niche space between current and future predictions and that there will be a larger shift in suitable niche space as emissions scenarios worsen and time increases.

If a shift in suitable niche space from current to future predictions is found for each individual species, then I expect that there may also be a shift in suitable niche overlap between the species, specifically between *V. membranaceum* and each of the bumble bee species. Aim 2 will be assessed using the difference in D-statistics of the future overlap between the plant and pollinator and the current overlap between the plant and pollinator. The difference in D-statistics will indicate whether there was a gain or a loss of overlap, with a negative number representing a loss and a positive number representing a gain. I hypothesize that there will be an overarching trend of loss of overlap between species, and that loss will be greater as both emissions scenarios worsen and time increases.

METHODS

Obtaining and Preparing Data

Occurrence Data

Occurrence point datasets are a compilation of locations where individuals of a species have been observed or collected. These datasets are often compiled from collected specimens that are housed in museum collections. Museums and other institutions often contribute their data to a publicly available database such as the Global Biodiversity Information Facility (GBIF), which synthesizes datasets from contributions of many institutions and individuals (*Data Quality*, n.d.). Occurrences for each species used in this study were downloaded from GBIF on September 20th, 2024, using the *rgbif* (Chamberlain et al., 2024) package in RStudio (GBIF, 2024a; GBIF, 2024b; GBIF, 2024c; GBIF, 2024d). 5,840, 13,254, 15,471, and 606 occurrence points were downloaded for *Bombus insularis, B. melanopygus, B. mixtus,* and *Vaccinium membranaceum* respectively. These downloads only included occurrences based on preserved museum specimens. Each set of occurrence points were cleaned in RStudio by removing duplicate records, NA values, and blanks (occurrences that were missing GPS coordinates) (Fig. 3, Fig. 4, Fig. 5, Fig. 6). In addition, occurrence point outliers were manually inspected against their GBIF database entries and removed if the location was improbable or errant. After this filtering process, 1532, 2460, 2082, and 492 occurrence points remained for *Bombus insularis, B. melanopygus, B. mixtus,* and *Vaccinium membranaceum* respectively.

Bioclimatic Raster Data

The environmental niche modeling in my study used climatic factors. WorldClim is a database that hosts downloadable current, future, and historical climate rasters. A raster is an image format that stores data within each grid cell. Future and current bioclimatic rasters with a 30 arc-second resolution were downloaded from WorldClim (Fick and Hijmans, 2017; Takemura, 2019). 30 arc-seconds is the smallest resolution possible and allows for the most fine-tuned ENM to be generated. Rasters for 19 bioclimatic variables were available for the current and future climates. These variables are derived from temperature and rainfall data and represent annual trends, seasonal variation, as well as extreme climate conditions. The 19 variables are as follows: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter.

The 19 rasters were downloaded for a variety of future climate scenarios that are all based on the MIROC6 climate model (Takemura, 2019). In this study, each emissions scenario at a different time point in the future is called a future climate scenario. The emissions scenarios, shared socioeconomic pathways (SSP), are determined by the IPCC. Each SSP estimates climate conditions calculated using different levels of climate protection (Lee et. al 2021). Rasters from three future emissions scenarios, SSP1-2.6, SSP3-7.0, and SSP5-8.5, each at three different time frames, 2041-2060, 2061-2080, and 2081-2100 were used. SSP1-2.6 is the best-case scenario in which the global surface temperature increases between 0.5 and 1.5 degrees Celsius due to high levels of climate protection being implemented (Lee et al., 2021). SSP1-2.6 was chosen for this study to represent a low emissions scenario because it is generally preferred over other low emissions scenarios (Lee et al., 2021). SSP3-7.0 and SSP5-8.5 both represent scenarios where there is a low level of climate protection being implemented (Lee et al., 2021). In SSP5-8.5, the global surface temperature increases between 2.4 and 4.8 degrees Celsius (Lee et al., 2021). SSP5-8.5 is the worst of the two scenarios and is considered to be unreasonable with our current level of protection (Hausfather & Peters, 2020). It was chosen for this study to represent the absolute extreme future climate scenario. In SSP3-7.0, the global surface temperature increases between 2.0 and 3.7 degrees Celsius as a result of minimal climate protection and a reversal of current policies (Hausfather & Peters, 2020; Lee et al., 2021). SSP3-

7.0 was chosen for this study because it is considered to be a better benchmark for the plausible extreme than SSP5-8.5 (Hausfather and Peters, 2020).

All of the bioclimatic rasters, current and future, were cropped and cleaned in R version 4.4.0 on the UMass Amherst Unity computing cluster. They were cropped using the package *terra* (Hijmans, 2024) to include only the relevant range of North America, notated in decimal degrees: west -176.353, east -32.158, north 83.527, south 12.812. Once cropped, the NA values in the bioclimatic rasters were made consistent across all raster layers using the package *ENMTools* (Warren and Dinnage, 2024).

Climate Niche Modeling with MaxEnt

MaxEnt was used to generate ENMs because it was shown to have the best results and non-significant bias when compared to other modeling softwares such as generalized linear models (GLM), the gradient boosting machine (GBM), and random forests (RF) (Broennimann et al., 2011). MaxEnt (Philips et al., 2006) uses the principle of maximum entropy to determine the relative probability of an individual in a species occurring in a specific location (Merow et al., 2013). It does this by assessing where the species is known to be compared to background points where it has not been sampled. Maximum entropy is a key piece of MaxEnt's algorithm and is particularly important when the total population size of the species is unknown, as is it in this study (Phillips et al. 2006).

MaxEnt Model Testing

MaxEnt was run in R version 4.4.0 on Unity using the package *dismo* (Hijmans et al., 2023), the cleaned occurrence points, and current raster layers. For each species, 100 replicates of the model were run to test for consistency and assess whether the MaxEnt approach was appropriate for the dataset. Each replicate used the subsampling method, where 70% of the occurrence points were used to build the model and the remaining 30% of the occurrence points were used to test the model. The remaining model parameters were kept at the default settings. The MaxEnt models for each species were assessed using both statistical measures and visualization. If the mean area under the curve, AUC, for the 100 replicates was >70%, the model was considered consistent and appropriate for the dataset. AUC is a measure of the model's accuracy, or its ability to discriminate between presence and absence. Additionally, the omission rate for the test data was visually checked for alignment with the predicted omission rate across all replicates. If the model replicates passed these assessments, then the model approach was deemed appropriate.

The MaxEnt models for each species were run one final time in order to use a single model for current and future model projections. In some cases this singularly generated model had to be rerun because of a combination of low AUC, poor alignment of testing, and predicted omission rate or jackknife analysis that showed outliers in variable importance.

To generate predictions of where suitable niche space is currently or would be in the future, the model was projected back onto the current bioclimatic rasters, and onto the future climate scenario rasters using the package *dismo*. These predictions resulted in rasters that contained a measure of probability of suitable niche in each grid cell. These rasters were used to generate maps of the predictions.

Niche Overlap

The current and future prediction rasters were used to assess niche overlap for both aims. For Aim 1, the level of overlap of suitable niche between the current and future climate scenarios for each species was quantified. Additionally, the gains and losses of suitable niche between current and future climate scenarios for each species were mapped. For Aim 2, the level of overlap between the suitable niche of *V. membranaceum* and each of its pollinators was quantified in the current climate and for each future climate scenario. Additionally, the gains and losses of suitable niche overlap between each plant and pollinator pair for the SSP3-7.0 climate scenario across time frames were mapped.

D-statistic

To quantify overlap in suitable niche space, a D-statistic (Warren et al. 2008) was calculated using the function nicheOverlap from the package *dismo* in R version 4.4.0 on Unity. The D-statistic, or the D similarly statistic, ranges from zero to one with values closer to zero indicating low overlap and values closer to one indicating high overlap (Hijmans et al., 2023). For each individual species, the D-statistics of each future climate scenario was compared to the current D-statistic to test the prediction that the overlap would decrease with increasing SSP intensity and time. For the cross-species analysis, the difference in D-statistics between future species overlap and current species overlap was calculated.

Mapping Overlap, Gains, and Losses in QGIS

All raster mapping of overlap, gains, and losses was done in QGIS (QGIS.org). To perform these analyses the grid cells in the rasters were first reclassified from a continuous probability between zero and 1 to one of three numeric categories: 0 - 0.25 = 0; 0.25 - 0.75 = 1; 0.75 - 1.0 = 2. These numeric categories represent no probability of suitable niche (0), low probability of suitable niche (1), and high probability of suitable niche (2). This reclassification of the current and future rasters simplified the mathematical calculations of overlap and gains and losses.

To conduct the gain loss analysis for each species and visualize the shifting location of the niche, the current suitable niche raster (containing values from 0-2) was subtracted from each of the future suitable niche rasters (also containing values from 0-2) to determine where there were gains and losses. This resulted in five categories of gains and loss: high loss (-2), low loss (-1), no change (0), low gain (1), high gain (2). This analysis was repeated for all future climate scenarios for every species.

SSP3-7.0 was the only emissions scenario used for the mapping analysis of overlap between species and the gain loss of that overlap. It was the only emissions scenario used because it represents a reasonable extreme scenario (Hausfather & Peters, 2020). To conduct the analysis of overlap between species, the rasters of two different species in the SSP3-7.0 climate scenario and the same time frame were multiplied together. This resulted in rasters with four categories: no overlap (0), shared low suitability (1), mixed suitability (2), and shared high suitability (4). To conduct the gain loss analysis of overlap between species, the current overlap maps (containing values from 0-4) were subtracted from the future overlap maps (also containing values from 0-4). This resulted in nine overlap gain loss categories: high loss (-4), moderate high loss (-3), moderate low loss (-2), low loss (-1), no change (0), low gain (1), moderate low gain (2), moderate high gain (3), and high gain (4).

RESULTS

Model Significance

The model approach was deemed appropriate for all species. All replicate models had an AUC above 90%, aligned omission rates with the predicted omission rate, and the jacknife assessments showed no outliers in variable importance. The singular *V. membranaceum, B. insularis, B. melanopygus,* and *B. mixtus* model runs used in the projections all had an AUC above 90%, as well as omission rates and jacknife assessments that were all consistent with the 100 replicate models. However, the singular *B. melanopygus* model had to be rerun for SSP3-7.0 at 2081-2100 and SSP5-8.5 in 2061-2080 due to inconsistencies with the replicate models. Additionally, the singular *B. mixtus* model had to be rerun for SSP3-7.0 at 2041-2060 due to inconsistencies with the replicate models.

Aim 1: Comparison of species current and future projections

Shifts in Suitable Niche Space

All of the D-statistics between the current and future climate scenarios for all species were less than 1, indicating a shift in suitable niche space for all species under all future climate scenarios (Table 1).

Shifts in Suitable Niche Across Time

Vaccinium membranaceum, Bombus mixtus, and *Bombus insularis* all had a larger shift in suitable niche as time increased for SSP3-7.0 and SSP5-8.5, but not SSP1-2.6. In both SSP3-7.0 and SSP5-8.5, the D-statistics for each species' suitable niche became smaller as time increased, indicating a larger shift in suitable niche space as time increased (Table 1). In SSP1-2.6, the D-statistics for each species' suitable niche decreased between the early-century and mid-century model projections, but then had a slight increase that was higher than the mid-century D-statistic but was still lower than the early-century D-statistic (Table 1). This indicates that while each species' suitable niche experienced an initial shift that became larger through the mid-century in SSP1-2.6, there was a small shift back towards the location of the current predicted suitable niche by the end of the century.

B. melanopygus, however, had a larger shift in suitable niche as time increased for SSP3-7.0, but not for SSP1-2.6 or SSP5-8.5. In SSP3-7.0, the D-statistic became smaller as time increased, indicating a larger shift in suitable niche space as time increased (Table 1). In SSP1-2.6, the D-statistic was low in the early-century model projection and increased across the mid-century and late-century model projections (Table 1). This indicates a large initial shift away from the location of the current predicted suitable niche and a shift back towards the location of the current predicted suitable niche as time increases. In SSP5-8.5, the D-statistic decreased between the early-century and mid-century model projections, but then had a slight increase that was higher than the mid-century D-statistic but was still lower than the early-century D-statistic (Table 1). This indicates that while there was an initial shift that became larger through the mid-century in SSP5-8.5, there was a small shift back towards the location of the current predicted suitable niche by the end of the century.

Shifts in Suitable Niche Across Emissions Scenarios

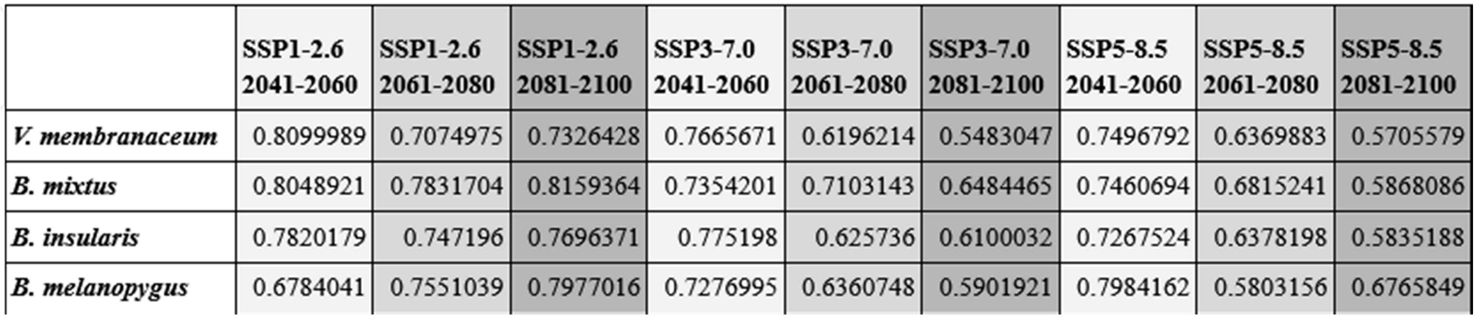
V. membranaceum had a larger shift in suitable niche space as emissions scenarios worsened in the early-century model projections, but not in the mid or late-century model projections. In the early-century projections the D-statistic became smaller across emissions scenarios, indicating a larger shift in suitable niche space as emissions scenarios worsen (Table 1). In the mid and late-century projections, the D-statistic was smallest in SSP3-7.0, followed by SSP5-8.5, with SSP1-2.6 having the largest D-statistic (Table 1). This indicates a larger shift in suitable niche space under both SSP3-7.0 and SSP5-8.5 than under SSP1-2.6, but a smaller shift under SSP5-8.5, the worst-case scenario, than under SSP3-7.0 in the mid and late-century projections.

B. mixtus had a larger shift in suitable niche space as emissions scenarios worsened in the mid and late-century model projections, but not in the early-century model projections. In the mid and late-century projections the D-statistic became smaller across emissions scenarios, indicating a larger shift in suitable niche space as emissions scenarios worsen (Table 1). In the early-century projections, the D-statistic was smallest in SSP3-7.0, followed by SSP5-8.5, with SSP1-2.6 having the largest D-statistic (Table 1). This indicates a larger shift in suitable niche space under both SSP3-7.0 and SSP5-8.5 than under SSP1-2.6, but a smaller shift under SSP5-8.5, the worst-case scenario, than under SSP3-7.0 in the early-century projections.

B. insularis had a larger shift in suitable niche space as emissions scenarios worsened in the early and late-century model projections, but not in the mid-century model projections. In the early and late-century projections the D-statistic became smaller across emissions scenarios, indicating a larger shift in suitable niche space as emissions scenarios worsened (Table 1). In the mid-century projections, the D-statistic was smallest in SSP3-7.0, followed by SSP5-8.5, with SSP1-2.6 having the largest D-statistic (Table 1). This indicates a larger shift in suitable niche space under both SSP3-7.0 and SSP5-8.5 than under SSP1-2.6, but a smaller shift under SSP5-8.5, the worst-case scenario, than under SSP3-7.0 in the mid-century projections.

B. melanopygus had a larger shift in suitable niche space as emissions scenarios worsened in the mid-century model projections, but not in the early or late-century model projections. In the mid-century projections the D-statistic became smaller across emissions scenarios, indicating a larger shift in suitable niche space as emissions scenarios worsened (Table 1). In the early-century model projections, the D-statistic was lowest in SSP1-2.6 and increased across emissions scenarios (Table 1). This indicates that the shift away from the location of the current predicted suitable niche is smaller as emissions scenarios worsen in the early century. In the late-century model projections, the D-statistic was smallest in SSP3-7.0, followed by SSP5-8.5, with SSP1-2.6 having the largest D-statistic (Table 1). This indicates a larger shift in suitable niche space under both SSP3-7.0 and SSP5-8.5 than under SSP1-2.6, but a smaller shift under SSP5-8.5, the worst-case scenario, than under SSP3-7.0 in the late-century projections.

Table 1. D-statistic measurements of current to future suitable niche overlap. The modeled suitable niche for each species is projected onto the current and future climates under three different emissions scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5) and at three different time frames (2041-2060, light grey; 2061-2080, medium grey; and 2081-2100, dark grey). Rasters from the projections were analyzed and a value of 1 indicates complete overlap and a value of 0 indicates no overlap.



	SSP1-2.6 2041-2060	**SSP1-2.6 2061-2080**	**SSP1-2.6 2081-2100**	**SSP3-7.0 2041-2060**	**SSP3-7.0 2061-2080**	**SSP3-7.0 2081-2100**	**SSP5-8.5 2041-2060**	**SSP5-8.5 2061-2080**	**SSP5-8.5 2081-2100**
V. membranaceum	0.8099989	0.7074975	0.7326428	0.7665671	0.6196214	0.5483047	0.7496792	0.6369883	0.5705579
B. mixtus	0.8048921	0.7831704	0.8159364	0.7354201	0.7103143	0.6484465	0.7460694	0.6815241	0.5868086
B. insularis	0.7820179	0.747196	0.7696371	0.775198	0.625736	0.6100032	0.7267524	0.6378198	0.5835188
B. melanopygus	0.6784041	0.7551039	0.7977016	0.7276995	0.6360748	0.5901921	0.7984162	0.5803156	0.6765849

Geographical Distribution of Suitable Niche Gains and Losses: Vaccinium membranaceum

The suitable niche of *V. membranaceum* had gains in the north and losses in the south across all emissions scenarios (Fig. 7, Fig. 8, Fig. 9). In SSP1-2.6, the mid-century and late-century projections each had greater losses in the south than the early-century projection (Fig. 7).

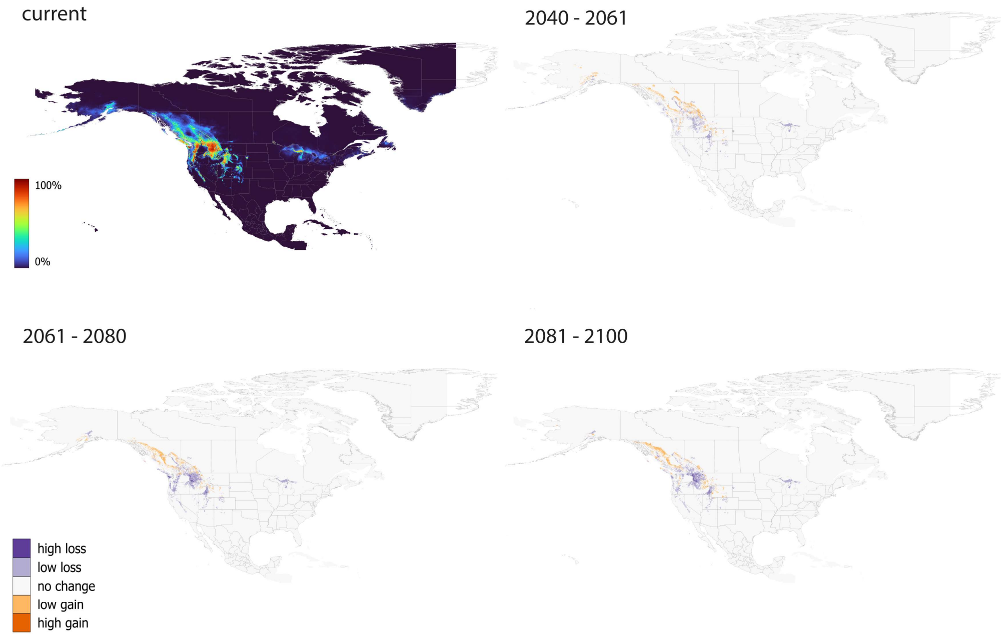


Figure 7. Suitable niche gain loss comparison for *Vaccinium membranaceum* under SSP1-2.6. The modeled suitable niche for *V. membranaceum* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP3-7.0 the mid-century and late-century projections each had greater gains and losses of suitable niche compared to the early-century projection (Fig. 8).

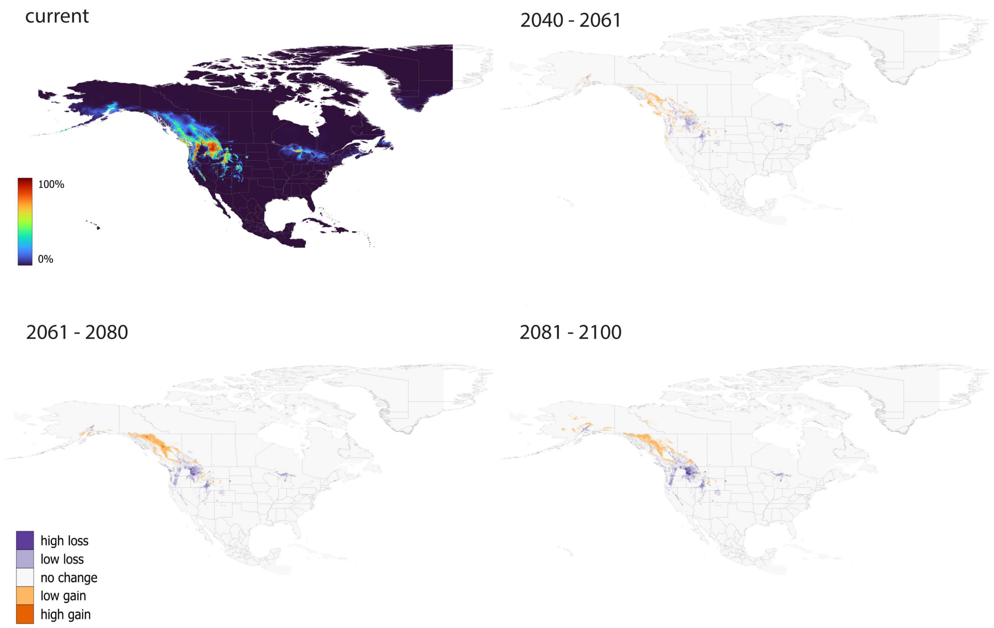


Figure 8. Suitable niche gain loss comparison for *Vaccinium membranaceum* under SSP3-7.0. The modeled suitable niche for *V. membranaceum* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP5-8.5 the mid-century and late-century projections each had greater gains and losses of suitable niche compared to the early-century projection (Fig. 9).

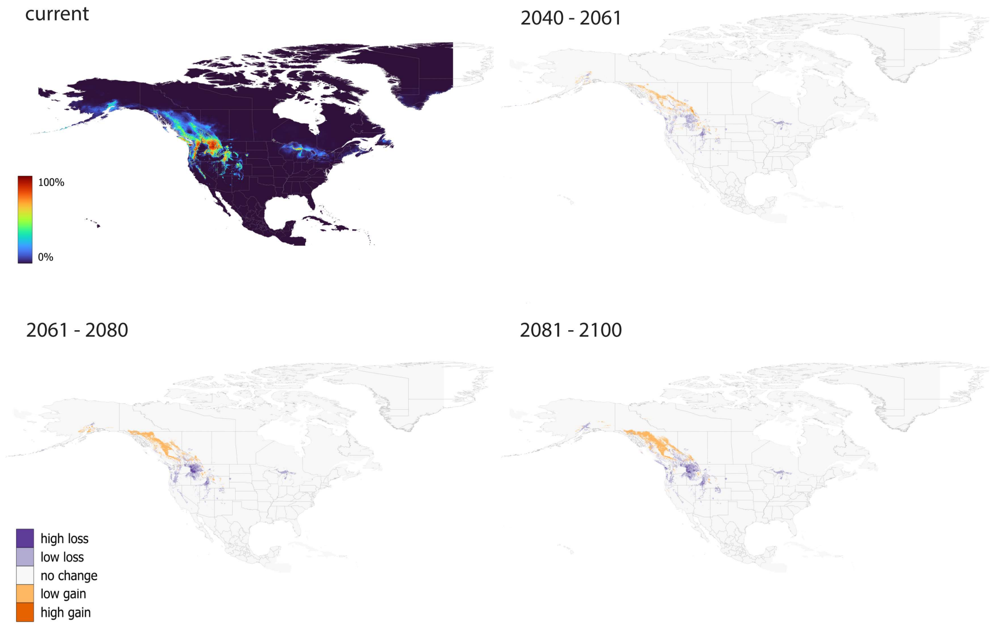


Figure 9. Suitable niche gain loss comparison for *Vaccinium membranaceum* under SSP5-8.5. The modeled suitable niche for *V. membranaceum* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

Geographical Distribution of Suitable Niche Gains and Losses: Bombus mixtus

The suitable niche of *B. mixtus* had geographically interspersed gains and losses across all emissions scenarios, with some concentration of loss at higher latitudes (Fig. 10, Fig. 11, Fig. 12). In SSP1-2.6, the gains and losses were visually similar across all three timeframes (Fig. 10).

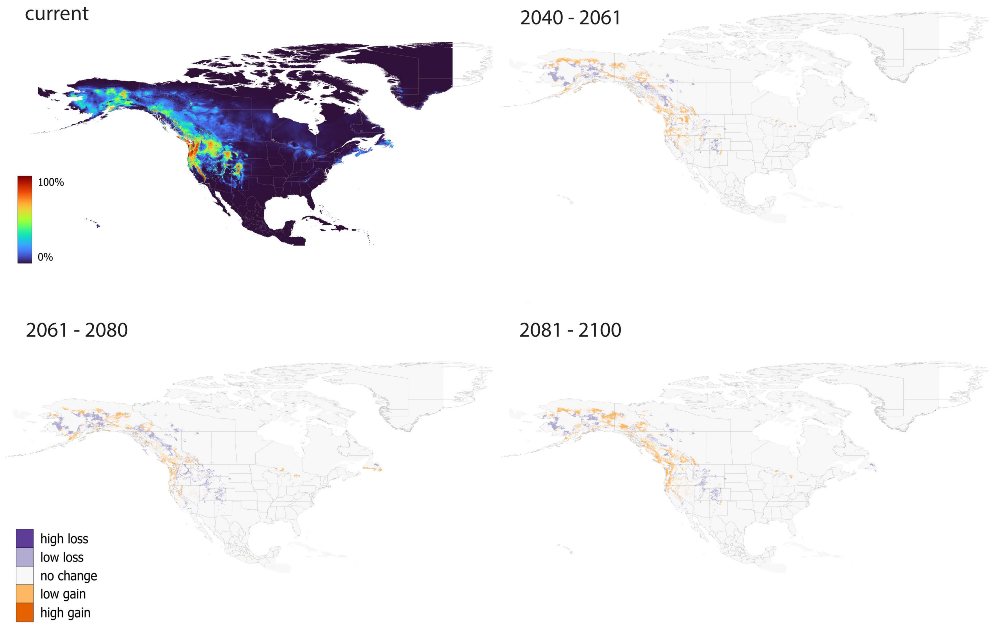
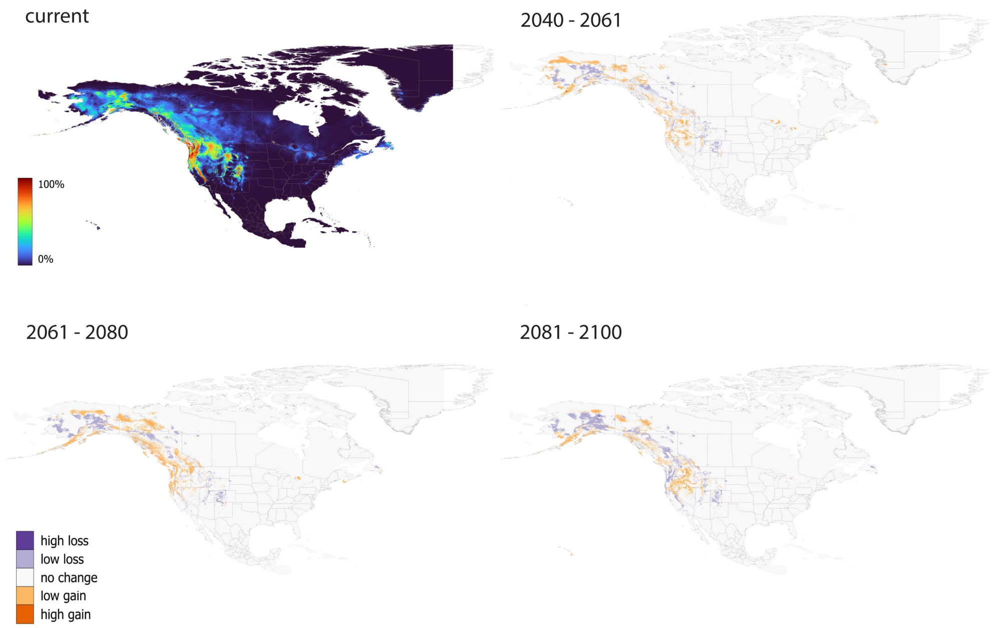


Figure 10. Suitable niche gain loss comparison for *B. mixtus* under SSP1-2.6. The modeled suitable niche for *B. mixtus* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP3-7.0 the gains and losses were slightly more dramatic in the mid-century and late-century projections than the early-century projections (Fig. 11). There were noticeably more losses in Alaska for the mid-century and late-century projections as well as slightly more high gain areas across the suitable niche. Additionally, in the early-century projection there was a section of gained suitable niche overlap in Alaska that was not present in the mid-century or late-century projections.


current

2040 - 2061

2061 - 2080

2081 - 2100

Figure 11. Suitable niche gain loss comparison for *B. mixtus* under SSP3-7.0. The modeled suitable niche for *B. mixtus* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP5-8.5 the southern gains and losses were greater in the mid-century and late-century (Fig. 12). The northernmost patches of suitable niche overlap gain that were present in the early and mid-century, mostly disappeared in the late-century. In addition, there was an increase in loss in the north.

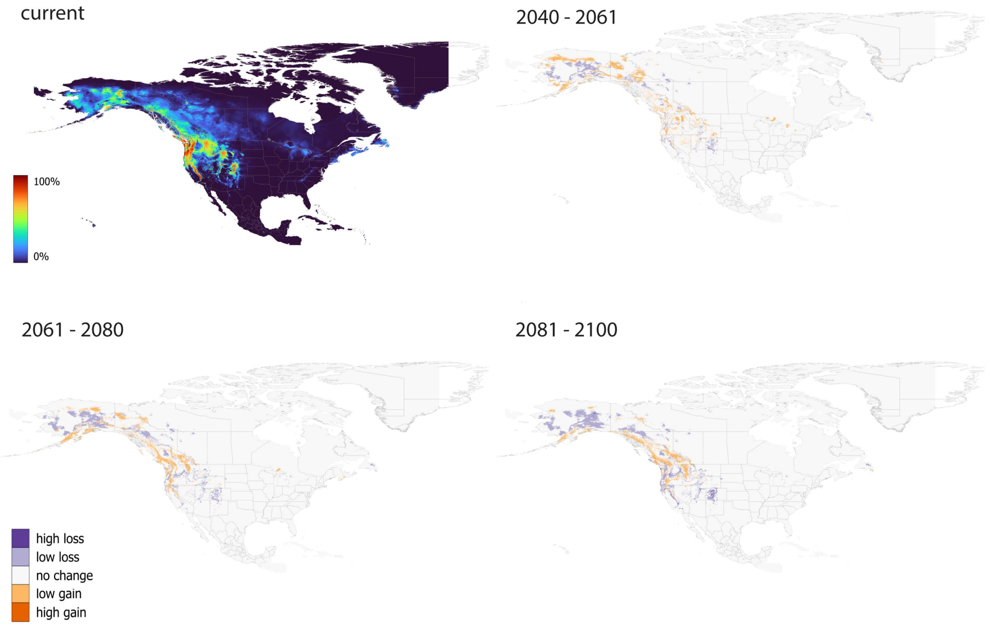


Figure 12. Suitable niche gain loss comparison for *B. mixtus* under SSP5-8.5. The modeled suitable niche for *B. mixtus* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

Geographical Distribution of Suitable Niche Gains and Losses: Bombus insularis

The suitable niche of *B. insularis* had gains in the north and losses in the south across all emissions scenarios (Fig. 13, Fig. 14, Fig. 15). In SSP1-2.6 the gains and losses of suitable niche were visually similar across all three timeframes (Fig. 13).

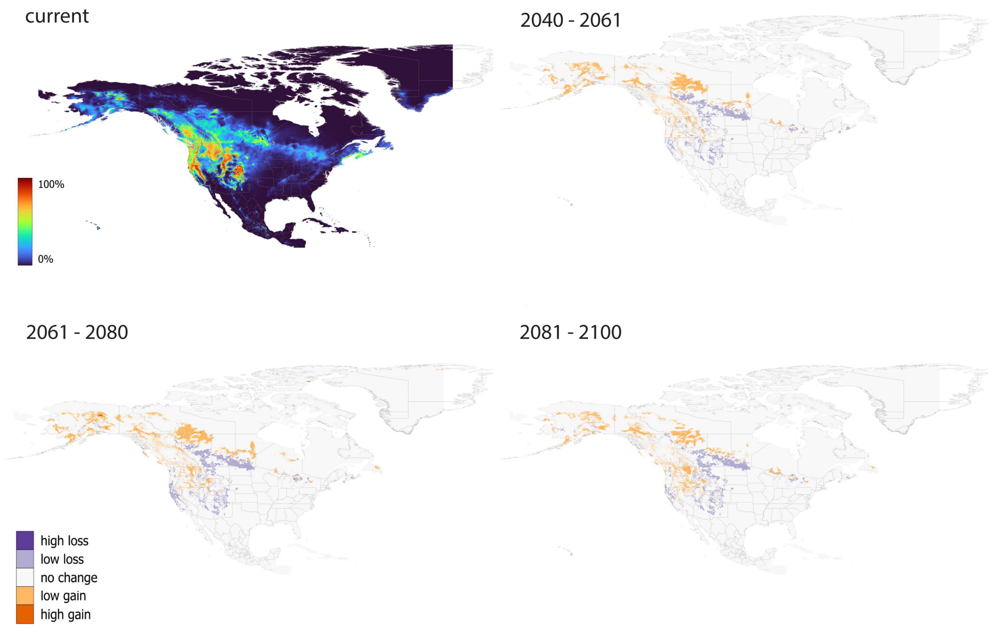


Figure 13. Suitable niche gain loss comparison for *B. insularis* under SSP1-2.6. The modeled suitable niche for *B. insularis* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP3-7.0 the mid-century and late-century projections each had greater northern gains of suitable niche compared to the early-century projection (Fig.

14). In addition, the late-century projection had greater loss in the south compared to early-century and mid-century projections.

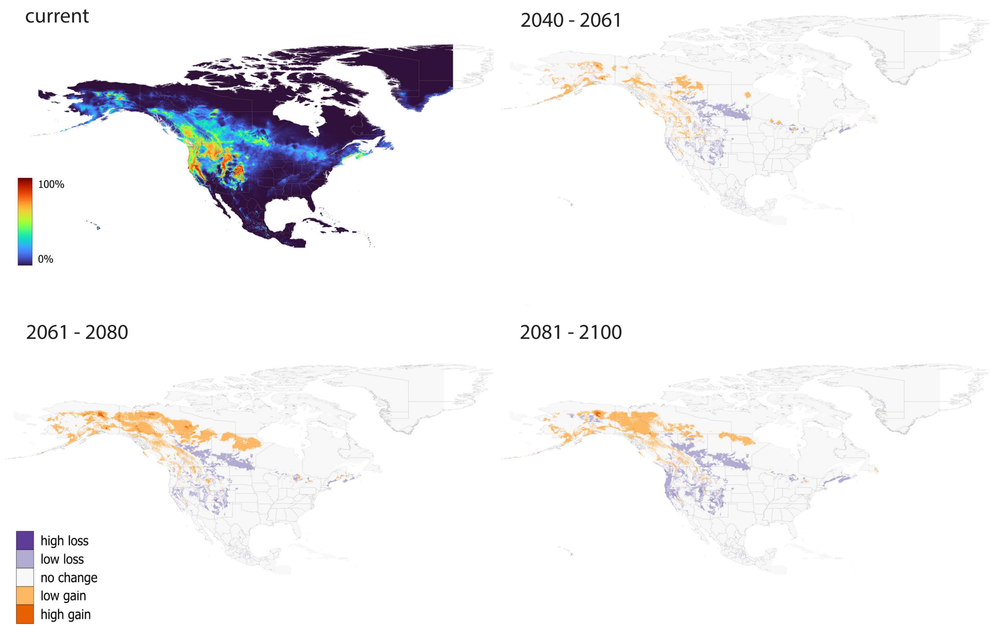


Figure 14. Suitable niche gain loss comparison for *B. insularis* under SSP3-7.0. The modeled suitable niche for *B. insularis* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP5-8.5 the gains and losses of suitable niche were visually similar across all three timeframes (Fig. 15). However, the southern losses were greater in the mid-century and late-century projections compared to the early-century projection.

Additionally, the mid-century and late-century projections each had greater gain in the north than the early-century projection.

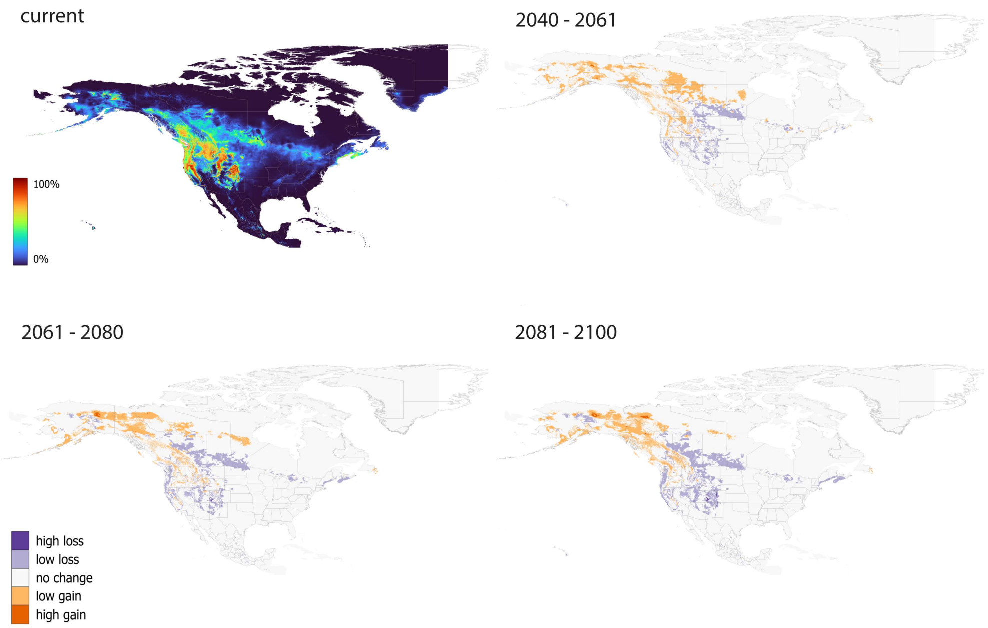


Figure 15. Suitable niche gain loss comparison for *B. insularis* under SSP5-8.5. The modeled suitable niche for *B. insularis* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

Geographical Distribution of Suitable Niche Gains and Losses: Bombus melanopygus

The suitable niche of *B. melanopygus* had geographically interspersed gains and losses across all emissions scenarios (Fig. 16, Fig. 17, Fig. 18). In

SSP1-2.6, there were greater losses in the early-century projection than in either the mid-century or late-century projections. The late-century projection appeared to have the most gain of suitable niche (Fig. 16).

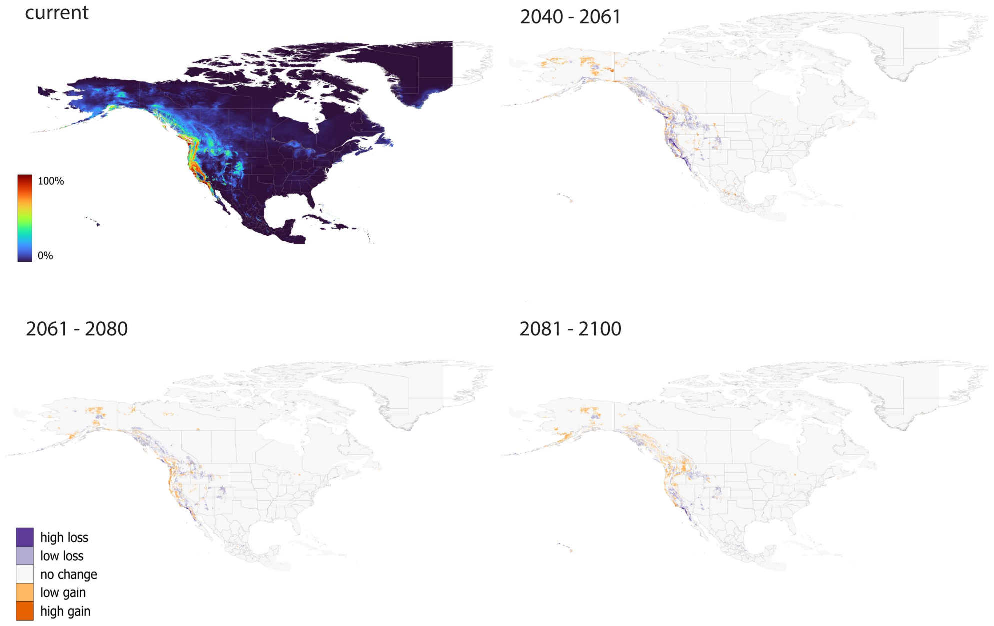


Figure 16. Suitable niche gain loss comparison for *B. melanopygus* under SSP1-2.6. The modeled suitable niche for *B. melanopygus* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP3-7.0, the suitable niche gains were concentrated near the areas of current high suitable niche probability (Fig. 17). The visual spread of the suitable niche gains increased as time increased.

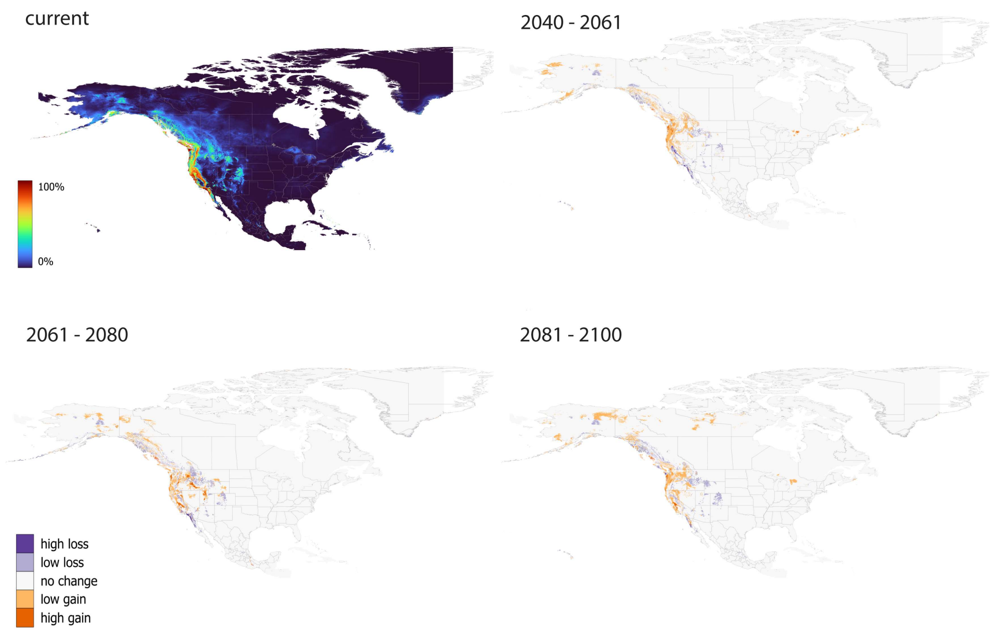


Figure 17. Suitable niche gain loss comparison for *B. melanopygus* under SSP3-7.0. The modeled suitable niche for *B. melanopygus* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

In SSP5-8.5 the suitable niche gains were concentrated near the areas of current high suitable niche probability (Fig. 18). The mid-century and late-century projections had greater loss and gain than the early-century projection.

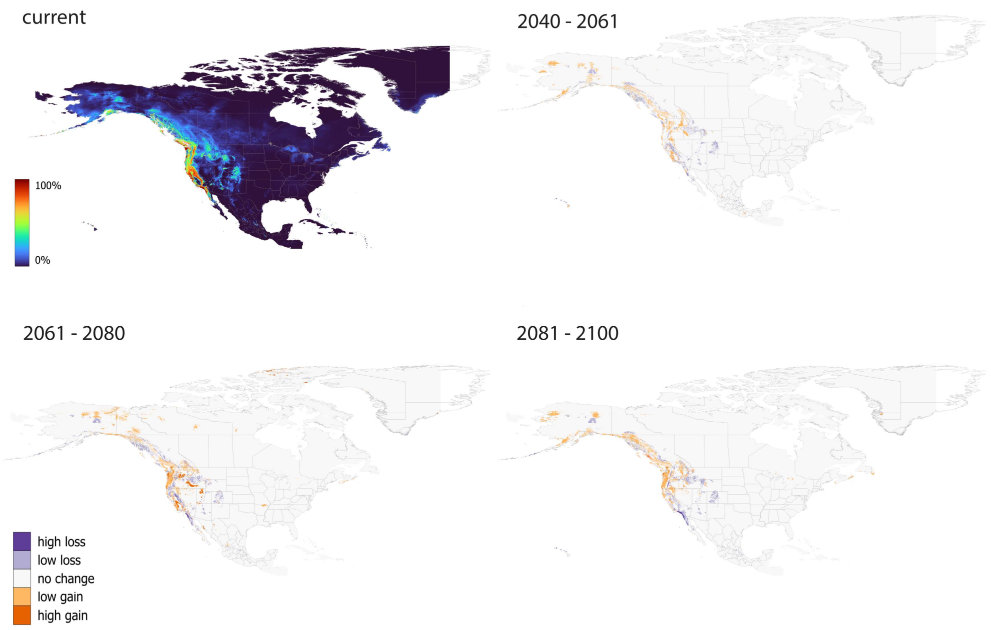


Figure 18. Suitable niche gain loss comparison for *B. melanopygus* under SSP5-8.5. The modeled suitable niche for *B. melanopygus* is projected onto the current climate to map current suitable niche probability. Warmer colors represent high probability of suitability and cooler colors represent low probability of suitability. The gains and losses of suitable niche at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing model projections onto the climate from these time periods to projections onto the current climate (top left). Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in five possible categories of change. Dark purple represents high loss, and dark orange represents high gain.

Aim 2: Comparison of species overlap

Shifts in Plant and Pollinator Suitable Niche Space Overlap

There was a loss of plant and pollinator suitable niche overlap in every future climate scenario for the *B. insularis*/*V. membranaceum* and *B. melanopygus/V. membranaceum* species overlap comparisons but not for the *B. mixtus/V. membranaceum* comparison. The difference in D-statistics for both *B. insularis*/*V. membranaceum* and *B. melanopygus/V. membranaceum* were negative in all future climate scenarios compared to the present, indicating an overarching loss of suitable niche overlap (Table 2, Table 3). The difference in D-statistics for *B. mixtus/V. membranaceum* was negative under SSP1-2.6 at the mid and late-century, SSP3-7.0 at the early and late-century, and SSP5-8.5 at the early-century (Table 4). However, it was positive under SSP1-2.6 at the early-century, SSP3-7.0 at the mid-century, and SSP5-8.5 at the mid and late-century (Table 4). This indicates that there was no overall trend of loss of species overlap in future climate scenarios for *B. mixtus/V. membranaceum.*

Suitable Niche Overlap Comparison: Bombus insularis and Vaccinium membranaceum

The comparison between *B. insularis* and *V. membranaceum* showed an increasing loss of suitable niche overlap over time under SSP1-2.6, but not under SSP3-7.0 or SSP5-8.5. Under SSP1-2.6, the difference in D-statistics was increasingly negative over time, indicating a loss of suitable niche overlap over time (Table 2). Under SSP3-7.0 and SSP5-8.5, the difference in D-statistics was negative for all timeframes, however after becoming increasingly negative between the early and mid-century comparisons, it became slightly less negative in the late-century comparison while still being more negative than at the early-century (Table 2). This indicates an overall loss of suitable niche overlap, with a slight regain of suitable niche overlap in the late-century under both SSP3-7.0 and SSP5-8.5.

The comparison between *B. insularis* and *V. membranaceum* showed an increasing loss of suitable niche overlap as emissions scenarios worsened in the early-century, but not the mid-century or late-century. In the early-century, the difference in D-statistics was increasingly negative as emissions scenarios worsened, indicating an increased loss of suitable niche overlap as emissions scenarios worsened (Table 3). In the mid-century, the difference in D-statistics was negative under SSP1-2.6, became more negative under SSP3-7.0, and then less negative under SSP5-8.5 though still more negative than SSP1-2.6 (Table 2). This indicates an overall loss of suitable niche overlap, but not a consistent decrease in suitable niche overlap as emissions scenarios worsen. In the late-century, the difference in D-statistics was negative under SSP1-2.6, became less negative under SSP3-7.0, and then again became more negative under SSP5-8.5 though not as negative as SSP1-2.6 (Table 2). This indicates an overall loss of suitable niche overlap, but not a consistent decrease in suitable niche overlap as emissions scenarios worsen.

Table 2. Differences in D-statistic measurements of overlap between *V. membranaceum* and *B. insularis* comparing future scenario overlap to current overlap. The future scenarios included SSP1-2.6, SSP3-7.0, and SSP5-8.5 at all three time frames (2041-2060, 2061-2080, and 2081-2100).

B. insularis and *V. membranaceum*			
current overlap 0.4404038	**SSP1-2.6 difference in overlap**	**SSP3-7.0 difference in overlap**	**SSP5-8.5 difference in overlap**
2041-2060	-0.01818	-0.02723	-0.03891
2061-2080	-0.03394	-0.08354	-0.0447
2081-2100	-0.0794	-0.04165	-0.04332

Under SSP3-7.0, the location of the suitable niche overlap between *V. membranaceum* and *B. insularis* had a northward expansion over time, but maintained the southern edge of overlap in California (Fig. 19). However, the range of overlap is smaller in the mid-century and late-century projections than the current and early-century projections. Additionally, the areas of high suitable niche overlap are decreasing over time (Fig. 19).

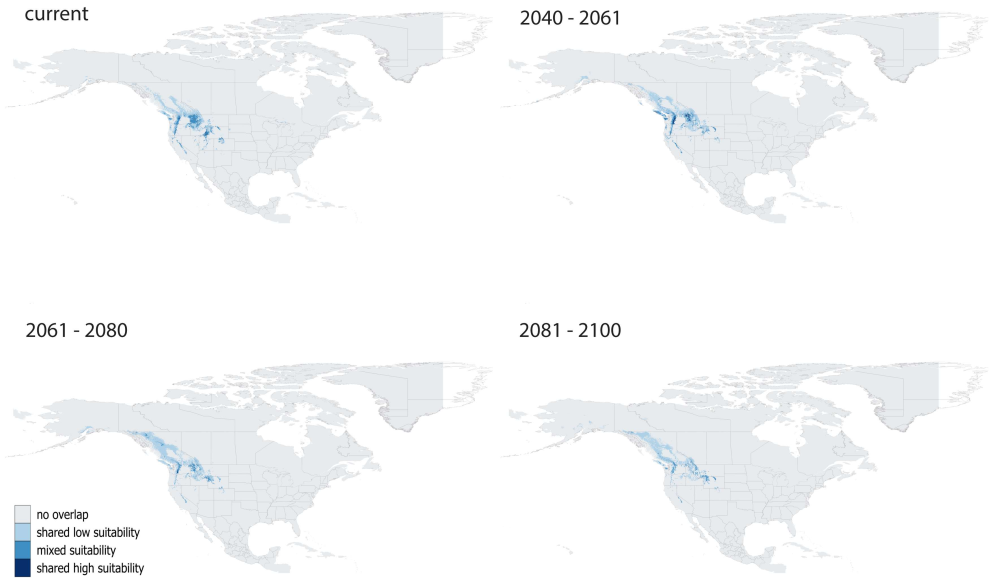


Figure 19. Suitable niche overlap between *Vaccinium membranaceum* and *Bombus insularis* under SSP3-7.0. The suitable niche overlap between the species at the present (top left), early century (top right), mid century (bottom left), and late century (bottom right) was calculated by comparing *V. membranaceum* model projections onto the climate from a given time period to those for *B. insularis*. Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in four possible categories of suitability overlap. The blue shading indicates suitable niche overlap, with darker blue indicating a higher level of shared suitability.

Suitable Niche Overlap Comparison: Bombus melanopygus and Vaccinium membranaceum

The comparison between *B. melanopygus* and *V. membranaceum* showed an increasing loss of suitable niche overlap over time under SSP3-7.0, but not under SSP1-2.6 or SSP5-8.5. Under SSP1-2.6, the difference in D-statistics was negative for all timeframes, however the difference became overall less negative over time (Table 3). This indicates a decrease in loss of suitable niche overlap over time. Under SSP3-7.0, the difference in D-statistics was increasingly negative as time increased, indicating a loss of suitable niche overlap over time (Table 3). Under SSP5-8.5, the difference in D-statistics was negative for all timeframes, however after becoming increasingly negative between the early and mid-century comparisons, it became slightly less negative in the late-century comparison while still being more negative than at the early-century (Table 3). This indicates an overall loss of suitable niche overlap, with a slight regain of suitable niche overlap in the late-century.

The comparison between *B. melanopygus* and *V. membranaceum* did not show an increasing loss of suitable niche overlap as emissions scenarios worsened. In the early-century, the difference in D-statistics was negative under SSP1-2.6 and became less negative as emissions scenarios worsened (Table 3). This indicates that there is an overall loss in suitable niche overlap, but the amount of loss decreases as emissions scenarios worsened. In both the mid-century and late-century, the difference in D-statistics was negative under SSP1-2.6, became more negative under SSP3-7.0, and then less negative under SSP5-8.5 though still more negative than SSP1-2.6 (Table 3). This indicates an overall loss of suitable niche overlap, but not a consistent decrease in suitable niche overlap as emissions scenarios worsened.

Table 3. Differences in D-statistic measurements of overlap between *V. membranaceum* and *B. melanopygus* comparing future scenario overlap to current overlap. The future scenarios included SSP1-2.6, SSP3-7.0, and SSP5-8.5 at all three time frames (2041-2060, 2061-2080, and 2081-2100).

B. melanopygus and *V. membranaceum*			
current overlap 0.4640853	**SSP1-2.6 difference in overlap**	**SSP3-7.0 difference in overlap**	**SSP5-8.5 difference in overlap**
2041-2060	-0.10558	-0.05451	-0.04834
2061-2080	-0.09602	-0.14079	-0.13236
2081-2100	-0.08665	-0.2005	-0.1127

Under SSP3-7.0, the location of suitable niche overlap between *V. membranaceum* and *B. melanopygus* stayed relatively consistent over time (Fig. 20). There are more areas of shared high suitability at the early-century compared to the present, however by the late-century those areas of shared high suitability have decreased (Fig. 20). Overall, the range of suitable niche overlap decreases over time (Fig. 20).

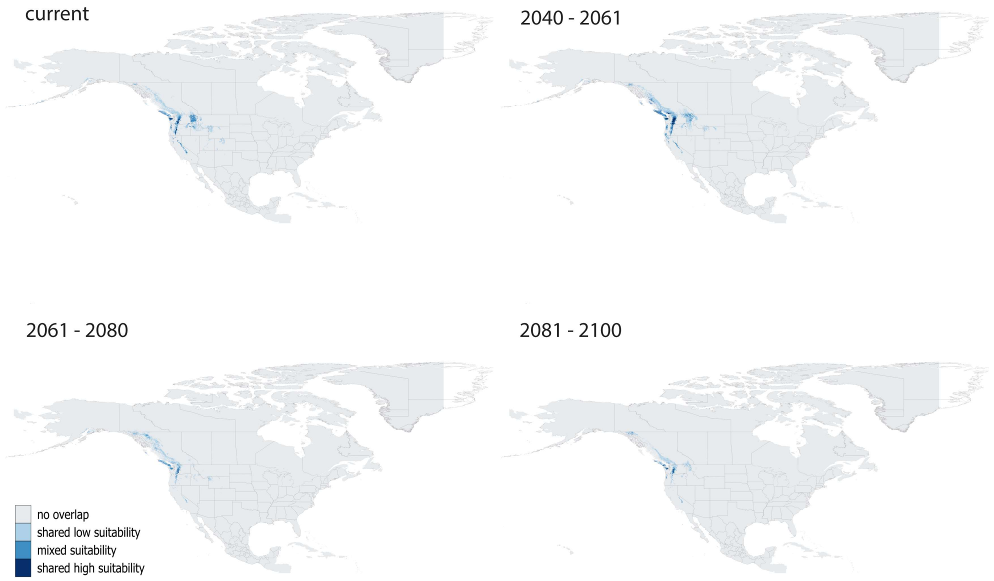


Figure 20. Suitable niche overlap between *Vaccinium membranaceum* and *Bombus melanopygus* under SSP3-7.0. The suitable niche overlap between the species at the present (top left), early century (top right), mid century (bottom left), and late century (bottom right) was calculated by comparing *V. membranaceum* model projections onto the climate from a given time period to those for *B. melanopygus*. Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in four possible categories of suitability overlap. The blue shading indicates suitable niche overlap, with darker blue indicating a higher level of shared suitability.

Suitable Niche Overlap Comparison: Bombus mixtus and Vaccinium membranaceum

The comparison between *B. mixtus* and *V. membranaceum* did not show an increasing loss of suitable niche overlap over time. Under SSP1-2.6, the difference in D-statistics was positive for early-century compared to present, indicating a small gain of overlap in the early-century (Table 4). However, the difference in D-statistics was increasingly negative in the mid and late-century comparisons under SSP1-2.6, indicating a loss of suitable niche overlap that increased slightly in magnitude from the mid to late-century (Table 4). Under SSP3-7.0, the difference in D-statistics was negative in the early-century comparison, positive in the mid-century comparison, and again negative in the late-century comparison (Table 4). This indicates an initial loss of suitable niche overlap in the early century, followed by a slight gain in the mid-century and then another slight loss. Under SSP5-8.5, the difference in D-statistics was negative for early-century compared to present, indicating an initial loss of suitable niche overlap in the early-century (Table 4). However, the difference in D-statistics was increasingly positive in the mid and late-century comparisons for SSP5-8.5, indicating an increase in suitable niche overlap in the mid and late-century (Table 4).

The comparison between *B. mixtus* and *V. membranaceum* did not show an increasing loss of suitable niche overlap as emissions scenarios worsened. In the early-century, the difference in D-statistics was positive under SSP1-2.6, became negative under SSP3-7.0, and then slightly less negative under SSP5-8.5 (Table 4). This indicates a loss of suitable niche overlap as emissions scenarios worsened from SSP1-2.6 to SSP3-7.0/585, and a gain of suitable niche overlap from SSP3-7.0 to SSP5-8.5. In the mid-century, the difference in D-statistics was negative under SSP1-2.6, became positive under SSP3-7.0 and increasingly positive under SSP5-8.5 (Table 4). This indicates increasing suitable niche overlap as emissions scenarios worsen. In the late-century, the difference in D-statistics was negative under SSP1-2.6, became less negative under SSP3-7.0, and then positive under SSP5-8.5 (Table 4). This also indicates increasing suitable niche overlap as emissions scenarios worsen.

Table 4. Differences in D-statistic measurements of overlap between *V. membranaceum* and *B. mixtus* comparing future scenario overlap to current overlap. The future scenarios included SSP1-2.6, SSP3-7.0, and SSP5-8.5 at all three time frames (2041-2060, 2061-2080, and 2081-2100).

B. mixtus and *V. membranaceum*			
current overlap 0.4811042	**SSP1-2.6 difference in overlap**	**SSP3-7.0 difference in overlap**	**SSP5-8.5 difference in overlap**
2041-2060	0.016633	-0.03786	-0.00656
2061-2080	-0.01538	0.007788	0.025329
2081-2100	-0.04222	-0.01875	0.087374

Under SSP3-7.0, the location of the suitable niche overlap between *V. membranaceum* and *B. mixtus* had a northward expansion over time, but maintained the southern edge of overlap in California (Fig. 21). The degree of overlap is smaller in the mid-century and late-century projections than the current and early-century projections (Fig. 21). The areas of high suitable niche overlap decreased over time (Fig. 21).

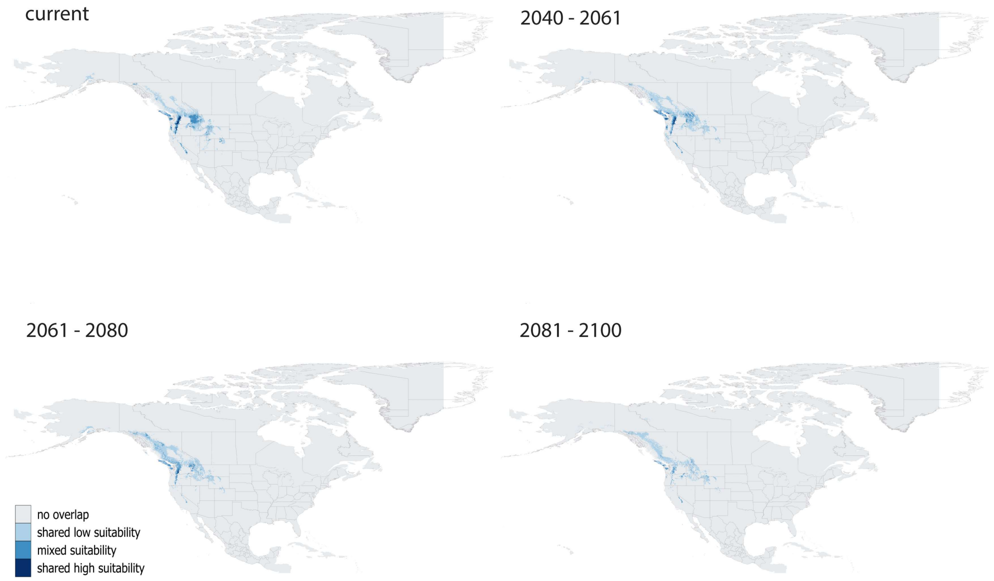
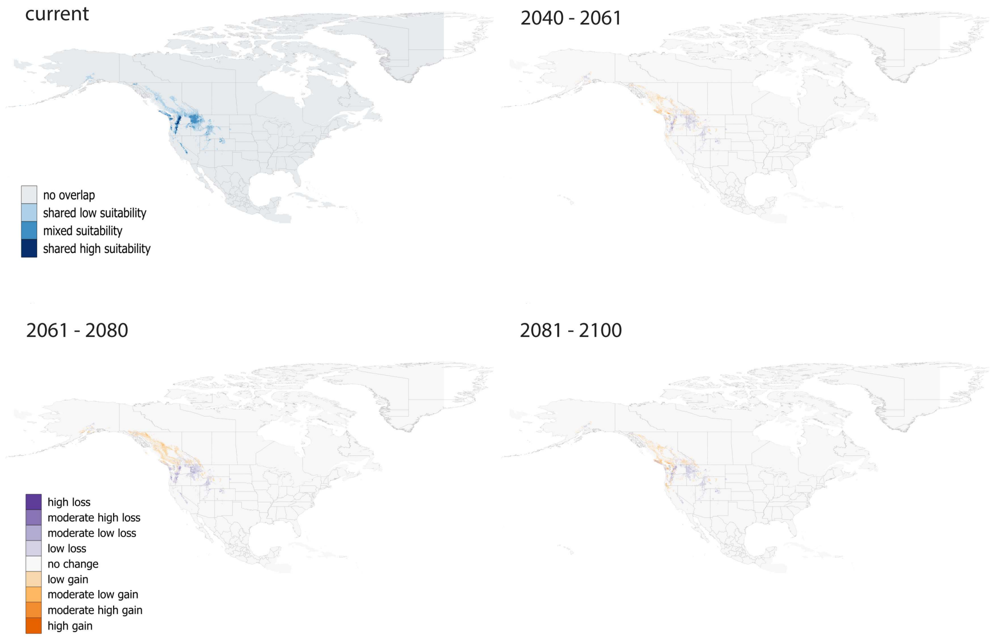


Figure 21. Suitable niche overlap between *Vaccinium membranaceum* and *Bombus mixtus* under SSP3-7.0. The suitable niche overlap between the species at the present (top left), early century (top right), mid century (bottom left), and late century (bottom right) was calculated by comparing *V. membranaceum* model projections onto the climate from a given time period to those for *B. mixtus*. Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in four possible categories of suitability overlap. The blue shading indicates suitable niche overlap, with darker blue indicating a higher level of shared suitability.

Gain and Loss of Suitable Niche Overlap for SSP3-7.0

The suitable niche overlap of *V. membranaceum* and *B. mixtus* displayed gains of overlap in the north and losses in the south and were similar across all timeframes (Fig. 22). The mid-century had a greater gain in the north than the early-century and late-century (Fig. 22).


current

2040 - 2061

2061 - 2080

2081 - 2100

Figure 22. Gain and loss of suitable niche overlap between *Vaccinium membranaceum* and *Bombus mixtus* under SSP3-7.0. The current suitable niche overlap (upper left) was calculated by comparing the *V. membranaceum* model projection onto the current climate to the *B. mixtus* model projection onto the current climate. Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in four possible categories of suitability overlap. The blue shading indicates suitable niche overlap, with the darker blue indicating a higher level of shared suitability. The gains and losses of suitable niche overlap at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing the species niche overlap in these time periods (see Figure 21) to the species niche overlap in the present (top left). These calculations resulted in nine categories of gains and losses. Dark purple represents high loss, and dark orange represents high gains.

The suitable niche overlap of *V. membranaceum* and *B. insularis* displayed gains of overlap in the north and losses in the south across all timeframes (Fig. 23). The mid-century and late-century had greater gains and losses and spread of gains and losses than the early-century (Fig. 23).

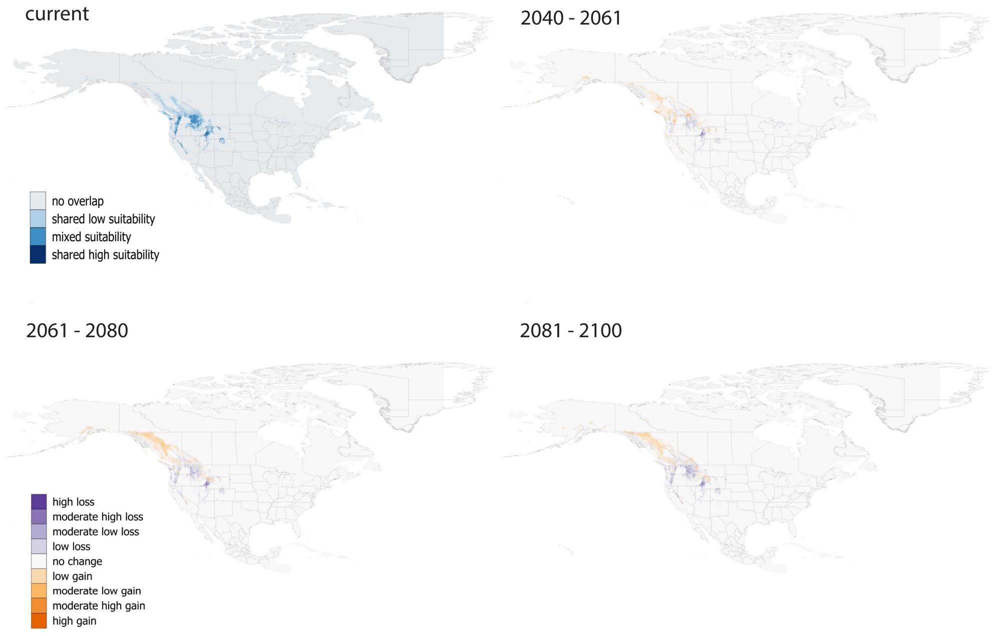


Figure 23. Gain and loss of suitable niche overlap between *Vaccinium membranaceum* and *Bombus insularis* under SSP3-7.0. The current suitable niche overlap (upper left) was calculated by comparing the *V. membranaceum* model projection onto the current climate to the *B. insularis* model projection onto the current climate. Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in four possible categories of suitability overlap. The blue shading indicates suitable niche overlap, with the darker blue indicating a higher level of shared suitability. The gains and losses of suitable niche overlap at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing the species niche overlap in these time periods (see Figure 19) to the species niche overlap in the present (top left). These calculations resulted in nine categories of gains and losses. Dark purple represents high loss, and dark orange represents high gains.

The suitable niche overlap of *V. membranaceum* and *B. melanopygus* was different in each time frame, but overall the gains were concentrated in the north and losses were concentrated in the south. The early-century had the most gain in suitable niche overlap, with some areas of loss at the southern edge (Fig. 24). The mid-century had gains in the north and losses in the south (Fig. 24). The late-century map had similar loss in the south as the mid-century map, and additional loss in the north near the areas of gain at the mid-century (Fig. 24).

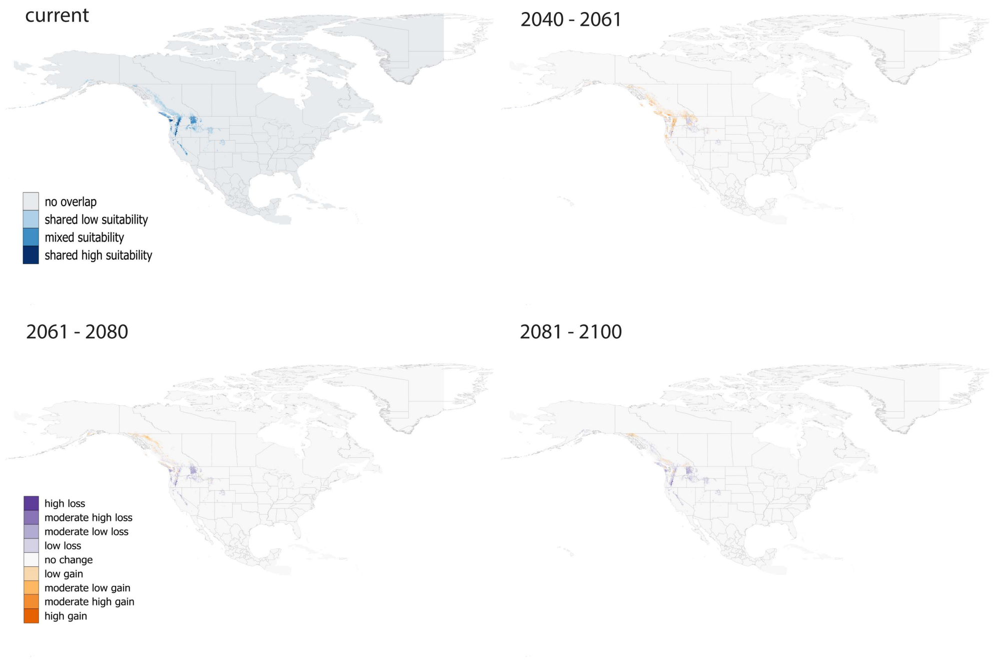


Figure 24. Gain and loss of suitable niche overlap between *Vaccinium membranaceum* and *Bombus melanopygus* under SSP3-7.0. The current suitable niche overlap (upper left) was calculated by comparing the *V. membranaceum* model projection onto the current climate to the *B. melanopygus* model projection onto the current climate. Probabilities of suitability were binned into three categories to simplify the comparison calculations, resulting in four possible categories of suitability overlap. The blue shading indicates suitable niche overlap, with the darker blue indicating a higher level of shared suitability. The gains and losses of suitable niche overlap at the early century (top right), mid century (bottom left), and late century (bottom right) were calculated by comparing the species niche overlap in these time periods (see Figure 20) to the species niche overlap in the present (top left). These calculations resulted in nine categories of gains and losses. Dark purple represents high loss, and dark orange represents high gains.

DISCUSSION

Aim 1: Comparison of species current and future projections

Shifts in Suitable Niche Space: D-statistic

The hypothesis that the location of suitable niche would shift in future climate scenarios was supported for all species in all future climate scenarios. The location of suitable niche was predicted to shift for every species in every future climate scenario, with some variation in the patterns of shift. No matter what level of climate protections are implemented, the location of suitable niche will change. However, in each emissions scenario the shifts have different magnitudes with SSP1-2.6 overall having the least amount of difference in suitable niche location from current to future scenarios. Additionally, all of the species experienced a shift back towards their current suitable niche location in SSP1-2.6. This may be due to the degree of global surface temperature change in SSP1-2.6 being below zero by the end of the century (Hausfather, 2019). With climate protections in place that are aligned with SSP1-2.6, it is possible for the effects of climate change on the suitable niche to be slightly reversed. However, in the other two more severe scenarios the shifts were larger than SSP1-2.6 by the end of the century. Without sufficient climate protections in place, the location of suitable niche of these species will be greatly changed.

Vaccinium membranaceum, *B. mixtus*, and *B. insularis* all displayed the same trends in the way their predicted suitable niche shifted across time in future climate scenarios. However, the way their suitable niche was impacted as emissions scenarios worsened was not consistent. This may have been impacted by the SSP's that were chosen for this study. SSP3-7.0 and SSP5-8.5 have different mean warming amounts, 4.1 degrees Celsius and 5.0 degrees Celsius respectively; however, their overall range of predicted degree increases overlaps (Hausfather, 2019). If temperature plays a large role in the environmental niche model, they may be too similar to display a trend of increased suitable niche shift across emissions scenarios.

Bombus melanopygus was an outlier in comparison to the other three species. While it still displayed a shift in suitable niche and followed some of the trends, there were a few key differences that set it apart. In SSP1-2.6, it had a larger initial shift than the other species, but over time its suitable niche continuously shifted back towards its current prediction. In SSP5-8.5 it was the only species to experience a shift back towards its current suitable niche at the end of the century. The difference between *B. melanopygus* and the other species could be because the unique factors that make up a species' suitable niche can greatly affect the way it will be impacted by climate change. Each species will respond differently to climate change based on its abiotic and biotic requirements, and while there will be overall trends it is important to not over generalize.

Shifts in Suitable Niche Space: Gains and Losses

The locations of gains and losses of suitable niche in future climate scenarios were different in each species, however there were two general categories of the distribution of gains and losses. *Vaccinium membranaceum* and *B. insularis* both had predicted losses in the south and gains in the north. This follows the trend of species ranges shifting poleward due to increasing temperatures from climate change (Chen et al., 2011). Despite having very similar patterns in D-statistics to *V. membranaceum* and *B. insularis*, *B. mixtus* had a very different pattern of gain and loss distribution. *Bombus mixtus* and *B. melanopygus* both displayed interspersed gains and losses that did not seem to have any north-south pattern. It is possible that the environmental niche models of these species depend more heavily on different variables. This might be a demonstration of how differences in niche requirements can affect the response that a species has to climate change.

In all species, the gains and losses became both larger in range and intensity in SSP3-7.0 and SSP5-8.5 compared to SSP1-2.6. This is consistent with the patterns of larger shifts in D-statistics in the higher emissions scenarios and smaller shifts in the lower emissions scenarios. Some species had clear differences in gains and losses between SSP3-7.0 and SSP5-8.5, but others displayed very similar trends between the two scenarios. This is potentially due to the similarities between the two SSP scenarios (Chen et al., 2011). These differences in reaction to emissions scenarios are in line with the idea that each species' unique climate requirements that make up its model causes each species to have a unique reaction to climate change.

Vaccinium membranaceum has a disjunct, or discontinuous, distribution between western North America and the Great Lakes region. This was reflected in its current suitable niche prediction. There is a large area of suitable niche in the Pacific Northwest, which is where the plant is more widespread. The future predictions of suitable niche shifts in this region were consistent with previous studies modeling the future environmental niche of *V. membranaceum* in the Pacific Northwest (Prevéy et al., 2020). My study looked at the Great Lakes region populations in addition to those from the Pacific Northwest. In the current prediction, there was an area of suitable niche located near the Great Lakes region where the plant is found. However, in all future climate scenarios this area experiences dramatic loss with no substantial surrounding gain. The potentially low genetic diversity of populations in that region due to the small size of the population and cloning ability of the plant, which make it less able to adapt to environmental changes, coupled with losses of suitable niche, may mean the plant cannot persist in the Great Lakes region as climate change continues.

Studies on bumble bee suitable niche, as impacted by climate change, display varying results in terms of direction of shift (Martins et al., 2014; Suzuki-Ohno et al., 2020; Martínez-López et al., 2021; Ghisbain et al., 2023). However, the lack of studies on future distribution of bumble bees in North America makes it difficult to make direct comparisons between studies. Sirois-Delisle and Kerr (2018) modeled the distribution of bumble bee species in North America taking into account modeled dispersal ability, however they did not discuss the location of suitable niche shift. Our findings are consistent with their findings that bumble bees may experience range constriction in future climate scenarios. Kerr et al. (2015) analyzed the historical shifts of bumble bee ranges in response to climate change, and their finding that there has been a contraction in the southern range is consistent with my predicted future suitable niche of *B. insularis*. *Bombus mixtus* and *B. melanopygus* both had southern losses, but they were paired with southern gains, northern losses, and northern gains, making their pattern of predicted suitable niche change not consistent with the general historical shifts of bumble bees.

Aim 2: Comparison of species overlap

Future Plant and Pollinator Suitable Niche Space Overlap

The hypothesis that there would be loss of plant and pollinator suitable niche overlap in every future climate scenario was supported for the *B. insularis*/*V. membranaceum* and *B. melanopygus/V. membranaceum* species overlap comparisons, but not for the *B. mixtus/V. membranaceum* comparison. For all species, the current overlap D-statistics between species were low. This may be because all of the bumble bee species are being compared against *V. membranaceum*, which has a smaller suitable niche than the other species. The size of the suitable niche of *V. membranaceum* would limit the potential overlap between species.

Bombus insularis/*V. membranaceum* and *B. melanopygus/V. membranaceum* both followed the hypothesis that there would be a decrease in overlap in all emissions scenarios and time frames. However, there was not a consistent trend in the magnitude of this loss across time or emissions scenarios. *Bombus mixtus/V. membranaceum* did not follow the hypothesis, as some future climate scenarios experienced a gain of suitable niche overlap in future scenarios. The inconsistent impacts of climate change on species suitable niche overlap indicates that each species interaction would need to be considered individually to fully understand how their spatial relationship will change in the future.

The D-statistic measurements only show a small part of the changes to species suitable niche overlap, as it is a summary overlap measurement. The cross species geographic analysis of suitable niche overlap showed a decrease in high shared suitability regions over time in SSP3-7.0. This was consistent across all species. By the end of the century, the predicted overlap between *B. melanopygus/V. membranaceum* was substantially smaller in both size and areas of high shared suitability than their current overlap. The *B. insularis*/*V. membranaceum* and *B. mixtus/V. membranaceum* comparisons are harder to differentiate in terms of size, however the southern areas of shared suitability are much smaller than the current overlap in those areas. In order to interact, the species must be in spatial contact. As the level of shared high suitability and overall amount of overlap decreases, the ability of the species to interact will be negatively impacted. The regions of low and mixed shared suitability will still provide regions where spatial contact is possible. However, the areas of shared high suitability provide a high probability of interaction and interaction may be less likely to occur in the other regions of overlap.

All of the species pairs displayed gains of overlap in the north and losses in the south to varying degrees. However, *B. melanopygus/V. membranaceum* followed that trend less strongly than the rest. This trend is likely due to the pattern of northern gains and southern losses in the future predicted suitable niche for *V. membranaceum*. The only species that had predicted current suitable niche overlap with *V. membranaceum* in the Great Lakes region was *B. insularis*. Compared to the other bumble bee species, the distribution of *B. insularis* has the most occurrences in the Great Lakes region, with the spread of samples being consistent from east to west (Fig. 6). Additionally, its distribution of occurrences is most similar to *V. membranaceum*, and it has more suitable niche space in the Great Lakes region than *B. mixtus* and *B. melanopygus*. The current suitable niche overlap between *B. insularis* and *V. membranaceum* makes sense when considering these factors. However, the suitable niche overlap is lost in SSP3-7.0 at every time frame. This loss is likely due to a combination of losses of suitable niche in the Great Lakes region in both species under SSP3-7.0 (Fig. 8, Fig. 14).

The data showing that these bumble bee species pollinate *V. membranaceum* came from observations in Montana (Lichtenberg and Graves, 2023). It is possible that *B. melanopygus* and *B. mixtus* do not pollinate *V. membranaceum* in the Great Lakes region. However, in the raw occurrence data for these two species there are occurrences in the Great Lakes region and even farther east (Fig. 4, Fig. 5). Additionally, their current suitable niche models show at least a low level of probability of having suitable niche space near the Great Lakes (Fig. 10, Fig. 16). The low level of suitability for *B. melanopygus* and *B. mixtus* in the Great Lakes region is potentially a result of fewer samples being collected in that region and contributing to the model. However, it is not clear whether the smaller number of collected samples in the Great Lakes region is due to a sampling bias or smaller populations in that area. However, since they do have current predicted suitable niche near the Great Lakes region, the lack of species overlap for these two bumble bee species is likely due to the reclassification thresholds that set any probability between 0 and 0.25 as 0. Therefore, it is possible that they are pollinating *V. membranaceum* in those regions, but not as likely as *B. insularis*.

Dispersal Into Gained Suitable Niche

While all species are predicted to have gains of suitable niche in every future climate scenario, if they cannot disperse to those areas and establish in them, then the amount of gain and whether or not it offsets the losses is irrelevant.

Dispersal Ability of Vaccinium membranaceum

Vaccinium membranaceum is capable of dispersal through animal mediated movement. Thinleaf huckleberries are food sources for a variety of woodland wildlife including birds, small mammals, and game mammals (Martin et al., 1961, 357). Some of these animals eat not only the berries but the leaves and bark (Martin et al., 1961, 357). The berries of *V. membranaceum* have been documented to be consumed by grizzly bears and coyotes (McLellan and Hovey, 1995; Yang et al., 2008). The consumption of *V. membranaceum* berries by animals facilitates the dispersal of the plant seeds through the animals' scat (Yang et al., 2008). There have been minimal studies on the potential dispersal distances of *V. membranaceum*, however a study on the recolonization of the plant after the Mount Saint Helens eruption, located in Washington, found that it had been able to disperse from neighboring populations (Yang et al., 2008). The plant had traveled, likely through coyote scat, an average of 4.2 km (Yang et al., 2008). The highest amount of dispersal was over 10 km and the lowest was 1.5 km (Yang et al., 2008). The rate of this dispersal was not expressed by the study, however they expected that all of the founding individuals of *V. membranaceum* had accumulated over approximately 15 years (Yang et al., 2008). It is possible that the *V. membranaceum* would be able to disperse north into its gained suitable niche in future climate scenarios. The reliance on other organisms to facilitate the dispersal may be a limiting factor as the animal may not drop the seeds in an area of suitable niche.

Dispersal Ability of Bombus spp.

Bumble bees are only able to disperse their genetic material through queen and male dispersal (Kraus et al., 2008; Lepais et al., 2010). As the males do not overwinter, their dispersal is only relevant in terms of reaching mates that would prevent inbreeding. Through overwintering herself, the queen carries the genetic material forward when founding a new colony in the spring. Due to this, the dispersal of the queen is most relevant for overall colony dispersal. The queen is able to disperse during three life stages: searching for a mate, searching for a hibernation site post mating, and searching for a nesting site after emerging from hibernation (Mola and Williams, 2025). The majority of the queen's dispersal is expected to occur after the hibernation stage during the search for a new nesting site (Mola and Williams, 2025). Two species of bumble bee had been found to hibernate within a few meters of their natal nest or even within the nest (Boone et al., 2022; Pugesek et al., 2023). If this trend is consistent across species, then dispersal when searching for a nesting site would be particularly important for overall dispersal distance measurements.

The dispersal distance of bumble bee queens is dependent on the species, but across multiple studies the maximum dispersal distance ranged from 1.3 km to 8 km (Lepais et al., 2010; Hagen et al., 2011; Carvell et al., 2017; Mola et al., 2020). A minimal dispersal distance was reported in only one study, and they found it to be 85 m (Mola et al., 2020). These studies on other *Bombus* species may help inform the dispersal potential of *B. mixtus* and *B. melanopygus*. *Bombus* *insularis* is a parasitic social insect and therefore may have a different dispersal potential than other *Bombus* species. The *B. insularis* queens do not disperse to search for their own nesting site, they instead disperse to search for a host site. This unique life cycle may make it more difficult to measure dispersal potential from the natal site, however other proxies have been made. One study comparing the location of host sites for *B. insularis* found full sibling queens in separate host colonies 7.04 km apart (Koch et al., 2021). This provides evidence that *B. insularis* queens have a relatively similar dispersal potential as other bumble bee queens.

Sirois-Delisle and Kerr (2018) modeled the range and dispersal of bumble bees in future climate scenarios and predicted that the range loss of bumble bees would shrink even in high dispersal scenarios. They found that range loss would be most prominent in areas with increased land use and human disturbance (Sirois-Delisle and Kerr, 2018). There were some areas in the future climate scenarios where multiple bumble bee species were predicted to disperse into new range successfully (Sirois-Delisle and Kerr, 2018). These areas were mostly undisturbed; however they were not under conservation protection (Sirois-Delisle and Kerr, 2018). The species of my study were included in this analysis and were predicted to have range constrictions under all dispersal scenarios (Sirois-Delisle and Kerr, 2018). Prioritizing the conservation of areas where bumble bees are able to either maintain their current range or disperse into expanded range should be a priority as the climate continues to warm.

While bumble bee queens are able to disperse during certain life stages, the actual success of this dispersal in tracking gains of suitable niche space is minimal. Historical analysis on changes to North American bumble bee populations as a result of climate change show overall contractions in range size (Kerr et al., 2015). North American bumble bees are not dispersing into their expanding suitable niche as their cool thermal limits warm (Kerr et al., 2015). They are concurrently losing southern range, which is contributing to an overall range constriction (Kerr et al., 2015). Bumble bee species have also experienced population size declines, however, there are some species that have maintained their abundance (Cameron et al., 2011). These declines may not be solely due to climate change as pathogens have also become an increasing concern for bumble bee survival (Cameron et al., 2011).

The predicted future suitable niche for each of the bumble bee species in this study followed the pattern of southern losses found in the historical analysis by Kerr et al. (2015). Since these southern losses are already occurring, it is likely that the future predictions of southern loss will occur. The lack of historical expansion into warming cool thermal limits indicates that the bumble bees of this study may not be able to expand into their gains in suitable niche.

In the Context of Pollinator Plant Interactions

Pollinator-Plant Suitable Niche Overlap: A Limited Field

While environmental niche modeling has been done for many species, understanding potential suitable niche overlap between species using ENM is limited. This is especially true for modeling plant-pollinator interactions. Other than one study modeling the future species overlap between *Agave* and its bat pollinator, this concept is novel (Gómez-Ruiz and Lacher, 2019). Therefore, the results of the species suitable niche overlap analysis cannot be compared against results from previous studies.

Utilizing species' modeled suitable niche in order to assess future species overlap may become increasingly useful in the face of climate change. It can act as a predictor for potential to interact in future climate scenarios, which is especially important when considering species that have closely intertwined relationships. However, the environmental niche model comparisons from my study only reflect the overlap in climatic requirements of the species, which does not take into account the other points of interaction. When considering modeled suitable niche overlap with other factors, like phenology, a better understanding of the plant pollinator interaction can be reached.

Pollinator-Plant Phenology

The phenology of the pollinator life cycle and the blooms of flowering plants must be aligned so that pollinators are foraging when the flowers are blooming. This alignment allows their mutualism to be carried out. If there is a mismatch between the pollinator and plant phenology, it could impact the ability of the organisms to interact. Climate change, mainly the associated warming temperatures, has caused phenological shifts for both bee pollinators and bee pollinated plants (Bartomeus et al., 2011; Kudo and Ida, 2013; CaraDonna et al., 2018; Weaver and Mallinger, 2022). In some cases, these shifts are happening in the same direction and at the same rate between interacting organisms, which allows for a continuation of their interaction (Bartomeus et al., 2011; Weaver and Mallinger, 2022). In other cases, these phenological shifts have caused mismatches (Kudo and Ida, 2013; Weaver and Mallinger, 2022). These mismatches have the potential to negatively impact the success of the species (Kudo and Ida, 2013).

There have been documented shifts in blooming time for species in the genus *Vaccinium* (Weaver and Mallinger, 2022). These shifts were significantly associated with warming temperatures in three out of four of the species studied (Weaver and Mallinger, 2022). The flowering date of these three species advanced between 4.82 and 0.23 days with every degree Celsius increase (Weaver and Mallinger, 2022). *Vaccinium membranaceum* has not been specifically assessed, however its phenological shifts have been modeled for future climate scenarios. Prevéy et al. (2020) predicted that the flowering times of *V. membranaceum* would increase by a mean of 21 days through the end of the century in the representative concentration pathway (RCP) 4.5 and a mean of 35 days in RCP 8.5. RCP 4.5 is a more conservative emissions scenario and RCP 8.5 is more extreme (Chen et al., 2021). The SSPs are updated versions of the RCPs for the Sixth Assessment Report and are not directly comparable to the RCPs (Chen et al., 2021).

Bumble bees have had documented phenological shifts in their spring emergence that have been associated with climate change (Bartomeus et al., 2011; Koppel and Kerr, 2022). A study looking at 20 bumble bee species found that from the baseline of 1954-1970 to the modern period of 2004-2012, the average emergence time across species has shifted earlier by 3.4 days (Koppel and Kerr, 2022). *Bombus insularis*, *B. mixtus,* and *B. melanopygus* were all a part of that study. From the baseline to the modern period, the average emergence day advanced by 23.12 days for *B. insularis* and 3.66 days for *B. mixtus* (Koppel and Kerr, 2022). Interestingly, the average emergence day of *B. melanopygus* was 6.14 days later in the modern period than the baseline period (Koppel and Kerr, 2022). *Bombus melanopygus* typically begins nesting earlier than other species (Williams et al., 2014). The delay in their emergence time may cause this to change.

It is not possible to make a direct comparison between the phenological shifts of *V. membranaceum* and its bumble bee pollinators using these data, however some inferences can be made. All species in this study have experienced or are predicted to experience a shift in their spring phenology. The documented and predicted advance of *V. membranaceum*, *B. mixtus,* and *B. insularis* in spring phenology may mean that the interactions between these species will advance similarly. However, if the emergence of *B. melanopygus* continues to be delayed later into the spring season, it is possible that there will be a greater mismatch between this bumble bee and *V. membranaceum* in future climate scenarios. The average date of bee emergence and flowering time would have to be assessed and compared in order to accurately determine potential mismatch between phenologies using these shift data. It is possible that by the bee emerging later in the season, the phenology of *B. melanopygus* and *V. membranaceum* aligns more rather than less. The reverse is also possible for the overlap in phenologies of *V. membranaceum* and *B. mixtus* or *B. insularis*.

Future Directions

Modeling Significance

In environmental niche modeling, the models are checked for accuracy and consistency during the replicate phase of model generation. After the model is confirmed to be accurate and consistent, the current projection and future projections are done using a singular run of the model. That singular run of the model does not average across multiple model replicates. While these singular models can be compared against the replicated model for accuracy and consistency, they may not reflect the mean of the initial repeated environmental niche model. Replicating the singular model for analysis could be able to account for model uncertainty (Buisson et al., 2010). This would allow for statistical significance in change of suitable niche between current and future scenarios to be tested, which would improve the quality of the analysis.

MaxEnt is one of many approaches for environmental niche modeling. Assessing the environmental niche across multiple approaches can result in a more comprehensive study (Hao et al., 2020). An ensemble approach creating a summary model across multiple softwares, such as generalized linear models (GLM), the gradient boosting machine (GBM), and random forests (RF), is another way to expand the scope of the study (Hao et al., 2020). Assessing the environmental niche of a species using multiple softwares is one way to address the differences in predictive performance among the different approaches (Hao et al., 2020).

Great Lakes Region

Despite all of the bumble bee species having occurrence data points and predicted current suitable niche in the Great Lakes region (Fig. 4, Fig. 5, Fig. 6, Fig. 10, Fig. 13, Fig. 16), *B. insularis* was the only species to maintain predicted suitable niche space when the current predicted suitable niche was reclassified. Additionally, the predicted suitable niche space of *V. membranaceum* in the Great Lakes region experienced majority or total loss in all future climate scenarios (Fig. 7, Fig. 8, Fig. 9). While these results are not unexpected, there is a chance it is not fully accurate. Every species in the study displays a much larger concentration of individuals in the Pacific Northwest than the Great Lakes region.

This pattern of lower concentration of bumble bee occurrences in the Great Lakes region, especially for *B. mixtus* and *B. melanopygus*, may indicate a sampling bias. On the other hand, the occurrences in and near the Great Lakes region could be at the limits of the bumble bee's suitable niche, which would explain the lower sample size. *Vaccinium membranaceum* is known to have much smaller populations in the Great Lakes region than the Pacific Northwest, so its difference in concentration of occurrences is likely not due to a sampling bias (Drummond et al., 2022).

The difference in concentration of *V. membranaceum* individuals between the Pacific Northwest and the Great Lakes region may be influencing the environmental niche model. There may be minor differences in the suitable niche requirements of populations in the Pacific Northwest and populations in the Great Lakes region due to the regions being disjunct and going through multiple generations without gene flow between them. The disproportionate sample size between the two regions could bias the model towards climate from the Pacific Northwest region, potentially skewing the probability of identifying suitable niche in the Great Lakes region. Modeling the suitable niche of the Great Lakes region alone and projecting that model to future climate scenarios could provide greater detail to how that population may react to the changing climate.

Additional Niche Requirements

The environmental niche models in this study used climatic data to predict the suitable niches of the species. These variables are only one part of the environmental requirements these species need to survive. *Vaccinium membranaceum* has specific soil requirements for its survival. To prevent leaf necrosis, the soil it grows in must have a pH between 4 and 6 (Nelson, 1974). It thrives in nitrogen rich soil, especially when high nitrogen levels are paired with high levels of phosphorus and/or potassium (Nelson, 1974). However, high potassium levels in low nitrogen soil can be harmful to the plant (Nelson, 1974). In contrast, high levels of phosphorus makes no difference in the success of *V. membranaceum* at low nitrogen levels (Nelson, 1974). It is possible to incorporate additional variables, such as soil pH and composition, into environmental niche models to assess these other factors.

Hamilton et al. (2024) generated environmental niche models that incorporated soil and topography variables for five berry plants including two species in the *Vaccinium* genus. Across all of the berry plants, elevation and soil variables were important model predictors while the climate variables had a varied level of importance for each berry (Hamilton et al., 2024). The *Vaccinium* plants both had elevation, soil pH, available water storage in soil, and percent of clay in soil in their top five predictors (Hamilton et al., 2024). One of the species had mean temperature in January within its top five and the other had mean temperature in July (Hamilton et al., 2024). *Vaccinium membranaceum* may have a more finely tuned predicted suitable niche if soil and topographical measures are included in the generation of its environmental niche model. The soil may be of particular importance when considering its specific pH and nitrogen requirements. Adding in these additional variables would make it more likely that the calculated suitable niche gain in future climate scenarios are actually places that meet all of the plant's growth requirements.

The non-climatic niche requirements of bumble bees are more difficult to fully understand than those of plants. However, there may be nesting and overwintering site environmental requirements that could add to the complexity of their environmental niche models. The nesting and overwintering habitats of bumble bees are understudied (Liczner and Colla, 2019). Liczner and Colla (2019) compiled data from studies on bumble bee nesting and overwintering habitats conducted around the world to find commonalities within the genus. Nesting sites were found in a wide variety of habitats and there was no pattern in landscape preference (Liczner and Colla, 2019). The nests were underground, above ground, and on the ground surface, among the species analyzed, indicating no clear preference (Liczner and Colla, 2019). Availability of floral resources may be a predictor of nest location and survival (Suzuki et al., 2007; Suzuki et al., 2009). This variable would be difficult to add into an environmental niche model. Overwintering sites had more overall patterns across the *Bombus* genus than nesting sites. A large majority of the queens overwintered underground, with only a few outliers found above ground (Liczner and Colla, 2019). They tended to choose overwintering sites that did not have dense vegetation and were on a northward slope (Liczner and Colla, 2019). The emergence of the queens from hibernation is impacted by the temperatures around them, with depth of underground hibernation, soil type, and exposure to sun being factors that may determine early or late emergence of bumble bee species (Alford, 1969). Including topographical and soil variables into the bumble bee environmental niche models could make them more accurate when considering overwintering sites for queens. However, the sampling of bumble bees does not always happen at their nesting or overwintering sites as many are collected during their foraging bouts. If topographical and soil variables were included in an environmental niche model, it may be better practice to categorize the occurrences by where they were collected so the foraging occurrences do not skew the model.

Areas of No Change and Minimal Loss

The gain and loss analysis in this study does not encompass the nuance of the changes to suitable niche because it does not depict the differences between areas of no probability and no change or the differences between the areas of minimal loss and total loss. This is true for both the analysis of gains and losses in individual species' suitable niche in future climate scenarios as well as the analysis of gains and losses of suitable niche overlap between species.

In the individual species current suitable niche gain-loss analysis, the areas where there was current suitable niche probability that did not change in future climate scenarios were not accounted for on the visual map of gains and losses. This includes areas that maintained a high probability of suitable niche (2) or a low probability of suitable niche (1) between the current and future climate scenarios. On the gain-loss maps, these areas would be indistinguishable from areas that maintained no probability of suitable niche (0) between the current and future climate scenarios as all calculations would result in a value of zero (0 - 0 = 0, 1 - 1 = 0, 2 - 2 =0), which is represented by the color grey (Fig. 7). In the gain-loss analysis of suitable niche overlap between species the areas that maintained shared low suitability (1), mixed suitability (2), and shared high suitability (4) between the current and future climate scenarios were also not accounted for. As with the individual gain-loss maps, these areas would be indistinguishable from areas that maintained no overlap (0) between the current and future climate scenarios as all calculations would result in a value of zero (0 - 0 = 0, 1 - 1 = 0, 2 - 2 =0, 4 - 4 = 0), which is represented by the color grey (Fig. 22).

Additionally, areas that only had minimal loss of suitable niche probability were indistinguishable from areas that had total loss of suitable niche probability on the gain-loss maps. For the individual species current suitable niche gain-loss analysis, these are the areas that went from a high probability of suitable niche (2) in the current scenario to a low probability of suitable niche (1) in the future scenarios. These areas would be the same color, light purple, as the areas that had a total loss of low probability of suitable niche between the current and future climate scenarios as all calculations would result in a value of -1 (1 - 2 = -1, 0 - 1

= -1) (Fig. 7). In the gain-loss analysis of suitable niche overlap between species these are the areas that went from shared high suitability (4) to mixed suitability (2) and the areas that went from shared mixed suitability (2) to shared low suitability (1), as they would be indistinguishable from areas that went from mixed suitability (2) to no suitability (0) and areas that went from low suitability (1) to no suitability (0), respectively. The areas that went from shared high suitability (4) to mixed suitability (2) and the areas that went from mixed suitability (2) to no suitability (0) would be in the same category, moderate low loss, because both calculations would result in a value of -2 (2 - 4 = -2, 0 - 2 = -2). The areas that went from mixed suitability (2) to shared low suitability (1) and the areas that went low suitability (1) to no suitability (0) would be in the same category, low loss, because both calculations would result in a value of -1 (1 - 2 = -1, 0 - 1 = -1).

The areas of no change and the areas of minimal loss are important to consider when trying to understand the areas where a species will maintain its suitable niche in the future. Considering the variation of dispersal potential among the species studied, locating these areas may be of particular importance when determining potential conservation needs. Additional geographic raster calculations and mapping techniques would need to be applied in order to assess these areas.

Conclusions

The results of this study predicted that the suitable niches of *V. membranaceum*, *B. mixtus, B. insularis,* and *B. melanopygus* will all shift in future climate scenarios and that these species will experience varying levels of gains and losses of suitable niche. It was also demonstrated that there would be a change in suitable niche overlap between the plant and each pollinator, which may decrease their ability to interact in future climate scenarios. These predictions, along with other habitat, genetic, and life cycle considerations, indicate that *V. membranaceum* and its bumble bee pollinators may experience not only population decline and range constrictions but a decreased ability to interact in future climate scenarios.

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