

Spatial Variation in Bee Abundance and Diversity Across Southern Rocky Mountain Habitats

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ABSTRACT

The structure of native bee assemblages and the nature of spatial variation of pollinator populations have direct effects on the reproductive success of plant species across their ranges and floral evolution. It is possible that changes in regional temperatures and precipitation are shifting foraging and nesting habitat preferences of bees. Very few studies have examined the habitat preferences of bees across variable landscapes and elevations, though the establishment of reference conditions is critical to future studies and the establishment of both plant and pollinator conservation schemes. Here, with the use of pan traps and hand netting, I sampled native bee populations across wet meadow, dry meadow, aspen understory and conifer understory as well as across an elevational gradient in an *Apis*-free region of the Western Slope of the Southern Rocky Mountains in Colorado, which has been experiencing increasing drought via reduced snowpack and earlier date of first bare ground. Floral phenology plots were also established at each site to track pollinator resources. In family-level analyses, when adjusted for sampling efforts, higher evenness was found in understories and higher variation in meadows. Floral diversity did not drive bee richness but did increase catch rates. Catch rates increased at higher elevation in dry meadows. Taken together, and in consideration of other observations and past studies, these data suggest a degree of spatial variation in bee community composition that is likely correlated with floral phenology and resource abundance.

Key words: bees, spatial variation, phenology, community composition, pollination

INTRODUCTION

Spatial variation in pollinator assemblages has reproductive consequences for the plants they visit and cascading ecological effects on the communities they exist within (Biesmeijer *et al.*, 2006; Kearns *et al.*, 1998). Spatial variation in the assemblages of pollinators across communities is commonly found (Eckhart, 1992; Guitian *et al.*, 1996; Fenster and Dudash, 2001; Moeller, 2005) and can lead to differences in pollen limitation and plant reproduction (Mustajarvi *et al.*, 2001; Gomez *et al.*, 2010). Studies involving long-term monitoring of bee populations and the availability of their associated resources are critically lacking. A greater understanding of the ecological and evolutionary causes and consequences of spatial variation in plant-pollinator interactions is dependent on the establishment of reference data revealing habitat preferences of pollinator groups, of which, in this study, bees are the focus.

Animal pollinators, of which bees are widely accepted as the most important, provide an imperative ecosystem service (Winfree *et al.*, 2011), with 90% of the world's flowering plant species, as well as 75% of the leading crop plants, requiring animal-mediated pollination to some degree (Axelrod, 1960; Klein *et al.*, 2007). Since 35% of the world's entire food supply requires the service of pollination (Klein *et al.*, 2007), conservation of pollinators can be viewed as a matter of national security and human survival (Kremen *et al.*, 2004; Munyuli *et al.*, 2013). The

persistence of native pollinators depends on high-quality habitats for foraging and nesting (Kennedy *et al.*, 2013) although the habitat preferences, ranges, phenology and abundance of many bee species remain poorly understood. From a conservation perspective, it is critically important that we understand the responses of bees to climate change as well as their current, and potentially variable or shifting, abundance and diversity between localized habitat types and elevations.

The last decades have shown pronounced changes in both global and localized climates (Luterbacher *et al.*, 2004), of which the effects on regional native bee assemblages are poorly understood. Climate change projections include decreased annual precipitation, increased surface temperatures, and increased occurrence and extremity of drought conditions (IPCC, 2007), which, in turn, directly affects floral resource availability for bees. Some deviations from historic weather patterns, such as atmospheric warming, are highly predictable throughout the 21st century, while regional changes in precipitation are less certain (Smith & Wagner, 2006; Root *et al.*, 2003). However, the Western USA, in particular, has experienced increasing frequency and intensity of droughts since the 1950's and it is predicted this trend will continue (Bates, 2008; IPCC, 2007). In order to monitor bee populations in the future, it is critical that baseline knowledge be established, especially in regions facing increased drought.

This study evaluates the abundance and diversity of bee families and wasps over a range of habitat types. Findings are compared across aspen understory, conifer understory, wet meadow and dry meadow as well as across an elevational gradient in dry meadow sites. The Colorado Bee List contains 946 species from 66 genera of bees, comprising ~25% of all the bee species found in USA and Canada (Scott *et al.*, 2011), and since this study will examine historically under-sampled understory habitats, it is important to determine what species are represented, especially if they hold habitat or plant species specialists. More broadly, this study may serve as a helpful reference for any future pollinator-focused climate change inquiries and will provide an invaluable supplemental dataset to further address both phenological and habitat preference questions as well as questions in community structure.

METHODS

Study System: The Upper East River Valley of Colorado, in which the Rocky Mountain Biological Laboratory (RMBL) and all field sites are situated, is comprised of interspersed wet and dry meadows, aspen stands and coniferous forests. The region suffered from 50% the average precipitation (Barr, RMBL data), and the resulting limited wildflower blooms in 2012, the year before this study, and provides both elevational gradients and variable habitat types for sampling. The absence of honey bee (*Apis mellifera*) populations allows a better look at native bee community structuring.

Study sites: Research was conducted in the vicinity of RMBL, Gothic, Colorado, USA (elevation: 2,890m), mostly within the boundaries of Gunnison National Forest. I established eight novel study sites in all: two within aspen (*Populus tremuloides*) stands, two within conifer (spruce-fir) stands, one in a wet meadow, and three in dry meadows across an elevational gradient (3023m, 3416m, and 3509m).

Design: Bees were sampled with pan traps and hand netting. Most methods are in accordance with the bee sampling protocol developed by LeBuhn *et al* (2003) in *The Bee Inventory Plot*. Two to three replicates of each habitat type were established at least 1km apart from another. However, two conifer sites were found to be only ~700m apart after initial sampling. To prevent edge effects, each site had at least a 15m buffer of that same habitat type surrounding it. In each site, two 45m transects were established with fifteen pan traps assigned to each. Yellow, blue and white pan traps were placed at ground level with color positions randomly assigned without allowing obvious grouping of the same color. Each trap was filled with soapy water (with Dawn™ blue dish soap). Upon collection, specimens were strained through a mesh bag and brought back to the lab and put in the freezer. When mesh bags were unavailable, specimens were placed in vials of ethyl alcohol labeled by pan trap color and stored in freezer to later be dried with a paper towel then a hair dryer aimed into a mason jar with a mesh lid for 30-50 seconds. Each specimen was pinned, labeled with relevant catch information including a unique identification number, and entered into a database. Any bees not identified to species during the summer will be identified by specialists over the winter.

In accordance with standardized bee sampling protocol (LeBuhn *et al*, 2003), to protect bee populations, I sampled each site bi-monthly. Traps were placed out upon arrival at site and retrieved at least six hours later, and the times at which the traps are placed out and picked up were recorded to calculate catch rates. At the time of both trap setting and trap collection, 60 minutes of hand-netting was completed. Weather events cut some sampling periods short, but all catch rates were calculated on a per hour basis. I sampled bees by net on the ground, on flowers and in the air. No more than five minutes was spent on any one patch of flowers. Data were collected on the host plant and/or any notable behavior of the bee, such as nest searching behavior or nest emergence. *Bombus* and *Psithyrus* species were recorded, marked with a paint pen to avoid counting them twice and then released.

In addition, I established six flower phenology plots, each 2m x 2m, at each site, with three plots along each of the two 45m transects. At each site visit, when pan traps were set, the number of flowers of each blooming plant species was recorded. Since there is often patchiness in distribution of understory vegetation, rough counts of blooming flower species outside the phenology plots, but within the immediate sampling site, were recorded as well.

I collected and recorded all data, and all collections were stored and processed, in exact accordance with the methods of the larger project which this research aimed to supplement. For most analyses, wet and dry meadow sites were combined and so were aspen and conifer understories.

Statistical software used includes R 3.0.1, SAS JMP and Excel 2010. I evaluated evenness and richness of bees and compared results between meadows and understories. To increase statistical power, for most analyses wet and dry meadows were grouped together as were aspen and conifer understories. Bootstrap procedures were used to compare these results. Bee abundance, estimated as number of bees caught and standardized by sampling effort (hereafter catch rate) was compared across bee families and sites. Floral richness of sites was also standardized by sampling efforts and a regression analysis was used to investigate potential correlation with bee

richness. An NMDS ordination was then generated to further investigate community composition.

RESULTS

In family-level analyses, when adjusted for sampling efforts, higher evenness of bee groups was found in understories (Fig. 1) and higher variation in meadows (Fig. 3). A non-parametric analysis using a bootstrap procedure ($n=10,000$) comparing the difference in evenness means between combined understory habitat and combined meadow habitats showed marginal insignificance (Fig. 2). The same analysis comparing the difference in richness means between combined understory habitat and combined meadow habitats revealed significant difference (Fig. 4).

Bee catch rate was highest in dry meadow habitats, but also notably high in aspen understory (Fig. 7). When viewed as catch rates by family (Figs. 5-6) the polarizing effects of Halictidae and Andrenidae on dry meadow catch rates can be clearly seen (also see Fig. 9). SP_Dry was a dry meadow site above Schoefield Pass where in two sampling periods a total of 935 Andrenidae, comprising mostly the same species of *Panurginus*, were caught. This is reflected by an Andrenidae catch rate of 72 bees per hour at that site (Fig. 6).

Floral richness, standardized by sampling effort, was highest at 2 of the 3 dry meadow sites and 1 of the 2 aspen understory sites (Fig. 5). Floral richness was not associated with family-level bee richness when standardized for sampling effort (Fig. 8), but did increase catch rates, especially at high elevation dry meadow sites (Figs. 5-7). Catch rates also seemed to increase in dry meadow sites with increasing elevation (Figs. 5, 7), especially if the catching of 935 *Panurginus* (Andrenidae) is recognized as a spatial anomaly.

DISCUSSION

Spatial Scale Matters

It is likely that both patch and landscape factors influence species richness (Hatfield & LeBuhn, 2007). Patch level factors may include area size, aspect, disturbances, vegetation structure and composition. Landscape-level factors may include elevation, isolation and the type and quality of the surrounding habitat matrix. The spatial scale of observations has been shown to affect α , β and γ diversity of cavity-nesting bees and wasps (Tylianakis *et al.*, 2006) and should be considered when interpreting results. In this study, contiguous habitat patches were at least 50m x 50m with at least a 15m buffer of the same habitat surrounding the sampled area. It is possible that sampling the center of larger patches of habitats would yield results that exclude some of the bee taxa foraging nearer the habitat margin. This is especially the case in the instance of aspen forest bordering meadow, as the plant communities have relatively undefined ecotones, and some flowering plant species can often be found occurring in both habitats. Hatfield & LeBuhn (2007) found that the portion of meadow surrounding habitat was the most consistent positive influence on both bumble bee species richness and abundance, and it's likely the portion and quality of meadow surrounding understory sites is a variable worth considering in future studies. Of the two aspen sites in this study, that with higher abundance did, in fact, have a slightly greater portion of its margin surrounded by a larger meadow than the aspen site with lower bee abundance (Fig. 5). Here I found higher evenness in understories and significantly higher variation in meadows (Figs. 1-4). Species-level analyses will soon illuminate these findings to a

greater degree. From identifying all specimens to family and observing morphotype similarities between understory and meadow sites, I believe that higher evenness will still be found in understories and an even more pronounced richness in meadow habitats. Future comparisons of aspen understories and meadow habitats are likely to find similar assemblages of species being driven by resource availability.

To further assess spatial variation in habitat preference, a non-metric multidimensional scaling ordination was created in R (stress: 0.07) showing family-level community composition between each of the eight sites (Fig. 9). The polarizing effects of Halictidae and Andrenidae catch rates can be clearly seen; as can the grouping of understory and meadow sites and the bee families caught within them. Bees of families Megachilidae and Colletidae were found primarily within understories, with Megachilidae being most strongly represented in aspen understories where they likely find more suitable nesting habitat (Fig. 5). Greater site replications in future studies with data collected on patch and landscape-level factors will illuminate these habitat preferences much more clearly. Future studies might also monitor not just floral resources but also nesting substrate availability (Potts *et al.*, 2002).

The abundance of Andrenidae at the dry meadow Schofield Pass site (SP_Dry) was likely a spatial phenomenon driven by the strong presence of a *Panurginus* species of which 933 confirmed specimens were caught (Fig. 6). There was a rocky outcropping comprising nearly $\frac{1}{2}$ of the SP_Dry site, providing what appeared to be very suitable nesting for the species. Over $\frac{1}{2}$ of the *Panurginus* caught were male and the population appeared to be exhibiting emergence behavior. If these *Panurginus* were to be removed from analyses, the catch rates of meadows and understories would be considerably more comparable (Figs. 5-7), the evenness of meadows would increase (Figs. 1-2), and the polarization of both the SP_Dry field site (#8 in ordination space of Fig. 9) and the family Andrenidae as displayed by NMDS community composition ordination (Fig. 9) would be reduced and their positions shifted down on axis 2 closer to the positions of other sites and bee families. It has been documented that a number of small-bodied bees perceive and respond to resources at small spatial scales (Greenleaf *et al.*, 2007; Gathmann & Tscharntke, 2002), but it is likely larger bees will travel farther to forage (Greenleaf *et al.*, 2007) and that bee functional groups will respond to resources in significantly different ways across different spatial scales and habitats (Jha & Vandermeer, 2009). It is therefore possible that investigating these habitats at multiple spatial scales may better detect the importance of landscape context for bee groups (Steffan-Dewenter *et al.*, 2002).

A final spatial consideration for further examination of these results or replication of this study should be grazing regimes. Bee abundances, particularly of ground-nesting bees, have been shown to be affected by grazing (Kearns & Oliveras, 2009; Potts *et al.*, 2002). This study was conducted almost entirely on the public lands of Gunnison National Forest where free-range cattle grazing is permitted each year in late summer and early fall months.

Pollinator Plasticity

Most pollination systems are currently perceived as relatively generalized (Waser *et al.*, 1996), and high levels of plasticity have been found in foraging preferences of native bees (Jha & Kremen, 2013). A 2012 study found that native bee foraging may be far more plastic and extensive than previously thought and that a simple optimal foraging strategy is not always followed (Jha & Kremen, 2013). Further, a 2011 review of pollination networks found that the

inherent plasticity of plant–pollinator interactions and network structure suggests that many species should be able to persist by responding to environmental changes associated with habitat loss, climate change and biological invasions quickly, even though the identity of their mutualistic partners may shift (Burkle & Alarcon, 2011; but see Brosi & Briggs, 2013). My results, while requiring species-level analyses with more habitat replicates to increase confidence, support the notion that bee habitat preference can vary, at least within family. Representatives of the five major bee families and wasps were found in all but one study site, in which Halictidae was not sampled in a conifer understory (Figs. 5, 6). However, using catch rates as a proxy for abundance, and comparing those findings to floral richness data suggests that similar bee assemblages may use both meadows and aspen understories. Species-level analyses will reveal this potential finding further later this year and future resampling that compares aspen understory to meadows will also likely strengthen this discovery.

Similar assemblages of bees were found in aspen understory as in dry meadows (Fig. 5) and common plant species were shared between aspen understory and surrounding meadows, especially at forest margins. It is likely pollinators will exhibit plasticity in habitat preference and forage wherever they find suitable resources. Here, floral richness, standardized for sampling effort, was considerably higher in meadows than understories. However, a regression analysis plotting floral richness against the richness of bees showed no correlation (Fig. 8, $R^2 = 0.03$). It is very likely that a stronger correlation will be seen after species-level identification of all specimens. The identification of oligolectic and narrowly polylectic bee species are also expected given the catch rates of Andrenidae and Halictidae. This data will again be compared to floral resource phenology availability.

Pollination Networks in a Changing Climate

Climate change is likely to alter plant-pollinator interactions through both temporal and spatial disruptions (Memmott *et al.*, 2007; Cleland *et al.*, 2007; Khanduri *et al.*, 2008), due in part to reduction in the floral resources of spring and summer blooms, which is correlated with reproductive failure in some native bee species (Pitts-Singer & Bosch, 2010; Fitzpatrick *et al.*, 2007; but see Williams *et al.*, 2012). Expressions of the drying associated with climate warming in montane regions are reduced snowpack and earlier dates of first bare ground (Sproles *et al.*, 2012; MacDonald *et al.*, 2012), which has been shown to limit floral resource abundance the following growing season with some plants failing to flower as abundantly or at all (Inouye & McGuire, 1991; Inouye *et al.*, 2002, 2008; Dunne *et al.*, 2003). RMBL has experienced reduced snowpack over the last 2 years (Barr, RMBL data), which, in turn, has reduced soil moisture and hence the abundance of floral resources via reduced growth and reproductive ability (Baude, 2011). It is suggested that warming and drying will drive both animal and plant species capable of dispersal to higher elevations and latitudes (Parmesan, 2006). In this study, although further analyses are yet to be performed, it can be clearly seen that catch rates in dry meadows increased with elevation (Figs. 5-7, 10). This finding is made clearer upon recognizing SP_Dry catch rates as a spatial anomaly. The highest site (VB_Dry, elev: 3509m) did not have the highest catch rate, but would if the *Panurginus* catches were to be removed from the SP_Dry (elev: 3416m) for analyses. This would reveal the increase in catch rates along the elevational gradient upon which dry meadows were sampled. In addition, the two sites with the highest floral richness were the two highest elevation sites (SP_Dry and VB_Dry).

Likely shifts in compositions of plant communities may exacerbate the potential threat to pollinators by an offset of phenological overlap (Abeli *et al.*, 2012; Forrest *et al.*, 2010; Root *et al.*, 2003). Community shifts at broad geographical scales due to drought are not yet well understood, but it is clear that various landscapes will be affected differently (Debinski *et al.*, 2013). A recent study in Colorado found surprisingly higher floral abundance in coniferous understories than in open meadows in 2012, a year with ~50% average snowfall, resulting in drought. Despite higher floral resource abundance in understory habitats, bee visitation rates remained higher in open meadows (Ortega, 2012). An understanding of potentially-shifting habitat preferences and spatial variation of pollinators, their floral resources and required nesting habitats in a changing climate will play an important role in the development of future conservation strategies for pollinators, plants and landscapes as well as prove useful in addressing questions of community composition functioning. It is therefore imperative that long-term bee monitoring and floral phenology studies be established and maintained.

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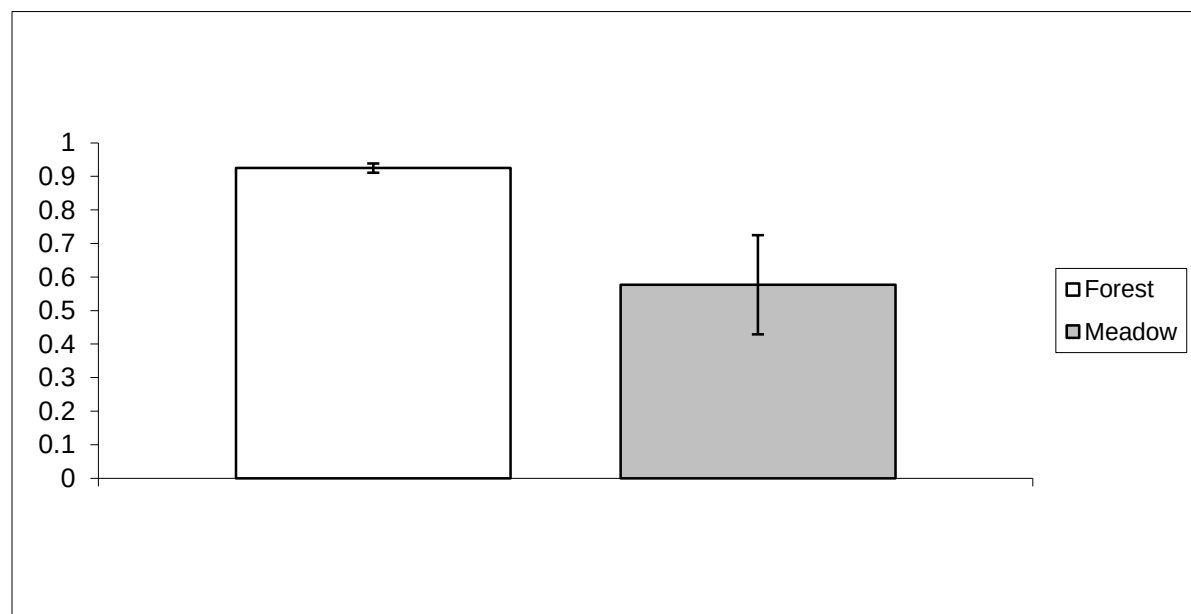


Figure 1 – Evenness – Calculated with Pielou’s evenness index. Forest understories (aspen and conifer) were grouped together as were wet and dry meadows.

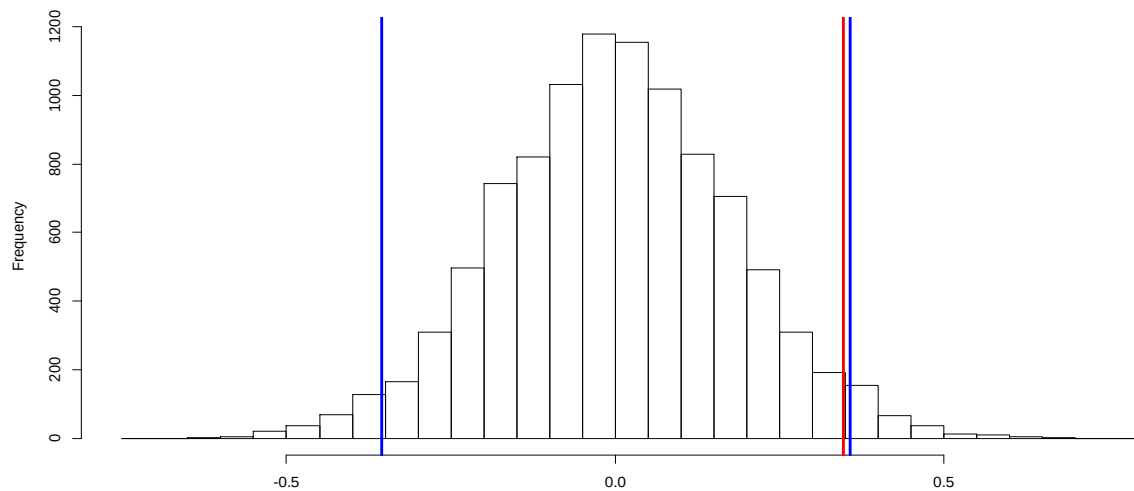


Figure 2 – Evenness - Non-parametric analysis using a bootstrap procedure (n=10,000) comparing the difference in means between combined understory habitat and combined meadow habitats. Blue columns represent 95% confidence intervals for the null distribution of the difference in means. The red column is the actual difference in means and marginal insignificance is indicated by the red line falling just within the blue lines.

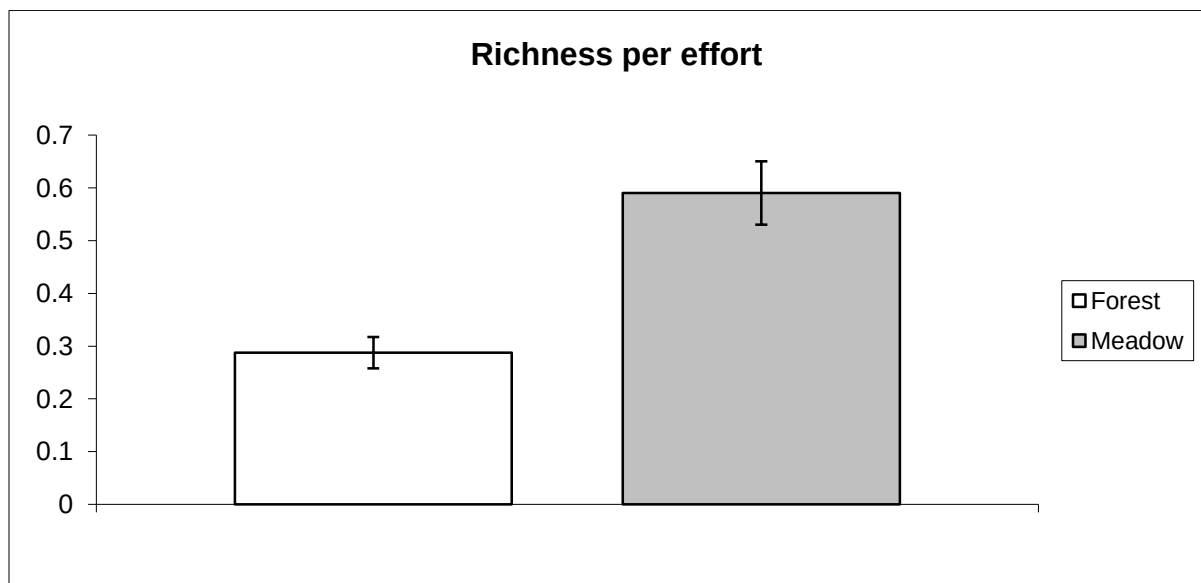


Figure 3 – Richness – Family-level richness (standardized by sampling effort) of bees caught in meadows (wet and dry combined) compared to richness of bees caught in understories (aspen and conifer combined). Sampling for one hour in a meadow would likely yield a richer sample of bees than in an understory.

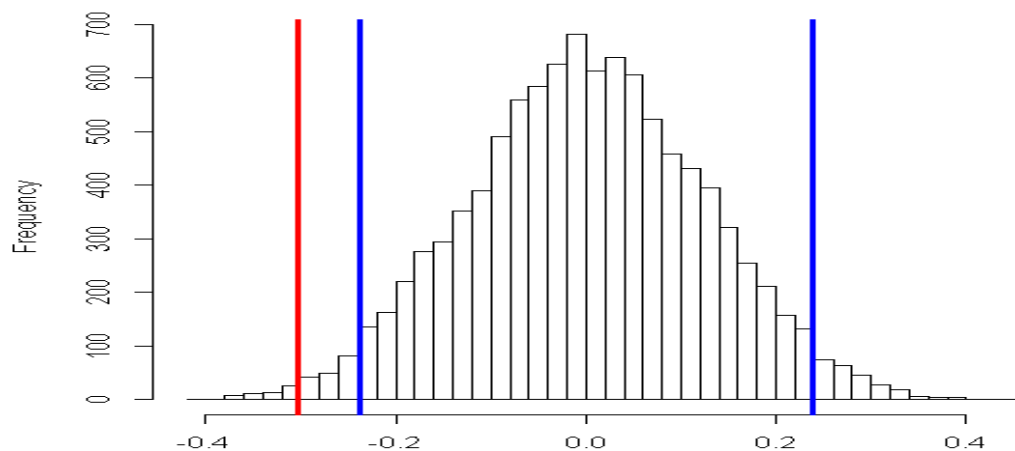


Figure 4 – Richness - Non-parametric analysis using a bootstrap procedure (n=10,000) comparing the difference in means between combined understory habitat and combined meadow habitats. Blue columns represent 95% confidence intervals for the null distribution of the difference in means. The red column is the actual difference in means and significance is indicated by the red line falling outside of the blue lines.

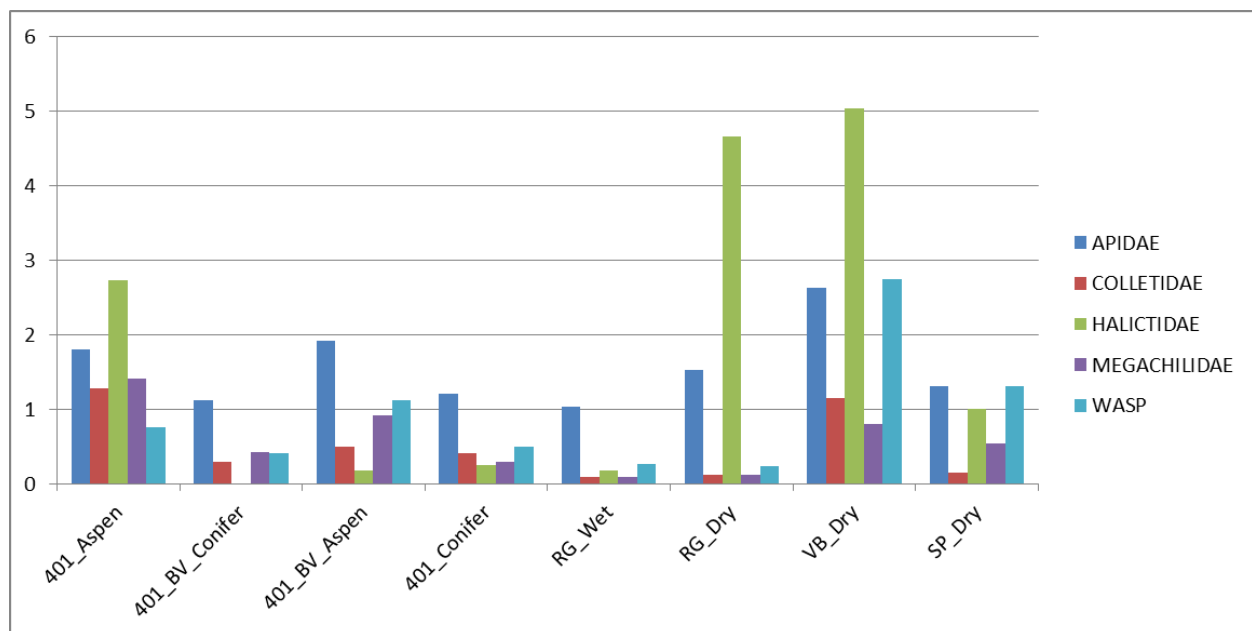


Figure 5 - Abundance, estimated as bee catch rate and standardized for sampling effort, was highest in dry meadow habitats, but notably high in aspen understory as well. Andrenidae was

omitted and appears in Figure 6. Total catch rates appear in Figure 7. The greatest floral richness (standardized for sampling effort) was found at two dry meadow sites (VB_Dry and SP_Dry) and one aspen understory site (401_Aspen).

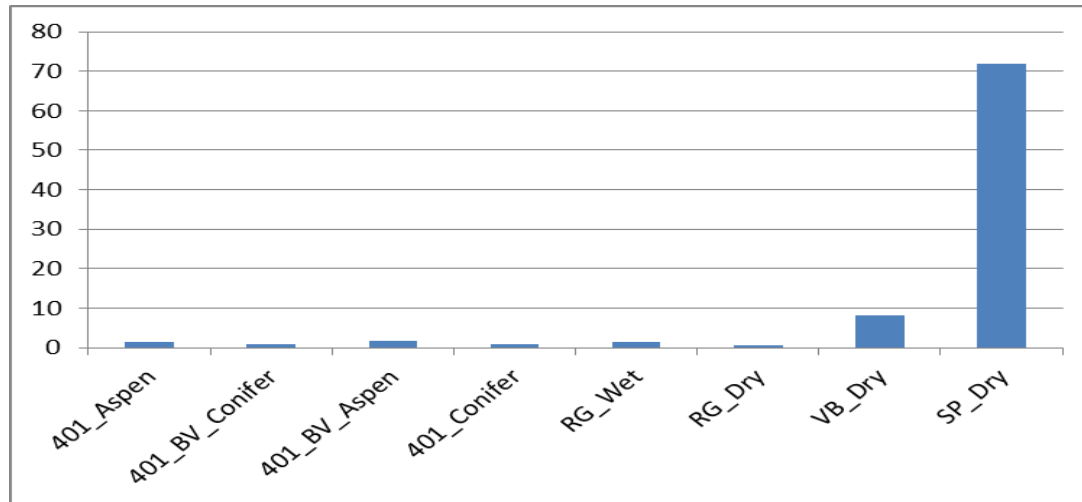


Figure 6 – Andrenidae catch rates. Schofield pass dry meadow site (SP_Dry) accounted for a total of 935 *Panurginus* sp., increasing Andrenidae catch rate at that site to 72 bees / hour. Dry meadow catch rates seem to increase with increasing elevation, especially if the SP_Dry *Panurginus* catches are recognized as a spatial anomaly. RG_Dry (Rustler's Gulch) = 3023m. VB_Dry (Virginia Basin) = 3509m. SP_Dry = 3416m.

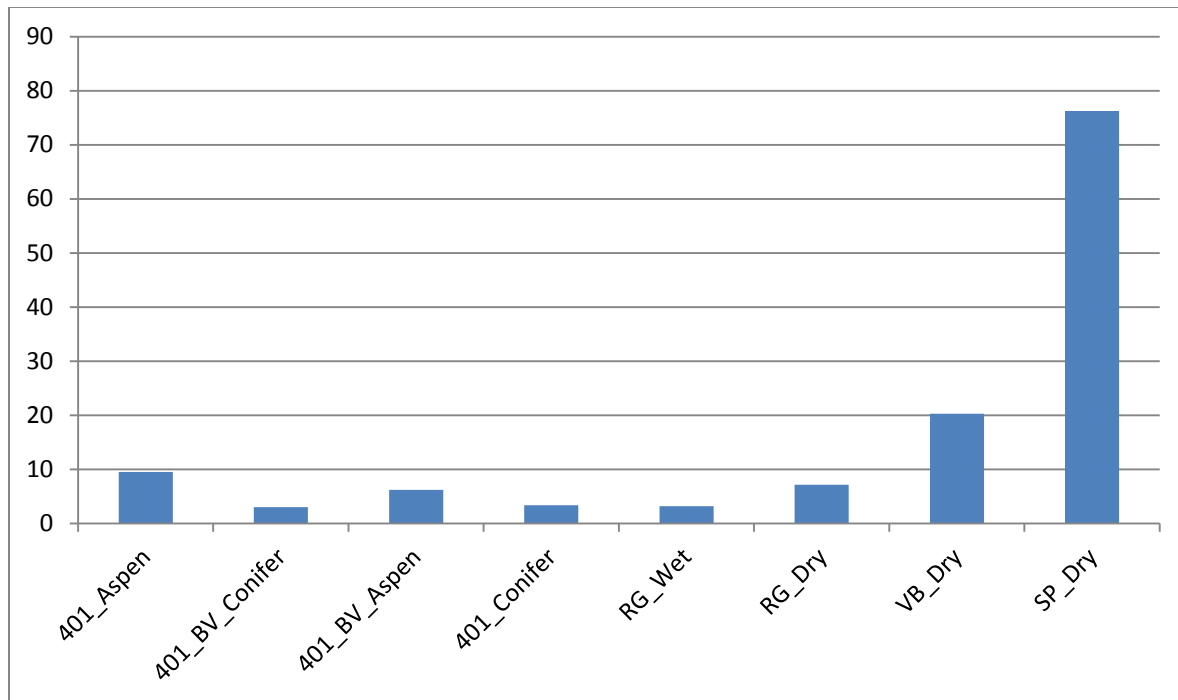


Figure 7 – Total catch rates (all bee families and wasps combined) at each site.

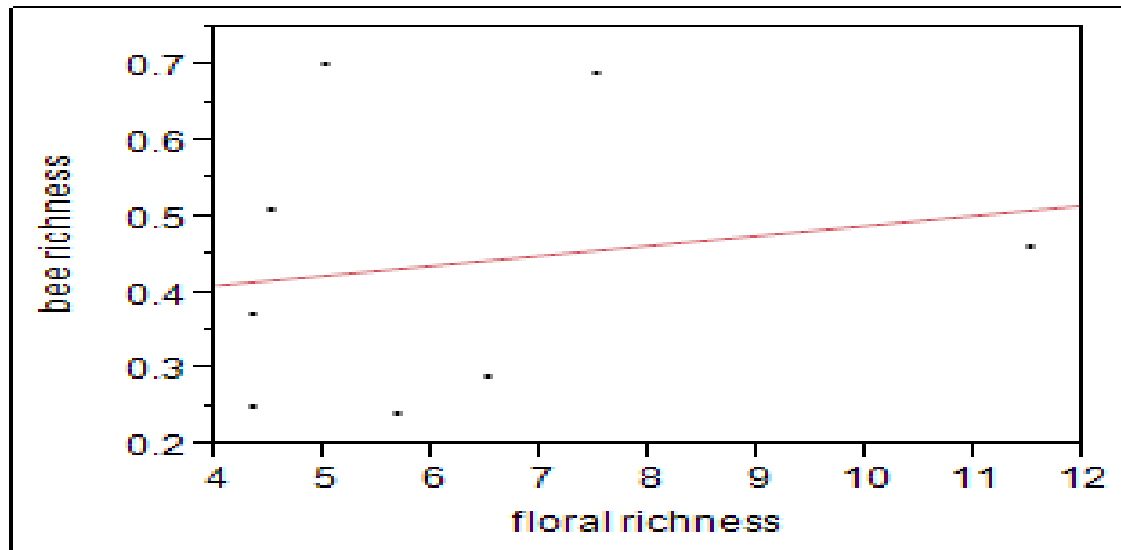


Figure 8 – Regression analysis ($R^2 = 0.03$) showing the lack of influence floral richness (standardized for sampling effort) had on family-level bee richness (standardized for sampling effort).

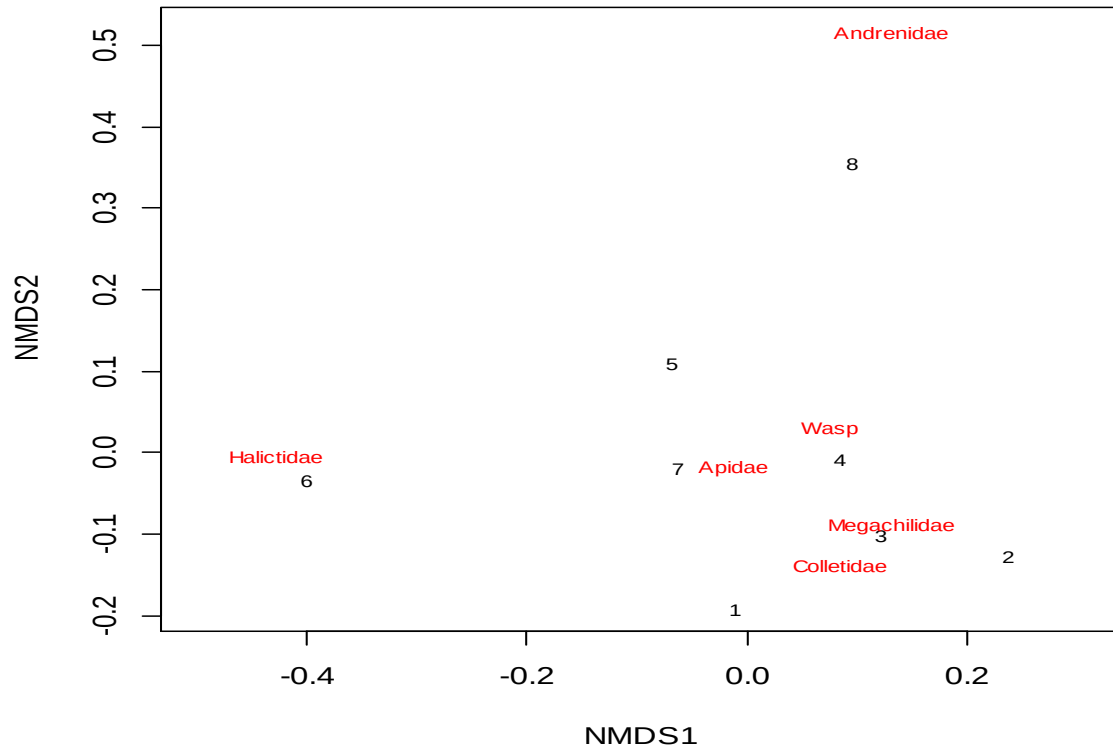


Figure 9 – NMDS ordination (stress: 0.07) showing family-level community composition between sites. Sites 1 and 3 are aspen understories, 401 and 401_BV respectively. Sites 2 and 4 are conifer understories, 401_BV and 401 respectively. Site 5 is the wet meadow and sites 6 through 8 are the dry meadows, RG, VB and SP respectively. The polarizing effects of Halictidae and Andrenidae catch rates can be clearly seen as can the grouping of understory and meadow sites and the bee families caught within them. Site #8 (SP_Dry) was where 935 *Panurginus* (Andrenidae) were caught.

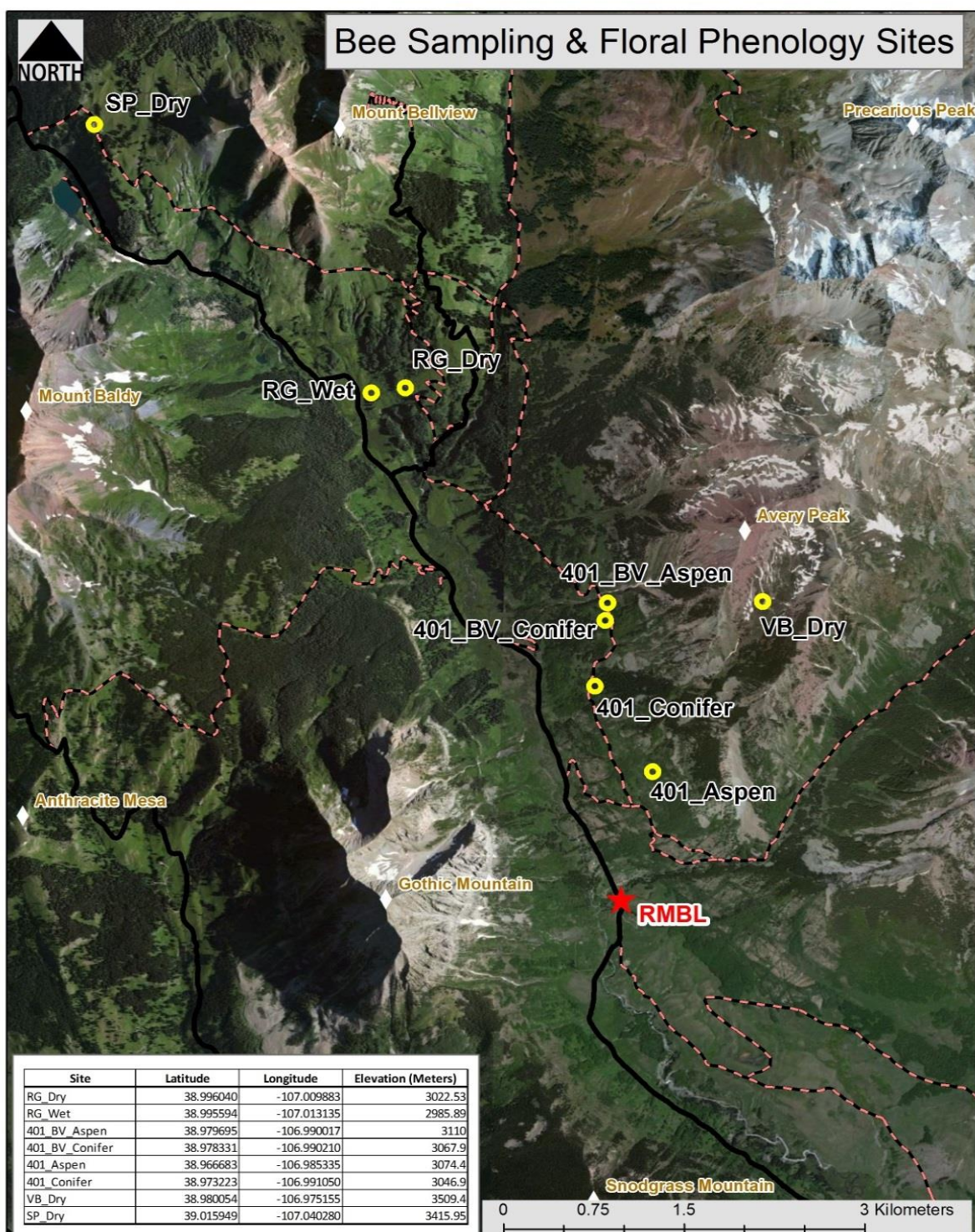


Figure 10 – Map of field sites with coordinates and elevations. Understory sites are named with either aspen or conifer and meadow sites with either wet or dry. BV=beaver ponds, RG=Rustler's Gulch, VB=Virginia Basin and SP=Schofield Pass.

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