# Plant-pollinator interactions characterized by diversity and abundance in grassland communities on the National Bison Range and the Flathead Reservation

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## Abstract

Plant-pollinator networks are an increasing focus of recent research due to Colony Collapse Disorder, which is caused by landscape change among other contributing factors. While it is well known that honey bee populations are in decline, the general wild bee population is also in decline. Wild bees not only provide crucial pollination services to natural plants in the environment but they enhance and maximize the pollination services provided by honey bees in crop fields. Therefore, this study was interested in the effect of floral habitat differences and disturbances on bee diversity and abundance on the National Bison Range and the Flathead Reservation. Grazed, ungrazed, and recreationally used tribal grassland were used as the study sites. Diversity and abundance of both plants and bees were recorded. No immediate trends were observed but patterns among grazed and ungrazed sites became evident when analyzed in daily comparisons. Ungrazed sites appeared to host a greater diversity and abundance of bees while grazed land appeared to have declining abundance in comparison to its floral diversity. Bees may have been pushed out of intensely grazed sites to ungrazed sites which is why this trend was occurring, although other plant phenology may have had an impact as well. This study showed that levels of disturbance and habitat composition can have an effect on bee composition and should be considered as more grassland is converted into agricultural fields.

## Introduction

Plant-pollinator networks are an increasing focus of recent research due to Colony Collapse Disorder, which is caused by landscape change among other contributing factors (NRC 2007). While bee research often emphasizes honey bee decline, general bee diversity has also depleted over time (Burkle *et al.*, 2013). These declines threaten plant reproductive success given its reliance on the pollination services provided by both wild bees and managed honey bees (Potts *et al.,* 2003). Honey bees derive their prestige from the crop pollination industry but they can neither replace wild pollinators nor maximize pollination services without them (Garibaldi *et al.,* 2013). Since wild pollinators are frequently overlooked, they were the center of this study.

Previous work has shown that floral reproductive success is associated with a greater diversity of pollinator visitors (Jordano, 1987; Memmot, 1999; Waser *et al.*, 1996). It is also found that diverse insect communities occur where pollen and nectar resource diversity is high

(Potts *et al.*, 2003). This mutualistic relationship suggests a correlation between the diversity of plant and pollinator communities (Ghazoul, 2006).

Flowering plants experience greater reproductive success in diverse and abundant plant communities indicating that plants benefit from a variety of coflowering species (Lazaro *et al.*, 2009). Heterogeneous plant communities may also facilitate the survival of rare plant species by using their nectar and pollen rewards as a beacon to attract pollinators to areas inhabited by the rare species (Ghazoul, 2006). As a result, both plants and pollinators benefit from the enhanced resource availability. Similarly, the competition theory for diversity suggests that consumer (pollinators) diversity is directly correlated to resource (plants) abundance and vice versa (MacArthur, 1972). This could mean that fluctuations in the bee community may impact the abundance and diversity of the corresponding plant community. Given the seasonality of blooming flowers and the life span of bees, these fluctuations occur frequently and require plant-pollinator relationships to be flexible. For example, the seasonality of blooming plants and lifespan of pollinating-insects often overlap for many species but rarely correlate exactly to sustain either plant or pollinator communities (Hegland and Boeke 2006; Lazaro *et al.*, 2009). In response, plants and pollinators will often generalize in order to maximize their pool of resources and to eliminate their reliance on a single blooming plant or active pollinator (Waser *et al.*, 1996). Disturbances within these communities of adjusted plant-pollinator relationships may therefore impact the diversity and abundance of bees (Hegland and Totland, 2005; Klinkhamer and de Jong, 1990). Bee life-history traits are known to respond to ecological disturbances which often alter bee composition (Williams *et al.*, 2010). This makes them a potential indicator species for changes in the environment or restoration treatments (Kuhlman, 2014).

In the same way, human land use and management often impact the diversity and abundance of plant-pollinator communities. Grassland communities especially are threatened by increased conversion to agricultural land. Additional grassland use and management efforts include habitat fragmentation, the introduction and spread of invasive species, recreation, and conservation efforts (Carvalheiro *et al*., 2010; Meyer *et al.*, 2014; Ricketts *et al*., 2008; Totland *et al*., 2006). Protected grasslands are maintained by rotational grazing, one of the three determinant factors of grassland vitality along with fire and precipitation. Moderate grazing can function as a control for plant biodiversity by subduing the spread of dominant species and providing opportunities for other species to grow (Knapp *et al.*, 1999). However, grazing may also result in homogenizing vegetation depending on the timing and intensity of grazing (Meyer *et al.*, 2014). Briske *et al.* (2008) alternatively suggests that grazing is an opportunity for the establishment of invasive species as well as other native species that may diversify the community. Due to the variability of grazing intensity, bee communities may respond to grazing either positively or negatively, depending on how grazing alters the plant community.

This study focuses on plant-pollinator communities in three types of protected grassland: bison grazed and ungrazed sites in the Palouse prairie on the National Bison Range and reserved tribal lands near the Flathead River in Charlo, Montana. The objective of this study is to answer two questions 1) are the diversity and abundance of flowering plant and pollinator communities correlated with one another? And 2) does the relationship between plant and pollinator diversity differ among these three grassland types? I hypothesized that areas of greater disturbance (grazed and reservation land) would be florally diverse but less abundant in association with a diverse and less abundant bee community. I assumed that grazing intensity was high and the reservation land experienced a high frequency of recreational traffic. I predicted less disturbed areas (ungrazed land) would have higher abundance of both bees and flowering plants given that these communities are more established and experience less intense grazing and traffic.

## Methods

### *Study Site*

I collected data in three habitat types: bison grazed, ungrazed, and tribal reservation land. Each habitat type was replicated three times. Bison grazed and ungrazed sites were located on the National Bison Range (NBR) (47.326299 N, -114.226053 W) managed by the U.S. Fish and Wildlife Service. The NBR is a rotationally grazed, unburned mixed bunch-grass Palouse prairie in the Flathead River Valley of western Montana. Bison grazing is highly influential on plant diversity and encourages heterogeneity especially within the forb and shrub communities in tallgrass prairie (Knapp *et al.*, 1999). Plant diversity is not influenced by bison grazing in the ungrazed sites, although they are frequented by natural browsers such as mule deer (*Odocoileus hemionus*) and white tailed deer (*Odocoileus virginianus*). Sites located on tribal land resided on the Flathead Indian Reservation, also in western Montana near the Flathead River. While these reservations are protected from urban development, they are open for public recreation and are subsequently highly disturbed. Reservation land is also subject to natural grazers and occasionally cows.

### *Field Sampling*

Each habitat type consisted of three randomly dispersed plots, each plot a 25 x 25 m grid. Within each grid, ten 0.25 $m^2$ quadrats were placed flush with the ground at randomly chosen points. All flowering plant species located inside each quadrat were recorded and counted to determine diversity and abundance of floral resources. Each plant in bloom was also counted and identified to species.

Bees were collected using a bowl traps. Six rebar-supported paper bowls, measuring 1.75 m in diameter, were randomly staked into the plots. The paper bowls were mounted onto thick metal wire twisted into a hoop and around the stake. The height of the traps was adjusted to the height of the surrounding flowering plants. The bowls were painted blue, yellow, or white using UV Wildfire Luminescent Paint. These colors were determined using the U.S. Forest Service's Pollinator Syndrome Traits Table for pollinator syndromes according to bees. Two bowls of each color were placed onto each plot and filled halfway with a water and dish soap mixture intended to immobilize insects for collection. The traps were left out for 24 hours on warm days devoid of precipitation. The collected bees were retrieved and stored in ethanol filled plastic cups. All samples were identified to genus and morpho species in the lab to determine diversity and abundance of bee pollinators at each site. Each site was sampled three times during the summer of 2015.

*Statistical Analysis*

Plant and bee diversity were calculated using the Shannon-Weiner Diversity Index. Plant abundance was represented as the average abundance of all 10 (0.25$m^{2)\text{ plots}}$ on a grid. Bee abundance was calculated as the total number of bees collected at each grid. Abundance of bloomed plants per grid was averaged among the 10 plots.

Linear regressions compared plant diversity and bee diversity, plant abundance and bee abundance, plant diversity and bee abundance, and plant abundance and bee diversity among all grids. Linear regressions also compared diversity and abundance data that was collected only at grazed and ungrazed sites during the same day. These regressions excluded data from sites that were sampled alone which included reservation sites and one grazed and ungrazed site. Bee diversity and abundance was also compared using linear regressions to the total number of bloomed plants at each grid.

A multi-linear regression compared variations of the variables plant diversity, plant richness, and plant abundance to bee diversity and abundance.

A one-way analysis of variance (ANOVA) compared bee diversity, abundance, and richness to habitat types and dates of sampling. ANOVAs were also used to compare plant diversity, abundance, and richness to habitat types. Diversity and abundance data collected only at grazed and ungrazed sites during the same day were compared to date of sampling and habitat types using ANOVAs as well.

**Results**

A total of 27 sites were sampled for vegetation and bee communities. Ungrazed, grazed, and reservation land were represented by three sites each with three grids at each site. A total of 33 plant species and 33 bee morpho species were observed. A total of 1800 bees were collected: 767 from ungrazed sites, 583 from grazed sites, and 407 from reservation land.

*Diversity and abundance among habitat types*

There was no significant relationship between plant and bee diversity among all 27 sites (Fig. 1). Neither was there a correlation between plant and bee abundance among all sites (Fig. 2). Singularly analyzing bee diversity, abundance, and species richness among habitat types did not produce any statistical difference (Fig. 3). Plant diversity, abundance, and species richness was also tested against habitat type but no significant difference was found either, suggesting constant plant composition among study sites and perhaps limiting its effect on bee composition (Fig. 4).

The competition theory of diversity was tested against bee diversity and plant abundance, which showed no immediate statistical significance (Fig. 5). Bee abundance and plant diversity were then tested against each other and Figure 6a shows the relationship is approaching significance ($p = 0.058$). The plotted data were separated by site and revealed that grazed sites were showing the strongest correlation between bee abundance and plant diversity in a negative trend ($p < 0.05$) (Fig. 6). Reservation land also displayed a trend, although not as strong as the grazed sites, positively correlating bee abundance and plant diversity. A multi-linear regression analyzed plant abundance and diversity against bee abundance and affirmed a significant interaction between plant diversity and bee abundance ($p = 0.058$) and no significant interaction between plant abundance and bee diversity ($p = 0.414$). The same test compared plant abundance and diversity to bee diversity but showed no interaction between neither plant abundance ($p = 0.257$) nor plant diversity ($p = 0.116$).

*Diversity and abundance through time*

Bee diversity and abundance were compared throughout sampling time (between 23 June and 13 July 2015) but no significant difference was observed ($p > 0.05$) (Fig. 7). Grazed and ungrazed sites only sampled together on the same day (6/23, 6/24, 6/25, 6/29, and 7/01) were then analyzed through time. This analysis excluded points from all the reservation sites and grazed and ungrazed sites that were sampled on separate days and not together in direct comparison with another habitat type. In this way, sites experiencing the same environmental conditions throughout the same period of time during the same day were compared, decreasing variation caused by day-to-day differences (Fig. 8). Ungrazed sites showed a significant relationship trending toward higher bee diversity consistently over time as compared to grazed sites ($p = 0.005$). When grazed and ungrazed sites specific to 6/23, 6/24, 6/25, 6/29, and 7/01 were compared to plant abundance and bee diversity, a significant positive correlation appeared ($p = 0.012$) (Fig. 9). When the plotted data was separated by habitat type, grazed sites appeared to be the most influential factor in determining this significance (Fig. 9). Because plant abundance was having such a significant effect on bee diversity and plant diversity was not, plant abundance was compared to plant richness and a significant positive relationship was found ($p < 0.001$) (Fig. 11). All habitat types responded in a similar way when the plotted data was observed separately by habitat type. A multi-linear regression then compared plant richness and plant diversity to bee diversity and a significant interaction was found between plant richness and bee diversity ($p = 0.042$). Another multi-linear regression compared plant richness and plant abundance to bee diversity showing an even more significant interaction between plant richness and bee diversity ($p = 0.007$) indicating that plant richness was the most influential factors in determining bee diversity among all sites (Fig. 12).

To account for seasonality variability, the average number of blooming plants per grid was compared to bee diversity over time (Fig. 10). No significant relationship was observed, although the graphed data appears to vary over time dramatically showing no distinct pattern ($p = 0.48$).

**Discussion**

Bee diversity did seem to increase as the number of plant species (species richness) increased as my hypothesis suggested, although plant diversity was not as influential as expected. The effect of more plant species, although they may not have been evenly dispersed, therefore, does seem to cause an influx of more bee species, especially in grazed habitat types overall. This contradicts my hypothesis that predicted ungrazed habitats would be more diverse in bee species. A bee monitoring program conducted by MPG Ranch in northern Montana actually reported in 2014 that bees were becoming more abundant in more disturbed areas and expanding their range (although “disturbed” was not defined) suggesting that bees are being pushed out of their natural habitat into different habitats. At first glance, bee diversity in this study seemed to follow the same trend as the MPG Ranch bees and were becoming more supported in, what this study classified as, more disturbed (grazed) areas. Potentially, bee species are expanding their range on or into the NBR and inhabiting more areas causing my study to register their movement as an increase in bee diversity.

Although bee abundance did not show any immediate significant difference among these habitat types, an interesting trend appeared when bee diversity was compared among grazed and ungrazed sites sampled on the same day which, in fact, shows bee diversity is higher in ungrazed habitats supporting my hypothesis. Selecting day-to-day specific data to analyze was decided when I realized that pooling all of the data I collected was masking interactions occurring between sites each day, not necessarily over time. This relationship suggests that less disturbed areas are more likely to host more diverse fauna. Because a day-to-day analysis was showing variability over time, I decided to interpret my data as it was compared to habitat types on the same day. This means that ungrazed sites were more diverse as compared to grazed sites and disregarded reservation site data. Future studies should be aware of this effect and notice day-to-day trends when sampling bee communities, even if weather is already controlled for.

Plant diversity was also correlated to bee diversity at ungrazed sites indicating that more attractive forces produced from the diverse plant life could be bringing in and supporting a more diverse bee community. This may imply that individual plants benefit from a bountiful co-flowing neighborhood of plant species as Lazaro *et al.* (2009) has reported.

Although the correlation between bee diversity is not as strong with plant richness or abundance in these ungrazed habitats, it does seem like this less disturbed, more established habitat can support a greater variety of bee species. This also alludes to other contributing factors effecting the distribution and composition of bees on the National Bison Range and on the surrounding tribal land. Plant phenology, for example, may be more important in determining bee community than simply amounts and variability counts. Reservation land, which observed the least abundance out of the three habitat types, was overrun by invasive plant species including *Centaurea maculosa* (spotted knapweed), *Hypericum perforatum* (St. John's wort), and *Linaria dalmatica (*dalmatian toadflax). This type of plant composition is not accounted for in diversity indexes and abundance counts so it may have impacted bee composition undetected by my data.

Reservation land also experiences a level of disturbance much greater than the grazed and grazed land on the NBR due to its recreational nature and proximity to the Flathead River. The fact that the crude numbers reflecting bee abundance was the lowest in this area is not surprising. However, tribal land did reflect a slight positive interaction between plant diversity and bee abundance which was opposite that of the grazed land which showed a negative correlation between these two variables. One reason for this may be the presence of bison at my grazed sampling sites during the time of sampling. Their presence may have caused a disturbance large enough to influence the bee community to shift away from my study sites to less disturbed floral territory. Because these "grazed" sites were distinguished as such by the NBR indicates that bison frequently graze in these areas throughout the year. Given that bison grazing may subdue dominant species and proliferate the survival of rare species may have caused these areas to become more diverse over time, as mirrored by my plant diversity versus plant richness data, and support diverse bee communities. Therefore, the low bee abundance observed during my sampling time period may be attributed to the intense grazing and general presence of the bison which pushed the bees away from these sites.

I only collected between 10 and 15 bees a day at one site where bison were consistently present as compared to the 50-100 bees I was collected at other grazed, ungrazed, and reservation sites that did not host bison. Therefore this trend may at first appear negative in that bee abundance decreases as plant diversity increases, but it may only be masked by the presence of the bison. However, bison grazing should not be disregarded either. The effect of their presence is important when determining grassland management and the fauna of other communities such as bees. Maybe bees were being pushed out of these intensely grazed bison sites to ungrazed sites which is why bee abundance was registering so high at the ungrazed sites.

Overall, plant composition did seem to correlate to bee composition but spatial and temporal effects made my data variable. The level of disturbance and the type of habitat change occurring at each site, whether it be overrun by invasive plants or intensely grazed by bison, should be taken into account when determining whether or not bee communities are expanding their range temporarily or permanently moving.

This study also applies to the advent of industry converting grassland into agricultural fields. Although agricultural fields were not directly observed, some of the conclusions made here may be applied to these areas of management. Evidently, agriculture decreases natural habitat for grassland plant and pollinator communities (Hegland and Boeke, 2006; Ricketts *et al*., 2008). My study showed that more disturbance caused bee communities to be less abundant. If bees are moving out beyond their natural range because of displacement, the new habitat they choose may be less suitable. The effect of these disturbances can be observed in bee life-history traits such as nesting (Williams *et al*,. 2010). The more land tilled for agriculture, for example, the less stable ground bees have to nest, a critical element in their life cycle. As crop monocultures dominate the land, native pollinator species become even more displaced. It pushes them farther away from crop fields because single species fields are not diverse enough to support them (Carvalheiro *et al*., 2010; Ricketts *et al*., 2008). The success rate of pollination decreases near monocultures as well, meaning that commercial honeybees cannot do the job alone (Ricketts *et al.*, 2008). Therefore, plant and pollinator diversity is crucial to maintaining successful plant-pollinator interactions in addition to an understanding of the disturbance level that could be effecting their community structure.

**Acknowledgements**

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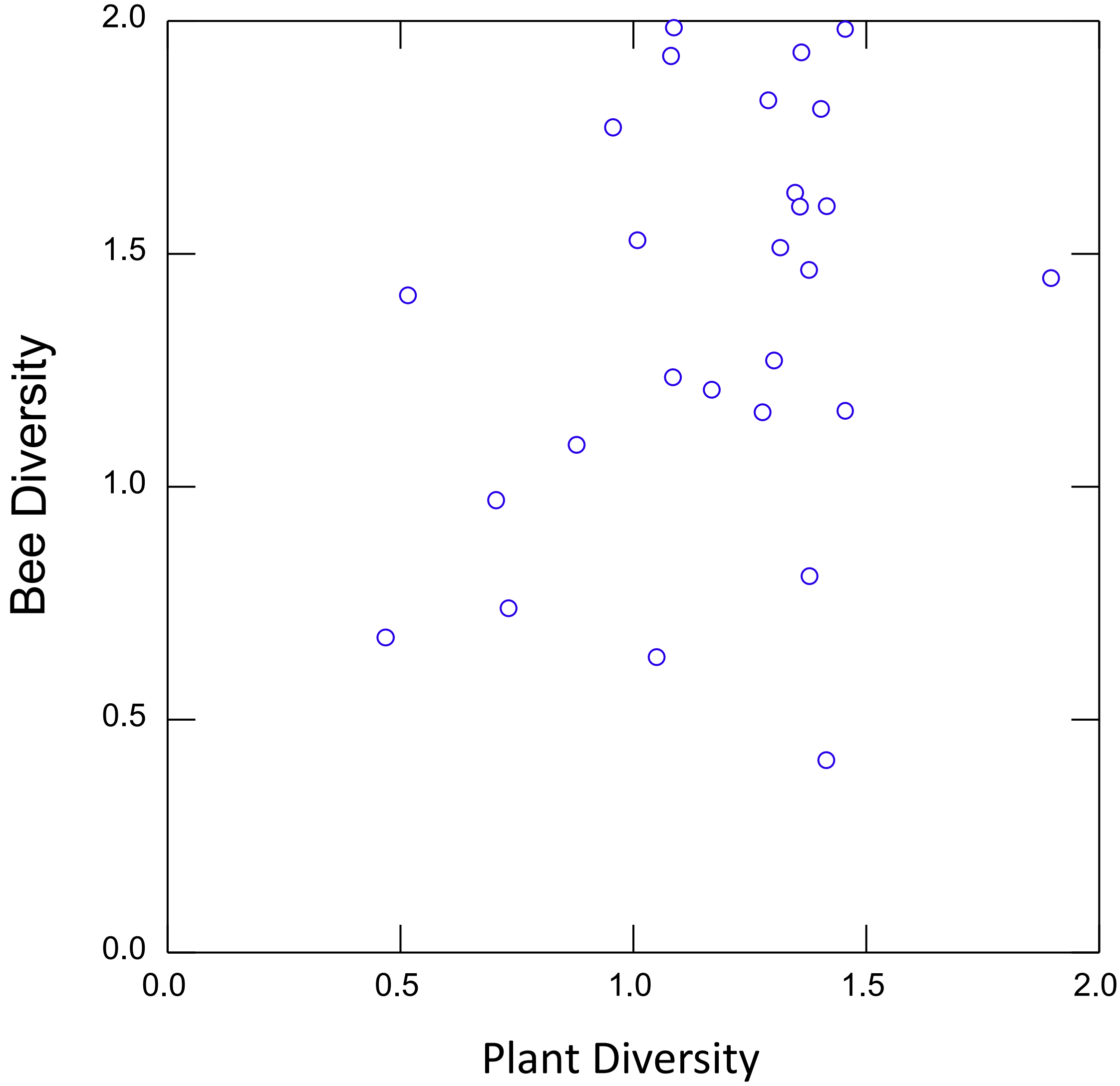


**Figure 1.** Plant diversity compared to bee diversity at all 27 grids (p = 0.122).

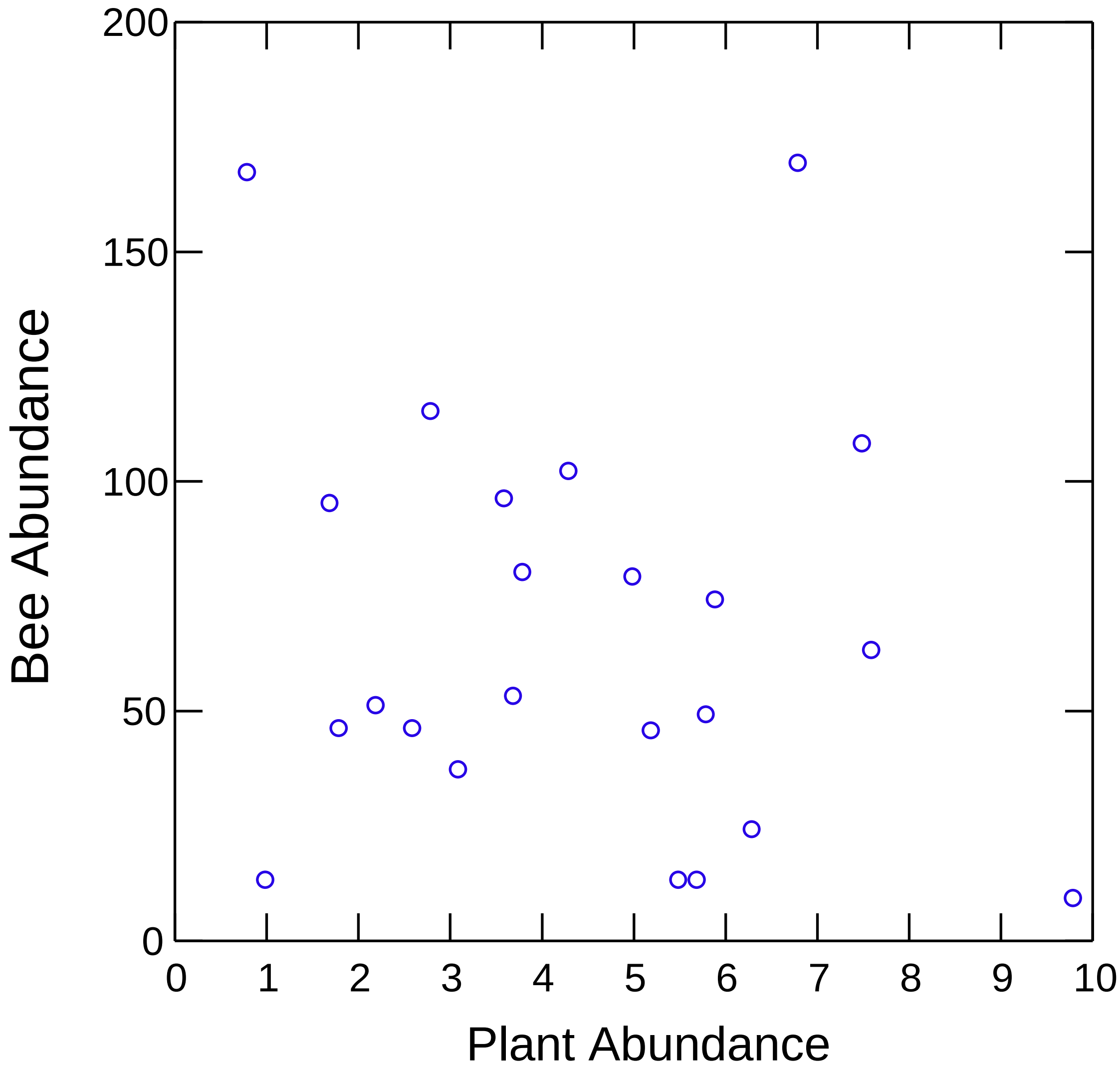


**Figure 2.** Plant abundance compared to bee abundance at 27 grids (p = 0.456).

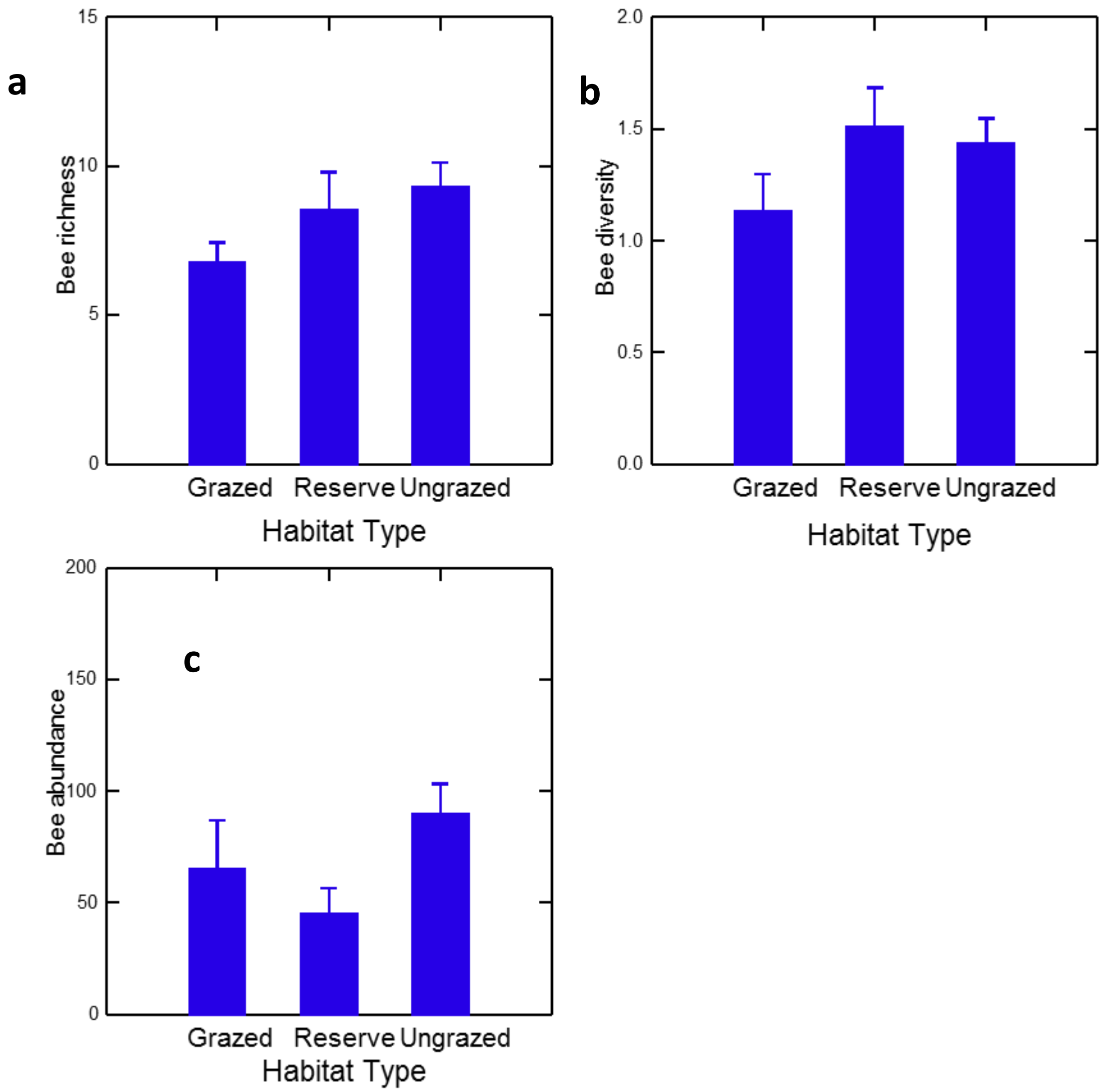


**Figure 3. a)** The effect of grassland habitat type on bee species richness. A slight positive trend favors ungrazed habitats but no statistical significance was found ($p = 0.150$) **b)** The effect of grassland habitat type on bee diversity. No significant difference was observed between types ($p = 0.168$). **c)** The effect of grassland habitat type on bee abundance. There appears to be slight trend favoring ungrazed habitats however, there was no statistical significance ($p = 0.144$).

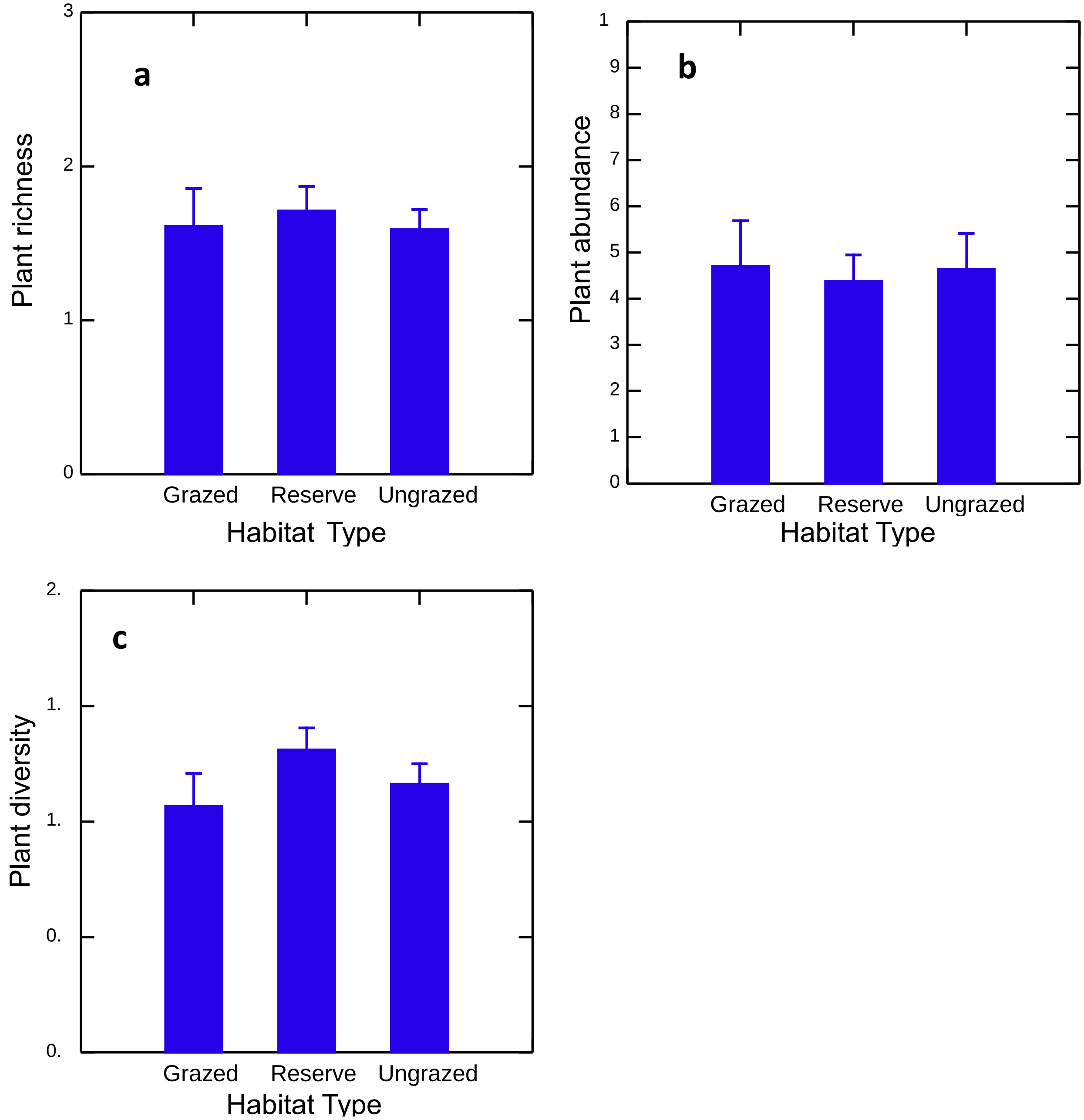


**Figure 4. a)** The effect of grassland habitat type on plant diversity. No significant difference was observed between types ($p = 0.275$). **b)** The effect of grassland habitat type on plant abundance. No statistical significance was found ($p = 0.947$). **c)** The effect of grassland habitat type on plant species richness. No statistical significance was found ($p = 0.869$).

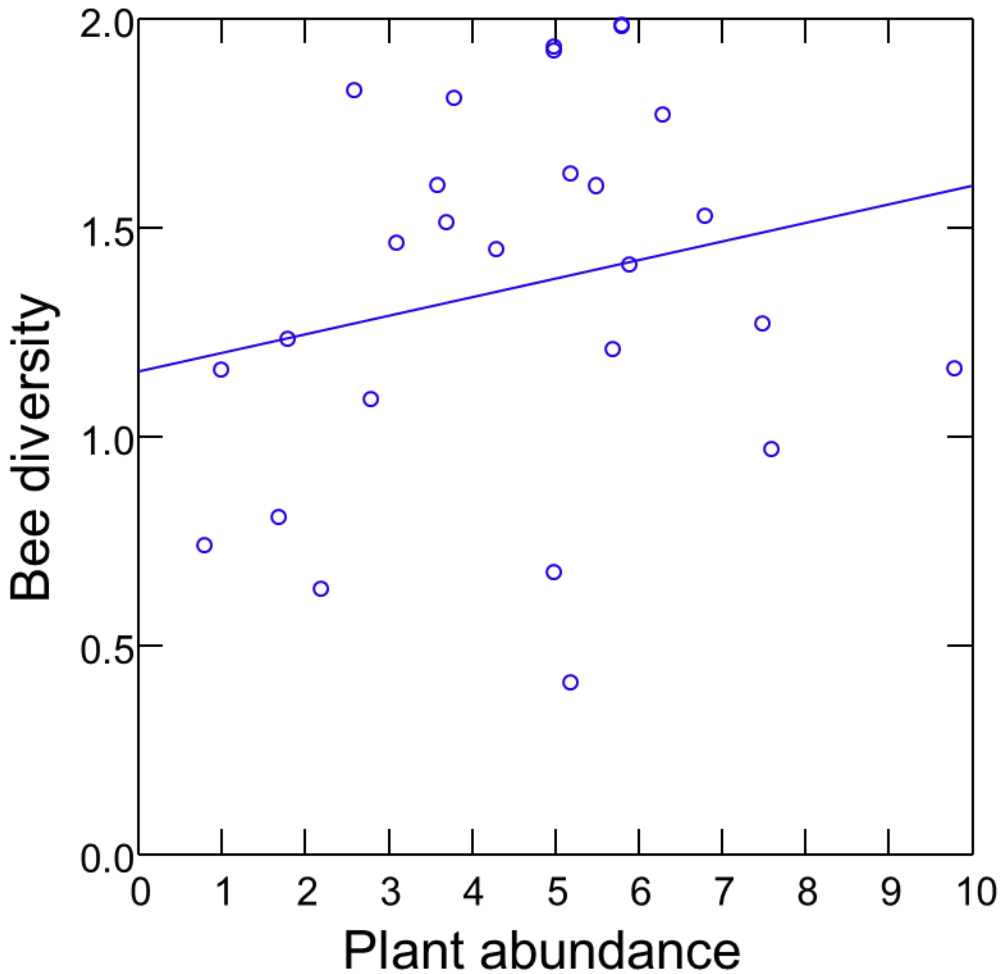


**Figure 5.** Plant abundance compared to bee diversity at all 27 grids (p = 0.282).

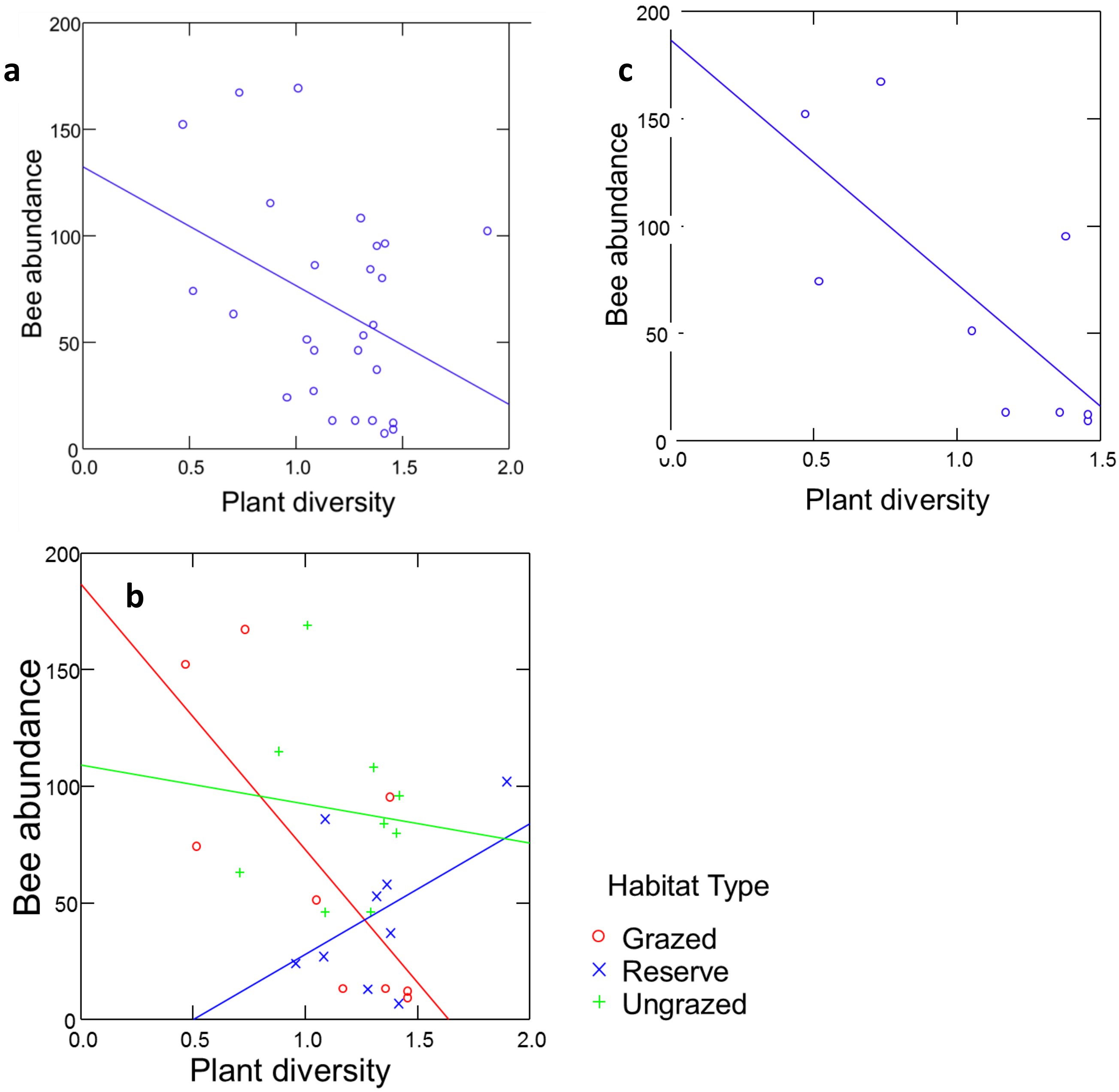


**Figure 6. a)** Plant diversity compared to bee abundance at all 27 grids showing a slight negative trend ($p = 0.058$). **b)** The effect of plant diversity on bee abundance at the three habitat types showing a negative trend at the grazed sites and a slight positive trend at the reserve sites. **c)** The effect of plant diversity on bee abundance only at the 7 grazed sites and showing a significant negative trend ( $p < 0.05$).

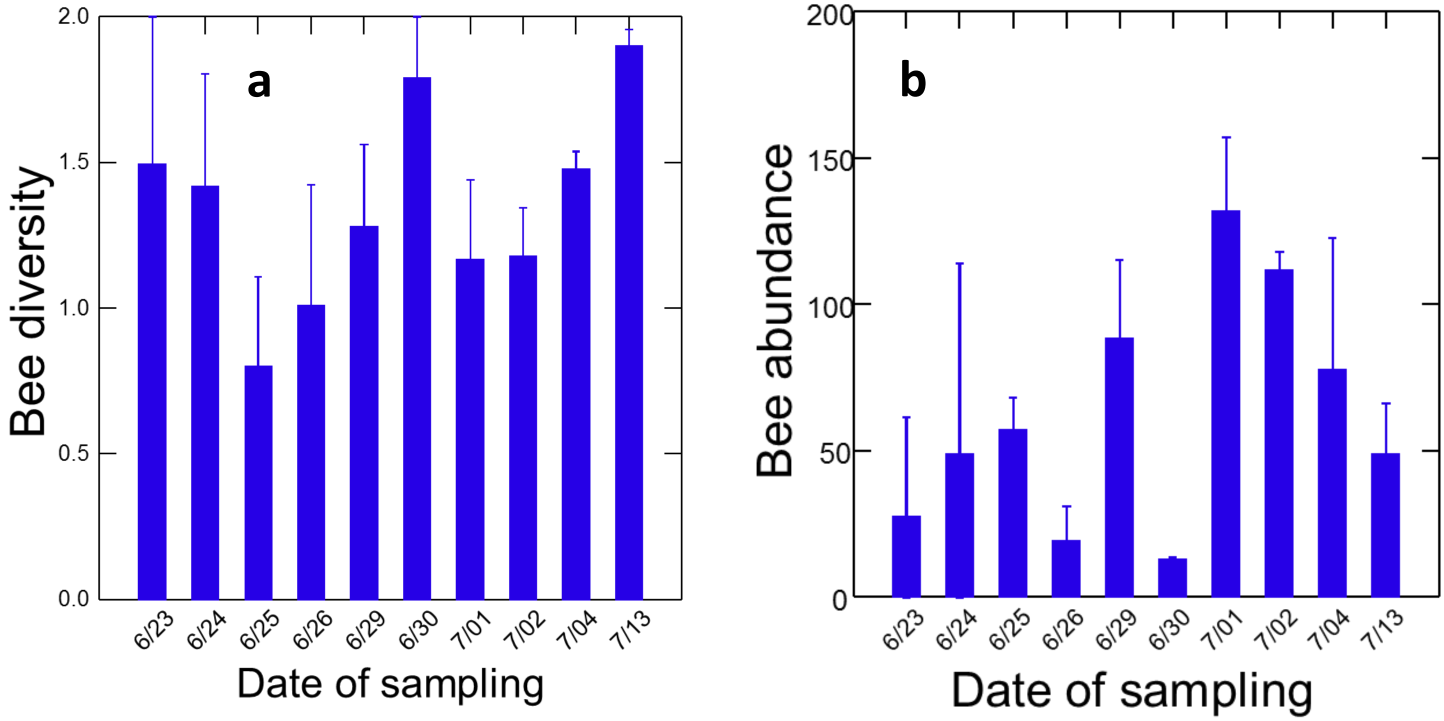


**Figure 7. a)** Bee diversity at all sites throughout the time of sampling. The results were fairly variable and not significant ($p > 0.05$). **b)** Bee abundance at all sites throughout the time of sampling. No significance was found ($p > 0.05$).

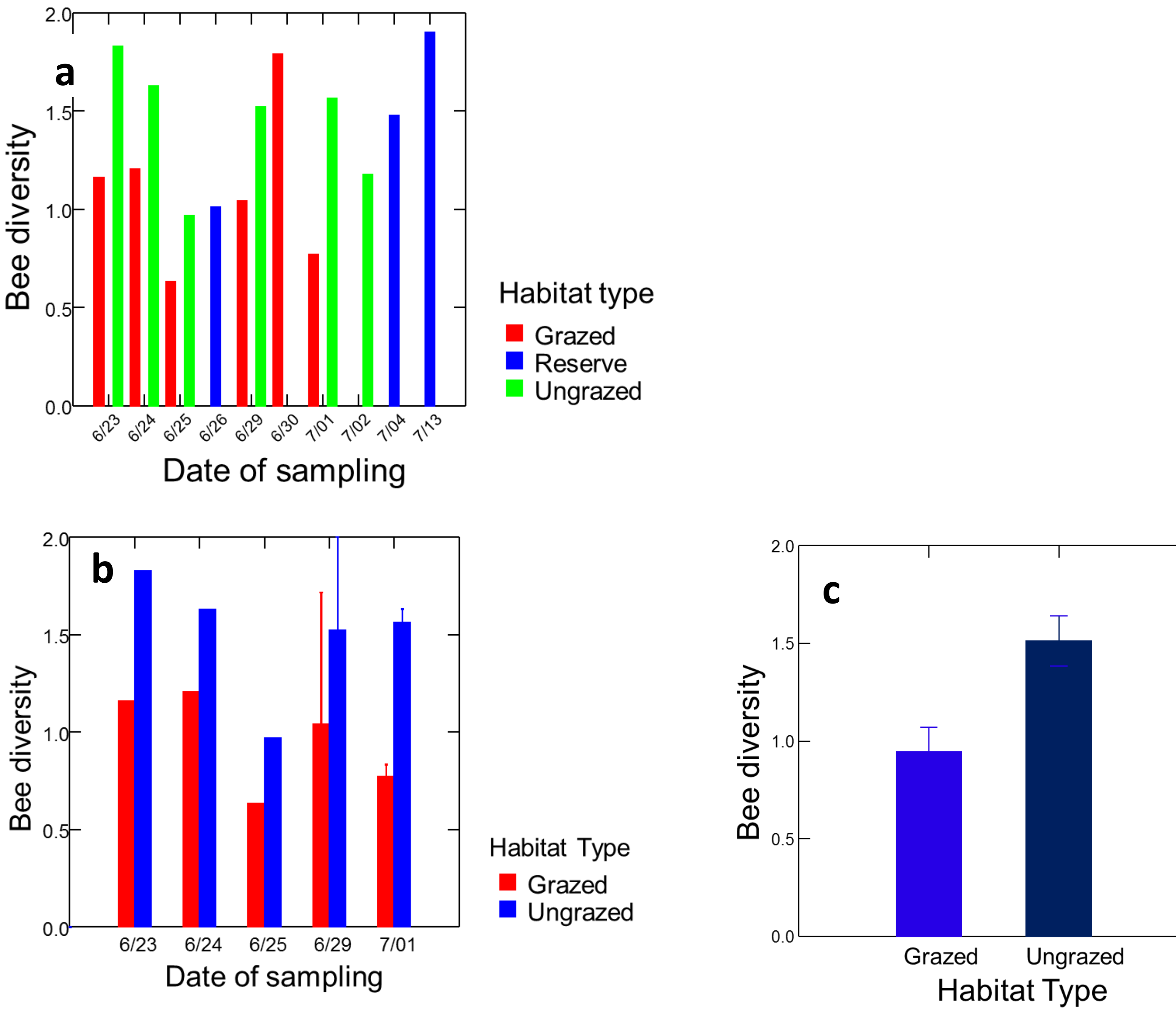


**Figure 8. a)** Comparing bee diversity throughout time during all sampling days separated by habitat type. **b)** Comparing bee diversity only at grazed and ungrazed sites sampled on the same day through time. Bee diversity is consistently higher at ungrazed sites. **c)** Bee diversity compared to grazed and ungrazed sites sampled on the same day showing a significant relationship ($p = 0.005$).

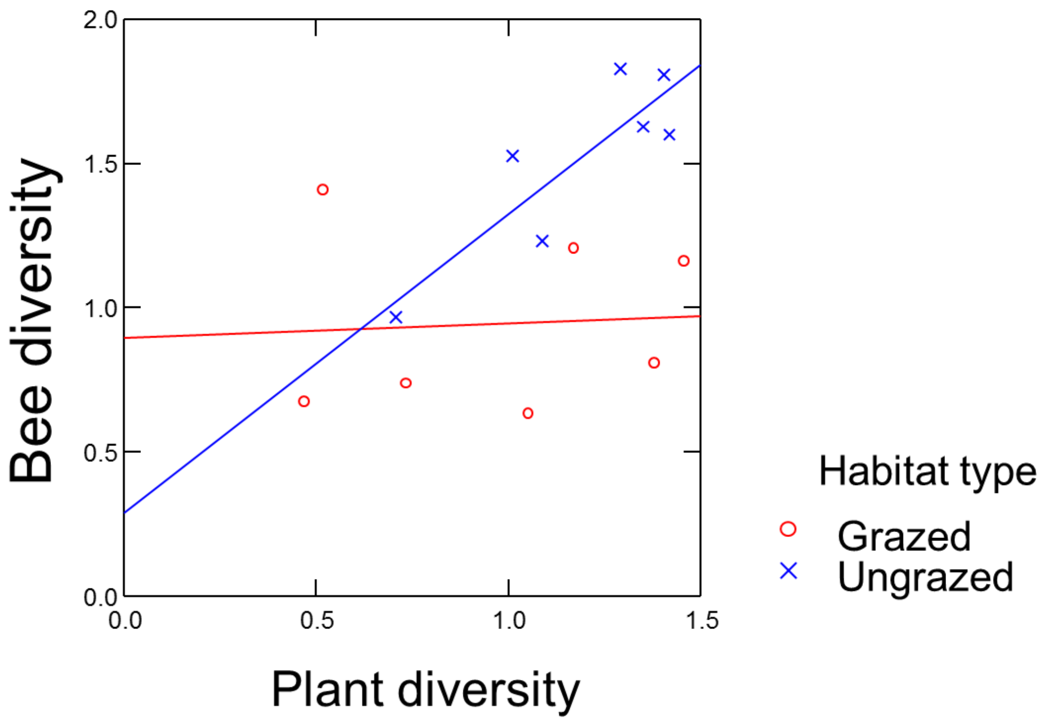


**Figure 9.** Plant diversity compared to bee diversity at grazed and ungrazed sites only sampled on the same day. Ungrazed sites showed a significant positive relationship (p = 0.012).

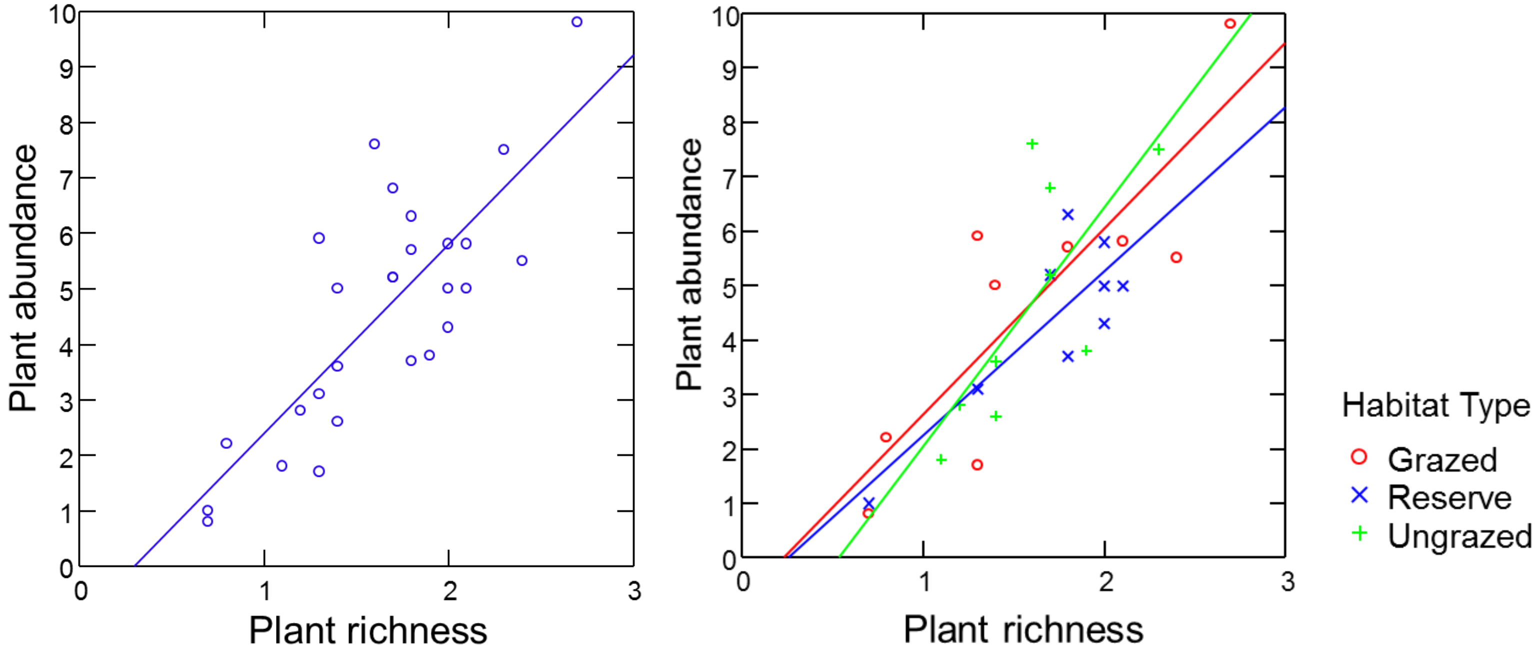


**Figure 11.** Plant richness compared to plant abundance at all 27 sites showing a significant positive relationship ($p < 0.001$). Each habitat type depicts the same positive trend.

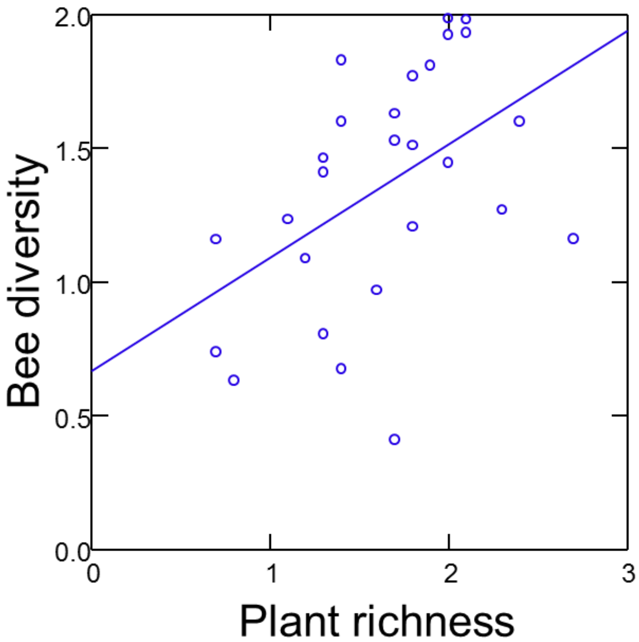


**Figure 12.** Plant richness compared to bee diversity at all 27 sites showing a significant positive relationship ($p = 0.012$). Each habitat type depicts the same positive trend although grazed sites have the most significant correlation ($p = 0.025$) compared to ungrazed ($p = 0.402$) and reservation sites ($p = 0.133$).

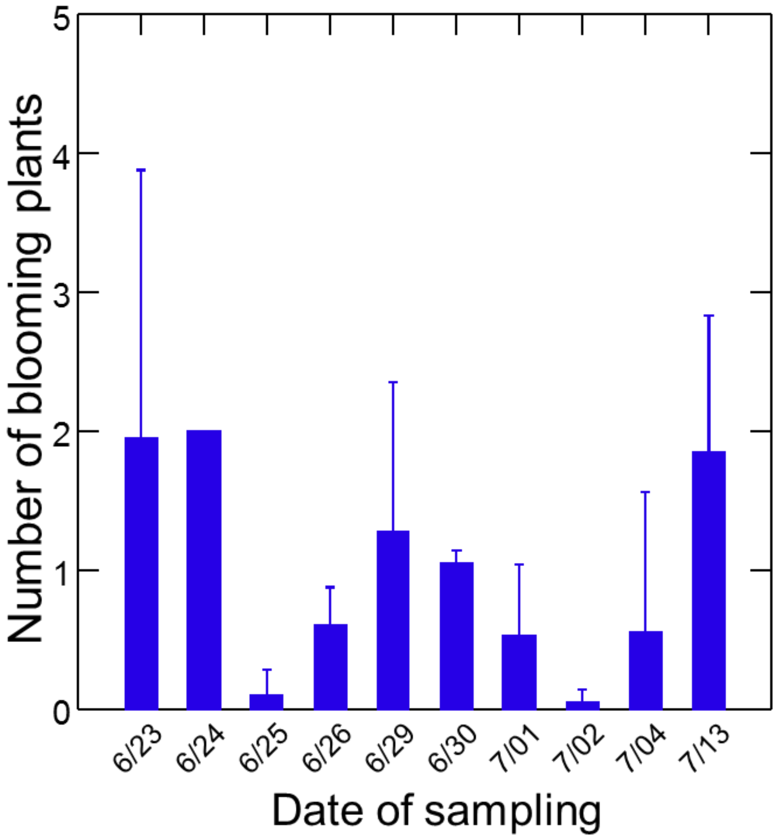


**Figure 10.** Number of blooming plants among all sites throughout the time of sampling between 23 June and 17 July 2015. No significant difference was observed among days (p = 0.48).