

Understanding the importance of coniferous understory habitat versus open meadows for
bees in times of drought

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Abstract. The occurrence and extremity of drought conditions are predicted to increase as a result of climate change. The western United States is expected to experience a decline in annual precipitation as well as an increase in drier, warmer years. Such changes could have numerous implications on Rocky Mountain subalpine ecosystems, including plant-pollinator interactions. During 2012, the Rocky Mountain West experienced severe drought conditions, and floral abundance was dramatically lower than in previous years. Floral abundance in coniferous understory habitats remained high compared to open meadows, possibly providing resources to pollinators. Open meadows had higher pollinator visitation rates, despite greater floral abundance in understory.

Keywords: climate change, drought, Rocky Mountains, subalpine ecosystems, plant-pollinator interactions, coniferous understory, open meadows, bees, floral abundance, pollinator visitation

INTRODUCTION

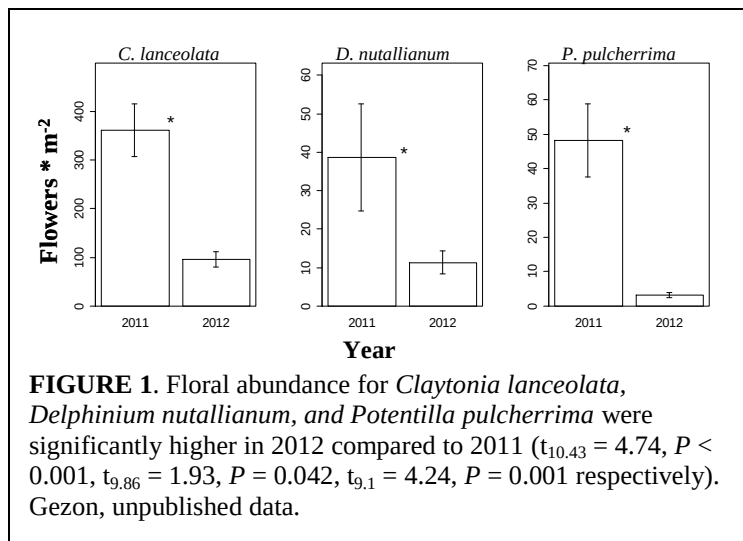
Climate change is predicted to cause a decrease in the annual amount of precipitation, an increase in surface temperatures, and an increase in the occurrence and extremity of drought conditions (IPCC 2007). Droughts have become more common in the Northern Hemisphere since the 1950s and it is expected that regions already experiencing drought will continue to have drier years (Bates 2007). The western United States has particularly experienced an increase in annual drought conditions (Bates 2007). Such climatic changes may have numerous effects on Rocky Mountain subalpine ecosystems, which depend on the time of snowmelt for normal summer seasonal progression.

Two leading causes of drought in the Rocky Mountains are a decrease in the annual amount of snow accumulation and a decrease in soil moisture (Bates 2007). Water is a vital resource for plant growth and reproduction (Baude 2011), and a decrease in annual water availability and soil moisture could consequently affect key processes, abundance, and biomass of various plant communities (Evans 2011, Johnson 2011). The

onset of drier years may have an impact on the variability of floral resources, which could consequently cause a shift in the foraging behavior of bees (Hegland 2009, Beismeyer 2006).

Drier, warmer climates have negatively impacted organisms and ecosystems in semi-arid and arid regions worldwide (Thomas 2010, Morrongiello 2011, Dulamsuren 2010). But surprisingly much remains unknown about the effects of drought conditions and drier soil at an ecosystem level, and how these conditions could affect plant-pollinator interactions (Beier 2012, Weltzin 2003). Many organisms rely, either directly or indirectly, on pollinators for food availability (Hegland 2009); therefore, it is important to understand if and how plant-pollinator interactions may be affected by the implications of climate change, specifically drought.

In the summer 2012, the western and midwestern regions of the United States had experienced an exceptionally dry year. From June 19, 2012 to July 31, 2012, the upper portion of Gunnison County, Colorado was classified as



having D3 (extreme) drought conditions (Heim 2012), and floral abundance in open meadows was abnormally low compared to previous years (Figure 1). Understory habitats, however, appeared to be less affected by the drought and floral abundance in understory remained high compared to open meadows. **The objective of my research was to understand the importance of coniferous understory versus open meadows for bees in times of drought** based on the following questions:

(1) How do abiotic conditions such as soil moisture and leaf temperature differ between understory and open meadow habitats? (2) How does floral abundance and richness in understory habitat compare with open meadows? (3) How do the rates of pollinator visitation differ between understory habitat and open meadows? (4) What are

the relationships between percent soil moisture, floral abundance and richness, as well as rate of pollinator visitation in understory and open meadows?

METHODS

Study Site

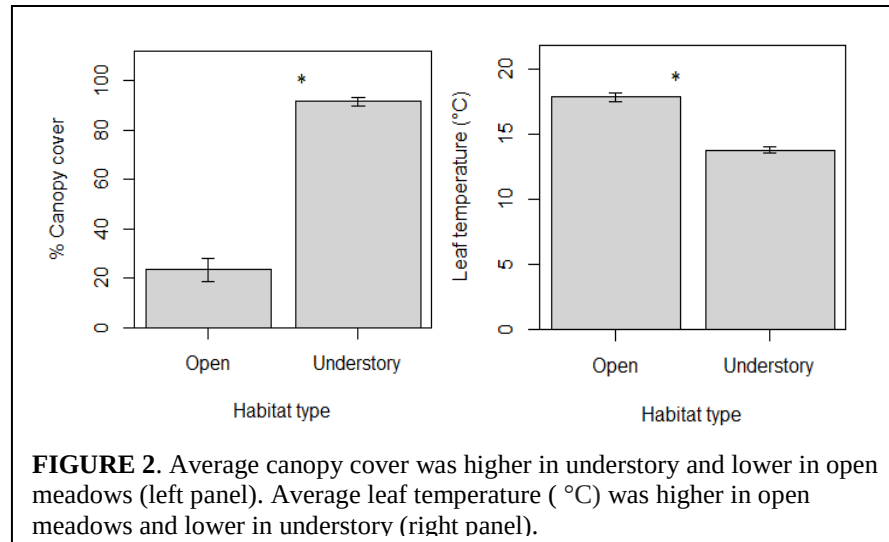
Research was conducted along Trail 401 near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado, USA (latitude 38°58'28.118"N, longitude 106°59'31.772"W, elevation 3047 meters). The study area was chosen based on the presence of open meadows and understory habitat, the amount of south and southwestern facing slopes, and the degree of slope. When choosing the site, I ensured that the area had enough open meadows and understory habitat for 6 open meadow plots and 6 understory plots. The area contained more south and southwestern slopes (64.3%) than north and northeastern slopes (5.9%) to avoid areas where temperatures may be cooler, consequently affecting insect abundance and activity. The degree of slope was small to prevent possible contamination of water runoff from slopes above the plots (79.2% of the slopes were 0-7.39 degrees).

Experimental Design

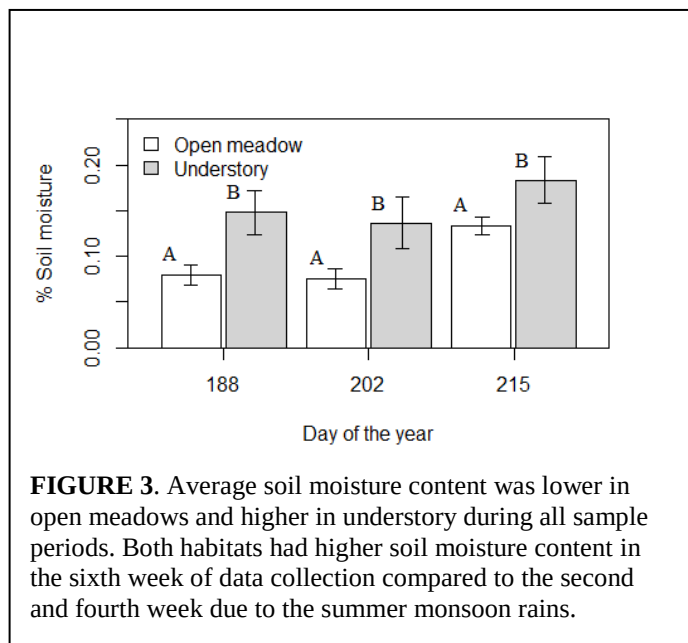
In each of six sites, I established two, 2x2 meter plots. Each site contained one open meadow plot paired with an understory plot – yielding a total of 12 plots. All understory plots were located within pine forests. Understory plots were chosen based on canopy cover (over 50%), presence of blooming flowers, and the existence of plants that would possibly bloom during data collection. Each open meadow plot was placed 8 meters from the forest edge with the same orientation as the understory plot and had less than 50% canopy cover.

I obtained weekly data on drought conditions based on the US Drought Monitor website (Heim 2012). Drought conditions were rated by the US Drought Monitor on a scale from D1-D4, with D1 being “abnormally dry” and D4 being “exceptionally dry” (Heim 2012).

To examine environmental differences between open meadows and understory, I measured percent canopy cover and leaf



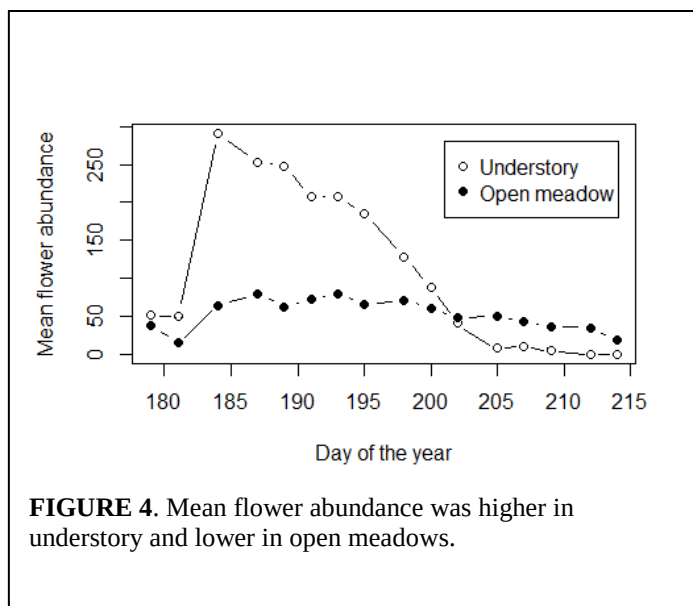
temperature of both habitats during the fifth week of data collection. Using a densitometer, I measured the overall percent canopy cover in both open meadow and understory plots. I measured the percent open area (not area covered by canopy) in each cardinal direction (North, West, South, East) of each plot and subtracted the open area from 100 to obtain total percent of canopy cover. I compared average percent canopy cover between understory habitats and open meadows using ANOVA, blocking for site. Insignificant terms were dropped from the final model. I measured leaf temperature (°C) with a handheld infrared thermometer. Plot means were determined by averaging the leaf temperature of three leaves on three different plant species. I compared average



leaf temperature between understory habitats and open meadows using nested ANOVA, with plot nested within site. All statistical analyses were performed using R statistical software version 2.14.1 with RStudio integrated development environment.

I analyzed percent soil moisture in open meadows and understory habitats to investigate the relationship between soil moisture content and flower abundance. Ten cm soil cores were sampled three times during the study (once every two weeks) and percent soil moisture was measured using a gravimetric method (Inouye 1993). I analyzed average soil moisture content as a function of habitat and time using repeated measures ANOVA, blocking for site.

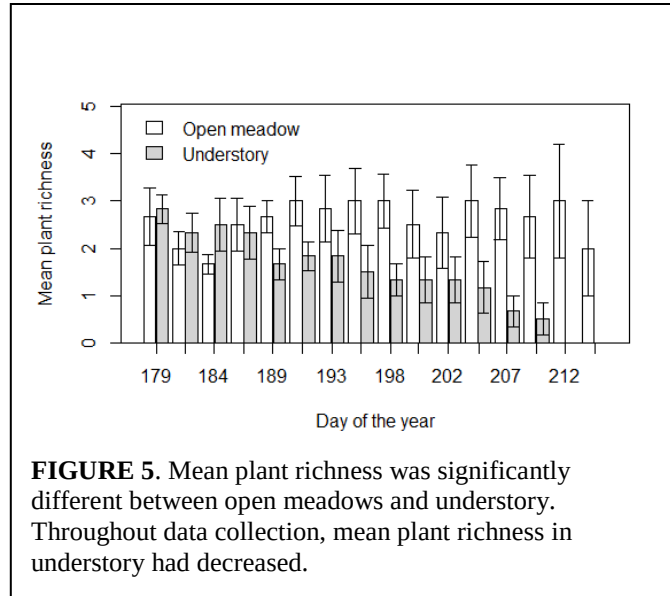
Every other day, I censused floral abundance in all plots. I identified all plant species in flower, recorded the average number of flowers per plants, and counted the total number of plants in flower of each species. I compared the overall abundance and richness of floral resources between open meadow and



understory habitats using repeated measures ANOVA, blocking for site.

To determine how bee abundance, activity, and rate of pollinator visitation in open meadows compare to understory, I conducted pollinator observations every week. Each plot was monitored for 80 minutes per week. Since pollinators may forage based on temperature and time of day, I conducted pollinator observations for 40 minutes in the morning and 40 minutes in the afternoon. The sites were randomized every day to prevent biased timing of pollinator observations. Understory and open meadow plots of the same site were monitored in the same hour, but understory and open meadow plots were also randomized. The bee pollinators were identified to the lowest taxonomic level. I used a tape recorder to document the plant species visited, the number of flowers the

pollinators visited, and the duration of flower handling. Pollinator visitation was quantified as total time spent foraging per plot on each day. To test for differences in pollinator visitation between habitat types, I used repeated measures nested ANCOVA with habitat type (open versus understory), day of the year, and



block (site) as factors, and floral abundance (flowers * m⁻²) as a covariate. Block was included to account for the pairing of plots within sites.

To identify the pollinators around the sites, I collected a representative sample of bees from either inside or around the plots. I collected 32 bees in the first four weeks of data collection and identified all specimens to the lowest taxonomic level using a dissecting scope.

TABLE 1. Identification and quantity of bees collected from understory habitat and open meadows, RMBL.

Habitat	Family	Subfamily	Genus	Quantity
U	Andrenidae	Andreninae	Andrena	3
	Anthophoridae	-----	-----	1
	Colletidae	Hylaeinae	Hylaeus	2
O	Andrenidae	Andreninae	Andrena	4
	Andrenidae	Panurginae	Panurginus	12
	Colletidae	Hylaeinae	Hylaeus	2
	Halictidae	Rophitinae	Dufourea	4
	Halictidae	Halictinae	Halictus	1
	Halictidae	Halictinae	Lasioglossum	1
	Halictidae	Halictinae	Sphecodes	1
	Megachilidae	Megachilinae	-----	1

Notes: Bees were collected from June 27, 2012 to July 20, 2012.

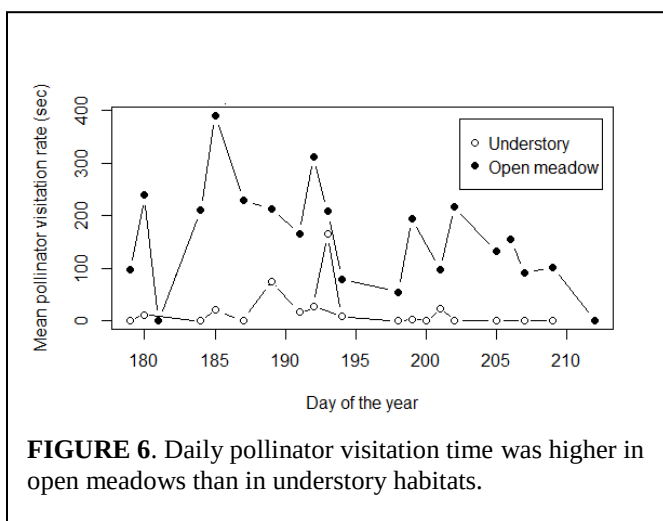
RESULTS

Drought conditions. – Drought conditions at Gothic, Colorado remained the same throughout data collection. The US Drought Monitor had classified the upper portion of Gunnison County as having D3 (extreme) drought conditions from June 19, 2012 to July 31, 2012 (Heim 2012).

Environmental conditions. – Average percent canopy cover was higher in understory habitat than in the open meadows ($F_{1,10} = 159.0$, $P = 1.8 * 10^{-7}$, Figure 2, left panel). Open meadows had a higher average leaf temperature ($^{\circ}\text{C}$) compared to understory habitats ($F_{1,10} = 18.8$, $P = 0.0015$, Figure 2, right panel).

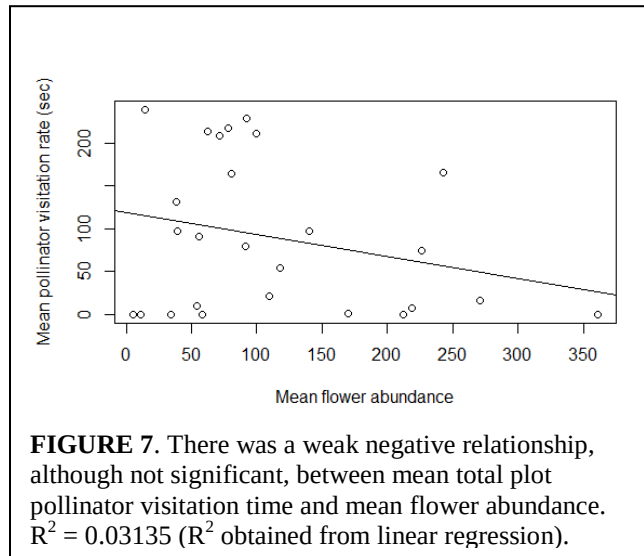
Soil moisture. – The average percent of soil moisture was significantly lower in open meadows than in understory habitat ($F_{1,32} = 19.03$, $P = 0.00013$, Figure 3) in all three sampling periods. Day of year significantly affected percent soil moisture ($F_{1,32} = 5.5$, $P = 0.0091$, Figure 3). The third sample time had higher percent soil moisture in both open meadows and understory habitats compared to the first two sample periods (Figure 3).

Flower abundance and richness. – The average flower abundance was significantly higher ($F_{1,428} = 7.85$, $P = 5.33 * 10^{-3}$, Figure 4) in the understory habitats than in the open meadows. Day of year did not affect floral abundance, and was therefore, dropped from the final analysis. Habitat did not have a significant affect on mean flower richness ($F_{1,10} = 3.6$, $P = 0.0968$, Figure 5). However, time of year did significantly affect flowering species richness ($F_{1,178} = 27.4$, $P = 4.57 * 10^{-7}$, Figure 5). The effect of time on flower richness varied between open meadows and understory habitats ($F_{1,178} = 46.4$, $P = 1.43 * 10^{-10}$, Figure 5). Average flower richness in understory habitat decreased as a function



of time (Figure 5).

Pollinator visitation. – Average time of pollination was significantly higher ($F_{1,8} = 5.94$, $P = 0.0408$, Figure 6) in open meadows than in understory plots. There was a negative regression, although not significant, between average time of pollinator visitation ($F_{1,24} = 1.8$, $P = 0.191$, Figure 7)



DISCUSSION

Overall, the environmental conditions – specifically, canopy cover, leaf temperature and soil moisture – were different between understory and open meadow habitats, meaning that even in times of drought, some habitats are more favorable for plant growth than others. My findings are supported by previous research which has found reduced daytime temperature in forested areas (Ferrez 2011, Renaud 2009), and suggest that forests may provide cool habitat during extremely dry conditions. Such environmental differences between both habitats are likely to occur in years of normal precipitation.

Floral abundance was greater in understory habitats than open meadows, but pollinator visitation was higher in open meadows. The low rate of pollinator visitation in understory could hinder the reproductive success of understory plants. In addition, the understory habitats were within bee foraging distance from the open meadow plots, but bees were not utilizing the floral resources in the understory. It is difficult to know exactly why bees were not utilizing these areas of higher resources, although there are several plausible explanations. Since bee activity tends to be higher in open, sunny areas (Louda 1996, Hegland 2009), the canopy cover and cooler temperatures of understory

habitats may have resulted in lower bee activity. It is also possible that the floral abundance in the open meadows may have been great enough as to not cause a shift in the foraging behavior of bees from open, sunny areas to shady habitats. Finally, the quality of floral resources could be lower in understory habitats versus open meadows. Further investigation is required to determine the reason that bees fail to utilize areas of high resource abundance during drought conditions.

Although floral abundance was higher in understory habitats, floral richness was not significantly different between habitat types. Understory floral richness, however, decreased over the course of the study (Figure 6). Decrease of floral richness in the understory habitats may be a result of soil properties in coniferous forests. Soil organic matter and nitrogen content, can increase plant richness (Laughlin 2007). Research has shown a decrease in plant species richness within pine forests due to lower amounts of organic matter and nitrogen content in the soil (Laughlin 2007). My results of flower richness in coniferous understory may, therefore, relate to the type of soil composition and would require further investigation to understand if soil properties affect plant richness.

To fully understand the implications of drought on plant-pollinator interactions in years of drought, it is important to continue this type of research in future years. Future research should focus on comparing floral abundance and pollinator visitation in years of drought versus years of normal precipitation. In addition, nectar content and quality, plant reproduction and pollen limitation should be compared between habitat types. Additional factors should be considered when conducting future research, such as other forest understory types. Aspen forests are known to have large amounts of soil organic matter and nitrogen content, resulting in greater floral richness (Laughlin 2007). For that reason, aspen forests could provide greater floral resources compared to open meadows in drier years. Since soil conditions affect floral abundance and richness (Laughlin 2007), it could be important to analyze other soil properties, such as nitrogen content, in addition to soil moisture. It would also be vital to measure daily or weekly air temperature between habitat types since bee activity depends on temperature. Leaf temperature had provided insight to the different environmental conditions between habitats, but it would have been more useful to measure air temperatures.

The implications of climate change include an increase in the severity and frequency of drought, especially in regions already experiencing dry conditions (IPPC 2007). Dry years may have numerous affects on the functions and processes of ecosystems in semi-arid to arid regions (Weltzin 2003, Bates 2007). It is, therefore, important to continue investigations into how drought conditions can affect certain species, communities, and ecosystems.

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