

Effect of location on plant species richness and diversity in Aspen (*Populus tremuloides*)
understory: edge vs. inner forest habitat

Student: Grace Glynn

Mentors: Rick Williams and Stephanie Zorio

RMBL Independent Research
Summer 2013

Abstract

Ecological theory holds that edge effects influence species composition and diversity along both anthropogenic and natural forest edges. These ecotonal zones provide abundant microhabitats and opportunity for increased biodiversity. Abiotic factors such as temperature, soil moisture and soil water-holding capacity often create edge environments conducive to a variety of life. This study examines whether plant understory diversity decreases with distance from the edge of *Populus tremuloides* stands. I inventoried diversity within 5/ 1m² quadrats along five 40m transects perpendicular to the forest edge at three sites in Colorado's East River Valley near the Rocky Mountain Biological Laboratory. Air temperature near ground level, soil moisture, and soil water holding capacity were also measured. Diversity and richness were not higher at the forest edge. However, species composition differed significantly between the forest and the edge and meadow habitats. The most abundant forest species were not found in the meadow habitat, and vice versa. Species composition was similar between the edge and the meadow, suggesting that aspen stands are expanding into the meadow habitat. There was a trend in soil moisture and water holding capacity being higher at the edge than in adjacent habitats. This study is important in understanding the progress and consequences of shifting habitat ranges in a unique and biodiverse system.

Introduction

Edge effects have long been studied as keys to understanding ecological variability across small spatial scales. Forest edges are areas of transition between adjacent, defined ecosystems across which variation in environmental factors such as soil moisture, soil organic matter, temperature, and light availability can be observed (Cadenasso et al., 1997). These abiotic parameters allow edge zones to exhibit an environmental heterogeneity absent in the forest interior, providing opportunity for greater levels of biodiversity. Studies have shown that understory plant species composition varies across edge gradients (Matlack 1994), and that species richness levels are higher at edge ecotones (Marchand, 2006).

Diversity inventories of highly productive, novel systems are crucial to a complete understanding of ecosystem processes. *Populus tremuloides* understory communities have gone relatively unstudied although they are thought to contain the second highest level of biodiversity in the western U.S.A. (Kay, 1997; Grant, 1996). Though clear-cut areas within aspen forests have been shown to exhibit distinctly different microclimates from the forest interior (Carlson & Groot, 1997), neither abiotic nor biotic effects of natural aspen forest edges have been studied. Aspen stands comprise a significant portion of the vegetation within the Upper East River Valley with greater understory diversity than the predominant Spruce-Fir forests. While aspen forest in the Rocky Mountain region is recognized as generally being successional to slower-growing coniferous forest (DeByle & Winokur, 1985), aspen acts as climax forest in the Upper East River Valley, where it grows in mature stands independently of spruce-fir forest. Aspen stands border both fescue grassland and sagebrush habitats in

the region, creating ecotonal zones with unique species assemblages at the fringes of mature stands (Langenheim, 1962).

Within these ecotonal zones, differences in soil moisture, water holding capacity, and relative humidity are likely driving forces in varying species composition. These environmental conditions are in turn influenced by elevation, slope, aspect, and geologic substrate.

This study seeks to test for edge effects within mature aspen stands bordering forb-dominated meadow habitats in the Upper East River Valley, Colorado. It is expected that microclimate gradients across edge zones will induce gradients of species richness and diversity in understory communities. It is further predicted that edge-related patterns (diversity and quadrat richness) will follow a decrease in species richness and diversity with distance from the edge. It is expected that ambient temperature data will exhibit more dramatic daily fluctuations towards the open meadow habitat as compared to the inner forest. Observations of edge effects will have implications for human-induced fragmentation and future range shifts due to climate warming, as local biodiversity levels will be affected by such ecological change. An understanding of the determinants of diversity variance on fine spatial scales is always of ecological interest, but is particularly crucial in an age of rapid environmental change.

Methods

Study Sites and System

Three mature aspen stands were chosen in the Upper East River Valley near the Rocky Mountain Biological Laboratory based on similar aspect and elevation (Fig 1). At each study site, edge effects were measured within twenty meters on both sides of the edge. The specific location of the edge, as defined by Cadenasso (1992), was determined by the location of the canopy dripline, the outer reach of mature canopy tree branches.

Plant Community Sampling

Five 40m transects were established perpendicular to the forest edge, centered on the canopy dripline and 10m apart. Five 1m² quadrats were then positioned on each transect at 0m (edge point), 10 and 20m into the forest and 10 and 20m out into the meadow. Within each quadrat, percent cover was recorded for each species. Stem counts were also carried out, and stems within dense clumps were counted as one plant. Voucher specimens were collected and entered into the database in the Rocky Mountain Biological Laboratory herbarium.

Measurement of Abiotic Factors

Data loggers (HOBO inc., Bourne, MA) were utilized to measure ambient temperature over the course of one week; loggers were tied six inches above ground level at the forest edge, 20m into the meadow, and 20m into the aspen stand, located at

transect three at each site. Nine soil samples were collected from each site with the use of 10cm soil corer. Samples were taken from the forest edge, 20m into the stand, and 20m out at the northernmost transect, the southernmost transect, and the middle transect. Soil samples were prepared by removing chaff through a 2mm sieve, and soil moisture content was quantified by weighing sieved samples before and after baking for 24 hours at 100°C. Soil water holding capacity was determined by saturating soil samples to capacity before re-weighing them. Field sites were mapped using a handheld GPS and GIS software.

Analysis

Diversity was measured according to the Shannon-Wiener Index, using percent cover values for each species. Percent cover values from quadrats 10m and 20m into the meadow were combined and defined as meadow habitat, and values from 10 and 20m into the forest were combined to classify forest habitat. I compared plant understory diversity between meadow, forest edge, and inner forest habitat types using a one-way ANOVA in JMP (Version 10, Cary, NC). Soil water holding capacity was also compared amongst forest, edge, and meadow habitats using a multi-factor ANOVA in JMP. A Tukey Post-Hoc test was used to determine differences between sites and between habitats overall.

Results

Plant Communities

In sampling across three sites, seventy-two species were encountered overall. Species richness was highest on the edge in site 1; there were 26 species present in comparison to 23 in the meadow and only 15 in the forest (Figure 2). However, species richness at the other two sites was variable amongst habitats, differing from the predicted outcome of higher species richness in the edge ecotone.

According to the Shannon-Wiener index, understory diversity was not higher at the edge (Table 1). Diversity was highest in the meadow at sites 2 and 3, but highest in the forest at site 1. When diversity was calculated combining habitats across all sites, highest diversity was found in the forest, followed by the meadow, with the edge habitat having the lowest understory diversity.

Species composition varied significantly between the edge and the forest and between the meadow and the forest (Table 2). Plant communities in the edge and the meadow did not differ significantly.

Of the five most abundant species found in each habitat across all sites, most species were found predominantly in either the meadow or the forest (Figure 3). Of these top five, the meadow and the forest did not share any species. *Thalictrum fendleri* was the most abundant species in the forest, while *Festuca thurberi* was most abundant on the edge and *Heracleum sphondylium* was most abundant in the meadow.

Festuca thurberi, *Erigeron speciosus*, and *Ligusticum porteri* were more abundant in the edge than in forest and meadow habitats. No species were less abundant at the edge than they were in both the forest and meadow.

Abiotic Factors

Water holding capacity of soils differed significantly amongst habitat types overall (f ratio=5.1380, $df=2$ $p=0.0148$), with higher capacity for water retention on the edge (Figure 4). Water holding capacity differed significantly across sites, with site 1 soils showing higher overall water holding capacity when compared to sites 2 and 3 ($f=12.8973$, $p=0.0002$). There was a trend in soil moisture, with the edge habitat exhibiting the highest mean value for soil moisture across sites (Figure 5). Soil moisture was lower in the forest than in the edge, and lowest in the meadow.

Mean daily fluctuations in temperature differed with distance from the edge (will refer to Fig), with more dramatic fluctuations found in the meadow habitat. The meadow also had a higher temperature high during the day.

Discussion

In a comprehensive study of the flora of the Gothic area in the late 1940s, Dr. Jean Langenheim (1962) inventoried percent cover of understory species within ecotonal zones where aspen borders fescue grassland. She reported the habitat to be dominated by, in order of decreasing average percent coverage, *Festuca thurberi*, *Bromus ciliatus*, *Thalictrum fendleri*, *Vicia americana*, *Ligusticum porteri*, and *Lathyrus leucanthus*. This study reports four of these species (*F. thurberi*, *L. porteri*, *T. fendleri*, and *L. leucanthus*) in the top five most abundant species in the edge zone. After finding the grass *Festuca thurberi* to be abundant at the ecotonal zone, Langenheim concluded that most of the aspen stands had invaded fescue grassland and were transitioning to maturity. However, it is commonly believed that fire suppression is threatening the regeneration of aspen in the west, as vegetative reproduction is known to be stimulated by fire (Brown and DeByle, 1987). Evidence for the decline of aspen communities was provided by Shepperd 1990, who classified aspen stands in the central Rocky Mountains, Colorado and found 14% young stands (<40 years), 23% middle aged stands (50-60 years), 60% mature stands (80-100 years), and only 4% old stands (>140 years). This aging trend supported the stand simulation model created by Bartos et al. (1983), which predicted peak aspen biomass after 100 years and succession to conifer forest after 200 years. Despite this general predicted trend, Langenheim's observations on a finer spatial scale suggest an exception in the aspen stands of the Upper East River Valley. My results suggest an expansion of aspen forest at some sites, with meadow and edge habitats exhibiting similar species composition as opposed to significantly different edge and inner forest habitats. Edge abundance of *F. thurberi* and the presence of young aspen saplings growing into the meadow also suggest that aspen forest stands continue to expand into fescue grassland.

Forest structure may explain the higher species richness level in the edge at site 1 and variable richness at the other sites. Sites 2 and 3 were less mature and with more saplings expanding into the meadow. While site 1's edge was clearly defined and had

very few root suckers emerging at the border of the meadow and the stand, the edges of sites 2 and 3 were less linear, with many young aspens in the meadow habitat. There were also more open canopy spaces at the less mature sites 2 and 3. Unlike site 1, the edge habitats at site 2 and 3 showed lower or identical species richness when compared to adjacent habitats. Edge effects may be visible only in well-established edges, and the edges of sites 2 and 3 may be colonized by more species as they mature. Future studies may benefit from standardizing stand maturity and edge definition, and from conducting surveys at a larger scale, as ecotonal edge zones are likely larger in recently expanded stands.

Langenheim (1962) noted that aspen groves in the Gothic area correlated with limestone and shale substrates, and that shales appeared to be a more favorable parent material for aspen groves when compared to clastics. In this study, sites 2 and 3 were located on shale. These sites exhibited higher levels of plant diversity than site 1, which is located on coarse glacial deposits. This discrepancy may be attributed to geologic substrate, though more research is needed to determine the favorable traits of shale, and the local Mancos shale formation specifically, as a substrate for aspen stands.

Varying topography may have caused species composition and diversity to differ across sites. Studies have suggested that steeper slopes may more effectively buffer against invasion by competitive species and therefore encourage higher diversity levels (Bennie et al., 2006). Sites two and three were significantly steeper than site 1, and both showed higher levels of diversity than site one (Table 3). Site two, with the steepest slope, had the highest diversity index.

Higher soil moisture and water holding capacity levels are also thought to allow greater species richness and diversity. Soil holding capacity was highest at the edge, probably due to exposure and the dripline effect in combination, and this water retention would influence species composition. Soil moisture was also highest at the edge, though not significantly. Differences between site 1's habitats may have been influenced by the fact that they were collected just after rainfall, while sites 2 and 3 were sampled on drier days with no rainfall. Future studies would collect soil from all locations on the same day to eliminate this confounding variable. Though soil moisture did not vary significantly across sites, a larger sample size would likely detect differences due to parent rock material.

As stands mature, aspen have been shown to be a soil-improving species of tree. In the Rockies, soil in aspen groves is deeper than that of conifer stands, and this difference becomes greater as the aspen stand matures (Hoff, 1957). Deepness and richness of soil is likely a strong determining factor in understory plant composition, and may have contributed to higher richness values at site 1. Further studies would benefit from conducting more extensive soil analysis to better illustrate differences across the edge gradient.

Sampling methods were refined after sampling of site 1 to count closely clustered groups of stems as one plant, which may have resulted in inaccurate stem counts, especially in grasses. With increased sampling size, differences in diversity across an edge gradient would be more accurately illustrated. The edge also may have been defined inaccurately; the ecotonal edge zone may extend ten meters or more into what was defined as meadow or forest habitats, and is likely larger in less mature stands.

In conclusion, similar species composition between meadow and edge communities and the presence of root suckers at stand edges suggest that aspen groves have continued to expand into meadow habitats since the 1940s. Forest and meadow habitats harbor distinct species assemblages, and their dominant species have opportunity to inhabit the same region in ecotonal edge zones, creating potential for higher richness in these areas, especially in mature, well-established stands. The aspen understory is an important system in the study of biodiversity, as both its inner forest and edge habitats exhibit high levels of species richness and diversity as compared to other major habitats locally such as conifer understory.

Figures

Table 1: Shannon-Weiner diversity index values for each site and habitat and values combining all sites, based on plant understory species richness and % coverage by species within 1m² quadrats.

Habitat	Site 1	Site 2	Site 3	Overall
Forest	2.743	2.7663	2.7301	3.1847
Edge	2.1773	2.4352	2.224	2.9436
Meadow	2.0658	2.9899	2.7988	3.0991

Table 2: Results of paired t-test illustrating differences in understory communities between habitats based on % cover inventories

	Mean Difference	t-Ratio	DF	p value
Meadow-Edge	26.176	3.72145	49	0.0005*
Forest-Edge	-38.229	-3.53092	49	0.0009*
Meadow-Forest	-10.757	-1.01215	54	0.316

*significant results

Table 3: Mean values for slope, aspect, and elevation at each edge point across sites.

Site	Slope	Aspect	Elevation
1	6.888	270.116	2942.4
2	29.204	250.372	2953.48
3	15.598	229.888	2949.12

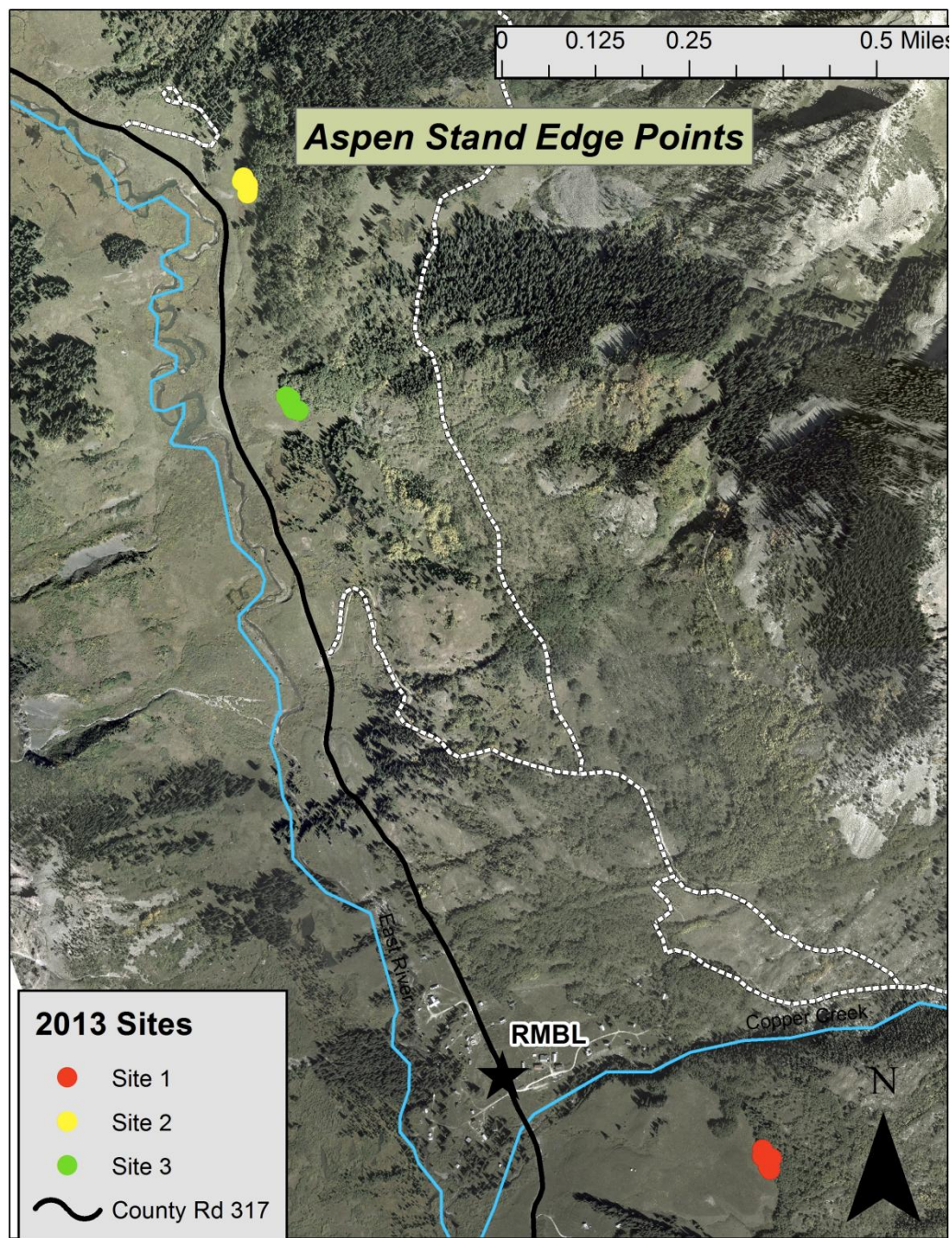
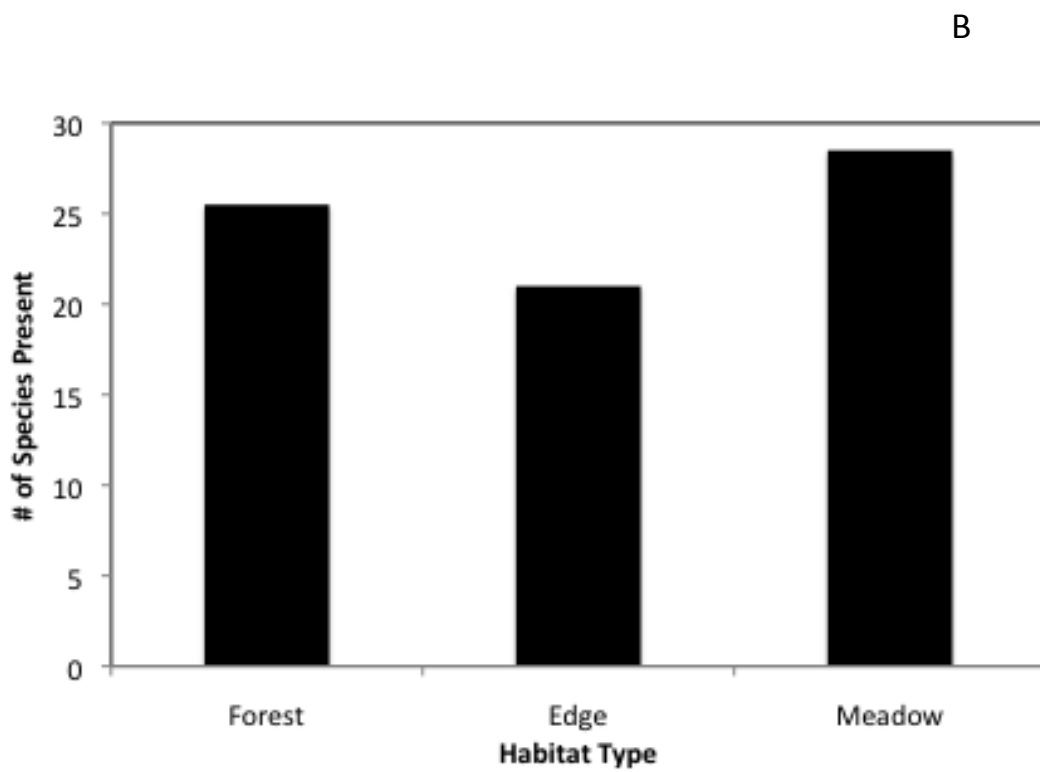
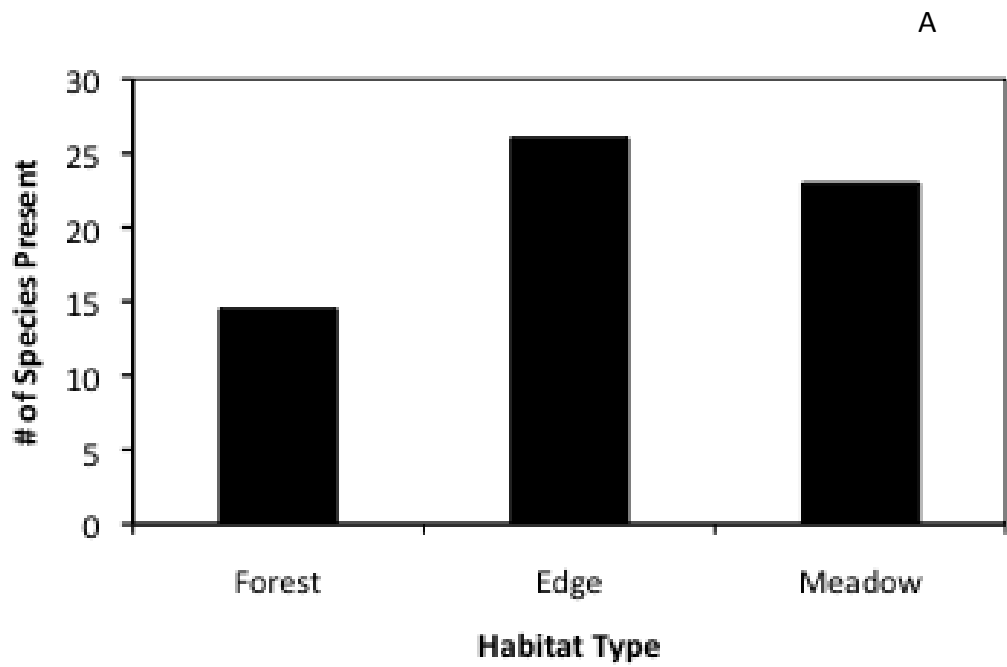


Figure 1. Study sites



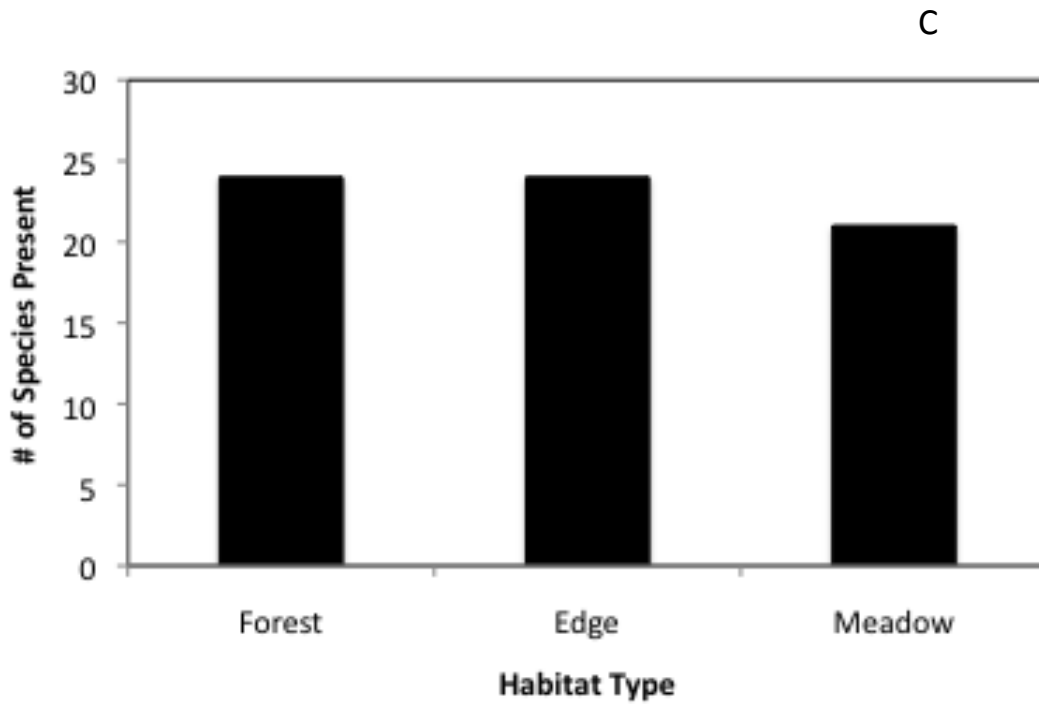


Figure 2. Species richness, or total number of species found in quadrats within Site 1 (A), Site 2 (B), and Site 3 (C)

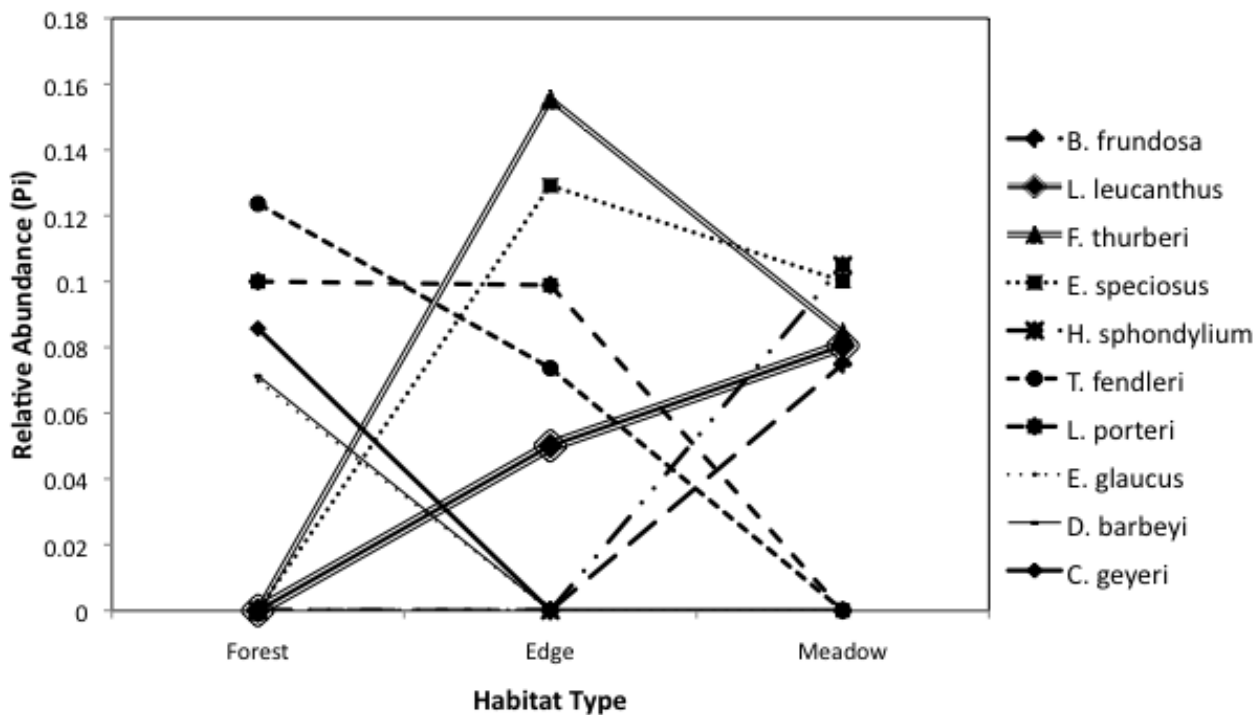


Figure 3. Relative abundance of top five species found in each habitat type across all sites

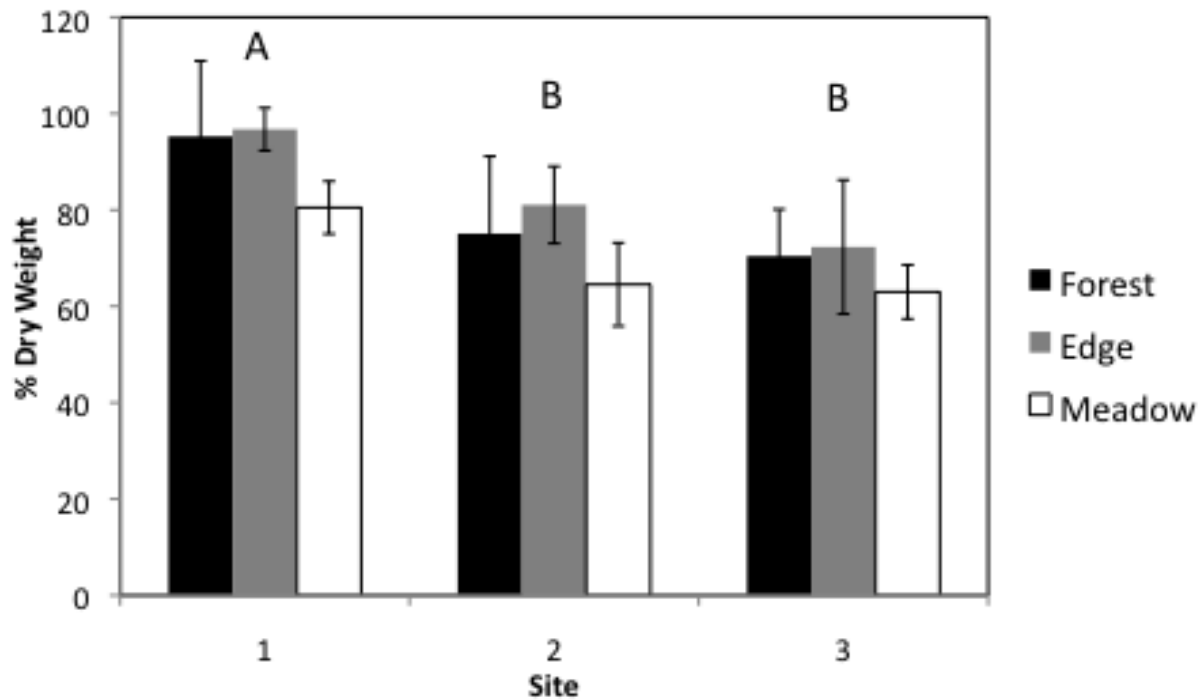


Figure 4. Water holding capacity of soil across habitat types within each site. Site 1 differed significantly from sites 2 and 3.

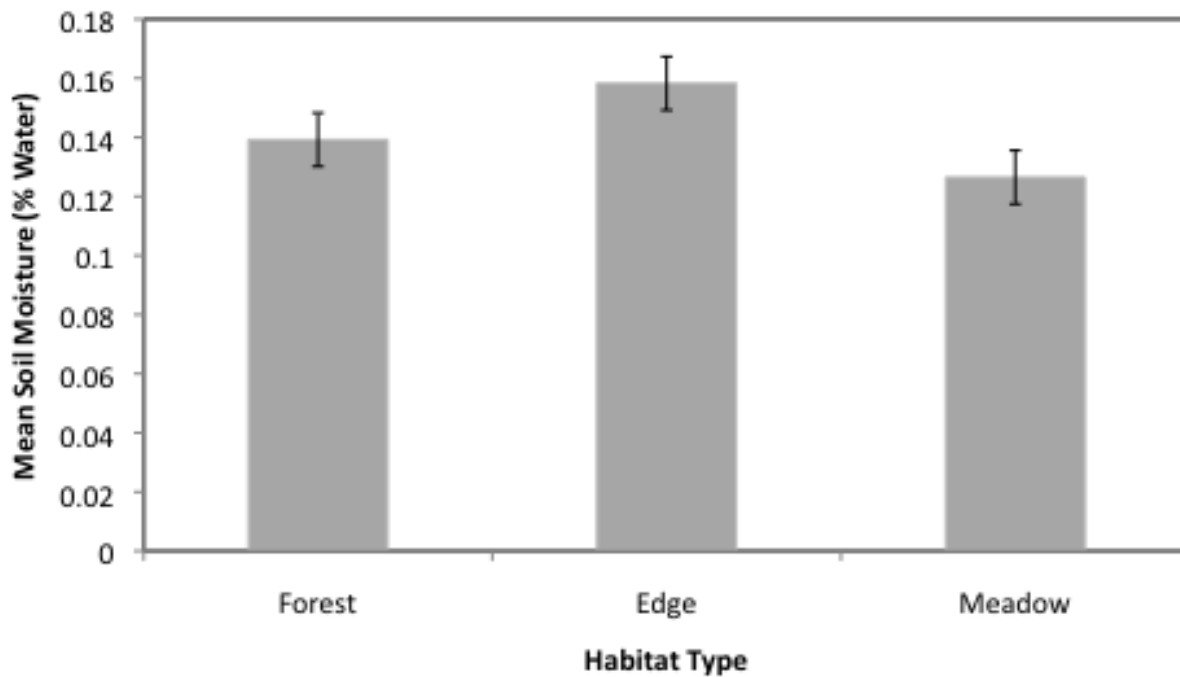


Figure 5. Mean and standard error values for soil moisture for habitat types across all sites. Differences between habitats were not significant ($p=0.069$).

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