Promotion of herbaceous plant communities by forest canopy gaps

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Abstract

A distinguishing characteristic of second-growth forests is the paucity of large gaps. Many studies have suggested that smaller gaps do not promote biodiversity like large gaps within an old-growth forest. Biodiversity within a forest depends on management practices to restore plant communities back to that of old-growth forests. The purpose of our study is to examine whether canopy gaps in second-growth forests increase understory herbaceous composition. Also we wanted to determine whether gaps increase understory herbaceous composition because of increased rates of reproduction. We tested this hypothesis by sampling a plot <20 m^2 under a canopy gap then sampling a neighboring plot 10-30 m away under the intact forest canopy. We found that herbaceous plant biodiversity is increased on the understory under canopy gaps and that canopy gaps act as engines of reproduction. Biodiversity is essential to the forest ecosystem because herbaceous plant communities can increase forest services. Canopy gaps are one step to maintaining a diverse forest ecosystem.

Introduction

In old-growth northern forests, natural disturbances such as windstorms are essential to the biodiversity of the land. These natural disturbances create gaps in the canopy of the forest, increasing light availability and other valuable resources on the forest ground (Kern et al. 2014). Without such disturbances, loss of biodiversity can occur due to lack of resources, limiting the understory to shade-tolerant species (Schnitzer et al. 2008). However, species diversity, which is the abundance and variety of different types of organisms found in an area, can be dependent on gap size (Nuttle et al. 2013). Smaller canopy gaps tend to prohibit recruitment because existing shade-tolerant species utilize all available resources and fill in the gaps (Nuttle et al. 2013). It has previously been hypothesized that larger canopy gap openings increase understory diversity by promoting regeneration and recruitment of species from different classes of shade tolerance while prohibiting lateral growth from reaching the center of the gap (Nuttle et al. 2013).

In second-growth forests, there is a paucity of large canopy gaps, which in turn may lead to loss of species diversity (Royo et al. 2010) or invasion of exotic species. Exotic species pose a threat to biodiversity of many ecosystems due having the ability to invade a forest with their advance regeneration characteristics and tolerance of disturbances (Knapp and Canham 2000). Luckily, exotic species do not pose a major threat on the biodiversity of many forests, such as forests located in Northern Wisconsin and Michigan, because of their minimal exposure to the public.

Although exotic species do not pose a major threat to biodiversity, lack of canopy gaps does. Biodiversity is a hot topic for understory composition and communities. But, the richness of the communities as well as the abundance of those species is also an important aspect in forest structure. Forest floor vegetation contributes to increasing vital carbon and nutrient cycling as well as acting as a main source of food for herbivores (Hedwall et al. 2013) indicating that a larger abundance of vascular plants could improve over all forest conditions.

Forest floor vegetation is dependent on the forest structure. Forest management and land use have altered the structure of forests to create monospecific, shade-tolerant, fast growing forests. These management practices increase stand density and create shorter rotation periods (Hedwall et al. 2013). However, increased stand density reduces resource availability to understory communities and decreases primary production on the forest floor while also leading to a loss in vascular species density and richness, leading to an inevitably decrease in biodiversity.

It has been suggested previously that, "gaps drive the forest cycle" because they are essential for regeneration and survival of diverse and stable plant communities within a forest (Schnitzer et al. 2008). With increased availability of resources under gaps, species with life constraining traits such as shade intolerance or high nutrient requirements are able to compete and coexist (Kern et al. 2014). This is due to the ability of plants to partition an influx of resources, allowing for increased species diversity in gaps that would otherwise be absent from the forest (Schnitzer et al. 2008). Schofield (1997), found that herbaceous species were present under the most open canopy and absent from habitats under closed canopies, verifying that canopy gaps increase biodiversity on the forest ground.

The purpose of our study is to examine whether canopy gaps in second-growth forests increase understory herbaceous composition. Specifically, we wanted to determine if gaps increase abundance, diversity, density, and richness of understory herbaceous plants compared to the intact forest understory. We also wanted to investigate whether gaps increase understory composition due to increased rates of reproduction. We hypothesize that forest canopy gaps will act as engines of reproduction and understory herbaceous biodiversity will be greater under canopy gaps than under the intact forest canopy in a second growth forest in the Upper Peninsula of Michigan.

Methods

I conducted this study in the 7500 ha second-growth forest at the University of Notre Dame Environmental Research Center (UNDERC) field site in Gogebic County, Northern Michigan, USA. All plots were located in the forest west of Tenderfoot creek, which has the most desirable conditions for sampling under gaps. On the UNDERC site, the forest west of Tenderfoot creek contains stable ground with fewer lakes and vernal ponds. Plots were located in three forest types, maple dominated, aspen dominated, and mixed hardwood. Twelve sets of plots were sampled, each with an area of 20 m^2. A set of plots was defined as one plot under a canopy gap and a neighboring plot under an intact canopy, both in similar forest types with approximately 10-30 meters between the two plot types. For this study, a canopy gap was defined as an opening in the canopy with a snag or fallen tree, large enough for sunlight to reach an area > 20 m^2. All herbaceous plants within each plot were identified and counted, distinguishing those plants that were flowering at the time of data collection.

For statistical analysis, I utilized R-software (R Core Team 2014). I used a paired t-test to determine whether there was a significant difference (p-value < 0.05) in diversity, richness, total density, percent and density flowering and total abundance between the pairs of plots. I used the Shannon's diversity index to calculate diversity between the pairs of plots. I also used a paired t-test to determine whether there was a significant difference (p-value < 0.05) in abundance and density between the pairs of plots for Canada mayflower *(Maianthemum canadense),* starflower *(Trientalis borealis),* and bunchberry *(Cornus Canadensis).* These three species were chosen as focal species because they were the most common species found within the plots.

Results

Across all plots, the understory contained 15 herbaceous, primarily native species. Among them, 10 were identified to species and 5 were identified to genus.

Diversity and Richness

The mean diversity of the herbaceous community was 1.12±0.00151 in the gap plots and 0.812±0.00187 in the intact plots (Table 1). The mean diversity was significantly different between the gap and intact plots (t = 4.5954, df = 11, p-value = 0.00077). In gap plots, mean richness was 6.75±0.0168, while in the intact plots mean richness was 4.67±0.0104, indicating a significant difference in richness between gap and intact plots (t = 3.1727, df = 11, p-value = 0.0088, Table 1).

Density

The total density, which includes all identified herbaceous stems, was 38.7±0.155 stems/m^2 in gap plots and 14.4±0.0228 stems/m^2 in intact plots indicating a significant difference (t = 4.1871, df = 11, p-value = 0.0015, Table 1).

The density of Canada mayflower was significantly different (t = 3.2155, df = 11, p-value = 0.0082, Figure 1), with gap plots at 15.9±0.0860 stems/m^2, having almost double the density of Canada mayflower. The density of starflower between the set of plots was not significantly different (t = 1.5993, df = 11, p-value = 0.138, Figure 1). However, a Shapiro-Wilk normality test determined that there was a non-normal distribution for the starflower density. The density of bunchberry was significantly different (t = 2,884, df = 11, p-value = 0.014, Figure 1) between the pairs of plots. The mean density of bunchberry in gap plots was 11.5±0.0944 stems/m^2 where as intact plots had a mean density of 0.375±0.00306 stems/m^2. However, a Shapiro-Wilk normality test determined there was a non-normal distribution of bunchberry.

Abundance

The relative abundance of Canada mayflower is significantly higher (t = -2.4562, df = 11, p-value = 0.031) in the intact plots than the gap plots. There was a higher proportion of Canada mayflowers (50.57%) in the intact than in gap plots (35.94%, Figure 2). The abundance of starflower was not significantly different (t = -0.7095, df = 11, p-value = 0.49, Figure 2) between the pairs of plots. The abundance of bunchberry was significantly higher (t = 2.8989, df = 11, p-value = 0.014, Figure 2) in gap plots than intact plots. Gap plots were comprised of 21.99% bunchberry compared to 3.38% bunchberry in intact plots. However, the Shapiro-Wilk normality test determined a non-normal distribution of the bunchberry abundance.

Flowering

The percent of herbaceous plants that had flowered was not significantly different (t = 0.4909, df = 11, p-value = 0.63) between the set of plots. In gap plots, 33.62% of herbaceous plants had flowered and 29.05% had flowered in intact plots. The density of herbaceous plants flowering was significantly different (t = 3.0754, df = 11, p-value = 0.0105, Table 1) between the pairs of plots. The mean density of herbaceous plants that were flowering in gap plots was 13.0±0.0809 flowers per m^2 and 4.18±0.0228 flowers per m^2 in the intact plots (Table 1). However, a Shapiro-Wilk normality test determined a non-normal distribution of herbaceous plants with flowers.

Discussion

Large canopy gaps in old-growth forests have been found to enhance herbaceous plant diversity (Royo et al. 2010). As stated previously, gaps are suggested to be drivers of the forest because they are foci for regeneration (Schnitzer et al. 2008). The purpose of this study was to explore if: (1) second-growth forests contain diverse understory layers despite a lack of large canopy gaps and (2) whether small canopy gaps can act as engines of reproduction by increasing the abundance of flowering plants in the understory. I hypothesized that forest canopy gaps would act as engines of reproduction and promote understory herbaceous plant biodiversity compared to intact forest canopies.

In a forest ecosystem, plant diversity is essential to the biodiversity of all other communities, such as insects and mammals. A more diversified ecosystem will have greater resilience and faster recovery time following a disturbance. The majority of past studies done in forest ecosystems mainly focus on tree species diversity when discussing biodiversity. However, trees only represent one-third of the forest vascular plant community (Royo et al. 2010). Schnitzer and Carson (2001) reported that gaps are vital for maintaining woody species diversity, such as lianas and pioneer tree species. Each individual species plays an important role in promoting the success of other species as well as the success of the ecosystem. Thus, it is vital to understand what leads to lack of biodiversity within a forest ecosystem.

Resources, such as light and water availability, influence growth patterns and success rates among species (Kern et al 2014). When forests consistently have closed canopies that restrict the amount of sunlight penetrating to the forest floor, the understory community will shift slowly to shade tolerance species. Unfortunately, this causes a decrease in plant diversity because plants that need ample amounts of sunlight to survive will be outcompeted by shade-tolerant species (Nuttle et al 2013).

Canopy gaps are created by natural disturbances, such as windstorms or heavy snowstorms that knock down branches or trees. Consistent gaps increase biodiversity because they allow for the survival of shade-intolerant species, while also supporting the services shade-intolerant species provide (Schnitzer et al. 2008). When a forest has an understory that transitioned to mainly shade-tolerant species, it is difficult for shade-intolerant species to regenerate under the new canopy gap leading to a decreased biodiversity.

I found that gaps in a second-growth forest promote diversity as well as species richness among the herbaceous plant community. Variation between plots can be attributed to forest type, and the amount of resources available. There were some gap plots located under maple-dominated forests that had low species richness and had similar diversity values to the paired intact plot because the shade tolerant species were able to regenerate faster. Nuttle (2013) suggested in the gap hypothesis, that canopy gaps in a second-growth forest are too small to support the regeneration or recruit anything but shade-tolerant species. The paired plots that were located in a mixed hardwood forest had higher species richness and higher values of diversity.

In addition to species richness and diversity, density of herbaceous plants was substantially higher under canopy gaps. The density and abundance of the three focal species varied. Density of Canada mayflower was higher under canopy gaps. However, because Canada mayflower was the dominant species in intact plots, it had a higher relative abundance in intact plots than in gap plots. Although Canada mayflower had lower abundance in gap plots, the herbaceous community benefits from this because multiple species are able to thrive; Canada mayflower is not dominating or using all available resources. This is an example of species coexistence and effects of species diversity (Kern et al. 2014). Kern (2014) suggested that in addition to species diversity, it is important for forest vegetation to include a range of trait diversity. Increased species richness in gap plots would increase the chances of a larger trait diversity range.

A part of the gap hypothesis suggests that gaps act as an engine of reproduction (Schnitzer et al. 2008). It has been predicted that individual species under a canopy gap will have higher fecundity and will reach reproductive maturity quicker than those individuals under an intact canopy (Schnitzer et al. 2008). The density of herbaceous plants that were flowering was higher under canopy gaps than intact forest. This could be due to canopy gaps having greater species richness and greater density of herbaceous plants compared to intact forest understories. Unfortunately, the 33.62% of herbaceous plants that were flowering in gap plots were not significantly different than the 29.05% of herbaceous plants that were flowering in intact plots. I accept my hypothesis that gaps act as engines of reproduction. Although the percentage of herbaceous plants flowering was not significantly different, there was a higher density of herbaceous plant individuals that had flowered in gap plots than intact plots.

Canopy gaps play a huge role in promoting biodiversity, however gaps are not the only factor. Fire and deer are two huge influences on a forest ecosystem. Controlled burns and reduced deer browsing increase a forests biodiversity within all communities (Royo et al. 2010). However, recent studies show that unless all three factors- gaps, fires, and deer browsing- are at historic interaction levels, historic biodiversity can never be reached (Nuttle et al. 2013). That does not mean forestry management cannot continue to increase biodiversity within forest ecosystems.

Forestry management has been a huge debate for America and many other countries across the world. The public is demanding shorter rotation periods for timber production but higher diversity within forests (Puettmann and Tappeiner 2013). It is hard to find a balance. For example, Sweden's temperate forests are facing an increase in canopy cover in the tree layer structure, but this causes a decrease in favorable growth conditions, limiting success of the next generation of trees. In addition to Sweden, Germany and Finland found trends of steady declines in abundance of important vascular plant species on the forest floor since the forest structure began changing towards increased stand density and shorter rotation periods (Hardwell et al. 2013). One of the main reasons for this decline is light radiation availability for forest vegetation. Negative relationships were found between forest floor vegetation abundances and broad leaf tree cover. Hardwell et al. (2013) suggested that a way to combat this problem would be to increase forest thinning and promote the growth of trees that have open crowns that allow more light penetration.

With increased public understanding of ecological services and historical regimes, many silvicultural practices have been proposed to promote understory species diversity and variability within current policy and economic settings. Puettman and Tappeiner (2013), suggest one important point from their proposed guidelines is that any silvicultural regime must be viewed through the context of natural disturbances. This is vital because it considers natural disturbances as a good thing rather than an obstacle to overcome (Puettmann and Tappeiner 2013). It is important that silviculture management considers how valuable natural disturbances are on the trees as well as the forest floor vegetation.

It is possible to achieve species diversity with combined efforts and a greater understanding of all the factors. Species diversity and richness benefits the forest ecosystem because of the increased services provided by each individual species. Forests that are prone to natural disturbances but have a fast recovery time are an idea forest type for forestry managers. Canopy gaps can increase biodiversity within the herbaceous plant community as well as other plants an animals. Canopy gaps are one element of the larger picture to increase and maintain forest biodiversity.

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Tables

Table 1 The average values and standard error of diversity, richness, density, and flowering density between gap and intact plots, where bold values indicate significant differences.

Plot	Diversity	Richness	Density	Flowering Density
Gap	**1.12±0.00151**	**6.75±0.0168**	**38.7±0.155**	**13.0±0.0809**
Intact	0.812±0.00187	4.67±0.0104	14.4±0.0787	4.18±0.0228

Graphs

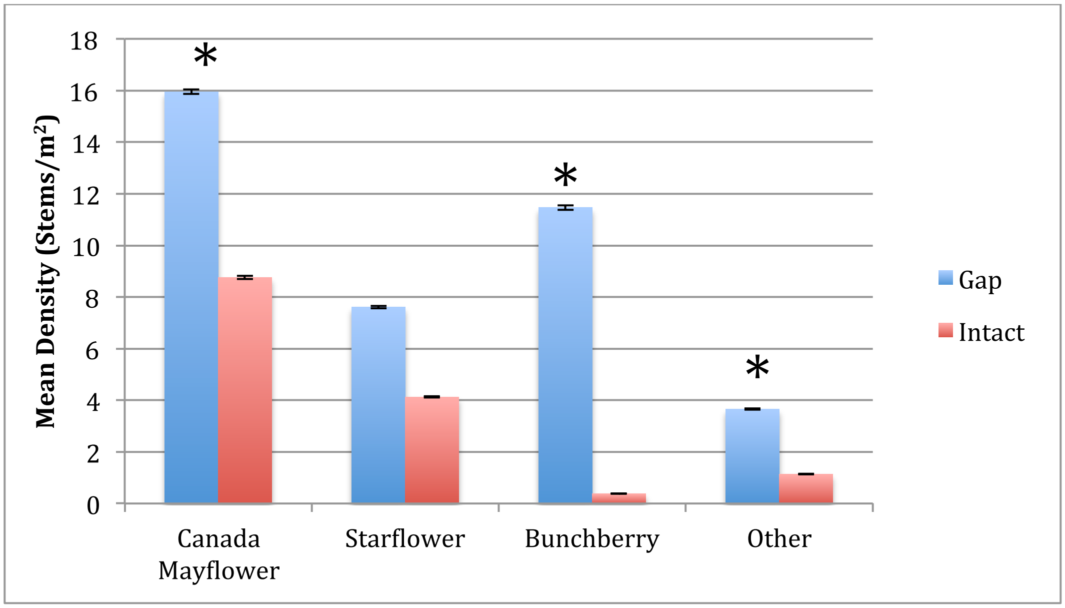

Figure 1 The mean densities of Canada Mayflower, Starflower, Bunchberry and other in gap plots and intact plots. An "*" indicates a significant difference.

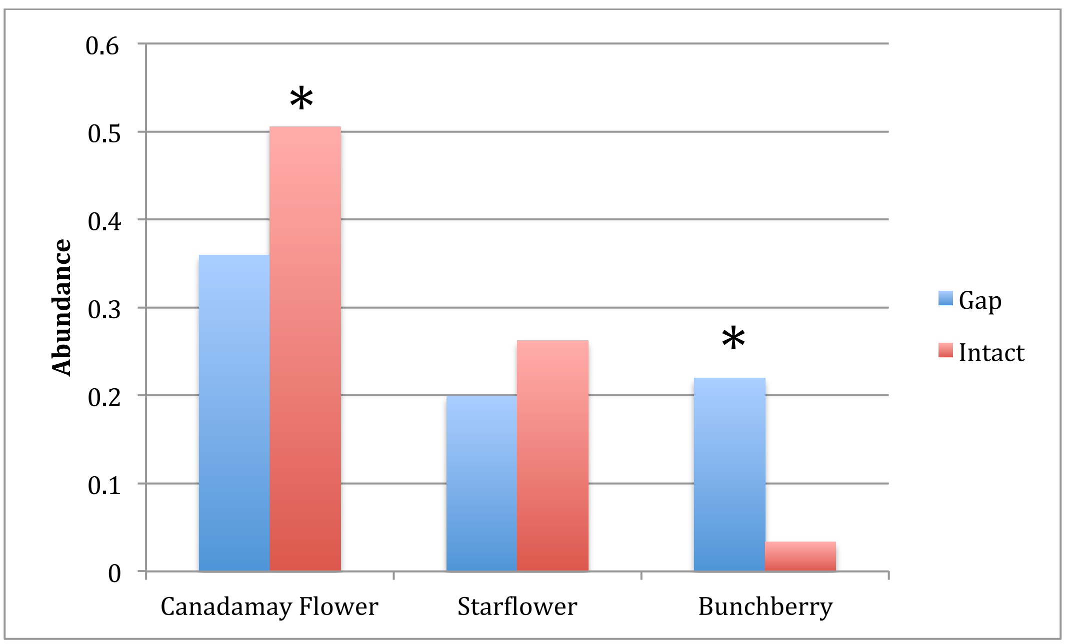

Figure 2 The mean abundances of Canada Mayflower, Starflower, Bunchberry and other in gap plots and intact plots. An "*" indicates a significant difference.