

*Abundance and Distribution of North Woodland tree species with relation to
Canopy Gaps at UNDERC*

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Abstract

Despite numerous studies looking at canopy gaps and their impact on tree species diversity, the dynamics of these light-gaps are still widely debated. Furthermore, a basic understanding of canopy gap dynamics would greatly aid in developing appropriate forest management plans. This study posits that gaps are not essential in maintaining species diversity in forests. To substantiate my hypothesis I surveyed woody juvenile stems in 24 gaps and 24 paired non-gap control sites. After recording the species, height, and browse condition of each stem in my plots I found that species diversity was not different between gap and non-gap control sites. Furthermore, shade tolerant species did not show a dichotomy in their recruitment patterns on a percent basis. This suggests that, at least in the northern hardwood forest around UNDERC, the gap regime is not rigorously linked with maintenance of species diversity. Further study should be undertaken to determine whether latitudinal or spatial gradients have an effect on gap dynamics

Introduction

One major factor in niche partitioning of woody species is the amount of light available for photosynthetic use. Using tropical forest patches in Belize, MacDougall (1992) demonstrated that five out of six of the species tested had specific preferences with relation to the amount of light available. Moreover, there is evidence that patterns of recruitment amongst trees are more dependant

upon light availability than soil moisture or soil nitrogen levels (Pacala et al. 1996). Because canopy gaps allow for additional light to enter forest understories, many understand canopy gap dynamics to be a significant driving force in species diversity maintenance within in forest ecosystems (Clark et al. 1993, Schnitzer and Carson 2001).

Some researchers have concluded that canopy gaps allow for shade intolerant pioneer species to exist and compete with shade tolerant trees and thus help maintain overall species diversity in the forest(Schnitzer and Carson 2001, Anderson and Leopold 2002). However, Midgley et al. (2001) found that in the Knysna Forest of South Africa there was random recruitment of juveniles in the gaps.

Additionally, it has been shown that in Barro Colorado Island (BCI), spatial and temporal variation among gaps had no influence on the local tree species diversity (Hubbell 1999). These examples appear to indicate that, at least in some scenarios, gap dynamics are not essential for the continuation of species diversity in a forest ecosystem. However, comparisons between gap and non-gap control sites Hubbell (1999) found that although species richness was higher per unit area in gap vs. non-gap sites the species richness per stem remained the same for both sites. This suggests that the gap disturbance regime is important by virtue of providing a venue for an increase in community wide establishment of seedlings.

Furthermore, research done in San Carlos de Rio Negro, Venezuela shows that advanced regeneration growth has a significant impact on the species composition of a treefall gap (Uhl et al. 1988). In single treefall gaps the advanced regeneration accounted for 97% of all woody growth after four years and in multiple treefall gaps 83% of growth after four years resulted from advanced regeneration (Uhl et al. 1988). This study further serves to beg the question: Are canopy gaps as rigorously coupled with maintenance of forest species richness as currently thought?

The University of Notre Dame Environmental Research Centre (UNDERC) was subjected to intensive logging and subsequent fires, which have resulted in a forest community primarily composed of birch, maple, fir, et al. (Stearns 1950). In the several decades since these major disturbances the forest has naturally developed treefall gaps in which new growth has taken over. I propose that the gap disturbance regime will not prove to be a significantly important venue for maintaining forest biodiversity at UNDERC. Furthermore, I posit that this hypothesis will manifest itself by no significant difference being found in shade tolerant species¹ composition between gap and non-gap control sites. Specifically, if a dichotomy in recruitment patterns fails to become

¹ Shade tolerant species were defined specifically as eastern hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), leatherwood (*Dirca palustris*), alternate-leaf dogwood (*Cornus alternifolia*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and hop-hornbeam (*Ostrya virginiana*) (Barnes 1981).

apparent, it would serve to further call into question the current gap/ non-gap paradigm of biodiversity maintenance.

Methods

Site

Research was conducted on UNDERC property in the upper peninsula of Michigan. The 3000 ha. property has a variety of 30-90 year-old forests and access is limited to researchers only. Although more than 40% of the property is covered in lakes or other wetlands, there are canopy gaps that exist throughout the rest of the property's forests that served as study sites. Both single treefall and multiple treefall gaps were used and the age of the gaps ranged from approximately 1- 10 years of age. For the purposes of this study I used 24 canopy gaps, each paired with a non-gap site with full canopy cover in close proximity to the gap site being tested.

Procedure

After visually locating the centre of the gap, I measured three separate distances to the edge of the gap, representing the radii of three circles, the areas of which I averaged to estimate the size of the gap. Additionally the age of the gap was classified into either 0-3 years, 3-10 years, or greater than 10 years based on the condition of the downed tree that created the gap. The gap- making tree was also identified to species. Around the centre of the gap I laid out a 5m x 5m plot in

which I surveyed the juvenile² trees present, recording species, height, and the presence or absence of browsing on each stem. For selecting a non-gap control site a random compass bearing was chosen and 30 metres in that direction became the centre of a 5m x 5m non-gap plot. Given that the new location did not contain another canopy gap, vastly different geography, or another unacceptable quality, the same surveying process was repeated.

Statistics

After the data was collected it was analyzed using two-tailed paired t-tests to determine significant differential trends between gaps and their paired non-gap control sites. Also, a Shannon-Weiner Diversity Index was used to examine diversity in gaps and non-gaps followed by another two-tailed paired t-test to determine any significant difference in diversity between the gap and non-gap sites.

Results

Species

I identified a total of 3135 stems, comprising 29 species³ of woody plants. By far, *Acer saccharum*, *Acer rubrum*, and *Corylus cornuta* were the most common species in gaps while at non-gap sites *Acer saccharum*, *Corylus cornuta* and *Populus tremuloides* were the most common (Figure 1).

² For the purposes of this study a juvenile will be considered any tree of x height, where $30\text{cm} < x < 3\text{ m}$.

³ For a full list of species identified see Appendix A.

Species Abundance

I found that there was a significant difference in density of stems, with gaps having considerably more stems per m² than their non-gap control site (p-value = 0.007)⁴. Also, gaps had significantly higher species richness than their non-gap control sites, when measured on a per metre basis (p-value = 0.033). Similarly, a species-area curve visually confirms that there are more species per m² in the gap vs. the non-gap sites (Figure 2). In contrast, species richness, when calculated on a per stem basis, was significantly higher (p-value = 0.042) for the non-gap control sites. However, a paired t-test of the Shannon-Weiner Diversity Index values for all sites show that there is no significant difference (p-value= 0.406) in the diversity of species found at each site.

Shade-Tolerant Distribution

Also, there were significant differences in the number of shade tolerant trees present in gaps and non-gaps. The gap site was significantly more likely to have a greater number of shade tolerant trees (p-value = 0.022). However, when shade-tolerant tree distribution was measured as a percent and not with absolute values no significant difference between gap and non-gap sites appeared (p-value = 0.408).

⁴ For gap and non-gap mean data as well as corresponding error see Table 1.

Discussion

Species Abundance

With the data gathered in this survey, I fail to reject my hypothesis. I hypothesized that the gap regime would not be significantly important in the maintenance of biodiversity at UNDERC. Both stem density and species per m² were higher in gap sites than non-gap sites, as found by Hubbell et al. (1999). However, whereas species per stem diversity was identical in the Hubbell et al. (1999) between gap and non-gap sites this study found that there was more species per stem in control sites. Although there are more stems per m² in gaps and more species per m² in gaps, there is a factor of 4.7 differential between their p-values. Ergo, abundance of stems in gaps is considerable enough to cause a significantly lower species per stem ratio in gaps as opposed to non-gap control sites. As predicted by the identical species/ stem values between gaps and non-gaps (Hubbell et al. 1999) the Shannon-Weiner Diversity Index showed no significant difference between gap and non-gap sites.

Shade-Tolerant Distribution

One of the predictive elements of my hypothesis was that no dichotomy of recruitment would be evident in shade tolerant species between gap and non-gap sites. Contrary both to my prediction and to the entire gap/ non-gap paradigm, there were more shade tolerant trees per m² at the gap sites than at non-gap control sites. However, when this is evaluated in light of the significant impact

advanced regeneration has on recolonization (Uhl et al. 1988) the data then assimilates with expected patterns. Uhl et al. (1988) showed that 83%-97% of treefall gap stems are from advanced regeneration. If, in the northern hardwood forest of UNDERC, shade-tolerant *Acer saccharum* dominates the understory then the gap regime will allow it to immediately sequester the newly available light resource and grow. Since juveniles were counted as only those greater than 30 cm and much of the understory remains below this threshold level, then increased growth from new light availability will cause growth of the advanced regeneration. With this additional growth, stems gain the height required to be counted in the survey. However, if all stems were counted regardless of size, similar stem numbers might become apparent between gap and non-gap sites.

Although the number of shade-tolerant individuals was significantly different between gaps and non-gaps the percent composition of shade-tolerant individuals was not significantly different between sites. This could be because, even though more juveniles are reaching the survey threshold height of 30 cm, shade intolerant trees are able to recruit their seedlings at some parts of those gaps. This would support the findings of Hubbell et al. (1999) that show gaps increase the community-wide recruitment of seedlings. Also, Uhl et al. (1988) shows that microhabitat within the gap did not seem to have an effect plant establishment, which suggests support for the community-wide recruitment paradigm.

However, even though shade intolerant species were able to recruit some seedlings in gaps amidst the advanced regeneration of other shade-tolerant species there were many shade-intolerant plants found in the non-gap control sites. One possible explanation for this is the ghost of gaps past. Because there is no record of when or where gaps may have previously appeared in the canopy the non-gap control sites might have been in an area where a gap had been present in the recent past. Some of the shade-intolerant species found in the control sites could have been stems that colonized during a previous gap disturbance regime.

Suggestions for Future Study

Although I failed to reject the proposition that the canopy gap regime is not essential to for maintenance of biodiversity, there is still much research to be done before the gap/ non- gap paradigm is completely decoupled from the preservation of forest diversity. One of the limitations of this study was that it dealt with relatively small gaps of maximally five downed trees. Perhaps a similar study using gaps of various sizes, ranging from single-tree disturbances to several ha. blowdowns would be able to correlate gap size to the type of regeneration a gap experiences. It has been shown by Uhl et al. (1988) that species composition in single-treefall gaps is more affected by advanced regeneration than that of multiple-treefall gaps. However, in the Uhl et al. (1988) study the number of replicates was low for both single and multiple-treefall gaps (n=5,1 respectively).

Hopefully with further study the tentative relationship between spatial gradients and species composition during regeneration could be substantiated.

Much research has been done regarding the gap/ non-gap paradigm in neotropical forests though there may be substantive differences between gap dynamics in temperate climate forests which have lower species diversity. Differences found between neotropical gap recruitment and temperate gap recruitment would serve to support Midgley et al. (2001) who found that in a South African forest there did not seem to be a dichotomous recruitment pattern between gap and non-gap sites. It might be possible that along latitudinal gradients there exists a shift in gap dynamics.

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Tables

Table 1. Mean and error data regarding several variables for gaps and control sites

		Species/ 25m ²	Stems /m ²	Species/ Stem	# Shade Tolerant	% Shade Tolerant	Shannon Weiner
Control	Mean	5.42	1.48	0.26	16.25	0.48	1.09
	Stdev	2.65	1.26	0.26	19.43	0.31	0.53
Gap	Mean	6.46	3.75	0.15	59.13	0.59	1.18
	Stdev	2.15	4.04	0.14	93.98	0.63	0.48

Figures

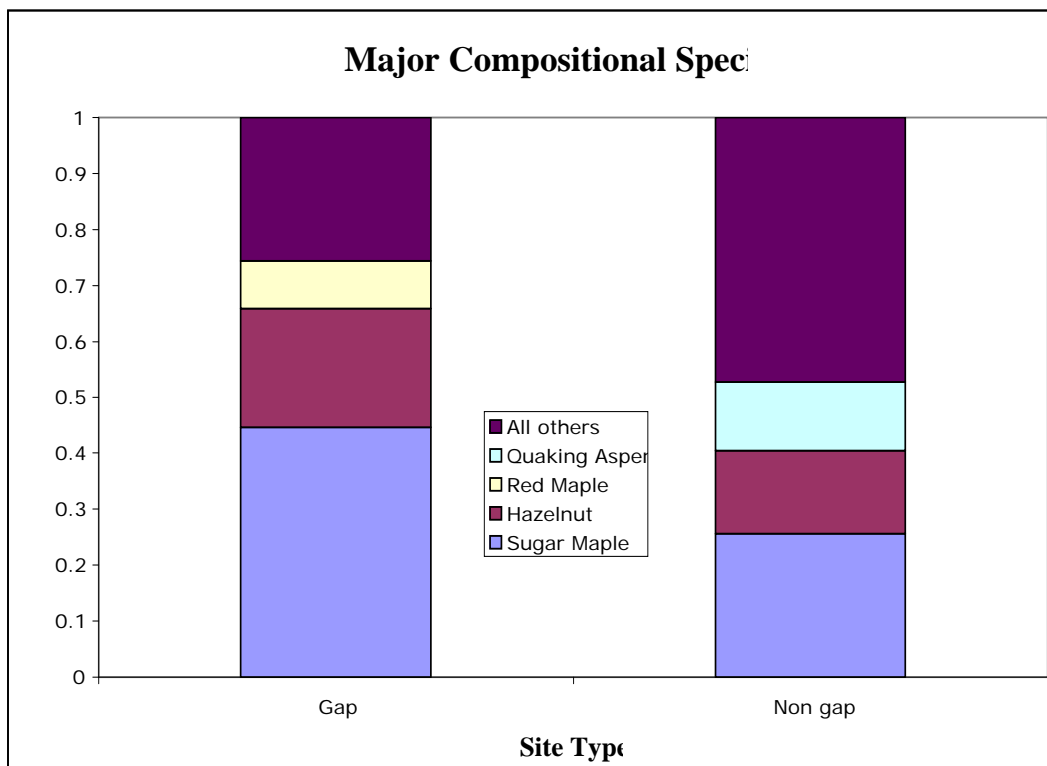


Figure 1. The compositional structure of several major species at gap and non-gap sites

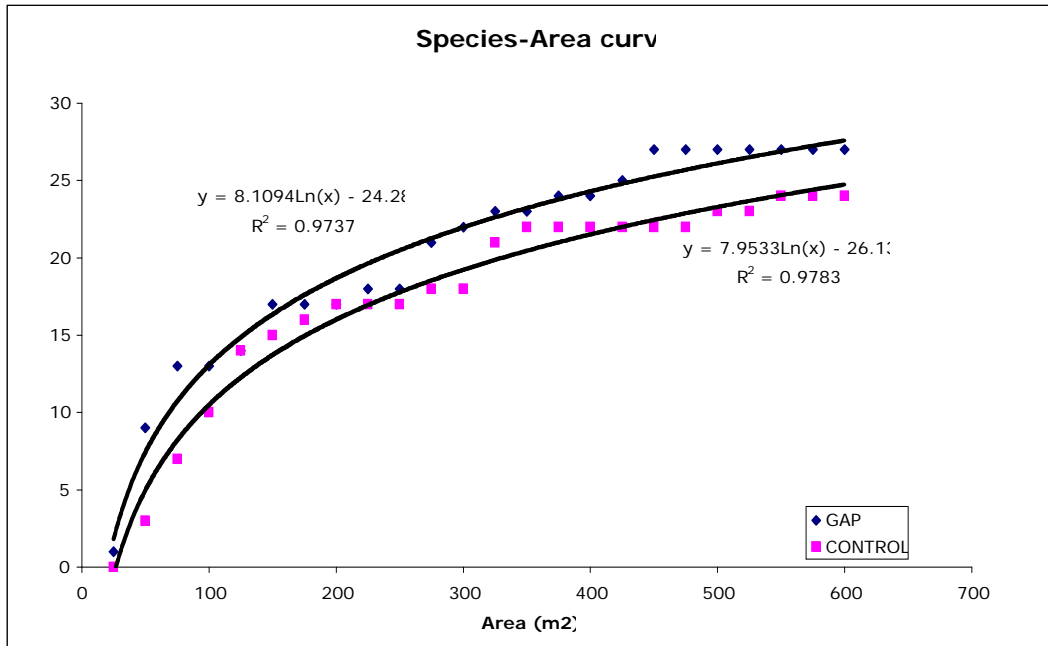


Figure 2. A graph showing the increasing amount of total species present in gap and non-gap environments as greater amounts of area are surveyed.

Appendix A: List of Scientific and Common names of Species found

Common Name	Scientific Name
White Birch	<i>Betula papyrifera</i>
Quaking Aspen	<i>Populus tremuloides</i>
Big-toothed Aspen	<i>Populus grandidentata</i>
Balsam Poplar	<i>Popula balsamifera</i>
Hazelnut	<i>Corylus cornuta</i>
Pin Cherry	<i>Prunus pensylvanica</i>
White Ash	<i>Fraxinus americana</i>
Black Ash	<i>Fraxinus nigra</i>
Black cherry	<i>Prunus serotina</i>
Yellow birch	<i>Betula alleghaniensis</i>
Hop-hornbeam	<i>Ostrya virginiana</i>
Basswood	<i>Tilia Americana</i>
Sugar maple	<i>Acer saccharum</i>
Red maple	<i>Acer rubrum</i>
Amercian elm	<i>Ulmus Americana</i>
Serviceberry	<i>Amelanchier arborea</i>
Choke cherry	<i>Prunus viriniana</i>
Alternate-leaf dogwood	<i>Cornus alternifolia</i>
Leatherwood	<i>Dirca palustris</i>

Raspberry

Ribes triste

Gooseberry

Vaccinium sp.

Blueberry

Abies balsamea.

Balsam Fir

Picea glauca

White Spruce

Picea mariana

Black Spruce

Pinus strobes

White Pine

Tsuga canadensis

Eastern Hemlock

Rubus sp.