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Assessing the Impacts of Commercial Clearcut on Freshwater Invertebrate Communities

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ASSESSING THE IMPACTS OF COMMERCIAL CLEARCUT ON FRESHWATER INVERTEBRATE COMMUNITIES

by

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ABSTRACT

Forest harvesting can impact the environment in many ways, one of which is causing a loss of subsidies and increased light intensity to freshwater ecosystems. This can have a major impact on freshwater invertebrate communities that may rely on subsidies to survive. In this study, I tested two effects of commercial clearcut, changes in light availability and detrital resources, on freshwater invertebrate communities. Cattle tanks containing freshwater invertebrates were given detritus from two different plots: one which underwent commercial clearcut over 50 years ago, and one which underwent commercial clearcut 2 years ago. Tanks were also placed in two areas of differing canopy: one shaded, another open. The abundance, richness, and composition of the invertebrate communities were measured. There was no significant difference between the 50-year and 2-year clearcut leaf subsidy treatments, but there was a significant difference between the shaded and opened canopy treatment. This indicates that a lack of canopy over a freshwater ecosystem in autumn or winter alters freshwater invertebrate communities through light availability rather than through a lack of detritus.

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Supplemental Figure 1. The total mean abundance in each tank at the end of the experiment for the canopy treatment (open canopy-white bars, closed canopy-grey bars) and leaf subsidy treatment (2 years after clearcut and 50+ years after clearcut) of (a) Amphipoda, (b) Choronimidae, (c) Coleoptera, (d) Zygoptera, (e) Anisoptera, (f) Ephemeroptera, (g) Hemiptera, (h) Plecoptera, (i) snails, and (j) Trichoptera. Bars indicate standard error of the mean.

INTRODUCTION

Cross-ecosystem subsidies are resources that move from one ecosystem into another (Richardson et al. 2010). For example, insects emerge from streams into the terrestrial riparian zone around it, which can provide 25-100% of the energy or carbon to the terrestrial organisms that will feed on them (Nakano and Murakami 2001, Baxter et al. 2004, 2005). Terrestrial ecosystems can also provide subsidies to freshwater ecosystems through terrestrial insects falling into streams, providing nutrients for the organisms in the streams (Baxter et al. 2004, 2005).

Terrestrial subsidies are very important to freshwater ecosystems. Terrestrial subsidies to freshwater can provide half the annual energy for large organisms, such as salmonids (Nakano and Murakami 2001, Baxter et al. 2005). Fish in freshwater ecosystems feed on terrestrial insect subsidies, causing aquatic insects that would normally be consumed by the freshwater fish to be more abundant (Baxter et al. 2004). Reducing subsidies can cause predators to shift to preying on aquatic insects, decreasing their numbers (Nakano et al. 1999). As aquatic insect density decreases, there can be increases in algal biomass (Nakano et al. 1999), leading to complex interactions that are dependent on changes to trophic guilds, such as trophic cascades. One type of terrestrial subsidy is leaves that fall from trees.

Terrestrial leaf litter is an important subsidy to freshwater ecosystems. Many taxa feed exclusively on decaying leaf litter (Richardson et al. 2010). Benthic invertebrate abundance can be greatly reduced when there is no leaf litter, and may be a limiting factor in some systems (Richardson 1991, Dobson and Hildrew 1992, Wallace et al. 1999). Dissolved organic material (DOM) from leaf inputs can also cause freshwater invertebrate larvae to grow faster because DOM will provide extra energy that the freshwater invertebrate larvae can use for growth and development (Mann 1988, Cibrowski et al. 1997). This affect to growth can lead to more invertebrates emerging from the freshwater ecosystem as adults, which leads to further subsidies from the freshwater ecosystem to the terrestrial ecosystem (Compson et al. 2013). DOM also affects microbes. Species such as *Burkholderia cepacia* can increase in abundance when DOM is high, while other species, such as *Pseudomonas putida* can be inhibited by DOM (McNamara and Leff 2004). Almost 50% of energy in a stream can come from DOM (Fisher and Likens 1973). Leaves can also provide habitats for aquatic invertebrates (Mann 1988). Leaves must first be broken down before they are used for food.

Detritus is broken down by detritivores. The majority of detritivores are freshwater insects (Graça 2001). Some of these detritivores include lake flies (Chironomidae), mayflies (Ephemeroptera), stoneflies (Plecoptera) and Amphipods (Amphipoda) (Martin et al. 1981, Vos 2001). The most common freshwater invertebrates that feed and break down DOM are known as shredders, which include members from Amphipoda, Plecoptera, Trichoptera, and Diptera (Graça 2001). Shredders can help increase litter retention in freshwater ecosystems, which will let other organisms use the energy provided (Hildrew et al. 1991). Shredders are dependent on DOM as well, as the density of shredders can be controlled by the availability of DOM (Townsend and Hildrew 1988). Shredders will not be able to break down detritus, however, if there is no detritus to break down.

As detritus is such an important resource to freshwater ecosystems, these ecosystems can be highly affected by harvesting. Silviculture is the science of controlling the establishment, growth, composition, health, and quality of a forest in order to be sustainable to harvesting (Kenefic et al. 2014). There are many types of silvicultural practices, such as even-aged clearcutting which is when most of the trees in the section are harvested, while promoting regeneration from seeds or sprouts (Marquis et al. 1992, Kenefic et al. 2014). This can still have a major effect on the ecosystem because most of the trees are harvested, which initially causes faster growing shade-intolerant species to outcompete shade-tolerant species (Kenefic et al. 2014). However, there are harvesting practices that do not use sustainable silvicultural practices, such as commercial clearcutting, which is unregulated harvesting where all merchantable trees are removed from a stand without tending or attention to regeneration (Kenefic et al. 2014). Since it is unregulated, it is not a true silvicultural practice, and therefore, can have major consequences for terrestrial and freshwater ecosystems.

There is increasing interest on the impact of timber harvesting on both terrestrial and freshwater ecosystems (Greenberg et al. 1994, Harpole and Haas 1999, Richardson and Béraud 2014). Interestingly, silvicultural treatments such as even-aged clearcutting can have the same effect as a high-intensity wildfire disturbance (Greenberg et al. 1994). Organisms, such as salamanders, can decrease in abundance with various silvicultural treatments because of the lack of leaf litter (Harpole and Haas 1999). Leaf litter retains moisture after rainfall, which is crucial for the salamanders to survive (Harpole and Haas 1999). Harvesting can also have an effect on freshwater invertebrate communities. Insect density can increase after harvesting (Richardson and Béraud 2014). This may be due to an increase in the abundance in small-bodied species (Stone and Wallace 1998). Harvesting also effects light availability, as there is no longer a canopy limiting light. This in turn effects temperature. Some areas of a stream are inhibited from primary production due to canopy shading during the growing season (Mann 1988). However, this dynamic changes when the trees are removed. Streams without a riparian buffer can warm up 5.8 times faster than streams with a buffer due to an increase in light availability (Moore et al. 2005). Timber harvesting has significant effects on water chemistry and increases algae in freshwater ecosystems (Sweeney et al. 2004, Richardson and Béraud 2014). These effects are larger when the stream is thinner (Richardson and Béraud 2014). Riparian zones also prevent nonpoint source pollutants from entering the stream, but this effect will be diminished after harvesting (Sweeney et al. 2004). There will also likely be less leaf subsidies entering the freshwater ecosystem, which will effect freshwater invertebrate populations.

The purpose of this study is to investigate short-term verses long-term effects of commercial clearcut silviculture practices on leaf fall subsidies and light availability to freshwater invertebrate communities. I experimentally crossed the effects of leaf subsidy input and light availability in a tank experiment at the University of Maine Forest. Leaf subsidies were collected from two silvicultural treatments (2 years and 50+ years post even-aged clearcut) at the Penobscot Experimental Forest and placed into open or closed canopy tanks containing freshwater invertebrates. I predict that the increased amount of detritus from the 50+ year clearcut will increase abundance and alter community composition of freshwater invertebrates by providing more energy for a larger community compared to those containing leaf fall from the more recent clearcut.

METHODS

Site Description

The Penobscot Experimental Forest is in an intersection of forest regions known as the Acadian Forest. This forest ecoregion is located between 43 and 48 N latitude, from New Brunswick, Nova Scotia, and Prince Edward Island in Canada to Maine and higher elevations of the Appalachian Mountains in the United States (Loo and Ives 2003, Kenefic et al. 2014). It is located between the northern boreal coniferous forest and the primary deciduous forest (Loo and Ives 2003). The Acadian Forest contains a mixture of northern hardwoods and northern conifers (Kenefic et al. 2014). The Penobscot Experimental Forest (PEF) is an Acadian Forest with sections that were treated with even-aged clearcutting.

Experimental Design

A total of twenty 50 gallon cattle tanks were set up at the deer pens on the University of Maine campus due to water being more readily available on campus than in the Penobscot Experimental Forest. Ten tanks were set up under intact forest canopy and ten tanks were in an open field to mimic the light availability in the 50+ year area and the 2-year area, respectively. This was fully crossed with detritus from the 50+ year area and the 2-year area to represent subsidies that normally would fall in. Each tank was filled with tap water from campus and left to sit for one week to evaporate the chlorine. Then one cup of clean, store-bought sand was added to provide a substrate for the invertebrates to live on and mesh was placed over each tank to prevent unwanted leaf inputs. Leaf subsidy treatments were randomly assigned within each light-availability block; either shade or open. This led to 4 different treatments that had 5 tanks each; shade 50+ year, shade 2-year, open 50+ year, and open 2-year. A table showing this set up is seen in Table 1. The tanks were then left to sit for another week in order to let the sand settle.

Invertebrates were collected from a wetland in Sunkhaze Meadows National Wildlife Refuge near the University of Maine campus. To collect invertebrates, 100 cm by 60 cm d-net (1mm mesh size) sweeps were performed in homogenous habitats throughout the wetland. Large predators were removed in order to avoid community loss due to predation and leaves were removed in order to only have detritus from the silviculture sites. The remainder of the freshwater invertebrates and the smaller detritus were put into containers with wetland water for transport. A total of 21 samples were collected, 20 of which were randomly added to each tank.

Leaves for the leaf subsidy treatment were collected from the Management Intensity Demonstration section of the Penobscot Experimental Forest using leaf traps composed of two aluminum baking trays (52.1 x 8.4 x 33.0cm) joined along the long side with adhesive tape with 6 pinholes punched in along the bottom to allow for drainage of rain water. Each tray was weighed down with rocks to avoid blow over. Five trays were put out in two experimental clearcut blocks: the 50+ year clearcut and the 2-year clearcut (Everett Capstone Unpublished). Leaves were collected from the trays every two weeks. After leaves were dried at room temperature in paper bags, the two samples were separated into leaves and needles. The 50+ year treatment were given a total of 7 g of broad leaves and 4.3 g of needles, leading to a total of 11.3 g of detritus (Table 1). The 2-year treatments were given 0.9 g of broad leaves and 2.4 g of needles, leading to a total of 3.3 g of detritus (Table 1).

End of Experiment Processing

The experiment ran for 43 days and tanks were destructively sampled. At the end of the month, the invertebrates, broad leaves, needles, sand, and detritus from the tanks were collected into plastic bags and frozen until laboratory analysis.

Samples were thawed and sorted using 3 sieves with the measurements 4.00 mm, 1.00 mm, and 500 µm in order to separate invertebrates, broad leaves, and needles above 1 mm in size. Invertebrates were stored in 70% ethyl alcohol until identification.

Using a dissecting microscope, invertebrates were identified to order and counted to get abundance and taxa richness for each tank. Broad leaves and needles were separately dried in a drying oven at a temperature of 47 ^{o}C for at least 72 hours to get dry mass (g).

Statistical Analysis

A two-way Analysis of Variance (ANOVA) was used to compare the means and variance of the leaf subsidy treatments and the canopy treatments to test for a significant difference among the treatments. This was to look at the difference within and between each of the four treatments. The two-way ANOVA was used to calculate the significance of the change in the detritus mass, the abundance of freshwater invertebrates, and the richness of taxa in each treatment. The two-way ANOVA was run in R.

To test the effects of canopy and silviculture detritus on invertebrate community composition, I used non-metric multidimensional scaling (NMDS) ordination. Bray-curtis dissimilarity indices were used to reflect differences in relative abundances of invertebrates. Differences in invertebrate community structure between canopy, leaf subsidy, and their interaction was tested using permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations using the adonis function in the vegan package (Oksanen et al. 2017) in R (R Core Team 2016).

Table 1. A representation of the experimental design. There are 5 tanks for each treatment. Detritus inputs are also recorded in grams (g).

		Canopy light availability		
		Open	Closed	Detritus Inserted (g)
Time since clearcut	2 year	5	5	3.3
	50 + year	5	5	11.3

RESULTS

Detritus

The detritus mass changed over the course of the study. In both the open canopy treatments, as well as the shaded canopy 50+ year leaf subsidy treatment, there was a net decrease in total detritus mass (Figure 1). In the open canopy 50+ year leaf subsidy treatment, the average detritus mass decreased by 7.828 g, while in the shaded canopy 50+ year leaf subsidy treatment, the average detritus mass decreased by 5.184g (Figure 1). In the open canopy 2 year leaf subsidy treatment, the average detritus mass decreased by 1.764g (Figure 1). In the shaded canopy 2 year leaf subsidy treatment, there was a net increase in total detritus mass by 0.688g (Figure 1). The canopy treatments and the leaf subsidy treatment had significant effects on end detritus mass, with p values of <0.001 and 0.001 respectively. However there was no significant interaction between the treatments, with a p value of 0.853 (Table 2).

Community Composition

There was a significant difference in invertebrate community composition between the tanks (Figure 2). The canopy treatment significantly affected invertebrate community structure, with a p value of 0.003, but neither the leaf subsidy treatment nor their interaction significantly affected the invertebrate community structure, with p values of 0.111 and 0.357 respectively (Table 2). The area of the shape for each canopy treatment indicates how similar or different the treatments are, where tank points that are close together have a similar community composition (Figure 2).

Total Abundance

The total abundance of freshwater invertebrates per tank was significantly greater in the open canopy tanks than in the shaded canopy tanks (Figure 3; Table 2). The average total freshwater invertebrate abundance in the shaded canopy 50+ year leaf subsidy treatment was 11.2 freshwater invertebrates, while in the open canopy 50+ year leaf subsidy treatment, the average total freshwater invertebrate abundance was 34.6 freshwater invertebrates (Figure 3). In the shaded canopy 2-year leaf subsidy treatments, the average freshwater invertebrate abundance was 11.6 invertebrates and in the open canopy 2-year leaf subsidy treatments, the average was 23.8 invertebrates (Figure 3). There was a nonsignificant trend in difference between the leaf subsidy treatments, where the 50+ year leaf subsidy treatments had a higher average abundance than the 2-year leaf subsidy treatments (Figure 3, Table 2). The p value for this trend was 0.266 (Table 2). The interaction of both treatments also was not significant, with a p value of 0.233 (Table 2).

Invertebrate Taxa Richness

The invertebrate taxa richness (number of taxa per tank) was significantly greater in the open canopy tanks than the closed canopy tanks (Figure 4; Table 2). There was a small trend of more taxa in the 50+ year leaf subsidy treatment (Figure 4), but it was not significant (Table 2). There was no significant difference in the treatment interaction (Table 2).

Table 2. The statistical results from two-way analysis of variance models (ANOVA) on a) total end detritus (g), c) total invertebrate abundance per tank, and d) invertebrate taxa richness per tank, as well as non-metric multi-dimensional scaling analysis (NMDS) ordination on b) invertebrate community composition. F values are presented with (treatment degrees of freedom, total degrees of freedom). Bolded p Values indicate a significant difference.

Response Variable		F Value	P Value	r^2
a) Total end detritus (g)				0.72
	Canopy	$24.95_{(1,16)}$	**<0.001**	
	Leaf Subsidy	$15.87_{(1,16)}$	**0.001**	
	Canopy X Leaf Subsidy	$0.04_{(1,16)}$	0.853	
b) NMDS Ordination				n.a.
	Canopy	$2.85_{(1,16)}$	**0.003**	
	Leaf Subsidy	$1.62_{(1,16)}$	0.111	
	Canopy x Leaf Subsidy	$1.10_{(1,16)}$	0.357	
c) Total Abundance				0.54
	Canopy	$15.55_{(1,16)}$	**0.001**	
	Leaf Subsidy	$1.33_{(1,16)}$	0.266	
	Canopy x Leaf Subsidy	$154_{(1,16)}$	0.233	
d) Invertebrate Taxa Richness				0.35
	Canopy	$4.91_{(1,16)}$	**0.042**	
	Leaf Subsidy	$1.52_{(1,16)}$	0.236	
	Canopy x Leaf Subsidy	$2.18_{(1,16)}$	0.159	

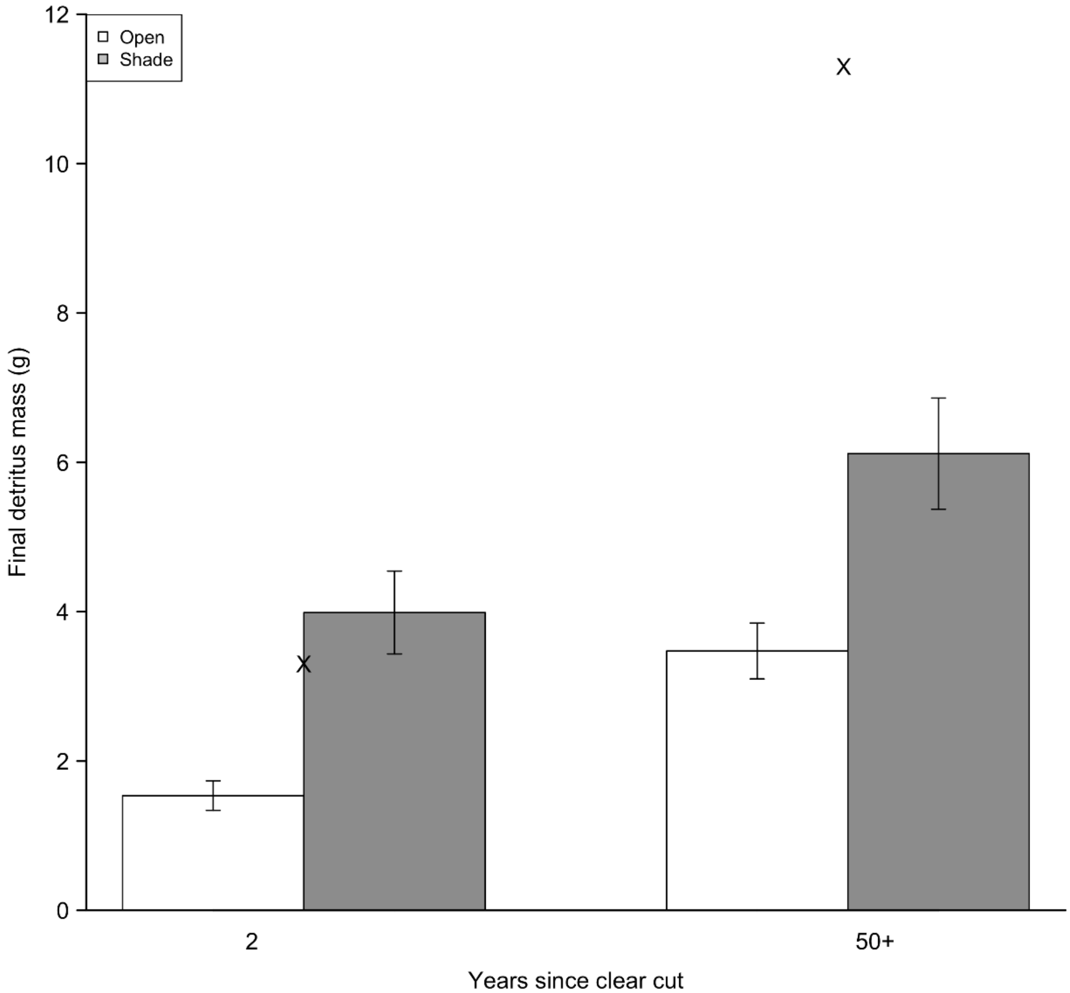

Figure 1. The total final detritus mass (g) in each tank at the end of the experiment for the canopy (open canopy-white bars, closed canopy-grey bars) and leaf subsidy treatment (2 years after clearcut and 50+ years after clearcut). The initial detritus is indicated with X for each leaf subsidy treatment. Bars indicate standard error of the mean.

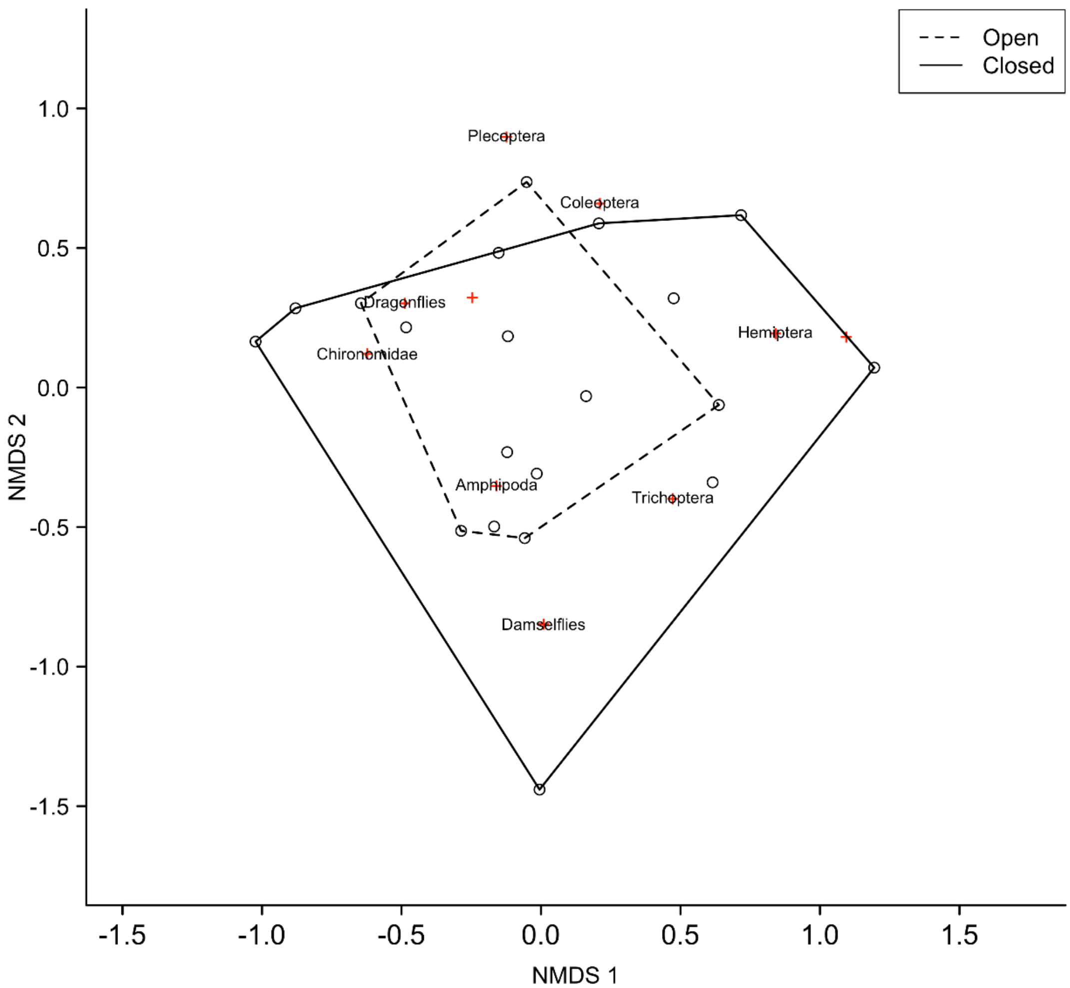

Figure 2. NMDS Ordination on tank community composition. Tanks are represented by open points and taxa represented by +'s. Open canopy tanks are enclosed in the dashed-line polygon and closed canopy tanks with the solid-line polygon.

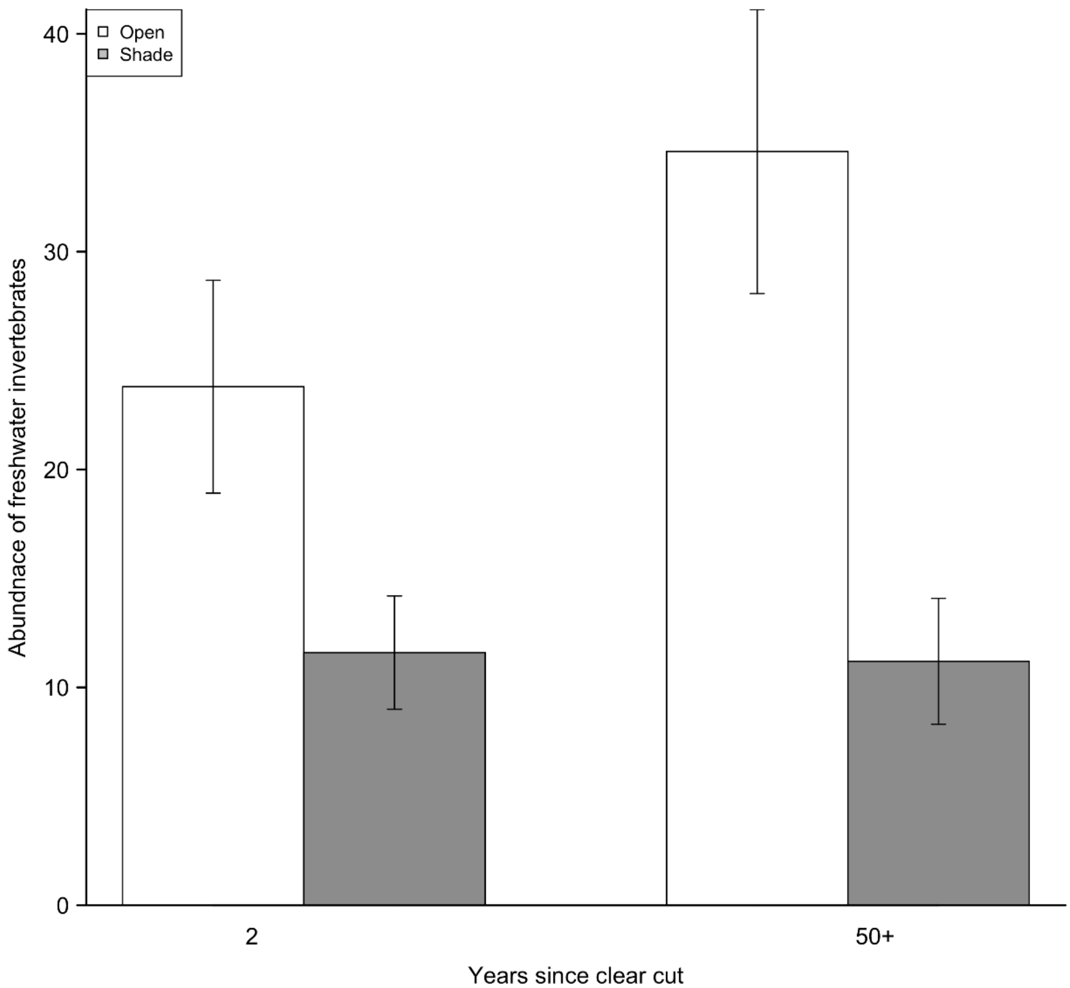

Figure 3. Mean total abundance of freshwater invertebrates in each tank at the end of the experiment for the canopy treatment (open canopy-white bars, closed canopy-grey bars) and leaf subsidy treatment (2 years after clearcut and 50+ years after clearcut). Bars indicate standard error of the mean.

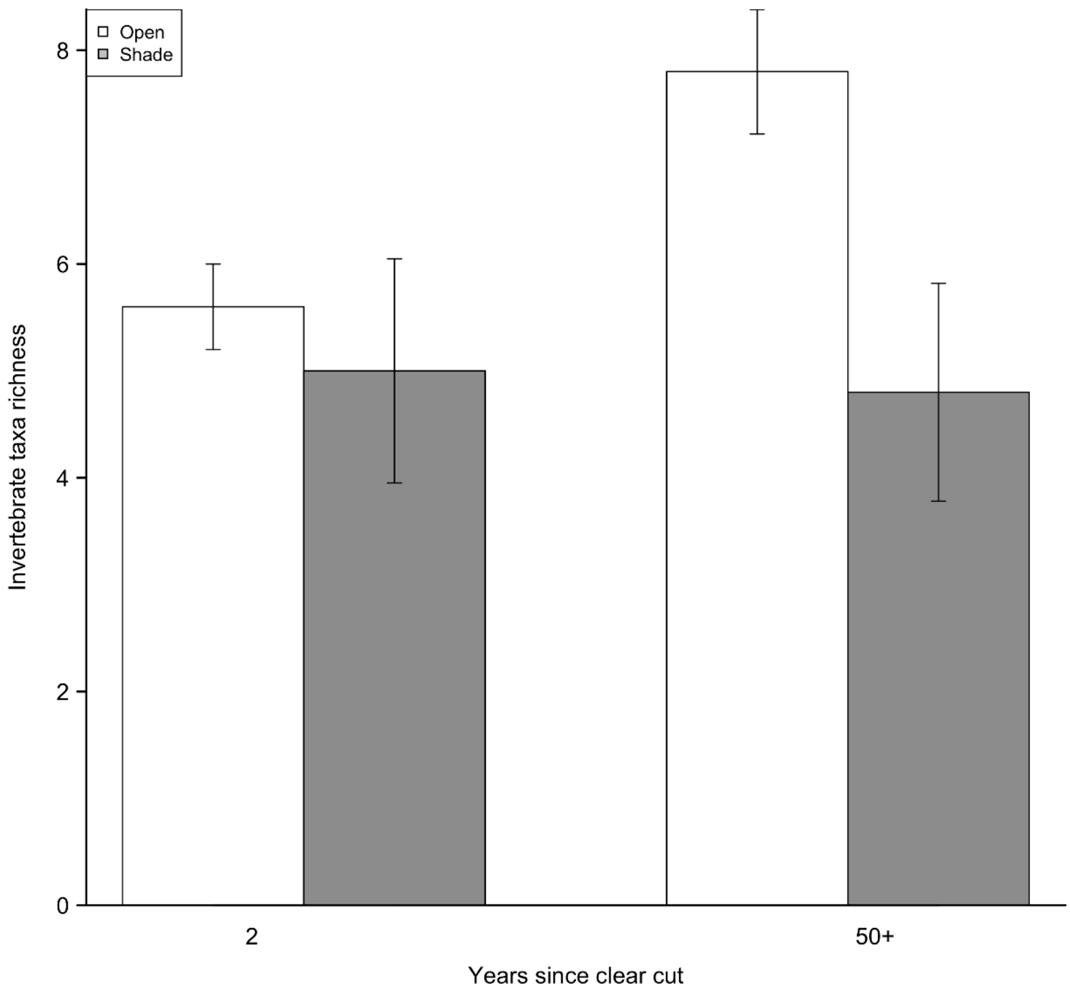

Figure 4. Mean invertebrate taxa richness to order and family in each tank at the end of the experiment for the canopy treatment (open canopy-white bars, closed canopy-grey bars) and leaf subsidy treatment (2 years after clearcut and 50+ years after clearcut). Bars indicate standard error of the mean.

DISCUSSION

This study tested two different effects of clear-cut silvicuture on freshwater ecosystems, changes in light availability crossed by changes in terrestrial leaf subsidies. The hypothesis that detritus from a 50+ year clearcut silviculture treatment would lead to more diverse freshwater ecosystems than a 2-year clearcut treatment was not supported. In open canopy treatments, with increased light availability, there was an increase in freshwater invertebrate abundance and richness of taxa compared to a shaded canopy treatment. The leaf subsidy treatment, however, did not have an effect on either richness or taxa. This implies that short-term effects on freshwater communities' diversity in late autumn is driven more by light availability than by detritus mass.

Detritus Subsidy Breakdown

The decrease in detritus in my experimental tanks is most likely due to breakdown by bacteria, fungi, and macro-detritivorous invertebrates. Leaves are one of the quickest plant part to break down, and it is especially fast with the presence of freshwater invertebrates (Webster and Benfield 1986). Freshwater invertebrates such as Plecopterans and Amphipods will use enzymes to break down detritus (Martin et al. 1981, Lepoint et al. 2006). These freshwater invertebrates can consume up to 33.2% of their body weight in one day (Cummins et al. 1973). These detritivores are essential to the ecosystem, and when leaf litter is excluded, there is a bottom-up effect propagated through detritivores, where the detritivores cannot survive without the detritus, and therefore cannot provide food for their predators (Wallace et al. 1997, 2015). The freshwater invertebrate detritivores found in this study include Amphipods, Chironomids, Ephemeropterans, and Plecopterans (Supplemental Figure 1a, b, f, h). In this study, the open canopy contained a higher abundance and richness of these detritivores than the closed canopy (Supplemental Figure 1 a, b, f, h). This likely led to the greater breakdown of detritus in the open canopy tanks (Figure 1).

Temperature can also affect leaf breakdown, with lower temperatures leading to slower breakdown due to a slower microbial process (Webster and Benfield 1986). In this study, this a likely reason why the leaves broke down more in the open canopy treatments. The closed canopy treatments may have experienced consistently lower temperature, causing a slower breakdown, while the open canopy tanks may have experienced extremes on both ends. In some cases there can still be rapid breakdown when invertebrates are present because they are not inhibited by lower temperatures as much as microbes are (Webster and Benfield 1986). In warmer streams, there is a lower carbon : nitrogen imbalance than in colder streams, which causes there to be more microbes and freshwater invertebrates in the streams (Mas-Martí et al. 2015). However, in some cases freshwater invertebrate densities can decrease with higher temperatures, and while there is faster development, there is a smaller size at maturity (Hogg and Williams 1996). Temperature was not measured however. Therefore, if this experiment will be performed again, temperature should be measured.

Despite bacterial, fungal, and invertebrate breakdown, the 2-year silviculture leaf subsidy shaded treatments showed an increase in detritus mass. This is likely due to leaves from the forest canopy entering the tanks, despite the mesh. A decrease happened in the 50+ year treatment because there was a slightly higher abundance of freshwater invertebrate detritivores in the 50+ year leaf subsidy shaded tanks than in the 2-year shaded tanks, though not enough to truly be significant (Supplemental Figure 1 a, b).

The quality of the detritus could have also played a role in differences between the sites. In the 2-year site, there were more coniferous trees, while the 50+ year site had more deciduous trees. This would also affect detritus breakdown. Harder substances like pine needles break down more slowly than broad leaves (Gholz et al. 2000). This is due to the lignin and nitrogen content in the different parts of the plant. Plants with more lignin, such as conifers like white pine, break down at a slower rate, while deciduous trees with less lignin, such as flowering dogwood, break down faster (Melillo et al. 1982). Additionally, plants with more nitrogen break down faster compared to those with less nitrogen (Melillo et al. 1982). Deciduous trees have higher nitrogen compared to coniferous trees (Melillo et al. 1982). Therefore, it made sense that the detritus from the 50+ year site, which contained mostly deciduous trees, had a higher level of break down than the detritus from the 2-year site, which contained higher levels of coniferous trees (Figure 1).

Invertebrate Community Structure

There was a significant difference in freshwater invertebrate community composition between open canopy tanks and shaded canopy tanks because the shaded canopy tanks had a wider variance in taxa (Figure 2). The main differences between the shaded canopy tanks were in the Zygoptera, Trichoptera, and Hemiptera abundance (Figure 2). Based on these findings, it is possible that we would be more likely to predict what invertebrates would be present in freshwater ecosystems under an open canopy than a closed canopy because the open canopy treatments had communities that were more alike than the closed canopy treatments. This may be due to differences in temperature or light availability. However, I do not have evidence for the mechanisms that are driving this difference. Further studies should look at these mechanisms.

I found that the invertebrate community composition, abundance, and richness was affected by light availability in open versus closed canopy, but not by the leaf subsidy treatment. This was unexpected, as increased detritus most often leads to increased invertebrates in freshwater ecosystems. Detritivore density increases during the months that leaf fall is common (Richardson 1991). In many freshwater communities, such as those found in streams, detritus is a limiting resource, meaning the abundance of the community is dependent on the detritus levels (Dobson and Hildrew 1992, Wallace et al. 1999). However, this contradicts what I found in this study. There have been some cases where taxa richness was slightly higher at clearcut streams (Stone and Wallace 1998, Banks et al. 2007).

In a previous study, it was found that in open canopy freshwater ecosystems, there was a higher abundance of most of the different guilds of freshwater invertebrates (Hawkins et al. 1982). Most importantly, there was a higher abundance of shredders in open canopy freshwater ecosystems (Hawkins et al. 1982). This is in line with what I found in this experiment. There was a higher abundance of shredders in the open tanks than the closed tanks (Supplemental Figure 1 a, b, f, h).

There are many reasons why I did not see a significant difference in freshwater invertebrate community composition between the leaf subsidy treatments, but did see a significant difference between the canopy treatments. One possible reason for the higher abundance and richness of the taxa in the open canopy treatments was a higher abundance of algae. There is a high specific growth rate of algae, such as *Chlorella* *sorokiniana*, at high light intensities (Schlesinger et al. 1981, Qiang et al. 1998, Cuaresma et al. 2009). Many species of algae, including *Asterionella Formosa*, *Cryptomonas marssoni*, *Tychonema bourrellyi*, *Staurastrum cingulum*, *Dinobryon divergens*, *Ceratium furcoides*, and *Eudorina unicocca* grow well at 25 ^{o}C, with some growing at higher temperatures as well (Butterwick et al. 2004). A higher abundance in algae can lead to a higher abundance of invertebrates, and in some cases, algae may be enough to keep communities abundant without the need of subsidies (Wallace et al. 1999). Freshwater fauna can show little change if there is enough algae or moss in the ecosystem (Wallace et al. 1997). There also may be differences in functional groups. Scrapers, which consume live plant matter, consume algae (Cummins and Klug 1979). One family of scrapers are the Trichopterans (Anderson and Cummins 1979). Trichopterans were found in all the treatments, but there were slightly more in the open canopy treatments (Supplemental Figure 1 j). This slight majority may be due to a higher level of algae. In my experimental tanks, there could have been enough algae to offset any effect the lack of detritus may have had. However, it is currently unknown if this is the case, as algae mass and temperature were not measured.

Another possible reason for the difference in freshwater invertebrate communities with canopy treatment in my study is an increase in the microbial or fungal conditioning of the leaves. Conditioning occurs when microbes or fungi partially decompose leaf litter (Bärlocher and Kendrick 1975). This conditioning is a necessary process in order to move nutrients to higher trophic levels (Danger et al. 2012). Microbes and fungi may have been able to colonize the open canopy tanks more than the closed canopy tanks. However, microbe and fungi abundance was not measured, so it is unknown if they truly had an effect. This is an idea that should be looked at in the future by running this experiment again to look at microbial community composition.

An alternative reason for the difference between freshwater invertebrate communities is an increased colonization of invertebrates in the open canopy. Colonization occurs when an organism moves from one home site to another permanently (Bilton et al. 2001). This colonization would increase the abundance and richness of the freshwater invertebrate communities (Bohonak and Jenkins 2003). Colonizing freshwater invertebrates also contribute to detrital breakdown (Chauvet et al. 1993). It is possible that the invertebrates could colonize the open canopy tanks more, possibly due to a lack of barriers between the open canopy tanks. In my research, however, I have not seen any indication of canopy effect on colonization studied, and I believe that the interactions between the freshwater invertebrates and the consumption of detritus altered abundance and richness more than colonization. One way to expand this experiment would be to monitor colonization rates between open and closed canopy treatments.

The lack of significance between the leaf subsidy treatments may be due to the length of my experiment. Most research on silviculture's effects were done over longer periods (Greenberg et al. 1994, Moore et al. 2005, Wallace et al. 2015). Detritus may not have had enough time to be conditioned enough to add resources because my experiment lasted 43 days. It can take 60-80 days for leaf toughness to decrease to a level that invertebrates can consume (Danger et al. 2012). There also may not have been enough time for some members of the invertebrate communities to reproduce. The invertebrates in my experiment were mostly juveniles that were unable to reproduce. Finally, there was likely not enough time for invertebrates to colonize the tanks. Exposure time is important to colonization, even more so that detritus types (Ligeiro et al. 2010). This would affect the abundance of the community.

The time of year can also have an effect on freshwater invertebrate community composition. This is because invertebrate abundance will be higher in months where leaf fall is common (Richardson 1991). The majority of leaf fall occurs in autumn (Benfield 1997). Research has indicated that there is also an increase in the abundance of invertebrates because water levels are high in the fall than in other seasons, as the water levels make it easier for colonizing invertebrates to find habitats (Brooks 2000). My experiment occurred in the fall, so the ecosystems should have experienced these effects. The next steps would be to expand this experiment to one year as opposed to 43 days. This would give the invertebrates time to reproduce and colonize the tanks.

Finally, the lack of significance between the leaf subsidy treatments may be due to the location of my experiment. The majority of research on silviculture is done in the location of the treatment (Greenberg et al. 1994, Harpole and Haas 1999). I likely would have seen different results if we had the tanks set up in the Penobscot Experimental Forest. While I would not be able to cross light availability with detrital inputs, there would have been a more accurate depiction of how much will fall into a freshwater ecosystem in the Penobscot Experimental Forest. Despite the mesh over the tanks, there was still the possibility of leaves and needles from the University of Maine Forest falling in, which could have caused and inaccurate measurement in end detritus levels. If I could set up tanks in the Penobscot Experimental Forest, I would not have to worry about unwanted material falling in.

Conclusion

My research indicates that a lack of canopy over a freshwater ecosystem in autumn and winter alters aquatic invertebrate communities through light availability. Changes in detritus does not have as much of an effect after only 43 days. When we are directly altering an ecosystem, we must keep in mind that we are also indirectly altering another ecosystem. We need to consider how our actions affect all ecosystems connected to the one we are altering.

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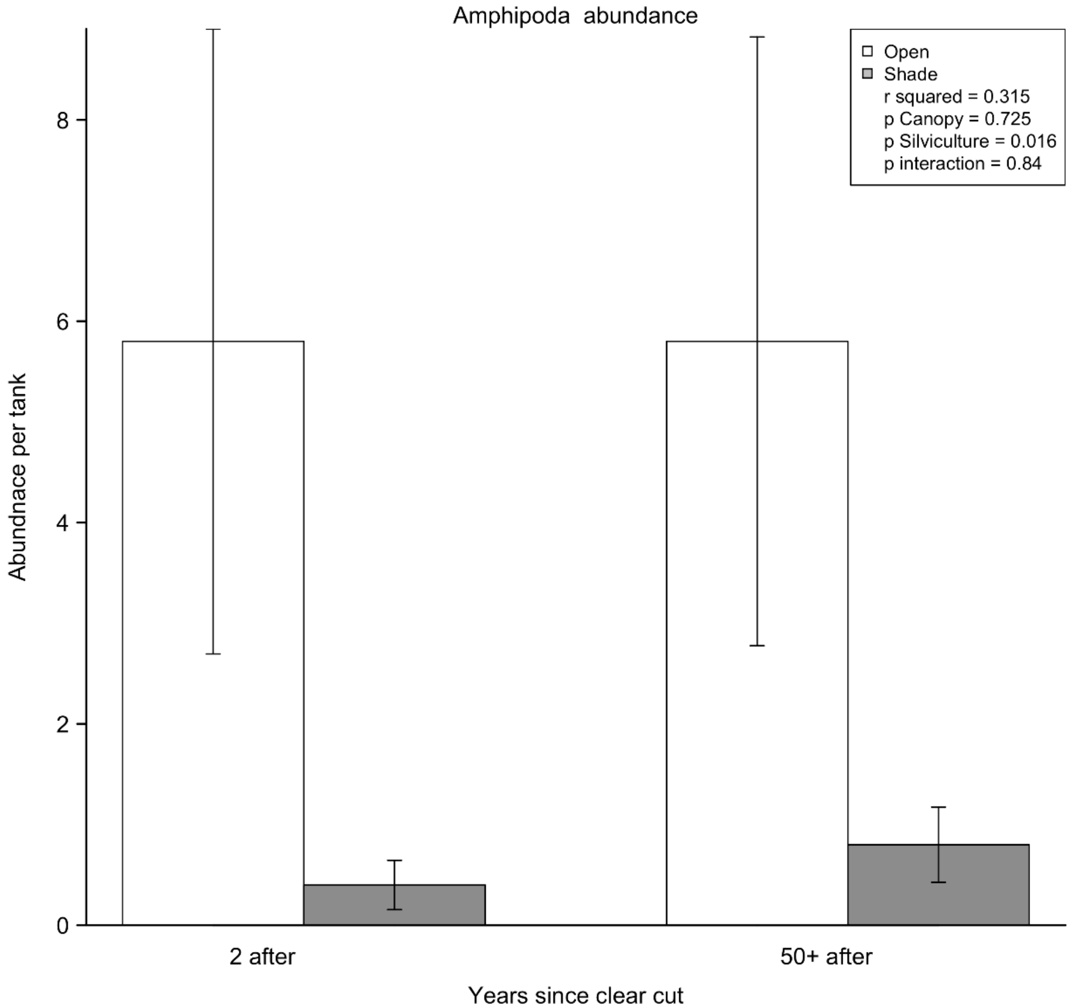
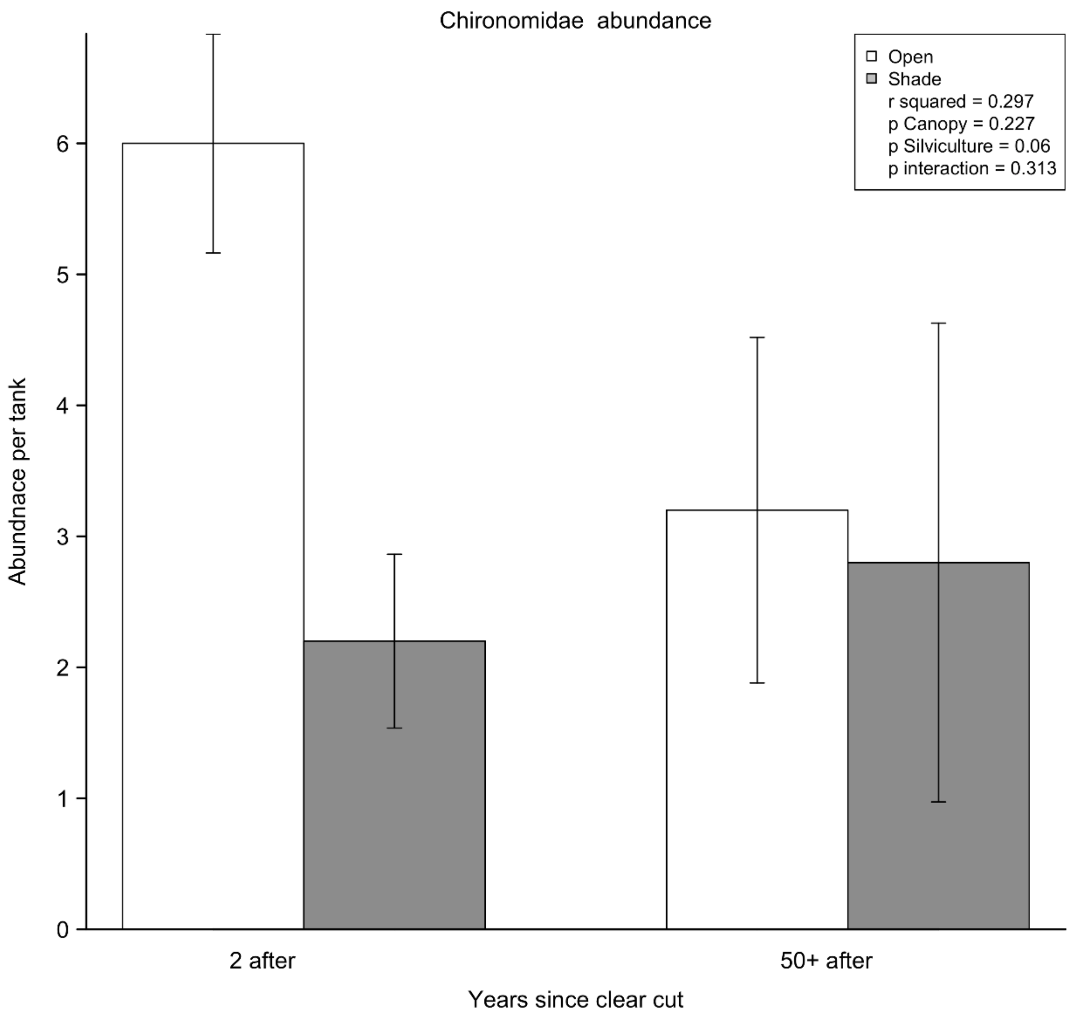
APPENDIX: SUPPLIMENTAL FIGURES

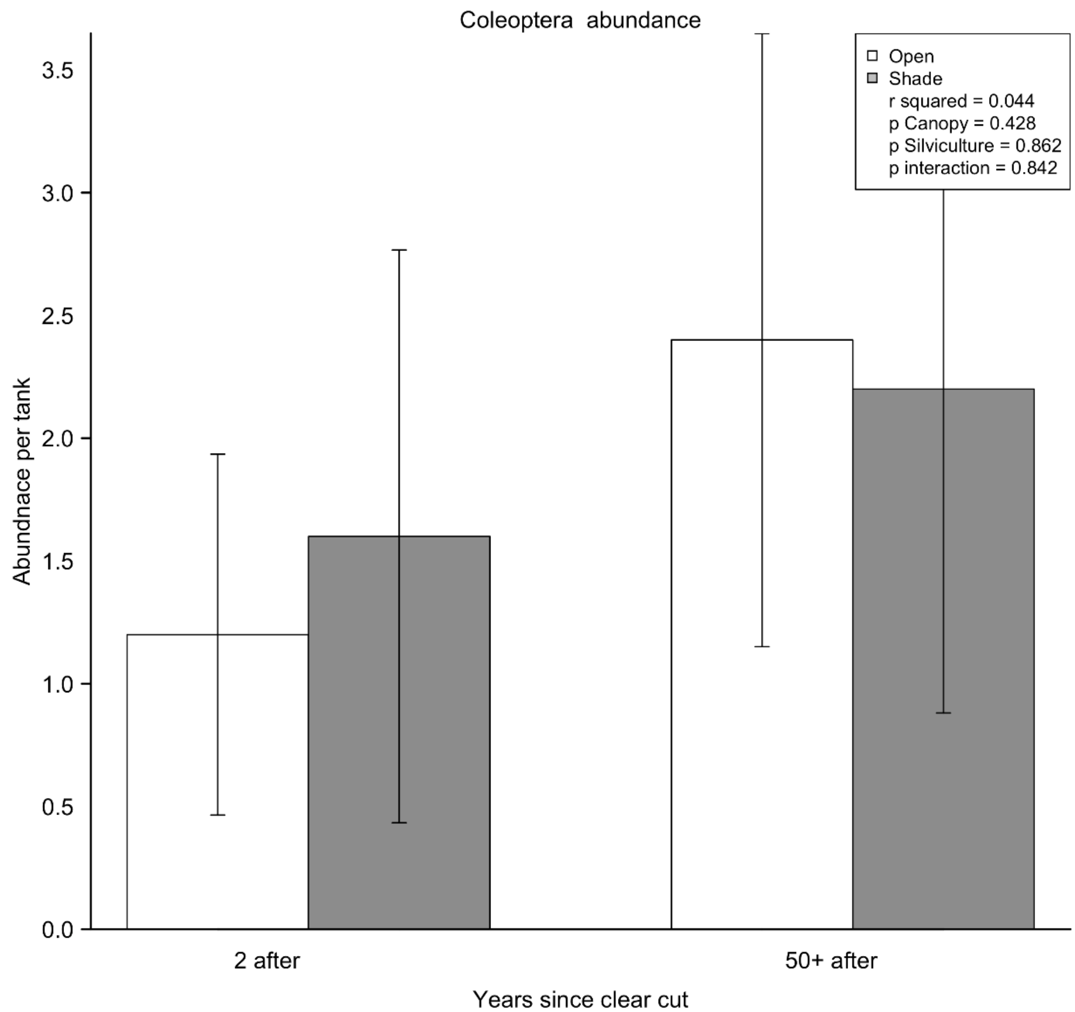
a)



b)

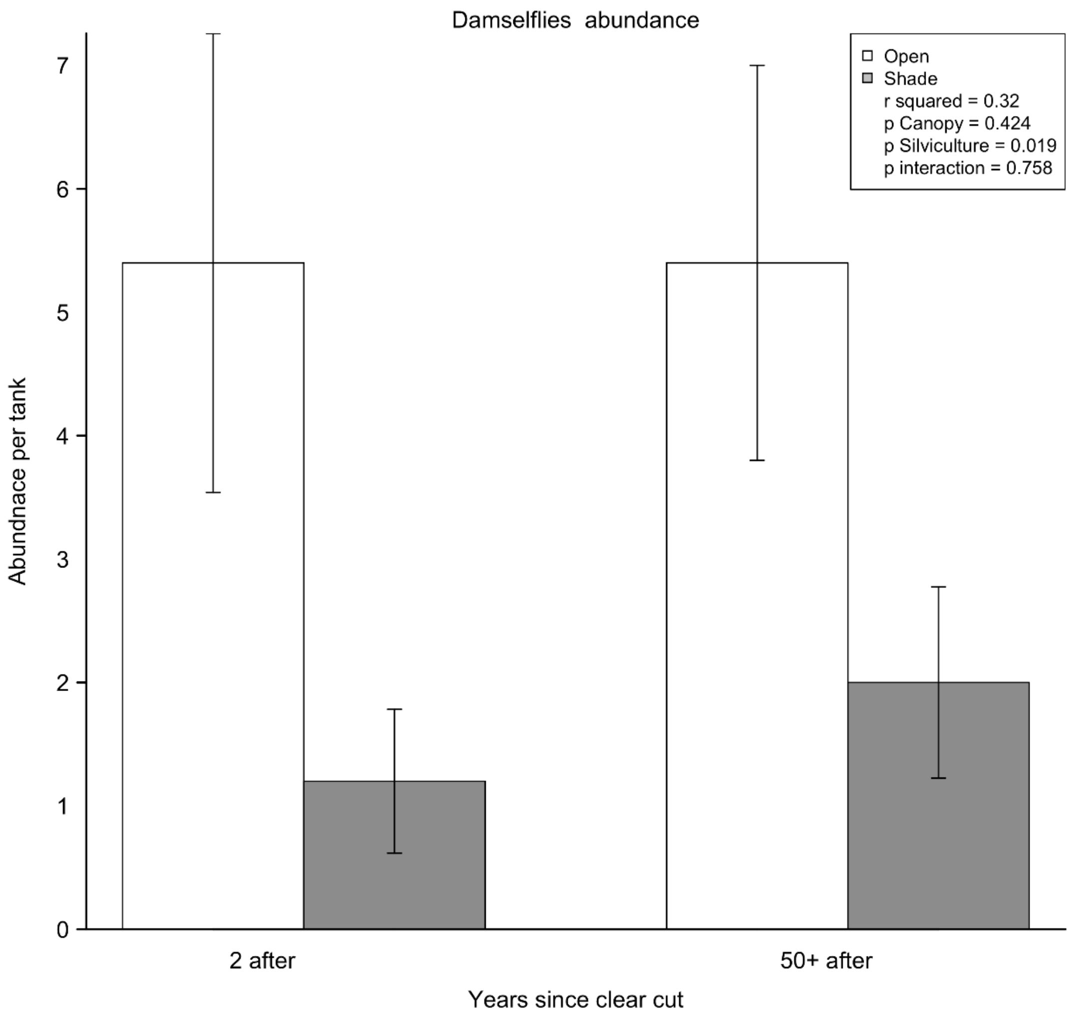

Chironomidae abundance
Open
Shade
r squared = 0.297
p Canopy = 0.227
p Silviculture = 0.06
p interaction = 0.313
Abundnace per tank
0
1
2
3
4
5
6
2 after
50+ after
Years since clear cut

c)

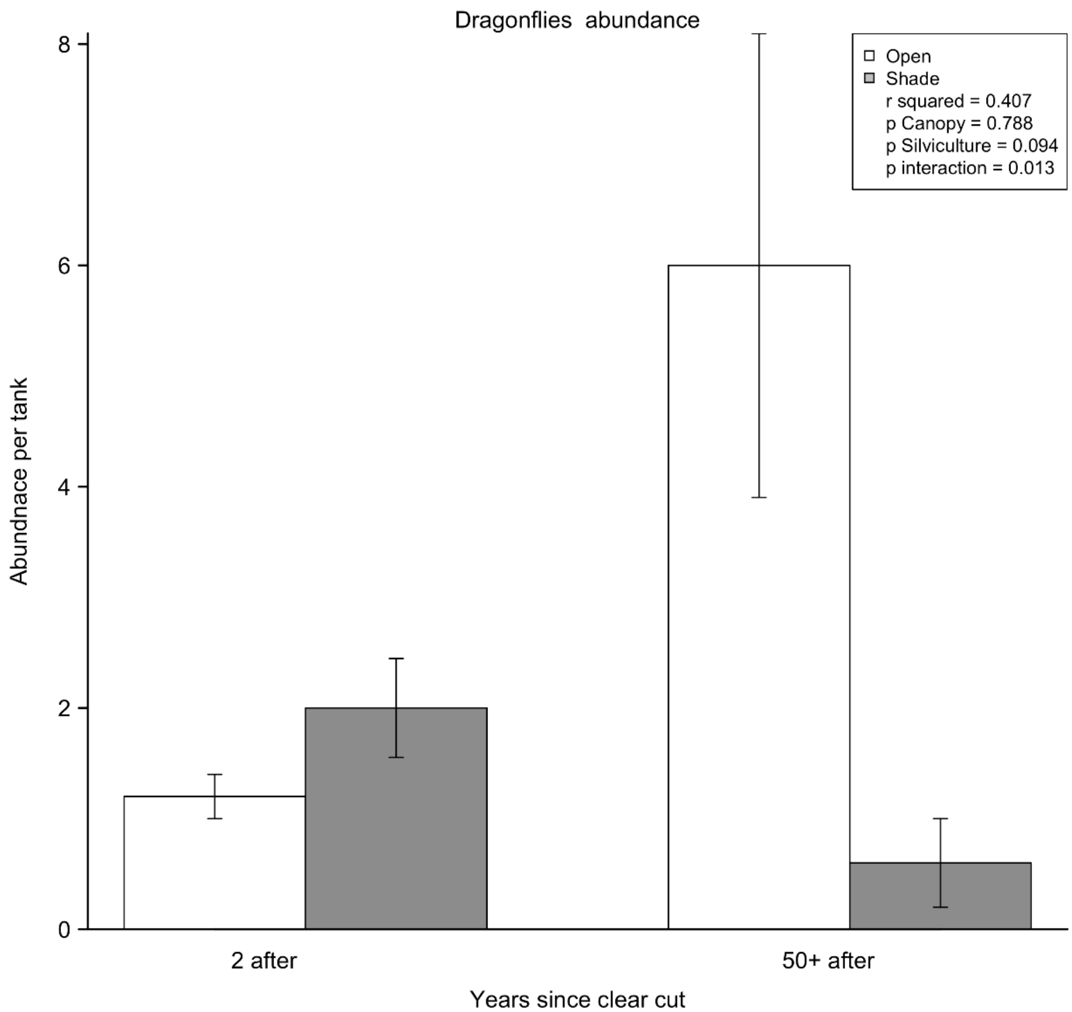


Coleoptera abundance
Open
Shade
r squared = 0.044
p Canopy = 0.428
p Silviculture = 0.862
p interaction = 0.842
Abundnace per tank
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
2 after
50+ after
Years since clear cut

d)

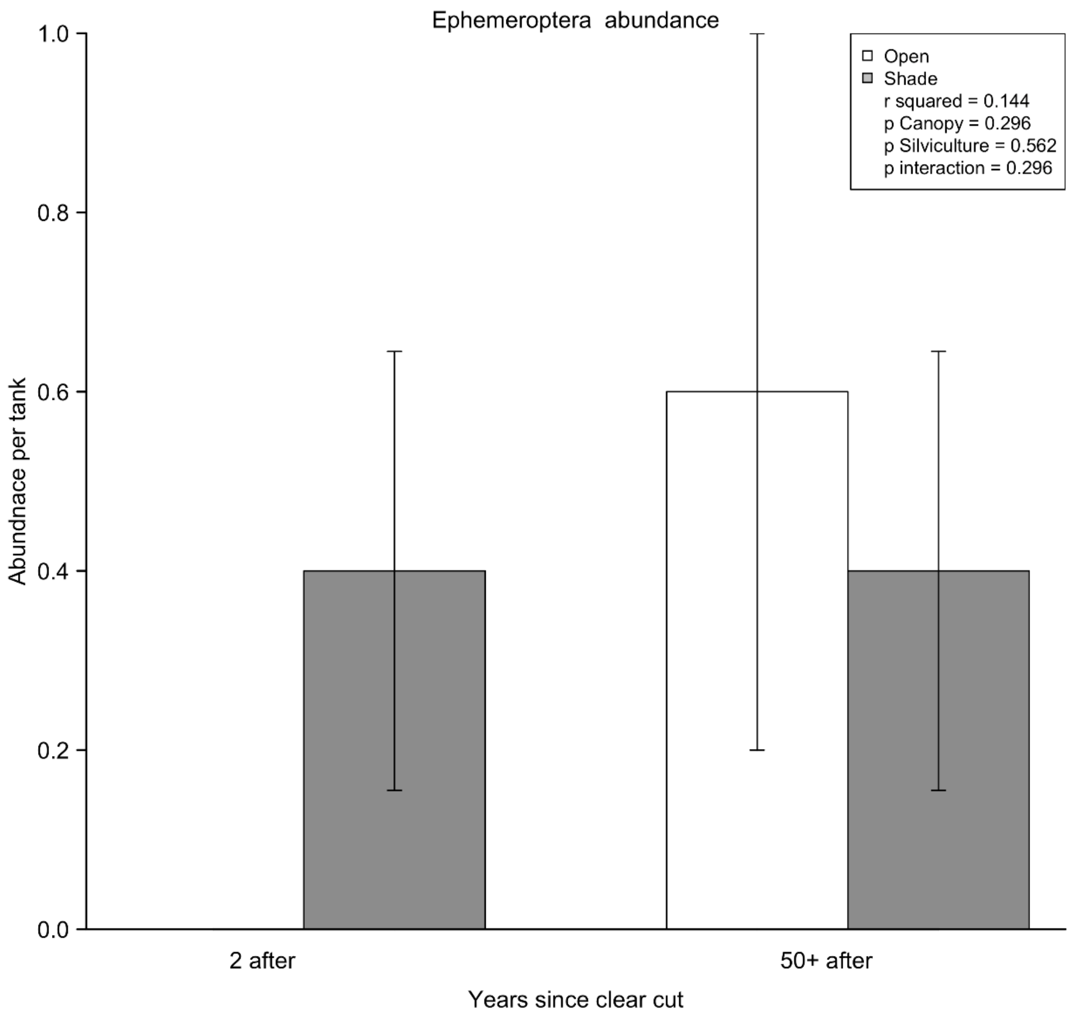

Damselflies abundance
Open
Shade
r squared = 0.32
p Canopy = 0.424
p Silviculture = 0.019
p interaction = 0.758
Abundnace per tank
0
1
2
3
4
5
6
7
2 after
50+ after
Years since clear cut

e)



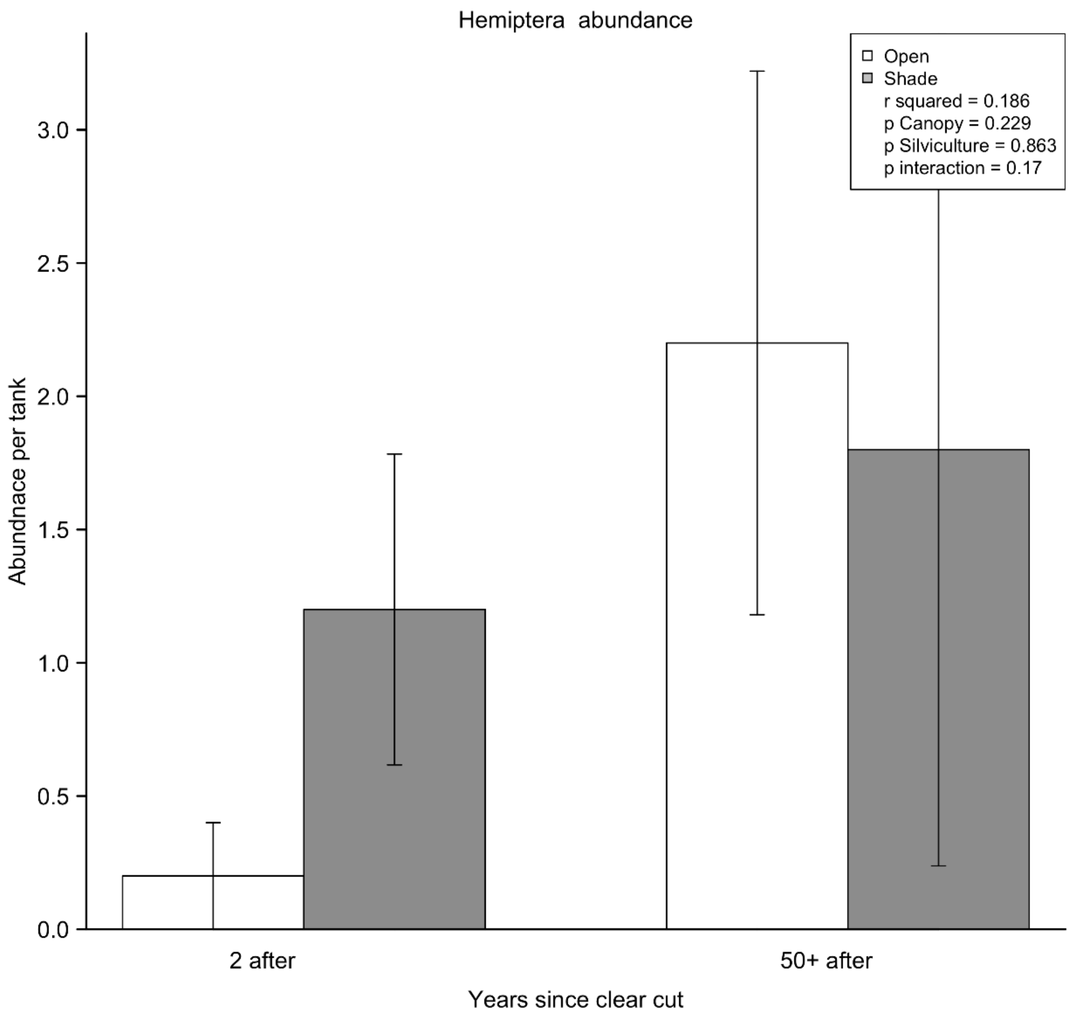
Dragonflies abundance
Open
Shade
r squared = 0.407
p Canopy = 0.788
p Silviculture = 0.094
p interaction = 0.013
Abundnace per tank
0
2
4
6
8
2 after
50+ after
Years since clear cut

f)



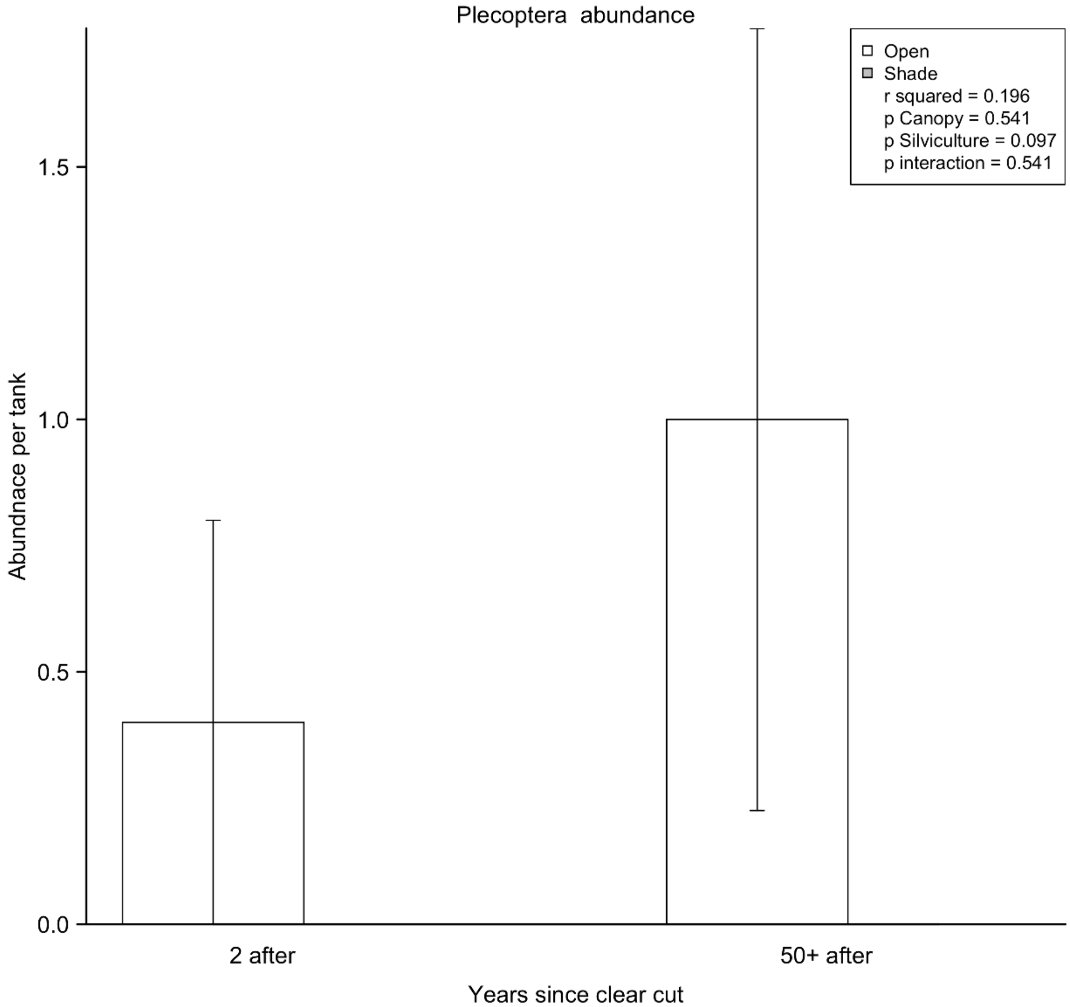
Ephemeroptera abundance
Open
Shade
r squared = 0.144
p Canopy = 0.296
p Silviculture = 0.562
p interaction = 0.296
1.0
0.8
0.6
0.4
0.2
0.0
Abundnace per tank
2 after
50+ after
Years since clear cut

g)

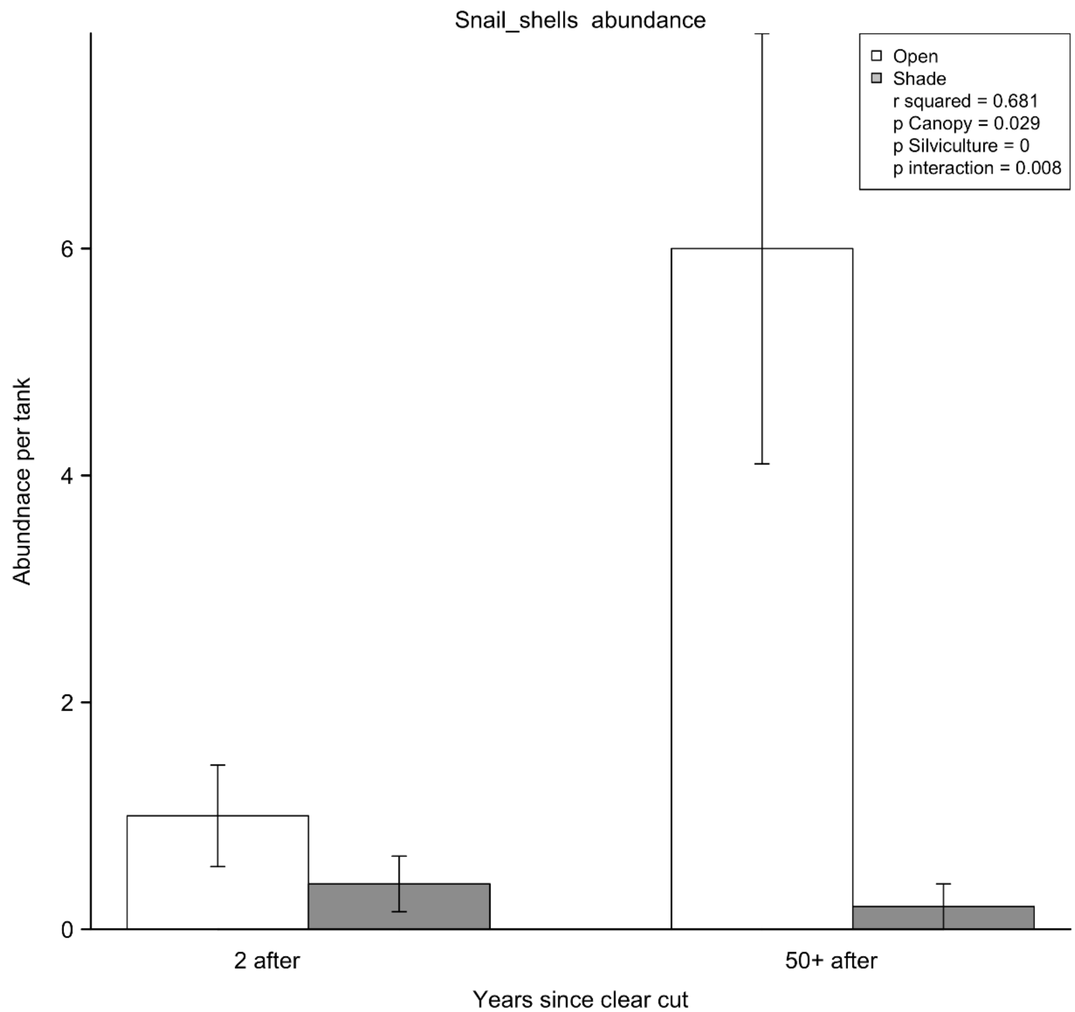


Hemiptera abundance
Open
Shade
r squared = 0.186
p Canopy = 0.229
p Silviculture = 0.863
p interaction = 0.17
Abundnace per tank
0.0
0.5
1.0
1.5
2.0
2.5
3.0
2 after
50+ after
Years since clear cut

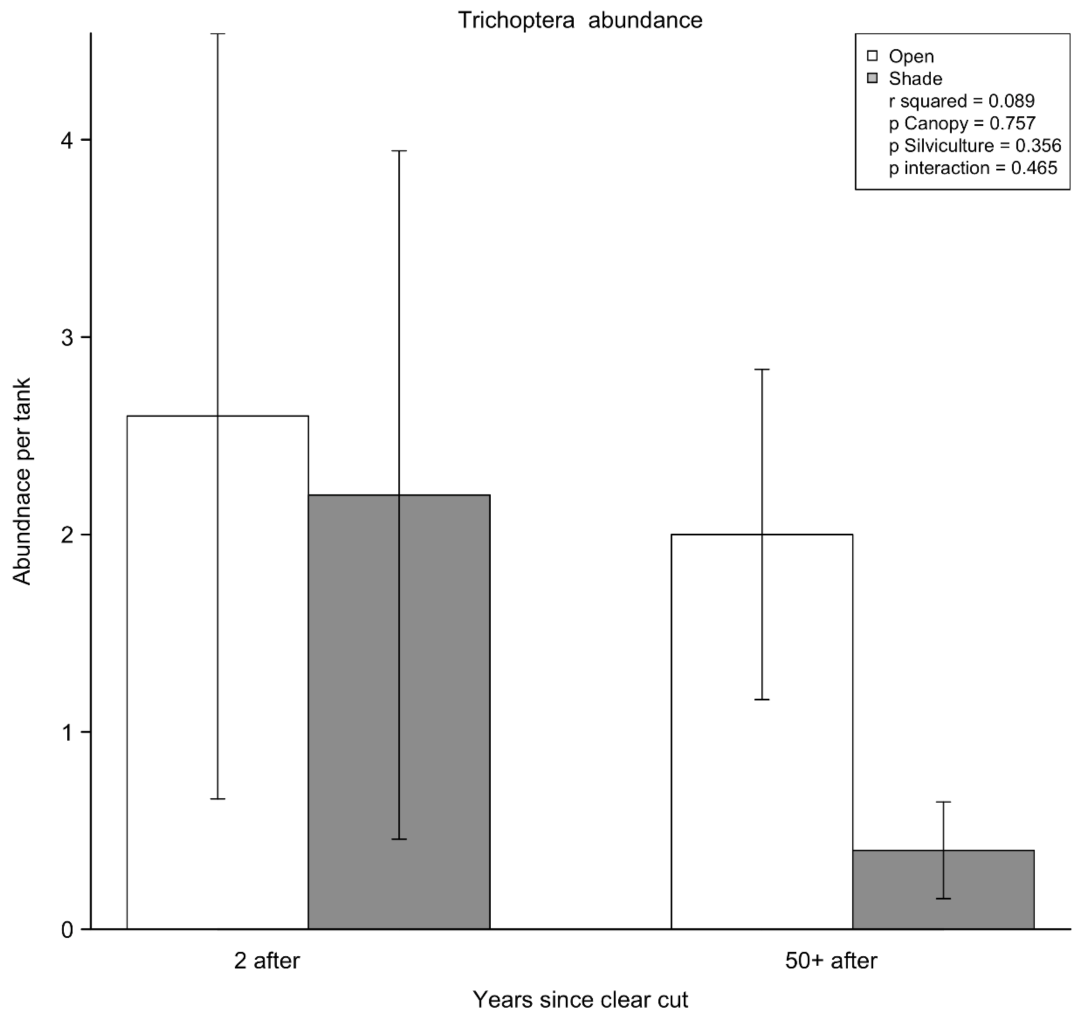
h)


Plecoptera abundance
Open
Shade
r squared = 0.196
p Canopy = 0.541
p Silviculture = 0.097
p interaction = 0.541
Abundnace per tank
1.5
1.0
0.5
0.0
2 after
50+ after
Years since clear cut

i)


Snail_shells abundance
Open
Shade
r squared = 0.681
p Canopy = 0.029
p Silviculture = 0
p interaction = 0.008
Abundnace per tank
0
2
4
6
2 after
50+ after
Years since clear cut

j)



Supplemental Figure 1. The total average abundance in each tank at the end of the experiment for the canopy treatment (open canopy-white bars, closed canopy-grey bars) and leaf subsidy treatment (2 years after clearcut and 50+ years after clearcut) of (a) Amphipoda, (b) Choronimidae, (c) Coleoptera, (d) Zygoptera, (e) Anisoptera, (f) Ephemeroptera, (g) Hemiptera, (h) Plecoptera, (i) snails, and (j) Trichoptera. Bars indicate standard error of the mean.

AUTHOR'S BIOGRAPHY

Nicholas J. Kovalik was born and raised in Stratford, Connecticut on December 27th, 1995. He graduated from Stratford High School and the Bridgeport Regional Aquaculture Science and Technology Education Center in 2014. Nicholas majored in zoology and minored in theatre. He is a member of the Biological Honor Society Beta Beta Beta. After graduation, Nicholas plans to educate the public about animals and conservation.