Influence of *Castor canadensis* on northern lower Michigan forest succession

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Abstract

Forests undergo a natural progression, called ecological succession, in which they experience a gradual change in community species composition (Luken 1990). As the tree community cycles through each stage of succession, the surrounding habitat cycles and transforms with it (Barnes and Wagner 2004). Our study focuses on how *Castor canadensis* (North American beaver) affects the direction of forest succession in northern lower Michigan. We counted, identified, and measured the diameter of standing and felled trees at four known beaver sites in the vicinity of Pellston, MI. In addition, we counted and identified 50 randomly selected juvenile trees at each site. Our results showed that *C. Canadensis* have a preference for *Populus tremuloides* (trembling aspen) (chi-square: p=0.008) and early successional tree species (chi-square: p=0.000) and show no foraging preference based on tree diameter (Mann-Whitney U: p=0.109). By comparing adult tree species to juvenile tree species, we also found that the species composition prior to and during beaver interference differs significantly from future forest species composition (chi-square: p=0.016). Given these results, we conclude that the foraging preferences of *C. canadensis* caused a premature progression of forest succession.

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Introduction

Significant disturbances to ecosystems often generate predictable changes in community composition. Species diversity within a habitat is important to examine because it offers insight into how the community functions as a whole. For instance, the species composition of the trees in a forest determines the amount of carbon a forest can sequester, what types of animals will live in the surrounding area, and what we can expect to find in the community in the future (Begon *et al* 2006). Forests go through a natural progression, called ecological succession, in which they experience a gradual change in the species composition of their community (Luken 1990). This process of physical change can occur over the course of hundreds of years. As the tree community cycles through each stage of succession, the surrounding habitat cycles and transforms with it (Barnes and Wagner 2004). The trajectory of this intrinsic process can be substantially altered with the introduction of an ecological disturbance into the habitat. Such a directional change in the succession of a forest can have an extensive affect on the entire ecological community (Luken 1990).

Few species are as capable of influencing a forest habitat as the beaver, the second largest rodent in the world. There are two species of beaver in existence today: *Castor canadensis* in North America and *Castor fiber* in Eurasia (Müller-Schwarze and Sun 2003). Our study will focus on the actions of the *C. canadensis*. Beavers are commonly referred to as 'ecosystem engineers'. Ecosystem engineers alter the physical state of the biotic or abiotic materials within a given habitat. In this way, they are able to reshape, maintain, and construct entire habitats (Jones *et al*. 1994). Beavers significantly alter their surrounding habitat by cutting down trees in the area to build their dams on rivers and streams (Müller-Schwarze and Sun 2003). This practice has large-scale effects on the species-diversity of the forest, the hydrological balance of the river, and the coexisting plant and animal species that share resources with the beaver (Raffel *et al*. 2009).

C. canadensis have been shown to practice selective foraging during the construction of their dams. For example, a study performed at Robinson's Lake in Wolverine, Michigan, found that beavers felled 100% of the *Populus tremuloides* (trembling aspen) in the surrounding area, in addition to a smaller percentage of the *Prunus serotine* (black cherry) population, displaying a clear species-specific preference. This study found that the tree diameter did not influence the foraging patterns of the *C. canadensis* (Kerin 1991). A similar study performed in Cheboygan, Michigan, found that *C. canadensis* showed a clear preference for *Populus grandidentata* (big-tooth aspen) over eight other species. Again, no correlation existed between tree diameter and preference (Fard 1991).

It is clear that beavers perform selective foraging. However, it is unclear as to how this practice influences the succession of the forest ecosystem. The tree species within a given forest are categorized as an early, mid, or late successional. For example, *P. tremuloides* and *Betula alleghaniensis* (yellow birch) are classified as early successional species in northern Michigan, while *Acer rubrum* (red maple) and *Acer sacchaum* (sugar maple) are late successional species (Mickler *et al*. 2000). This label reflects when they occur during the life cycle of the forest. The successional stage of a forest can be determined by observing both the relative abundances of adult species present and incoming juvenile species. As forest succession progresses, a new composition of juvenile species will emerge to replace the existing community.

In this study, we investigate how *C. canadensis* affects forest succession in northern lower Michigan. We do this by asking the following three questions.

1. Do beavers selectively forage for specific tree species?
2. Do beavers forage for trees within a certain successional category?
3. How does the selective foraging of the beaver affect the direction of forest succession?

Materials and Methods

Between the dates May 28th and June 5th 2010, we studied four beaver foraging sites to investigate whether or not beaver foraging preferences have an influence on the direction of forest succession in northern lower Michigan. All four sites varied in landscape characteristics in order to provide a wider variety of data: Site 1 (Figure 1, Table 1) was a lakeshore den at Grapevine Point on Douglas Lake, Site 2 was an elevated embankment on East Branch River, Site 3 was a steep embankment on Carp Creek, Site 4 was a swampy area on Carp Creek about 400 meters south of the previous location. All four sites were in the vicinity of Pellston, Michigan.

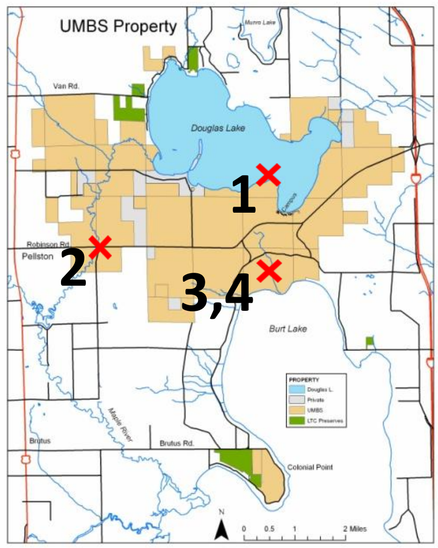

Figure 1. Map of beaver sites at Grapevine Point (1), East Branch River (2), and Carp Creek (3, 4).

All four sites were first evaluated for relative number of foraged trees to ensure sufficient data for analysis. We aimed to have at least 10 felled trees at each location. We determined the site size by locating the outer edges of beaver foraging while maintaining a local proximity to the nest area. All sites were at most 50 meters from each respective nest. This provided us with a sampling area containing felled and standing trees to reflect beaver preference. Sites varied between 12 to 15 meters wide and 10 to 20 meters in length (Table 1). The size of each location was determined depending on the approximated relative density of the felled trees in each given area.

Table 1. Site name, location, description, and size of each measured site.

Site	Location	Description	Size
1	Grapevine Point (Lat:45.56, Long:-84.68)	Lakeshore den	12 x 20 m
2	East Branch River (Lat:45.55, Long:-84.75)	Elevated embankment	12 x 8 m
3	Carp Creek (Lat:45.55, Long:-84.68)	Steep embankment, northern site	12 x 6 m
4	Carp Creek (Lat:45.55, Long:-84.68)	Swampy area, southern site	15 x 10 m

We first wanted to observe whether beavers practice selective foraging. After a site was measured and marked, we identified, counted, and categorized (early, mid, or late succession) all standing and felled adult tree species. To ensure that the tree was felled by a beaver and not by a natural cause, we looked for a conical shape at the top of the stump. In addition, to determine whether to classify the tree as standing or foraged, the tree trunk had to be completely detached from the main tree body mass. To differentiate between juvenile and adult, we classified any tree that was less than 2 meters in height as a juvenile. During the identifying process, we also measured the diameter of each standing and felled tree.

To observe whether the selective foraging of the beaver affected the direction of forest succession, we next quantified the juvenile species to see what will replace the felled adult trees in the future. A standardized count of 50 juveniles was conducted to ensure consistent relative proportions from each site. Because juvenile trees were significantly more abundant than adult trees, we counted and identified the juveniles in randomly selected 1 x 1 m areas until we had 50 specimens.

Statistical Tests

Although each site had a significantly different community composition, we combined the data from each site into a pooled data set to provide a representative sample of foraged beaver sites in northern lower Michigan. To determine if beavers selectively forage based on species, we created a contingency table and ran a Pearson Chi-Square test to compare the relative abundance of species of all felled and non-felled adult trees. We also ran a t-test on the diameters of all felled and non-felled adult trees to determine if diameter has any effect on beaver foraging preference.

To observe whether beavers foraged for trees within a certain successional category, we created a contingency table and ran a Pearson Chi-Square test to compare the relative abundance of felled trees and standing trees with respect to successional categories.

To determine the beaver's effect on the direction of forest succession, we created a contingency table and ran a Pearson Chi-Square test to compare the relative abundance of all juvenile trees and adult trees (both standing and felled) with respect to successional categories. The results of this test will provide insight to the differences between the standing forest and the forest that will replace it.

Results

H_0: Beavers do not selectively forage trees based on species.

With data compiled from all four sites, a total of 79 standing adult trees and 58 felled adult trees were recorded. The relative abundance of species between standing and felled adult trees was significantly different (Pearson chi-square = 87.431, d.f. = 8, p = 0.000). 11 standing adults and 8 felled adults were omitted from this statistical analysis because there were less than 5 specimens within the species type. The most abundant standing adult species were balsam poplar (32.35%), balsam fir (27.94%), and red maple (19.12%) (Figure 2). The most abundant felled adult species were trembling aspen (86.0%) and big-tooth aspen (14.0%) (Figure 3).

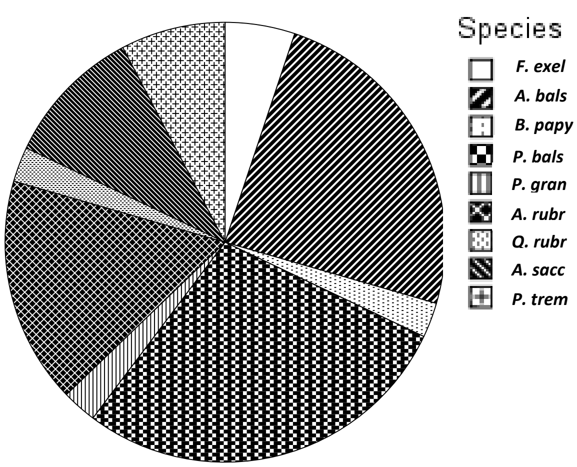

Figure 2. Species distribution of standing adult trees.

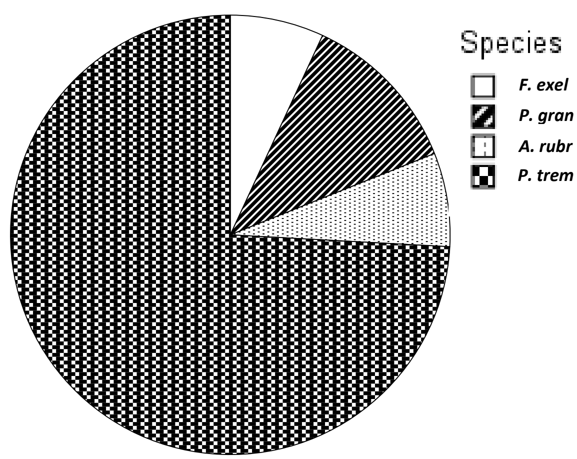

Figure 3. Species distribution of felled adult trees.

H_0: Beavers do not selectively forage based on tree diameter.

The diameter of each adult standing and felled tree was measured at each site. The data was tested for normality. The average means between the standing and felled adult trees were not significantly different (Mann-Whitney U = 1923.50, z = -1.601, p = 0.109).

H_0: Beavers do not selectively forage within a successional stage of trees.

All adult trees, both standing and felled, were categorized as early, mid, or late successional species. The relative abundance of successional species between standing and felled was significantly different (Pearson chi-square = 28.364, d.f. = 1, p = 0.000). The standing adults consisted of 40.51% early, 1.27% mid, and 58.23% late successional species (Figure 4). The felled adults consisted of 86.21% early and 13.79% late successional species (Figure 5).

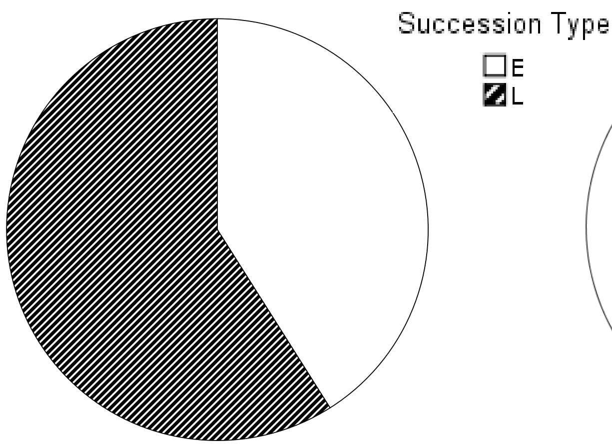

Figure 4. Successional species distribution of standing adult trees.

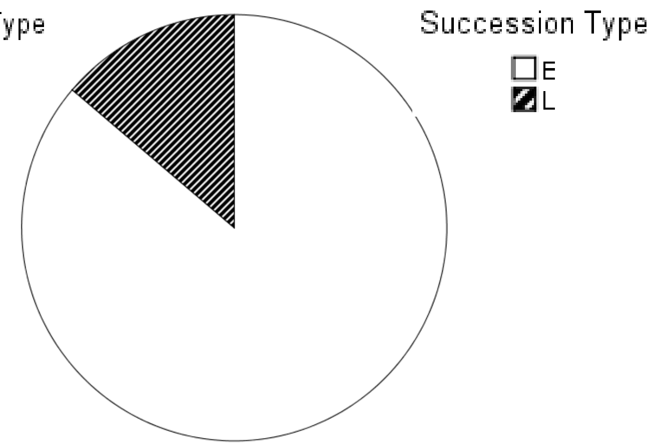

Figure 5. Successional species distribution of felled adult trees.

H_0: The foraging habits of beavers have no effect on forest succession.

A total of 199 juvenile trees were recorded between the four sites (1 specimen was omitted from the statistical analysis because there were less than 5 specimens in the successional category). Each juvenile tree was also categorized as either early, mid, or late successional. The relative abundance of successional species between all adults and juveniles was significantly different (Pearson chi-square = 45.065, d.f. = 2, p = 0.000). Within the adult trees, 60.29% were early and 39.71% were late successional species (Figure 6). Within the juvenile trees, 30.65% were early, 19.60% were mid, and 49.75% were late successional species (Figure 7).

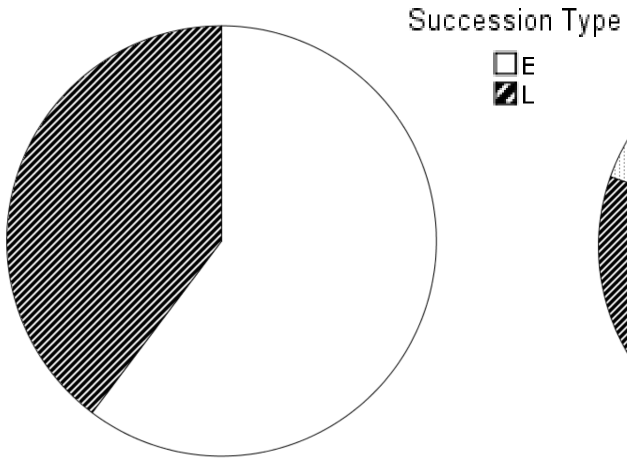

Figure 6. Successional species distribution of all adult trees.

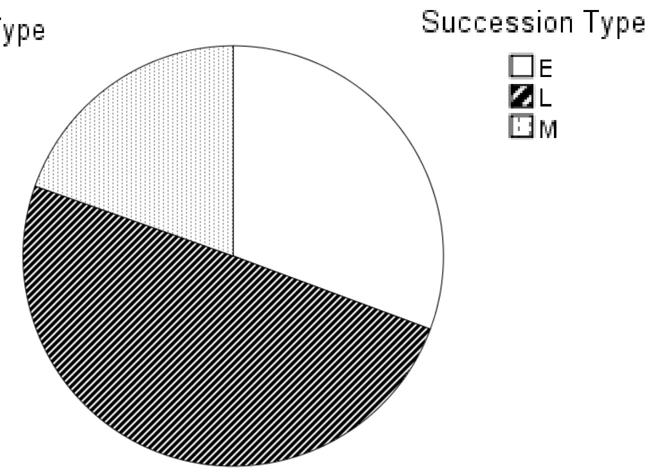

Figure 7. Successional species distribution of all juvenile trees.

Discussion

The American beaver is known to be a catalyst in forest composition flux, however little is known how their selective foraging habits influence the trajectory and rate of forest succession. Previous studies regarding *C. canadensis* have illustrated the beaver's selective foraging with regard to variables of tree species and tree diameter. However, the scope of this study was to expound upon previous research on the foraging habits of *C. canadensis* and observe whether they have any influence on forest succession.

We began our analysis by determining whether *C. canadensis* practice species-selective foraging. If there were no species preferences, we would expect to see the same relative abundance of species between standing and felled adults. Our results, however, showed a significant difference in the relative abundances of species between standing and felled adult trees, suggesting that *C. canadensis* selectively foraged for certain species of trees. Our data showed that *C. canadensis* preferred *P. tremuloides* in their foraging habits (86.0% of felled trees). Therefore, we reject our null hypothesis that *C. canadensis* do not selectively forage trees based on species.

In order to determine whether tree size influenced the selective foraging habits of *C. canadensis*, we compared the mean diameters of the standing and felled adult trees. Our results revealed that there was no significant difference between the mean diameter of the standing and felled adult trees. This suggests that the diameter has no effect on beaver preference and rules out tree size as a possible confounding variable. Therefore, we failed to reject our null hypothesis that *C. canadensis* do not selectively forage based on tree diameter.

Our results are consistent with the findings of other studies performed in the northern Michigan area (Krueger 2000, Hoeksema 1994, Gilbert 1994, Seidner 2000, McCarthy 1991, Dettling 2000, Harris 1994). Each study found a significant preference for aspen when given the option of a wide variety of tree species. In addition, each study found no correlation between the tree diameter and beaver preference.

After determining that *C. canadensis* practice species-selective foraging, we tested whether they foraged trees species within a certain successional category. We compared the relative abundance of early, mid, and late successional species between standing and felled adult trees. If there were no preferences within successional categories, the relative abundance would have been the same between standing and felled adults. Our results suggest that there is a significant difference between the successional compositions of the standing and felled trees. Our data show that the beavers preferred trees that were early successional species. Therefore, we reject our null hypothesis that beavers do not selectively forage within a successional stage of trees.

In order to determine if beaver preference for early successional species affected forest succession, we compared the relative abundance of juvenile species and adult species. Our results showed a significant difference between the successional species compositions of the juvenile and adult trees. The forest had a majority of early successional species before beaver foraging while it was composed of a majority of late successional species after beaver foraging. This suggests that the selective foraging of early successional species by *C. canadensis* influenced the rate of forest succession toward mid and late successional species dominance. Therefore, we reject our null hypothesis that the foraging habits of beavers have no effect on forest succession.

Given our results, we conclude that the foraging preferences of *C. canadensis* caused a premature progression of forest succession. Our research could be improved upon by conducting additional studies in regions outside of Pellston, MI. This would verify whether early successional species were preferred in other populations of *C. canadensis* with a different variety of tree species. While the sites we tested were comprised of a majority of late successional juvenile species, indicating accelerated forest succession, our conclusion could be stated with more confidence if this pattern was demonstrated throughout a larger number of sites. In addition, our research could have benefited from a sample of adult and juvenile trees in an area adjacent to the beaver site, but unaffected by beaver foraging. This would allow us to directly compare how beaver foraging affects the rate of forest succession within the same tree species community. This would also allow us to observe if the beaver has any effect on the juvenile species composition.

Presently, northern lower Michigan is largely dominated by aspens (Balisi 2009). Within the next 10 to 30 years, the aspen populations will senesce, causing forest composition to shift from early successional species dominance to mid and late successional species dominance (Karowe per comm). While this is a naturally occurring process, *C. canadensis* is significantly increasing the rate of change. As succession progresses, forest diversity increases due to colonization by mid and late successional species. This increase in species diversity continues until competition becomes overpowering and species diversity begins to decrease (Begon *et al* 2006). Therefore, in the years following beaver disturbance, northern lower Michigan forests could experience an increase in tree species diversity.

The implication that *C. canadensis* accelerates forest succession confirms and expands our understanding of the beaver as an ecosystem engineer (Jones *et al*. 1994). This ability to shape such an extensive area is of great relevance, especially when looking at the history of the *C. canadensis*. Consistent selection of early successionals over time may have influenced past forest habitats on a greater scale than previously recognized. While the current estimate for beaver population in North America is between 10 and 15 million, it is thought that the population once reached as high as 90 million (Müller-Schwarze, 2003). With up to nine times the present population, *C. canadensis* may have played a considerable role in shaping the forest landscape across their range of the North American continent. It is reasonable to regard *C. canadensis* not only as an engineer of its immediate habitat, but also as a species capable of exerting a significant influence on an overarching ecological process in its community. This should prompt further conversation about the role *C. canadensis* on both past and future forest composition flux.

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