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Seeing the Forest for the Deer: Plant Abundance and Diversity at the Gault Nature Reserve During a Spike in White-Tailed Deer

Abstract

Background: Deer populations have been rising across North America for decades. At the Gault Nature Reserve in Quebec, half of which is open to the public, the population of white-tailed deer (Odocoileus virginianus) has exceeded the region’s carrying capacity, estimated to be 5 deer/km², since 1996. Given that heavy grazing profoundly impacts forests, the purpose of this paper was to investigate the potential influence of white-tailed deer on plant abundance and diversity at the Gault Nature Reserve. We hypothesized that the abundance of deer, and by extension the effect of deer on vegetation, was negatively correlated with the proximity and frequency of human visitors on pedestrian trails. Our alternative hypothesis was that the effect of deer on vegetation was positively correlated with human disturbance, which is greater on the public side of the reserve.

Methods: We recorded the abundance and diversity of vascular plants along 14 transects of increasing distance from pedestrian trails on the public and private sides of the reserve.

Results: Contrary to our hypothesis, generalized linear models indicated that overall, plant abundance and diversity declined significantly as the distance from trails increased and that the effect of distance was significantly different on the two sides of the reserve. Pearson correlation tests revealed that there was not a significant correlation between distance and plant abundance and diversity on the public side, although there was a significantly negative correlation between these variables on the private side.

Limitations: White-tailed deer were not directly studied, which limited the inferences that could be made about their influence on plant abundance and diversity.

Conclusion: The distance from trails was a strong determinant of plant abundance and diversity on the private side of the reserve, but not on the public side, possibly because trail edges generally receive more sunlight and because the increased number of trails on the public side may have confounded our results. Although we did not find support for our hypothesis, the influence of trail edges on plant communities was reinforced. Researchers should continue to monitor the influence of white-tailed deer and forest managers should be mindful of edge effects when making decisions.

Introduction

In North America, white-tailed deer (Odocoileus virginianus) were extirpated from numerous areas and later reintroduced in the middle of the 20th century. (1-3) Their predators were also extirpated, but were not reintroduced. (1-2) In combination with restricted hunting seasons and laws, forest fragmentation, agricultural expansion, and the spread of exurban areas, deer populations have since reached an unprecedented density in many areas. Mont St. Hilaire in Quebec is one example of a region that has a high-density population of white-tailed deer. From 1996 onwards, the deer population in the area has exceeded the carrying capacity, i.e. the number of deer that a given amount of land can sustainably support (4), estimated to be 5 deer/km². (5) Although extensive surveys of the flora at Mont St. Hilaire have been completed (6), some questions remain about how the population of white-tailed deer impacts the Gault Nature Reserve.

The Gault Nature Reserve is located on Mont St. Hilaire, which is roughly 32 km east of Montreal and at the northern limit of the temperate deciduous forests of eastern North America. (7) The reserve is approximately 10 km² in size and consists of seven low peaks that form a ring around Lac Hertel. The western half of the reserve is designated for public use, while the eastern half is off limits to public visitors. Unlike the surrounding area, the forest on the mountain has experienced little human disturbance, such as tree removal for roads or properties (8). Numerous trees are more than 120 years old and sugar maples have been found that are over 400 years old. (8) Despite the reserve being well-managed and respected by local citizens, striking changes in species richness and evolutionary relationships have occurred over the past few decades. (6)

High densities of white-tailed deer dramatically affect woody and herbaceous vegetation (1, 3, 4, 9) along with insects, birds, and other mammals. (2, 3) At high densities, deer browsing can decrease vegetation density (1, 2) and lead to the extirpation of herbaceous species. (3, 4, 10, 11) Heavy deer browsing can also increase the spread of invasive species (12), alter forest succession (2), change forest regeneration (3), and modify micro-environments. (1, 9) Additionally, Takada et al. (2002) found that the presence of deer herbivory induced thicker spines in a spiny shrub, Damnacanthus indicus. (13) Since white-tailed deer negatively affect the distribution and abundance of numerous species and can influence community structure by impacting multiple trophic levels, white-tailed deer have been described as a keystone species. (3, 9) As a result, this paper aims to study how the high-density population of white-tailed deer could be impacting plant abundance and diversity at the Gault Nature Reserve. The experiment consisted of tallying the number of individual vascular plants and plant species found in circular plots (radius = 1 m) along 100 m transects at 5, 20, 40, 60, 80, and 100 m from the edges of pedestrian trails.

Fig. 1 illustrates our two hypotheses, which are based on the tendency of dense white-tailed deer populations to shrink plant abundance (1) and herbaceous species richness in the areas in which they reside. (1, 2) In our first hypothesis, depicted in Fig. 1a-b, we posited that deer were more concentrated on the private side of the reserve, possibly because they were...
avoiding the abundance of visitors on the public side. If this hypothesis was correct, we expected the plant abundance and diversity to be lower on the private side of the reserve. Moreover, we expected the plant abundance and diversity on the public side to be lower and to become approximately equal to the plant abundance and diversity on the private side after sufficient distance has passed to render the impact of people on deer negligible. Furthermore, in both hypotheses we proposed that plant abundance and diversity would remain the same along the transects on the private side because the private side had much less disturbance.

Before we started collecting data, we stratified the study area in order to reduce the types of forest and thus the number of variables being evaluated. The United States’ Forest Service employs a similar phase in their sampling procedure because the species composition in plots that straddle multiple forest types may be highly variable from plot to plot. (18) Since slope can impact the distribution of plants and communities, (7, 19), topographical maps of the Gault Nature Reserve were used to identify areas on the public and private side that had contour lines approximately the same distance apart. Moreover, because proximity to bodies of water can also impact plant communities (7, 20), maps were used to find areas on the public versus the private side of the reserve that were similar distances to Lac Hertel. Accordingly, seven transects were conducted on each side of the reserve, three of which started 10-50 m from the lake and four of which started more than 100 m from the lake, as shown in Fig. 2. All the transects near the lake had a similar slope and all those that were far from the lake had a similar slope as well. In the end, transects were set up in areas where American beech (Fagus grandifolia) and red maple (Acer rubrum) were consistently the dominant plants.

A detailed transect procedure was used to increase repeatability. The number of individual vascular plants and plant species in circular plots (radius = 1 m) were identified and recorded at 5, 20, 40, 60, 80, and 100 m from pedestrian trail edges. Circular plots were used because they have a smaller border per area than a square plot. As a result, circular plots have a smaller number of plants that could be along the border, which reduced the amount of variability introduced by making decisions about whether a plant was inside or outside the plot. (22) Furthermore, circular plots are utilized in the United States’ Forest Service sampling procedure (22) and are one of the methods discussed in Western Australia’s Department of Environment and Conservation standard operating procedure. (23) In addition, all the surveying was done between August 27th-29th, 2019 since plant diversity and abundance can vary over time. Lastly, roughly 30 minutes was spent on each transect to help standardize the surveying effort, similar to the sampling procedure used by the United States’ Forest Service. (18)

The transect length was intended to capture potential edge effects in order to explore how plant composition might change with an increasing distance from pedestrian trail edges. Edge effects refer to changes in population or community structure that occur at the boundary of two or more habitats (24), however, edge effects can vary in distance and impact depending on a variety of factors. (25) Elevated forest disturbance has been evident in some cases up to 400 meters inside fragment margins (26), though the most striking changes frequently occur within 200 meters of edges. (25, 27) Other studies have stated that edge effects may only reach 50 meters into boreal and temperate forests (28), or 15 meters into managed hardwood forests. (29) Ultimately, 100 meter transects were used because 100 meters appeared to be an intermediate distance among past assessments of edge effects and because it enabled more transects to be completed.

Methods

This study was conducted at the Gault Nature Reserve, located on Mont St. Hilaire, Quebec, Canada, in August 2019. The reserve is comprised of 10 km² of mature temperate forest divided into a public portion that features 25 km of pedestrian trails and a private portion that receives markedly less human traffic. (16) In between these two sides is Lac Hertel, a glacially formed depression that has a maximum depth of 9 m. (17) The climate of the region is humid continental with a mean annual temperature of 6 °C and a mean annual precipitation of 1000 mm. (4) There have been 600 species of plants and 800 species of butterflies identified at the reserve. (16) Additionally, 353 known types of minerals can be found at Mont St. Hilaire, which is considered one of the top mineralogical sites in the world. In 1978, the Gault Nature Reserve became the centre of the first Canadian reserve in the UNESCO Biosphere network. (16)

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Care was also taken to establish transects at distances from each other that would suggest independence. The most common species that was identified was American beech, which is known to have limited seed dispersal. (30) Although some small mammals may distribute seeds over short distances, and birds can potentially transport seeds several kilometers, most American beech seeds drop to the ground immediately around the tree. (30) Consequently, transects were established 50 m from each other, like in the procedure developed by Koivula et al. (28), and were assumed to be independent. The goal was to realize a “many and small” sampling scheme. (31) Having many, small surveyed areas yields accurate abundance estimates for the most common species, although species lists may be incomplete. Conversely, having fewer, large surveyed areas may result in a more complete species list, but the abundance of rare species could be underestimated. (31) As a result, the “many and small” scheme was implemented with transects being 50 m apart to avoid overestimating the abundance of rare species.

Plant surveying consisted of counting and identifying vascular stems that were under 1 meter in height. Although percent cover is a method of surveying plants that is quick and widely used by organizations like the United States’ Forest Service, estimates can differ among observers. (22) Individual counts were used because they can be well-suited to monitoring treatment effects. (22) Despite white-tailed deer being able to remove twigs and foliage up to a height of 6 feet (32), plants under 1 meter were the focus of our survey because white-tailed deer commonly eat large amounts of vegetation that are closer to the ground. (33) When the species of a plant was not readily identifiable, it was assigned a genus or unknown code and was collected for later identification, similar to the sampling procedure utilized by the United States’ Forest Service. (22) Next, when another plant was found that was not readily identifiable, it was compared to previous unidentified specimens to determine whether it constituted a new species or not. Lastly, surveying was done as a group to minimize the variation that can occur between observers. These steps facilitated the analysis of the potential effect imparted by the distance from trails and the side of the reserve.

After the plant survey was complete, the data was analyzed via generalized linear models (GLMs). GLMs are based on an assumed relationship between the mean of the response variable and the explanatory variable(s). (34) In addition, GLMs attempt to establish how the explanatory variable(s) cause the response variable to change. The interaction between explanatory variables can also be investigated via GLMs to explore whether they influence each other. In GLMs, data can be assumed to have a variety of probability distributions, like normal or Poisson. As a result, GLMs are considered more flexible and better suited for analyzing ecological relationships, which do not always fit a normal distribution. (34) The response variable in the first GLM was plant abundance, meaning the total number of plants. The explanatory variables were the distance from pedestrian trails and the side of the reserve, i.e. public versus private side. A Poisson distribution was used in this instance because plant abundance is an example of count data, which frequently follows a Poisson distribution. (34) The response variable of the second GLM was the Shannon diversity index, while the distance from pedestrian trails and the side of the reserve were once again the explanatory variables. The Shannon diversity index was calculated using the vegan package (35) in R (36), based on the following equation (Eq. 1). The Shannon diversity index was selected because it is a widely used diversity index in ecology that takes both species richness and evenness into account. (17) The second GLM used a normal distribution because the Shannon diversity index does not consist of count data.

\[ H = \sum \frac{n}{S} \ln \left( \frac{n}{S} \right) \]

Equation 1. The formula for the Shannon diversity index (H). In this equation, \( n \) is the number of plants of a particular species that were observed in a plot, \( N \) is the total amount of plants observed in a plot, and \( S \) is the total number of plant species that were observed in a plot. (17)

Finally, we used Pearson correlation tests to gain further insight into the relationships at play. Correlation tests quantify the direction and strength of the linear relationship between a pair of variables. (37) While GLMs could indicate whether the side of the reserve was a significant explanatory variable of plant abundance and diversity, they could not indicate whether the relationships between the distance from trails and plant abundance and diversity were stronger on the private or public side. In order to ascertain this, Pearson correlation tests were employed. Moreover, a Pearson correlation test was used to evaluate whether there was a significant relationship between plant abundance and diversity on the two sides of the reserves.

**Results**

A total of 623 plants and 22 plant species were observed on 14 transects in the Gault Nature Reserve between August 27th - 29th, 2019. The three most abundant species were American beech, red maple, and beech drops (Epifagus virginiana), which respectively accounted for 23%, 12%, and 9% of all the surveyed plants, as shown in Fig. 3.

The plant abundance data, depicted in Fig. 4, was used to perform a GLM in R (36) to gain insight into the relationships between plant abundance, distance from pedestrian trails, and sides of the reserve. Plant abundance decreased as the distance from trails increased on both the public and private side of the reserve, though plant abundance dropped off to a noticeably greater degree on the private side. When the GLM analyzed the overall change in plant abundance in the plots on both sides of the reserve as the distance from trails increased, distance was found to have a significantly negative effect on plant abundance, as is summarized in Table 1.
However, the side of the Gault Nature Reserve did not have a significant impact on plant abundance. Lastly, the side of the reserve and the distance from trails had a significant interaction, which means that the effect of the distance from trails was significantly different on the public versus private side of the reserve. In short, the first GLM revealed that an increasing distance from trails had a significantly negative impact on the combined number of plants that were observed and that the effect of distance was significantly different on the two sides of the reserve.

The Shannon diversity index data, illustrated in Fig. 5, was used to perform a second GLM in R (36) to explore the relationship between plant diversity, distance from pedestrian trails, and sides of the reserve. On the public side of the reserve, the Shannon diversity index seemed to increase as the distance from trails increased. When the second GLM, summarized in Table 1, analyzed the overall change in the Shannon diversity index in the reserve where public visitors are allowed, and the response variable was plant abundance. In the second GLM, the explanatory variables were the distance from pedestrian trails and the side of the Gault Nature Reserve, while the response variable was plant abundance. In the second GLM, the explanatory variables were the distance from pedestrian trails and the side of the Gault Nature Reserve, and the response variable was the Shannon diversity index. The interactions between the explanatory variables were also evaluated in these two GLMs.

The Shannon diversity index data, illustrated in Fig. 5, was used to perform a second GLM in R (36) to explore the relationships between plant diversity, distance from pedestrian trails, and sides of the reserve. On the public side of the reserve, the Shannon diversity index clearly decreased as the distance from trails increased. When the second GLM, summarized in Table 1, analyzed the overall change in the Shannon diversity index in the reserve where public visitors are allowed, and the response variable was plant abundance. In the second GLM, the explanatory variables were the distance from pedestrian trails and the side of the Gault Nature Reserve, while the response variable was plant abundance. In the second GLM, the explanatory variables were the distance from pedestrian trails and the side of the Gault Nature Reserve, and the response variable was the Shannon diversity index. The interactions between the explanatory variables were also evaluated in these two GLMs.

To summarize, the relationship between each of the response variables, plant abundance and diversity, and the explanatory variable, distance from trails, was different on the public side of the reserve versus the private side. The two GLMs supported this observation because they both indicated that the effect of distance was significantly different on the two sides of the reserve. To evaluate the strength and direction of correlations between the explanatory and response variables on the private side and public side, Pearson correlation tests were used. The results of these tests are summarized in Table 2. The tests revealed that the correlation between plant abundance and diversity from trails was significantly negative on the private side and insignificant on the public side. Likewise, the tests revealed that the correlation between the Shannon diversity index and distance from trails was significantly negative on the private side and insignificant on the public side. Lastly, Pearson correlation tests indicated that there was a significantly positive relationship between plant abundance and diversity on both sides of the reserve.

Table 1. Results of the generalized linear models, GLMs, in which the influence of the explanatory variables on the response variable was evaluated. In the first GLM, the explanatory variables were the distance from pedestrian trails and the side of the Gault Nature Reserve, while the response variable was plant abundance. In the second GLM, the explanatory variables were the distance from pedestrian trails and the side of the Gault Nature Reserve, and the response variable was the Shannon diversity index. The interactions between the explanatory variables were also evaluated in these two GLMs.

Table 2. Pearson correlation test results. Test #1 and #2 evaluated the relationship between plant abundance and the distance from pedestrian trail edges along fourteen 100 m transects split between the public and private side of the Gault Nature Reserve, Quebec, Canada. Test #3 and #4 assessed the relationship between the Shannon diversity index and the distance from trail edges along the same transects. Lastly, test #5 and #6 analyzed the relationship between the Shannon diversity index and plant abundance.

![Figure 5. The relationship between the distance from pedestrian trails and the Shannon diversity index of six circular plots (radius = 1 m) along fourteen 100 m transects at the Gault Nature Reserve, Quebec, Canada. The figure was fitted using a Gaussian distribution and the shaded areas represent the standard error of the mean. Private refers to the side of the reserve where public visitors are not allowed, and public refers to the side of the reserve where public visitors are allowed.](image)
serve. On the private side, Pearson correlation tests indicated that the plant abundance and Shannon diversity index were significantly greater close to the trail. Conversely, on the public side, Pearson correlation tests revealed that the plant abundance and diversity were not significantly correlated with the distance to trails.

A variety of factors might account for why our results differ from our hypotheses. The white-tailed deer in the Gault Nature Reserve may be more desensitized to the presence of people than anticipated, which could help explain why the side of the reserve was not a significant explanatory variable in the GLMs. Additionally, it is possible that people visiting the reserve could be acting as vectors for seed dispersal through seeds attaching to their clothes or equipment. This could be one of the reasons that plant abundance and diversity is generally greater near trails, where there is the highest human traffic. Elliott and Davies (2019) found that species richness on Mont St. Hilaire increased between surveys completed in 1958-1960 and 2012-2015. (6) Moreover, they found that the increased species richness could be attributed to people and other animals acting as vectors for seed dispersal and climate change impacting species distribution.

Differences in sunlight might have also contributed to our results. Researchers who investigated the environmental basis for canopy composition at Mont St. Hilaire found that slope and the amount of solar radiation, both of which influence soil moisture, were the main determinants of plot-to-plot variation. (7) Similarly, another study found that the difference in plant composition near trails is due to trail edges having lower canopy cover and therefore more sunlight reaching the understory. (29) Thus, the greater drop off in plant abundance and diversity on the private side of the reserve might be explained by the decreased disturbance it experiences, which may have caused less sunlight to reach the ground further from the trail. Correspondingly, it is possible that the increased presence of visitors could have contributed to the plant abundance and diversity not being significantly correlated with the distance from trails on the public side. If visitors were straying from paths and trampling vegetation, it could have caused more sunlight to filter through to the ground off the public paths over time. This increased amount of sunlight could have led to greater plant abundance and diversity.

Furthermore, our results could have been impacted by the numerous interconnecting pedestrian trails on the public side of the reserve, which leave smaller pockets of forest between them. At times, it was difficult to find areas on the public side where the end of the transect would be at least 100 m from every other trail while also having a similar slope and distance to Lac Hertel as the other transects. As a result, some of the public transects may have been conducted in areas where the end of the transect was too close to the edge of another pedestrian trail to reflect the actual conditions of the forest ecosystem 100 meters from a trail. Nevertheless, these three studies (29, 38, 39) and our results on the private side show that the distance to trails strongly influences plant abundance and diversity, while other research shows that the difference in sunlight may be one of the reasons why. (8, 29) Although the results on the public side may have been confounded by the increased number of pedestrian trails, the results on both sides of the reserve reinforce that edges have a powerful influence on ecosystems.

A few factors limit or impact the results of our plant survey. Species could have been overlooked because of low abundance at the time of the survey. There may have also been species that could not be identified due to their stage of development. The damaged condition of some plants rendered their identification more difficult as well. Factors such as these are inherent in essentially all plant surveys and contribute to a degree of uncertainty regarding species composition and diversity estimates. (22) Furthermore, the activity of white-tailed deer was not observed directly during this experiment, which made forming inferences about their impact more difficult. In the future observing deer directly with capture再来 might enable more causal conclusions to be drawn about their impact. Employing deer exclosures could also be informative. Finally, using percent cover as a means of surveying the Gault Nature Reserve might enable more transects to be evaluated and more plant species to be recorded. Future research could reduce the limitations that were encountered in this experiment by executing these changes.

Conclusion

Although we did not find support for our hypotheses regarding the impact of white-tailed deer on plant abundance and diversity at the Gault Nature Reserve, other sources clearly indicate that white-tailed deer can act as a keystone species. (1-3, 9-13, 17, 38) Future researchers should monitor how the overabundance of white-tailed deer impacts the ecosystem at the Gault Nature Reserve and elsewhere. If we disregard the keystone effects of deer on temperate and boreal forests, we risk losing the suite of species and processes needed to maintain ecosystem function. (9) Ultimately, our research underlined the influence that edges can have on plant communities. Individuals who manage ecosystems like the Gault Nature Reserve should be mindful of edge effects when making decisions.

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