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Stuck between the Mandibles of an Insect and of a Rodent: Where Does the Fate of Ash-Dominated Riparian Temperate Forests Lie?

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Abstract: The beaver (*Castor canadensis* Khul) is a key species that is known to shape the composition of riparian forests. Ash trees (*Fraxinus* spp.) can be abundant in these forests. However, invasion by the emerald ash borer (*Agrilus planipennis* Fairmaire) in North America threatens their survival. The disappearance of ash will have a large impact on the riparian forest composition in itself. It is not known what the consequences would be for the remaining forest if ash plays an important role in the beaver diet. Inventory plots across an ash gradient were measured in Plaisance National Park, Quebec, Canada, to collect data and to establish if (1) trees and saplings of this genus were selected or avoided by beavers, (2) if other genera had a lower or a greater probability of being consumed compared to ash, and (3) if ash density could affect the probability of consumption of other genera. Of all genera present in the park, ash trees were selected in the highest number of plots. Only two genera, *Carpinus* and *Populus*, had a higher probability of being consumed than ash. These genera are not abundant in the park, and neither in riparian forests of the temperate biome, and thus are not good candidates to replace ash as a staple for beavers. The most abundant genus in riparian temperate forests, along with ash, is *Acer*. In this study, *Acer* trees were not selected, and as for *Acer* saplings, were less likely to be consumed than ash. Mixed results were obtained about genera that could become more likely to be consumed as ash density decreases. It would seem that the disappearance of ash would not cause a switch to a single or a few genera in the future, which may be due to the high diversity of genera present in temperate riparian forests. However, ash may not disappear completely due to its capacity to sprout following the death of the aboveground portion of ash trees. This scenario is discussed in light of the susceptibility of intermediate-sized ash stems to be colonized by the emerald ash borer and of the greater likelihood of beavers to feed on these same-sized stems.

Keywords: *Castor canadensis*; *Fraxinus* spp.; emerald ash borer; feeding behavior; riparian forests; temperate biome

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1. Introduction

The emerald ash borer (*Agrilus planipennis* Fairmaire) (EAB) is an invasive species to North America [1] and Europe [2]. All North American ash species (*Fraxinus* spp.) are susceptible to attack, but green ash (*F. pennsylvanica* Marshall), white ash (*F. americana* Linnaeus), and black ash (*F. nigra* Marshall) are the hosts on which EAB is most able to complete its life cycle [3,4], with the consequence that the trees of those species die after being attacked for a few years [5]. These three species are the most abundant ash species and can make up a high proportion of the canopy of the eastern forests in both the USA [6] and Canada [7], highlighting the dramatic effects that EAB will have on many North American forest ecosystems.

In particular, riparian forests in eastern North America are often dominated by *ash* spp. and will be highly impacted by EAB [8]. Riparian forests are recognized to have a major ecological role as they are the interface between terrestrial and aquatic ecosystems, making them critical transition zones [9]. Despite their small size, their roles expand beyond their limits, making these areas important targets for conservation efforts [10]. Indeed, their roles are abundant and varied, from flood regulation to sediment retention, to the flux of nutrients [11,12]. Furthermore, riparian forests are known to shelter a high biodiversity of animal and plant species [13–15].

This high biodiversity, at least for the animals, can undoubtedly be partially attributed to ash trees. Gandhi et al., 2010 [16] reported that 43 arthropod species native to North America were completely dependent on *ash* spp., either to feed or to reproduce. Furthermore, the authors found in their review of the literature that 30 more species would become moderately to highly at risk, and that more than 200 other species could potentially be impacted as well, by the demise of ash trees in North America. A recent study also highlighted the potential effect of the disappearance of *ash* spp. on mammal and bird communities due to the risk of conversion of their habitat to non-forested wetlands and a concomitant decrease in connectivity for forest species [17].

A key species having a profound effect on riparian forests and its diversity is the beaver [18,19]. Beavers are often coined as ecosystem engineers, mainly because of the dams they built and the new water bodies they generate, which become a source of habitats for different plant and animal species. However, their role in shaping the environment in which they live extends to the riparian forests next to the existing and newly generated water bodies. There are two species of beavers, one native to Europe (the European beaver, *Castor fiber* Linnaeus), and the other to North America (the American beaver, *Castor canadensis* Khul). Both species of beavers are very similar, with respect to their morphology or general behavior [20,21]; therefore, the literature on both species is relevant to questions addressing resource selection and feeding behavior. Both species have been shown to be choosy generalists [22,23] which means that despite being able to feed on a very wide range of species, they exhibit a high preference for some items over others. Although preference may depend on the local abundance of certain species, two genera are recognized as favorite food items of the two species of beaver: poplars (*Populus* spp.) and willows (*Salix* spp.) [23–25].

Beavers are among the disturbances that generate gaps in the riparian forest [26] that can be filled with species adapted to these dynamics, such as some species of ash or maple (*Acer* spp.) [27,28]. However, by selecting some items over others, beavers favor the growth, and indirectly the relative abundance, of less selected items, thus affecting the future composition of the canopy [26]. In North America, this replacement process has often been reported, especially in mixed woods of the boreal forest where poplar species are highly selected, hastening forest composition towards coniferous dominance, or toward a shrub cover such as *Alnus* or *Corylus* when coniferous species are rarely present [26,29–32]. However, in temperate deciduous forests, especially when poplars and willows are absent or at low densities, selection by the beaver is not clear. Depending on the study, *Prunus* spp., *Fagus* spp., *Acer* spp., *Betula* spp., *Quercus* spp., *Carpinus* spp., *Alnus* spp. or *Ostrya* spp. are reported as selected, but not systematically [22,33–35]. Ash is also among the genera that can be positively selected by beavers [33] but this is not always the case [26,34]. The selection of *ash* spp. appears to depend on whether or not the beaver's favorite food items are present. These discrepancies in the literature highlight the need to better understand the importance of *ash* spp. in the diet of beavers, given how species of this genus are instrumental in supporting biodiversity in riparian temperate forests.

The fact that *ash* spp. can be highly selected by beavers in some areas, to a point where a drastic decrease in density is predicted [36], raises the question of what the disappearance of mature ash trees in the riparian forests caused by the EAB may have on the selection by beavers, especially if their favorite items are scarce. Indeed, if ash trees are one of the main sources of food for beavers, a sudden decrease in the density of this resource could potentially modify the feeding behavior of beavers, with unknown consequences for other tree and shrub species of riparian forests. Because the results of the beaver feeding behavior, in combination with the current invasion of EAB, are not well anticipated, it seems important to have a better understanding of the importance of *ash* spp. in the diet of the beaver. Indeed, understanding its importance would allow to be better prepared for the potential disappearance of *ash* spp. and its consequences. Furthermore, this could help to predict how the pressure on the riparian temperate forests exerted by the feeding behavior of beavers may be modified in the near future.

This study had three main objectives: (1) to establish whether *ash* spp.—but also other genera present in the diverse riparian forests at the study site—were selected for or selected against by the beavers. (2) to determine the odds for a genus to be consumed by the beavers compared to *ash* spp. (3) to examine, as *ash* spp. abundance decreases from high to low, whether some genera could exhibit a change in their probability of being consumed.

2. Materials and Methods

2.1. Study Site

This study was conducted in Plaisance National Park, Quebec, Canada. Created in 2002, it is a relatively small conservation park in Quebec, with an area of 28 km^2. Located along the Ottawa River (Figure 1), which has one of the highest river discharges in Quebec, the park is made up of a multitude of small islands and peninsulas with a cumulative length of banks of more than 100 km. Inland waters consist of several ponds and swamps. Only 400 ha of the emerged land in the park are classified as forest from aerial inventories by the Quebec Ministry of Forests, Wildlife and Parks. An extensive land inventory of the park's forests conducted prior to this study showed that there are more than 40 tree species, representing around two-thirds of the native tree species found in Quebec (F. Lorenzetti, unpublished results). Although the forested area of the park is small but diverse, it was estimated that half of the basal area of the trees (≥10 cm of DBH) is equally composed of *maple* spp. (*Acer saccharinum* L., *A. rubrum* L. and *A.* × *freemanii* E. Murray) and of *ash* spp. (*F. pennsylvanica*, *F. americana*, and *F. nigra*). However, the densities of maple and ash vary from scattered trees to dominant in the various stands.

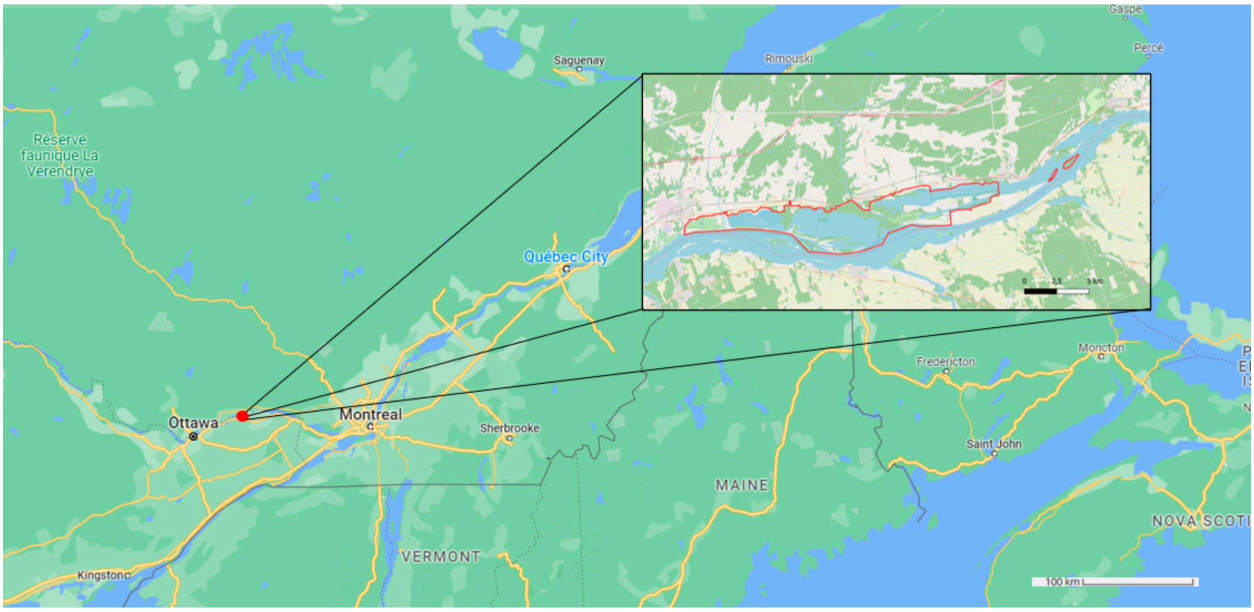

Figure 1. Location of Plaisance National Park on the Ottawa River, Quebec, Canada. Insert: park limits are drawn with a red line. Maps are based on images from © Google, 2022 (large scale) and © OpenStreetMap (small scale).

The density of beavers in the park is considered to be among the highest in Quebec in unexploited areas when compared to official inventories [37]. The inventories of the beaver lodges in the park clearly show an exponential increase over time: from 40 lodges in 2007, to 80 in 2014, and to almost 120 in 2018. The first two inventories were realized by the park staff, and the third by S. Rosner. All inventories involved reaching close to each lodge to mark its location. Two run-of-the-river dams on the Ottawa River, one upstream and one downstream of the park, regulate water levels. Although variations in water levels are dampened by dams, spring floods are recurrent, allowing the beavers to swim sometimes deeply into the flooded riparian forest. The study site in Plaisance National Park was considered to be one of the best possible opportunities to assess the importance of *ash* spp. in the diet of beavers in riparian forests of the temperate deciduous biome. Indeed, in addition of being representative of the compositional diversity of the forest of the ecological region of the Outaouais and St-Lawrence Rivers [38], *ash* spp. in the forest of the park ranges from low relative abundance to dominance, making it an ideal site to address the importance of that genus in the diet of beavers. Furthermore, the absence of beaver dams in the park ensures that most of the gathered stems are used as food, except for the small portion used to build the lodges.

2.2. Experimental Design

A total of 24 plots were set across the riparian forest of the park and inventoried over a period of four weeks in the summer of 2019, with two main goals: (1) to be representative of the tree composition found in the park, and (2) to cover an *ash* spp. gradient based on the basal area among plots so to make it possible to investigate if the abundance of ash influences the beaver's selection of tree and shrub items. The plots were set to be at least 150 m apart from each other. Each plot was 1500 m^2 in size: 30 m along the shoreline and 50 m deep into the forest (Figure 2). For every tree and shrub, the diameter was measured at 30 cm above ground since it appeared to be the typical height at which beavers cut most trees. Within each plot, every tree with a diameter >9 cm at that height was identified to the species, its diameter was measured and its distance from the shoreline assigned to one of the five 10 meters classes (0–10 m; 10.1–20 m; 20.1–30 m; 30.1–40 m; 40.1–50 m). Each tree was classified as consumed or not consumed. A tree was considered consumed if completely or almost completely, felled by beavers or if beavers have started to fell it and had removed most of the bark. Non-consumed trees were those with their bark intact or those that presented only a few bite marks.

Consumption of saplings and shrubs by beavers was also measured in subplots of the 24 main plots. Each main plot was subdivided into 60 subplots 5 m in diameter, 10 rows of 6 subplots parallel to the shoreline (Figure 2). One subplot was randomly selected from each row. As for the trees, this allowed to estimate consumption (i.e., consumed or not consumed) in relation to distance to the shoreline. All saplings and shrubs with a diameter at 30 cm above ground greater than 1 cm but less than 9 cm were identified to the species, assigned to a distance class from the shoreline, and categorized as consumed (i.e., a stem completely cut by a beaver) or not (i.e., undamaged stem by beavers). Stump sprouts were counted as individual saplings. The diameter was assigned to one of the four following classes: 1–3 cm; 3.1–5 cm; 5.1–7 cm; or 7.1–9 cm. Sapling and shrub stems from the 10 subplots were added and the sum per genus and per plot was used in the analyses. The subplot identity was only used as a proxy for the distance to the shore (for example, subplot 1 was always 0 to 5 m from the shore, and subplot 10 was always 45 to 50 m from the shore).

Due to the great heterogeneity of the forests in the park, and because the plots were selected to represent a large gradient of *ash* spp. sapling and tree densities, tree composition varied from one plot to another. *Ash* spp. was the only genus that was present as saplings and trees in each of the 24 plots. *Ash* spp. sapling abundance varied from 1 to 116 stems per plot (or 51 to 5908 stem/ha), with a median of 21 stems (or 1070 stem/ha). Ash tree abundance ranged from 16 to 258 stems per plot (or 107 to 1720 stems/ha) with a median of 63 stems (or 420 stems/ha). Tree genera that were present in the highest number of plots, after *ash* spp., were *Acer* (23 plots, range 3 to 64 stems, median = 21), *Ulmus* (21 plots, range 1 to 18 stems, median = 7), *Quercus* (16 plots, range of 2 to 34 stems, median = 6), *Tilia* (14 plots, range of 1 to 36 stems, median = 8), and *Populus* (13 plots, range 1 to 12 stems, median = 4). The eight other tree genera present in the inventories were found in less than 10 plots. Overall, 3 to 11 genera were found per plot, with six genera being the median number. In the case of the shrubs and saplings, *Ilex* (21 plots, range 2 to 192 stems, median = 43) and *Cornus* (19 plots, range 1 to 101 stems, median = 11) were the most frequent genera after ash ssp. followed by *Prunus* (14 plots, range 1 to 54 stems, median = 8), *Acer* (13 plots, range 1 to 43 stems, median = 4), *Tilia* (11 plots, range 2 to 23 stems, median = 8) and *Ulmus* (10 plots, range 1 to 4 stems, median = 1). Over the 20 genera identified for this layer, 13 were found in less than 10 plots.

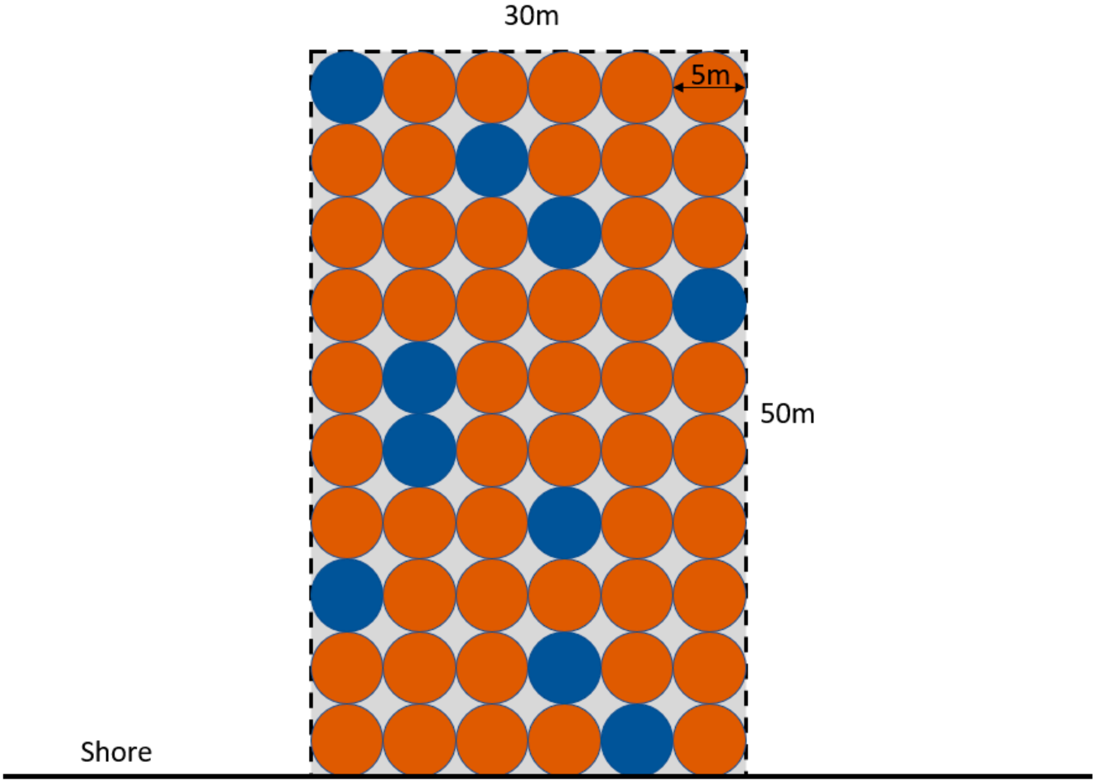

Figure 2. Schematic representation of a sampling plot (1500 m^2 in size) with randomized subplots for the assessment of beaver consumption of trees (whole-plot level) and of saplings and shrubs (subplot level). All trees with a diameter > 9 cm at 30 cm above ground were sampled. Blue circles represent randomly selected subplots (5 m in diameter) in which all saplings and shrubs < 9 cm in diameter at 30 cm above ground were sampled. One subplot in each of the 10 rows parallel to the shoreline was sampled.

2.3. Statistical Analysis

Although each tree, shrub and sapling was identified at the species level, all statistical analyses were performed at the genus level to increase sample size per genus. All analyses were performed separately for the trees and for the saplings and shrubs. The full data set was composed of 3423 tree stems counted over 14 genera (range 6 to 1992 stems per genera) and of 3840 shrub and sapling stems counted over 20 genera (range 1 to 1371 stems per genera). Depending on the objective, statistical analyses were performed at the genus level (objective 1) or at the stem level (objectives 2 and 3).

To establish which genera are selected for and against by the beavers (objective 1), a Jacobs' index value [39] was calculated for each plot for the most abundant genera. In fact, eight tree genera represented 98% of the tree stems and nine shrub and sapling genera accounted for 95% of stems in that stratum. A significant positive value of the Jacobs' index indicates that the item is positively selected by the beavers, meaning that it is consumed proportionally more than it is available among all the stems present. On the contrary, an item is selected against if the Jacobs' index is significantly negative, meaning that the item is consumed proportionally less than it is available among all the stems present. Significance was examined on a permutation-based Chi-square test.

To assess the odds of non-*ash* spp. being consumed relative to *ash* spp. (Objective 2), mixed effects logistic regressions were performed in which were included only the genera that had been consumed in at least five of the 24 plots, i.e., nine genera out of 20 for the saplings and shrubs and five genera out of 14 for the trees. These genera represented a large proportion of available stems (95% of the saplings and shrubs, and 90% of the trees) as well as of the consumed stems (93% of the saplings and shrubs, and 96% of the trees). To estimate the probability of a tree (n = 3068), a sapling or shrub (n = 3636) of non-ash genera to be consumed (coded '1′) or not (coded "0") relative to *ash* spp., the genus of each stem was included as a fixed effect variable in the models. This variable was coded as a dummy variable with ash genus set as the reference class in the analyses. The distance to the shore, as well as the diameter of the stem, are known to influence the feeding behavior of beaver [40]. Therefore, these two variables were included as fixed effects in the models to estimate the odds of each genus would be consumed relative to *ash* spp. while factoring in the effects of these two variables. The distance to the shore was set as a numeric variable (1 to 5 for the 10 m classes of the tree models, and 1 to 10 for the 5 m classes of the sapling and shrubs models). To test for a possible quadratic effect of the diameter on the probability of stems being consumed (see [34]), the variable diameter squared was also added as a fixed variable in the models. For saplings and shrubs, the diameter was included as a numeric variable based on the mid-class value. Given that no quadratic response has been detected for the trees, this variable was dropped from further tree models, but was kept for the shrubs and saplings as it was significant for that stratum. The effect of the interaction between distance and diameter was tested, as well as the interaction between genus and diameter, or genus and distance, on the probability of a stem being consumed, and none turned out to be significant. The distance to the nearest lodge might be a factor influencing the feeding habits of beavers, especially with respect to the preferred stem diameter [34,41]. To estimate the distance of the inventory plots to the nearest occupied lodge, the length of the shoreline between the lodge and the plot was measured using a georeferenced layer of the park lodges. Distances from a lodge varied between 5 and 500 m (median value = 117.5 m). This variable was included in the mixed logistic models, both as an independent factor, or in interaction with stem diameter. Neither term was found to be significant, and therefore, the results will not include this variable. Plot number was included as a random effect in order to take the non-independence of the data within a plot into account. The models were checked to verify whether spatial autocorrelation in the residuals was present, based on Euclidian distances between main plots. Spatial autocorrelation was detected only in the residuals of the shrub and sapling models. To correct this issue, the latitude and longitude of each plot was added in these models as a random effect. The effect of the different fixed variables on the odds of stems being consumed was estimated based on odds ratio (OR), which is defined as the ratio of the probability of being consumed over the probability of not being consumed. If OR = 1, it indicates no effect of the fixed variable on the probability of the stems being consumed. If the OR > 1, the fixed variable increases the odds that stems will be consumed, while an OR < 1 indicates the opposite. The 95% confidence interval (CI) of the OR was used to estimate whether the effect of the fixed variable is significant or not. When the 95% CI included the value of 1, it indicated a non-significant effect of the fixed variable on the odds of stems being consumed.

To determine if a decrease in *ash* spp. induces a shift in the selection of beavers for other genera (objective 3), it was tested whether the odds of a genus being consumed was affected by *ash* spp. abundance. Since there was no a priori information about the selection of items by beavers when the abundance of *ash* spp. varies, and since there were not enough data to test the effect of the interaction between each genus and each other variable, it was decided to run genus-specific models. Among the genera retained for the second objective, mixed effects logistic regression was run on each genus for which at least three different plots had at least 5 stems consumed. Based on this criterion, four genera of trees and five genera of shrubs or saplings were analyzed. At first, the same fixed and random variables as the models performed for the second objective were included in the models ran for this third objective but the number of *ash* spp. trees and *ash* spp. saplings per plot was added as a fixed variable for each stratum. Since the diversity of items present has been shown to influence food selection in other herbivore species, for example, an increase in plant diversity can result in a decrease in the selectivity of items by large herbivores [42,43], the Shannon index value of diversity was calculated for each plot and included as a fixed variable. Although the quadratic effect on stem diameter on the probability of shrub and sapling consumption was significant from the analyzes carried out for the second objective, this effect was not significant in the genus-specific models and was therefore not included in any of them. Multicollinearity among independent variables has been tested and detected only between the number of ash saplings and the Shannon index of the trees in the model analyzing the probability of consumption of *Carpinus* and *Acer*. The Shannon index was therefore removed from these models to be able to estimate the effect of the number of ash saplings on the probability of consumption of those two genera, which is the main objective of these analyses. Since no stems of *Ilex* or *Corylus* was larger than 5 cm, it was decided not to test the effect of the diameter in these two specific models. All mixed models were run using the glmmTMB package in R 4.1.0.

3. Results

3.1. Selection for or against a Genus by Beavers (Objective 1)

The selection of trees by beavers in Plaisance National Park was unambiguous since each genus had either a negative or a positive significant Jacobs' index values across plots (Figure 3). *Carya* and *Quercus* were the only two tree genera for which beavers did not express a significant selection for or against in any of the plots where they were present (8 and 16 plots, respectively). *Ulmus*, *Acer*, and *Tilia* trees were either not selected at all or significantly selected against, depending on the plot. Of the 21 plots tested, *Ulmus* was significantly selected against in only two of them. *Tilia* was significantly selected against in three of the 14 plots in which the genus was present. Finally, *Acer* was the genus that was significantly selected against the most consistently with nine plots out of 23 in which it was present. The trees of the three remaining genera, *Carpinus*, *Populus*, and ash, were either significantly selected for, or not selected at all. *Carpinus* was significantly selected for in one out of the seven plots where present, while *Populus* was significantly selected for in two out of the 13 plots in which the genus was found. Ash was significantly selected in 15 out of the 24 plots surveyed in this study, making this tree genus the most frequently selected for by beavers at the Plaisance National Park.

Jacobs' index values for saplings and shrubs (Figure 3) were less straightforward to interpret, as four out of nine genera had positive and negative significant values across plots: *Prunus* (one positive and two negative values out of 14 plots), *Cornus* (three positive values and three negative values out of 19 plots), *Tilia* (one positive value and one negative value out of 11 plots), and ash (eight positive values and one negative value out of 23 plots).

Acer and *Quercus* saplings were significantly selected in one plot out of 13 and 9 plots, respectively. *Carpinus* saplings and *Corylus* shrubs were significantly selected in three out of eight, and in two out of seven plots, respectively. *Ilex* was definitively the genus that was significantly selected against the most often, with eight plots with negative Jacobs' index values among the 21 plots in which it was present. Ash saplings stand out as the most selected by the beavers in Plaisance National Park, echoing the strong positive selection for ash trees that was found.

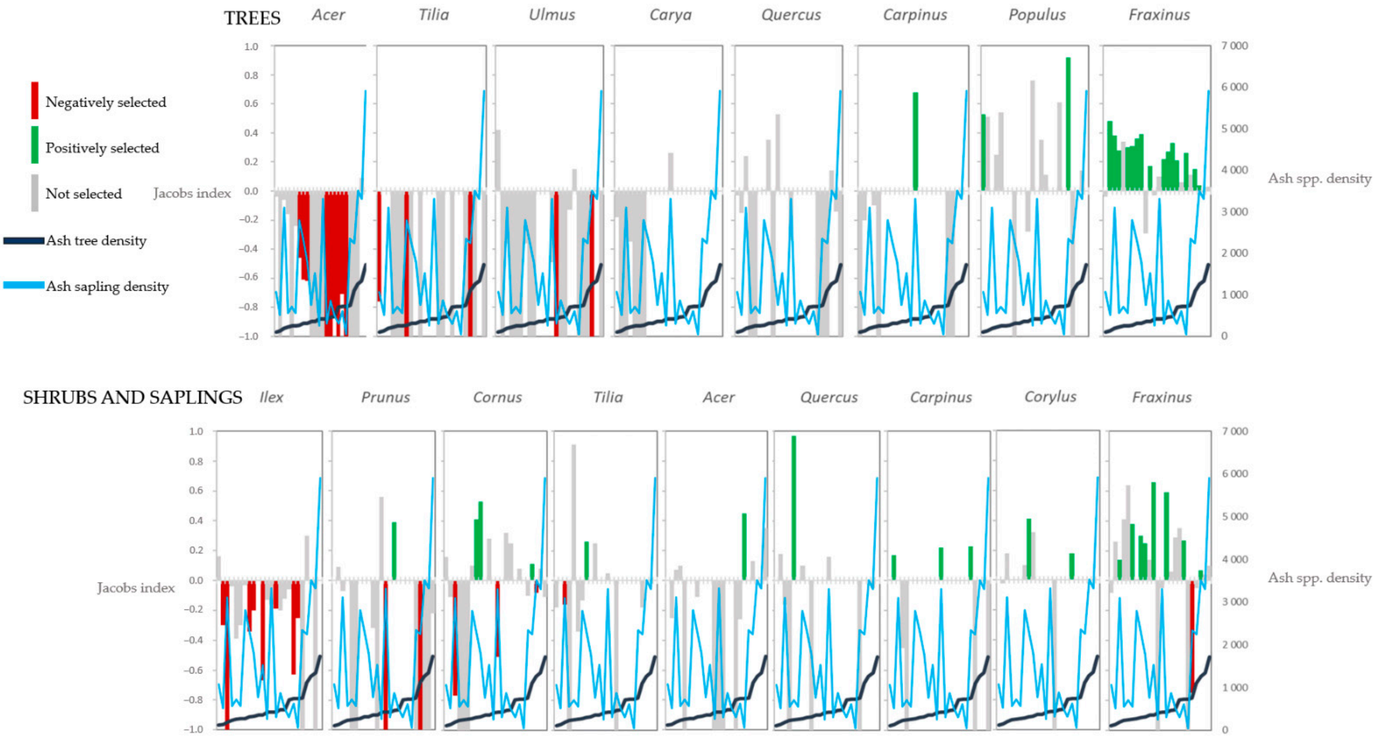

Figure 3. Selection of trees (**top** panel) and saplings and shrubs (**bottom** panel) by beavers in Plaisance National Park, Quebec, Canada. The Jacobs' index was used to establish whether a genus is selected for or against, or not all. A positive Jacobs' index value indicates selection of the genera in a given plot (significant values are shown by green vertical bars). A negative Jacobs' index value indicates selection against the genus in a given plot (significant values are shown by red vertical bars). Vertical bars in grey indicate Jacobs' index values not significantly different from zero and no selection. The black curve represents the density *ash* spp. trees (per hectare) and the blue curve represents the density of *ash* spp. saplings (per 0.1 ha).

The high occurrence of non-significant negative Jacobs' index values for both trees and shrubs/saplings is a consequence of these items being available in very small numbers and not consumed. Typically, in these cases, there were around five items or less in the plot, with none of them being consumed.

3.2. *Beaver Selection of Non-Ash Genera Relative to Ash* spp. *(Objective 2)*

From the inventory conducted in Plaisance National Park, the odds that a stem would be more or less consumed than *ash* spp. were significant for most of the genera tested, both at the tree (Table 1) and at the shrub and sapling (Table 2) strata. *Populus* trees were significantly and greatly more likely to be consumed than *ash* spp. trees, and *Carpinus* saplings were significantly more likely to be consumed than *ash* spp. saplings. *Acer* trees and *Ulmus* (Table 1) were significantly less likely to be consumed than the trees of *ash* spp. *Cornus*, *Ilex* and *Corylus* shrubs, and *Acer* and *Tilia* saplings, were all significantly less likely to be consumed than *ash* spp. saplings (Table 2). The odds of *Quercus* trees or saplings being consumed were not significantly different from *ash* spp. trees (Table 1) or saplings (Table 2). The probability of consumption was also not significantly different from that of *ash* spp. saplings (Table 2).

Table 1. The odds ratio and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for trees being consumed by beavers in Plaisance National Park, depending on their diameter or distance to the shore, and for a genus to be consumed compared to the consumption of ash trees. The model is based on inventories completed in the summer of 2019 in 24 plots 0.15 ha in size. Significant odds ratio are shown in bold. Consumption of *ash* spp. is set as the reference class for the genus, so an odds ratio > 1 for a genus indicates a greater odd of being consumed than *ash* spp., and an odds ratio < 1 for a genus indicates the opposite.

Variable	Odd-Ratio	Confidence Interval (95%)
Diameter	**0.95**	**0.94–0.97**
Distance to the shore	**0.21**	**0.18–0.25**
Acer	**0.07**	**0.05–0.11**
Ulmus	**0.13**	**0.07–0.25**
Quercus	**0.64**	**0.37–1.10**
Populus	**18.59**	**8.98–38.48**

Table 2. The odds ratio and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for saplings and shrubs being consumed by beavers in Plaisance National Park, depending on their diameter and squared-diameter values or distance to the shore, and for a genus to be consumed compared to the consumption of ash saplings. The model is based on inventories completed in the summer of 2019 in subplots across 24 plots 0.15 ha in size. Significant odds ratio are shown in bold. Consumption of *ash* spp. is set as the reference class for the genus, so an odds ratio > 1 for a genus indicates a greater odd of being consumed than *ash* spp., and an odds ratio < 1 for a genus indicates the opposite.

Variable	Odd-Ratio	Confidence Interval (95%)
Diameter	**1.74**	**1.43–2.11**
Diameter squared	**0.83**	**0.77–0.89**
Distance to the shore	**0.32**	**0.28–0.36**
Ilex	**0.16**	**0.12–0.22**
Acer	**0.41**	**0.25–0.70**
Cornus	**0.43**	**0.32–0.59**
Tilia	**0.45**	**0.25–0.80**
Corylus	**0.53**	**0.31–0.91**
Prunus	0.59	0.32–1.10
Quercus	0.79	0.29–2.17
Carpinus	**1.85**	**1.27–2.68**

The odds of a stem, be it a tree, a shrub, or a sapling, of being consumed decreased with increasing distance to the shore (Tables 1 and 2). The odds that a tree stem would be consumed also decreased with stem diameter (Table 1). The odds of shrubs and saplings being consumed was a quadratic function of stem diameter (Table 2).

3.3. *Effect of the Abundance of Ash* spp. *on the Chances of Other Genera Being Consumed by Beavers (Objective 3)*

The abundance of *ash* spp. saplings and trees did not significantly influence the odds that the stems of several other genera would be consumed, and when it did, the increase or decrease was 5 to 10% for each additional stem per plot (Tables 3 and 4). Ash sapling abundance increased the odds of *Acer* trees being consumed (*ash* spp. saplings ranged from 1 to 69 in those plots). The abundance of ash saplings increased the odds of *Carpinus* saplings being consumed (*ash* spp. saplings ranged from 10 to 116 in those plots) while ash trees decreased these odds (*ash* spp. trees ranged from 16 to 258 in those plots). Ash sapling abundance increased the odds of *Tilia* saplings of being consumed (*ash* spp. saplings ranged from 11 to 69 in those plots).

Table 3. The odds ratio and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for trees of being consumed by beavers at the Plaisance National Park, depending on their diameter, distance to the shore, on the abundance of *ash* spp. trees and saplings, and on the diversity of trees and saplings, based on the Shannon index. The model is based on inventories completed in the summer of 2019 in 24 plots 0.15 ha in size. Significant odds ratio are shown in bold. A significant odds ratio > 1 indicate a positive effect of the variable on the chances that a stem is consumed, while a significant odds ratio < 1 indicate the opposite.

Genus	*Acer*	*Quercus*	*Populus*
Intercept	**0.01 [2.11 × 10^{-5}–0.20]**	2009.20 [0.05–8.39 × 10^{7}]	38.16 [0.03–4.87 × 10^{4}]
Diameter	**0.96 [0.93–0.99]**	0.95 [0.90–1.01]	0.98 [0.94–1.02]
Distance to the shore	**0.29 [0.16–0.51]**	**0.47 [0.30–0.75]**	**0.43 [0.25–0.74]**
Abundance of ash trees	1.00 [0.99–1.01]	0.98 [0.95–1.01]	1.00 [0.98–1.02]
Abundance of ash saplings	**1.05 [1.03–1.07]**	1.03 [0.99–1.08]	1.00 [0.94–1.06]
Shannon index for trees	**7.07 [1.06–47.19]**	0.08 [0.00–6.81]	1.56 [0.11–21.52]
Shannon index for saplings	1.62 [0.65–4.04]	0.45 [0.04–5.21]	0.44 [0.08–2.49]

Table 4. The odds ratio and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for saplings or shrubs of being consumed by beavers in Plaisance National Park, depending on their diameter, distance to the shore, on the abundance of *ash* spp. trees and saplings, and on the diversity of trees and saplings, based on the Shannon index. The model is based on inventories completed in the summer of 2019 in 24 plots 0.15 ha in size. Significant odds ratio are shown in bold. A significant odds ratio > 1 indicate a positive effect of the variable on the chances that a stem is consumed, while a significant odds ratio < 1 indicate the opposite. The diameter was not tested for *Ilex* and *Corylus* since almost all the items available for these genera were in the lowest diameter class. The Shannon index for the trees was not tested for *Acer* and *Carpinus* due to the presence of multicollinearity.

Genus	*Acer*	*Carpinus*	*Tilia*	*Ilex*	*Corylus*
Intercept	0.19 [0.01–31.84]	1.69 [9.32 × 10^{-4}–3052.54]	1.02 [5.41 × 10^{-7}–1.91 × 10^{6}]	0.21 [8.65 × 10^{-4}–53.11]	422.36 [0.13–1.32 × 10^{6}]
Diameter	1.15 [0.86–1.54]	0.81 [0.65–1.01]	**1.49 [1.04–2.13]**	Not tested	Not tested
Distance to the shore	**0.69 [0.48–0.99]**	**0.77 [0.67–0.88]**	**0.56 [0.34–0.93]**	**0.62 [0.56–0.69]**	**0.74 [0.65–0.84]**
Abundance of ash trees	0.99 [0.97–1.02]	**0.95 [0.91–0.99]**	0.99 [0.96–1.02]	1.00 [0.98–1.02]	0.98 [0.96–1.01]
Abundance of ash saplings	1.03 [0.97–1.08]	**1.10 [1.01–1.20]**	**1.08 [1.02–1.15]**	1.04 [0.99–1.08]	1.03 [0.98–1.09]
Shannon index for trees	Not tested	Not tested	3.10 [0.01–879.43]	1.96 [0.12–32.16]	0.29 [0.00–18.26]
Shannon index for saplings	1.98 [0.14–28.03]	1.32 [0.02–77.36]	0.16 [0.00–5.38]	0.72 [0.08–6.76]	0.18 [0.01–4.07]

Factoring *ash* spp. abundance in the analyzes did not change that the distance to the shore significantly decreased the odds of a stem being consumed for all tree (Table 3) and shrub and sapling (Table 4) genera tested. However, this was not the case with the effect of diameter once the abundance of *ash* spp. was taken into account. The diameter of the tree stem decreased the odds that *Acer* spp. would be significantly consumed, but no such effect was found for *Quercus* and *Populus* spp. (Table 3). Sapling stem diameter also did not have a significant effect on the chances that *Acer* and *Populus* saplings were consumed but did significantly increase the odds of *Tilia* saplings consumption (Table 4). The diversity of tree genera, based on the Shannon index, greatly and significantly increased the chances that *Acer* trees to be consumed, but did not change the odds for other tree, sapling, or shrub genera tested (Tables 3 and 4). The diversity of the saplings, also based on the Shannon index, had no influence on the genera chances to be consumed.

4. Discussion

To summarize the results for each of the objectives of this study conducted in the riparian temperate forests of Plaisance National Park, it was found that (1) the tree genus most frequently selected for was *ash* spp. (63% of the time the genus was present in the study plots) and that the sapling genera most frequently selected for were *ash* spp. and *Carpinus* (at least one-third of the time the genera were present in the study plots);

(2) *Carpinus* saplings were also more likely to be consumed than *ash* spp. saplings and *Populus* trees were more likely to be consumed than *ash* spp. trees; and (3) the abundance of *ash* spp. trees and saplings had mixed effects on the likelihood of stems of other genera being consumed: *Carpinus* saplings were more likely to be consumed with the decrease in the abundance of *ash* spp. trees, while *Acer* trees and *Carpinus* and *Tilia* saplings were less likely to be consumed with the decrease in the abundance of *ash* spp. The odds of *Quercus* and *Populus* trees and of *Ilex* and *Corylus* shrubs, of being consumed were not influenced by the densities of trees or shrubs of *ash* spp.

This study has clearly shown that *ash* spp., in the context of a diverse riparian temperate forest such as the Plaisance National Park, are a large component of the beaver diet in such ecosystems. Ash trees accounted for 58% of the total amount of trees (1992 over 3423) but more than 80% of the consumed trees (586 over 729); meaning that almost 30% (586 over 1992) of ash trees were consumed. Ash saplings represented a smaller part of both the available and consumed stems, but still accounted for 20% of the total amount of saplings and shrubs (770 over 3840) and 29% of the consumed saplings and shrubs (412 over 1413), meaning that 54% of the ash saplings were consumed (412 over 770).

Ash spp. are not only largely consumed, but are highly selected for and across a large range of ash sapling and tree densities (Objective 1). In only one instance, *ash* spp. was selected against, a result that could be attributed to the high number of *Carpinus* saplings available in this particular plot where they represented 85% of the total consumed stems. Indeed, *Carpinus* saplings were also found to be 85% more likely to be consumed than saplings from *ash* spp. (Objective 2). *Populus* was the only genus of trees that was significantly more likely to be consumed than trees of *ash* spp. Although *Populus* trees were positively selected in only two of the 13 plots where the genus was present (Objective 1), *Populus* trees were more than 18 times more likely to be consumed than *ash* spp. trees (Objective 2).

The distinction between genus selected for and selected against is very clear for the trees, with 3 genera selected for (*Carpinus*, *Populus* and *Fraxinus*) and 3 genera selected against (*Ulmus*, *Tilia*, and *Acer*). The distinction between genera selected for and selected against is not as clear for saplings and shrubs as it was for the trees, especially for some genera that are selected for and selected against in a similar number of plots (Objective 1). However, *ash* spp. still remains the genus that is positively selected in the highest number of plots at the sapling stage, indicating that this preference for *ash* spp. is not dependent on stem height.

The varying abundance and dominance of *ash* spp. across the riparian forest stands in Plaisance National Park allowed to observe how the food items by beavers would change with this variable (objective 3). The abundance of *ash* spp. trees had a negative effect on the odds that *Carpinus* saplings would be consumed (i.e., OR = 0.95 which indicates a 5% reduction for the odds of *Carpinus* saplings of being consumed when the abundance of *ash* spp. trees increased by one stem at the plot level). On the other hand, the abundance of *ash* ssp. saplings had a positive effect on the chances of *Acer* trees to be consumed (a 5% increase for each additional stem at the plot level). Each increase of one *ash* spp. sapling at the plot-level also increased by 10% and 8%, respectively, the chances of *Carpinus* and *Tilia* saplings being consumed. It is not possible to rule out, in these cases, the possibility that *ash* spp. caused an indirect negative impact on other genera (apparent competition) [44]. Indeed, it cannot be excluded that as the abundance of *ash* spp. saplings increased, the plots became more attractive for beavers, increasing the chances that other genera would be consumed as well. In any case, the plot-level diversity of trees also increased the chances of *Acer* trees to be consumed. *Acer* trees may therefore still be targeted by beavers in highly diverse stands when *ash* spp. will disappear because of the EAB, since it appears that the Shannon index for the trees had a great impact on *Acer* chances of being consumed. It is unlikely that the abundance of other genera could have positively or largely influenced the patterns of consumption that were observed in the park, mainly because *ash* spp. was the only genus that was consumed systematically across the plots at both the sapling and tree levels. When feeding occurred in a majority of plots for other genera, their stems were generally not selected, or selected against.

One genus that was present in a majority of plots, at least at the tree level, and was found to have the same likelihood of being consumed as *ash* spp. trees, was *Quercus*. This could potentially mean that when available, it could be a genus that will replace *ash* spp. in the beaver's diet. This would be consistent with Raffel et al. (2009) [34] who found that *Quercus* was highly selected by beavers. However, in the case of Plaisance National Park, the relatively low abundance of *Quercus* will probably disqualify it from replacing *ash* spp. as a staple for beavers. More generally, northern red oak (*Quercus rubra* L.) and bur oak (*Quercus macrocarpa* Michx.), the two most abundant species of oaks present at the park, and the most frequent oak species in northern temperate woods, are not abundant in poorly drained soil. They are thus limited to mounds in riparian forests of the Canadian Great Lakes and St. Lawrence Lowlands. However, in some studies, *Q. rubra* can be described as abundant in some riparian forests stands [34,45]. In such cases, and if *ash* spp. was also abundant in those stands, it is possible to some extent that *Q. rubra* replace *ash* spp. as a food staple for beavers.

Although the three main objectives of this study were met, it is still difficult from the results to generate precise predictions about the future composition of riparian temperate forests, mainly because *ash* spp. stands out as the main staple item for beavers and no other genera can be shown to be an equivalent alternative, which is likely the consequence of these ecosystems (1) being diverse, (2) not abundant with more boreal dominant preferred items, such as *Populus* and *Salix*, and (3) not abundant with selected more meridional items such as *Carpinus*. Since *ash* spp. has a bleak future because of the impact of the emerald ash borer, the question about temperate deciduous forests has now more to do with the response of beavers to this disturbance than with the dynamics that the beavers generate by themselves in those ecosystems.

In regard of the future of *ash* spp., it seems that until the current seed bank and seed production are severely reduced, seedlings may remain abundant, although less so in lowland forests than in upland forests [46]. Ash could also be maintained from stump sprouts; however, the emerald ash borer was shown to be capable of recolonizing stems as small as 2 cm in diameter [47]. Given that the most selected for stem size by beavers in Plaisance National Park is in the 3.1–5 cm size class, both the beavers and the emerald ash borers will be in competition for the same resource, though it is not yet known what the colonization rate by the insect would be in relation to stem size in a world where ash is maintained as saplings or sprouts. Because the beavers in the park expressed a stronger selection for intermediate size saplings, it is also difficult to predict whether ash consumption rate would espouse a Type II [48] or a Type III [41] functional response when the resource is only present as saplings or resprouts. Despite the *ash* spp. sapling gradient in this study (51 to 5908 stems/ha), it was not possible to fit any type of functional response to the data. Since ash was not the only resource available to beavers when ash was at low densities, it may not be possible to clearly extract the functional response expressed by beavers. To project into the future, realistic manipulative experiments would be necessary [41,49,50]. This study is not sufficient to draw conclusions on the relative importance of saplings and trees in the beaver's diet. The fact that the quadratic effect on the diameter was significant only for the saplings implies that the preferred diameter for beavers is around 3.1–5 cm (across all the diameter spectrum, from saplings to trees). However, all the stems cannot be considered equal, and the fact that trees are less likely to be cut down than saplings does not necessarily means that they are less important in the beaver's diet, since the potential biomass that can be harvested on large trees is likely greater than what can be harvested on small saplings.

5. Conclusions

Beavers are well known to have the ability to shape the composition of riparian forests (e.g., [26,36]. In the case of Plaisance National Park, and more generally, the riparian temperate forest, it is considered that tree and shrub diversity could be the key to mitigate the potential damage that beavers could do to the forest. Being a picky generalist, it is possible that its diet selection will change depending on the most available genera—if not deterred to feed on it, allowing them to thrive in some areas. It is also important to note that despite the beavers being able to alter forest composition, their impact on the forest remains limited to the first meters from the shoreline.

Finally, to determine whether the intensity of the pressure caused by the beavers will remain the same over time, it could be relevant to determine how much *ash* spp., being the staple it is to beavers, increase the quality of the environment for them. It has already been shown that the preferred food of beavers could influence their population densities. For example, how *willow* spp. recovers rapidly after being browsed by beavers could have fueled the increase in the number of beaver colonies in Yellowstone National Park [25]. Furthermore, the density of *Populus* has already been shown to influence the number of kits per colony [51]. Because of the importance of ash in the beaver's diet, it is plausible that ash in the temperate deciduous forest may also influence the size of beaver populations. If that is the case, the disappearance of ash from riparian temperate forests will likely result in a general decrease in beaver density. Investigations are underway to determine whether this potential decrease will occur through an expansion of territory size or through a decrease in the size of the colony group. Regardless, a decrease in the density of beavers would necessarily reduce the browsing pressure on trees, saplings, and shrubs on the riverbank, reducing damage to the riparian forest.

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