Dynamics of Territorial Occupation by North American Beavers in Canadian Boreal Forests: A Novel Dendroecological Approach

Julie-Pascale Labrecque-Foy [1] [ID]**, Hubert Morin** [1] **and Miguel Montoro Girona** [2,3,]*[ID]

[1] Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555 boul de l'Université, Chicoutimi, QC G7H 2B1, Canada; julie-pascale.labrecque-foy1@uqac.ca (J.-P.L.-F.); hubert.morin@uqac.ca (H.M.)

[2] Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Campus of Amos, 341 Rue Principal Nord, Amos, QC J9T 2L8, Canada

[3] Restoration Ecology Research Group, Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), Skogsmarksgränd, 907 36 Umeå, Sweden

* Correspondence: miguel.montoro@uqat.ca; Tel.: +1-819-762-0971 (ext. 8038)

Abstract: *Research Highlights:* Our study highlights a new, simple, and effective method for studying the habitat use by beavers in Canadian boreal forests. Information regarding the presence of beaver colonies and their habitat occupation is essential for proper forest management and damage prevention in the boreal forest. *Background and Objectives:* The North American beaver (*Castor canadensis*) is a major element of natural disturbance, altering the dynamics and structure of boreal forest landscapes. Beaver-related activities also affect human infrastructure, cause floods, and lead to important monetary losses for forestry industries. Our study aimed to determine the spatiotemporal patterns of beaver occupation of lodges over time. *Materials and Methods:* Using a dendroecological approach to date browsing activity, we studied the occupation of two lodges per water body for eight water bodies located in the boreal forest of Québec, Canada. *Results:* Three sites showed alternating patterns of lodge use (occupation) over time, three sites (37.5%) demonstrated no alternating patterns of use, and two sites (25%) presented unclear patterns of lodge use. *Conclusions:* Alternating patterns of lodge use can be linked to food depletion and the need to regenerate vegetation around lodges, while non-alternating patterns may be related to fluctuations in water levels, the specific shrub and tree species surrounding the lodges, the size of the beaver territory, and the number of lodges present on a water body.

Keywords: engineer species; forest damages; habitat; natural disturbances; population dynamic; wildlife

1. Introduction

Natural disturbance regimes interact at multiple scales over time and determine the dynamics, structure, and composition of forests by altering ecosystem functioning, creating diversified habitats, and maintaining biodiversity [1–4]. The boreal forest is the second largest terrestrial biome in the world, and wildfires [5], insect outbreaks [6], and windthrow events are the main natural disturbances within these forests [7].

Another important disturbance in the boreal forest is the construction of dams by beaver (*Castor* sp.) colonies that raise the water level of lakes and rivers [8]. The increasing of the water level of lakes and rivers leads to land flooding [9]. Floods shape entire ecosystems that can be beneficial to many wetland-dependent organisms [10,11] and increase the quantities of deadwood [12]. However, it

can also affect human activities by damaging roads and houses, and beaver-related flooding causes important monetary losses for logging companies [13]. Even though this disturbance has major ecological and economic consequences, it remains an understudied element of forest ecology.

The North American beaver (*Castor canadensis*) has a wide distribution area within North America that stretches from Mexico to Alaska [13]. Beavers are ecosystem engineer species [14]; thus, they are able to modify their environment to make it more suitable for their survival by constructing dams and lodges [15]. Dam construction and the subsequent water level rise keep beaver lodge entrances underwater, allowing the colonies to be protected against predators, and the higher water level leaves enough living space under the ice in winter [13]. Beavers also build lodges, composed of sticks and mud, on the shore of the water body where the colony lives [13]. These environmental modifications contribute to the dynamic structuring of the boreal forest and provide habitats to many organisms [16,17] There are few lakes in Canadian boreal forests that lack a beaver presence; thus, this species has one of the most important roles in affecting water levels [18,19]. Nonetheless, despite the presence of beaver colonies on a territory having marked effects, studies have focused mainly on beaver habitat and behaviour [20,21].

Factors influencing the selection and the use of habitat by beavers are well documented: territoriality, food supplies, and water level fluctuations [22–24]. Territoriality affects the use of habitat by beavers [25]. Graf, et al. [26] found that the size of the territory influenced markedly the migration of a colony. The size of a beaver colony's territory depends on the size of the colony, the age of the beavers, and food quality [27]. Food supplies can also affect the pattern of use of the territory; as central place foragers, beavers rarely travel farther than 100 m from their lodges to feed [9]. Longer foraging trips are too energy-consuming and heighten risks of predation [28]. Thus, preferred food resources—poplar (*Populus* sp.), birch (*Betula* sp.), willow (*Salix* sp.), and maple (*Acer* sp.)—must be plentiful around the lodges [13]. Otherwise, as determined by Bluzma et al. [29], food depletion around a lodge can lead to the migration of the colony to another location. Bloomquist et al. [30], determined that the water level of the water body on which a lodge is located also influences a colony's use of the territory as levels change seasonally. Water levels should always be high enough for the lodge's entrance to be submerged and to leave enough living space in the winter [13].

Even if these listed factors are well documented, there is a lack of information regarding the dynamics of use of the territory by beaver colonies over time. Bluzma et al. [29] found that beavers alternate in their use of lodges on its territory, on average every 2.6 years, while Hyvönen and Nummi [31] found that it can take up to nine years before a lodge is recolonized by a colony. Studies focused on habitat use by beavers have concentrated mainly on beaver range and daily movements [26,30,32], leaving lodge use understudied.

Studying the use of the different lodges on a single territory (lake or river) can help determine whether a colony has been on this territory for a long time or just recently. This information can help prevent infrastructure damage and economic losses. Furthermore, as vegetation in the Arctic tundra is changing due to global warming [33], beaver colonies are migrating northward [34]. Therefore, further information can predict beaver-related effects in the expanded range.

This study aims to determine the dynamics of occupation of the territory by beavers in the North American boreal forest. More precisely, we determine the spatiotemporal patterns of beaver lodge–use on water bodies. As food depletion usually happens around a lodge when it has been occupied for several consecutive years, our hypothesis is that two lodges located on the same water body will be used in alternation every 3–4 years; this leaves enough time for the vegetation surrounding an abandoned lodge to regenerate before it is recolonized [35,36]. We expect to demonstrate alternance in the use of beaver lodges in our studied water bodies using a novel dendroecological approach.

2. Materials and Methods

2.1. Study Area

This study was conducted in the boreal forest of Quebec, Canada (Figure 1). The study sites were located in the Monts-Valin [37,38] and Simoncouche Research Station [39]. These two areas extend within the balsam fir (*Abies balsamea* (L.) Mill.)—white birch (*Betula papyrifera* Marsh.) and eastern black spruce (*Picea mariana* (Mill.) B.S.P.)—feathermoss bioclimatic domains [40]. The regional climate is subhumid subpolar having a short vegetation season of 110–135 days [41–43]. Annual mean temperature is 2.8 °C, and average annual precipitation is 930.6 mm [43]. Soil is mostly humo-ferric podzols, and the land surface is covered by a thick glacial till deposit [41]. The main natural disturbances in the study area are spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks [6], fire [5], and windthrow [7]. In this region, beaver density is around 0.01 to 0.27 colonies/km [44].
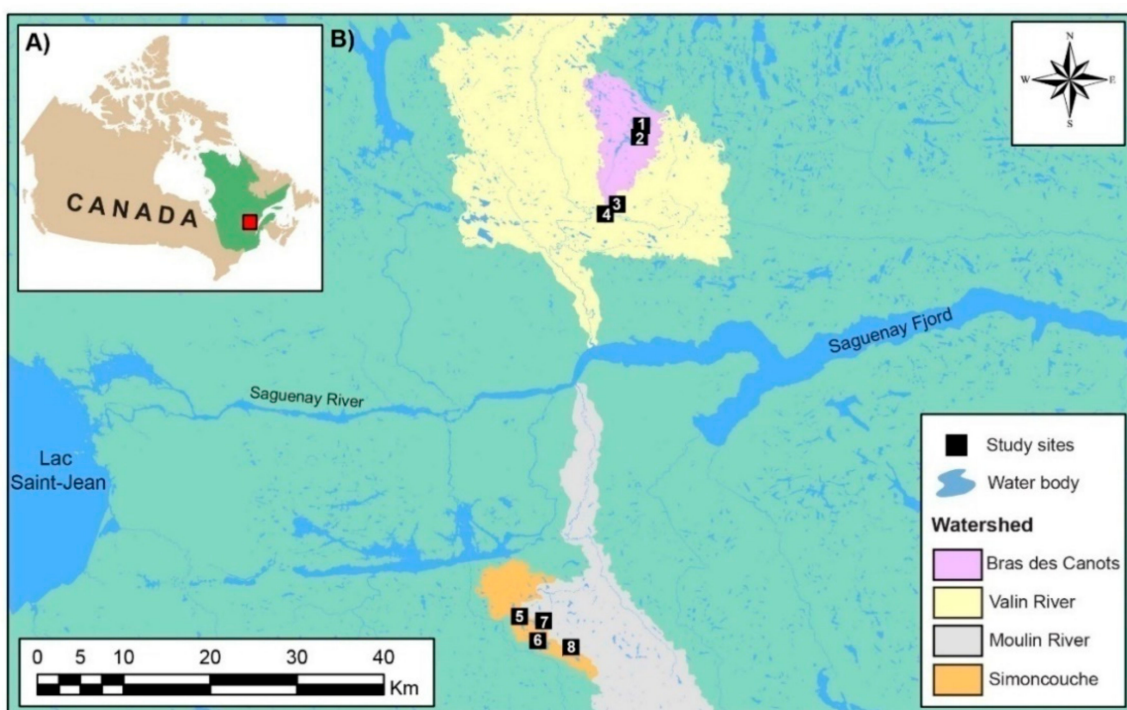
Figure 1. (**A**) Location of the study areas in North America, and (**B**) the experimental sites (1 = Martin-Valin, 2 = Culotte, 3 = Des Pères, 4 = Valin River, 5 = Simoncouche, 6 = Des Îlets, 7 = Flévy, 8 = Graveline).

### 2.2. Experimental Design and Site Selection

To evaluate beaver occupation in the study area, in 2018 we established an experimental design that covered four watersheds (two per study region: Mont-Valin and Simoncouche). We chose four watersheds to ensure that the results were representative of the natural variability and overall ecological conditions in the study area (Figure 1B). In each of these watersheds, we selected two lakes or rivers. Overall, we studied eight water bodies among the different locations; these sites varied in terms of altitude and geographic characteristics (Table 1). For each water body, we sampled two beaver lodges. Lodge selection was based on two criteria: (1) we selected the two most accessible lodges due to the difficult conditions of access (remote areas with limited trail net) and (2) the two lodges had to be >50 m apart to avoid any overlap of the study transects. We aimed to determine the pattern of use over time of the two different beaver lodges on a water body (lake or river) by the same beaver colony.

Table 1. Main characteristics of the studied water bodies.

Region	Watershed	Water Body (Name—Type)	Location	Size (ha)	Stand Type	Number of Lodges	Distance between the Studied Lodges (m)
Simoncouche	Simoncouche	Simoncouche—Lake	48°13′50.56″ N 71°15′02.32″ W	82.9	Trembling aspen	11	2200
		Des Îlets—Lake	48°11′57.90″ N 71°14′13.81″ W	167.7	Trembling aspen, balsam fir	2	1400
	Rivière du Moulin	Flévy—Lake	48°13′02.08″ N 71°12′58.86″ W	4.0	White birch, trembling aspen	2	200
		Graveline—Lake	48°10′55.18″ N 71°11′22.48″ W	4.0	Trembling aspen, black spruce	3	200
Monts-Valin	Bras-des-Canots	Culotte—Lake	48°38′18.31″ N 70°47′27.55″ W	11.1	Balsam fir, black spruce	4	180
		Martin-Valin—Lake	48°38′37.24″ N 70°46′46.14″ W	94.3	Balsam fir, black spruce	8	580
	Rivière Valin	Des Pères—Lake	48°35′10.17″ N 70°52′00.40″ W	2.0	Yellow birch, white birch, trembling aspen, balsam fir	2	240
		Valin River—River	48°34′42.29″ N 70°52′45.34″ W	——	Balsam fir, trembling aspen	6	730

2.3. Dendroecological Approach

A dendroecological approach can be effective in reconstructing the impact of natural and anthropic disturbances in forest ecosystems [6,7,45]. To better understand how beaver colonies used the territory over time, we applied dendrochronological analysis to the shrub and tree species located around the lodges. After beaver browsing, the annual segment of the main stem of a plant dies, and the plant often regenerates by activating a lateral bud to form a lateral branch (a new terminal bud) (Figure 2b) [46]. Based on this phenomenon, the year of activation of this lateral bud can be dated to determine the year of beaver browsing. Thus, by dating the years of browsing activity around a lodge, we can define the periods of occupation of the nearby beaver lodge. In 2013, we conducted a pilot experiment to test this new methodology; the study demonstrated that a much greater number of shrubs and trees around occupied lodges had been browsed in comparison to plants around unoccupied lodges (unpublished data).
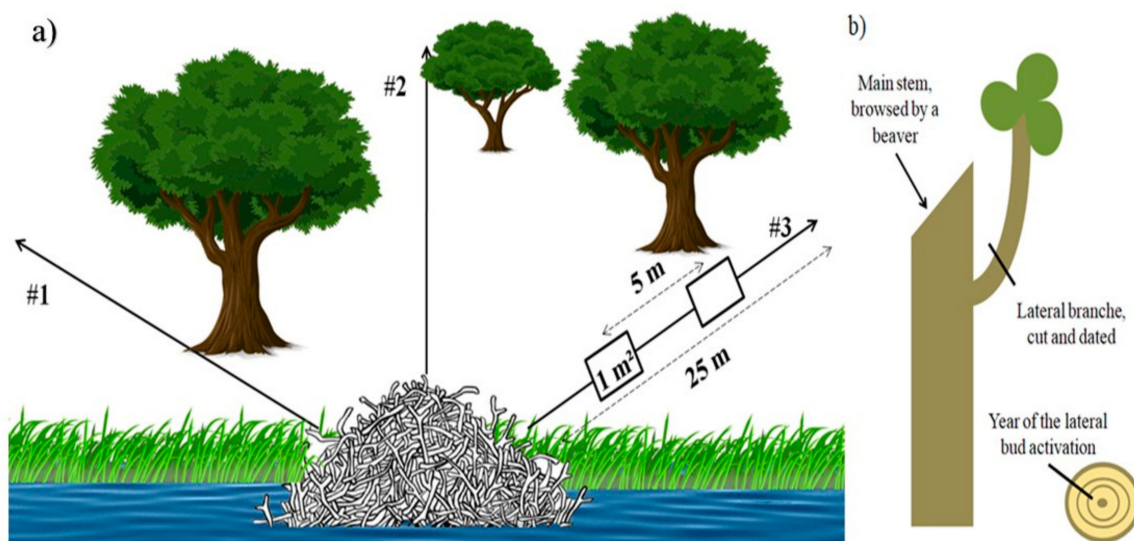

Figure 2. Sampling design. (**a**) Spatial distribution and location of transects and square plots around each beaver lodge, where squares represent the sampled plots and the bold arrows represent the three transects; (**b**) Representation of the dendroecological method used to sample and date stems browsed by beaver.

To date the browsing activity of beavers, we set up three transects (25 m) around each lodge, with an orientation of 45° between the transects. Five square plots (1 m^2) were installed on each transect, with 5 m between each of their centre, resulting in a total of 15 sampling plots per lodge (3 transects × 5 plots) (Figure 2a). In each sampling plot, each lateral branch formed by the activation of a lateral bud after beaver browsing was cut at the base level. Usually, beaver browsing is easily discernible from other animals browsing because the imprint of the teeth is apparent. If there was any doubt regarding the causal agent of browsing, the sample was discarded. The majority of the harvested lateral branches were from shrubs, while few were from deciduous saplings. Their diameters ranged between 0.5 and 5 cm, with average diameter of about 1 cm. We counted the number of annual growth rings of each sampled lateral branch from pith to bark, where the tree ring closest to the bark represented the last year of growth. The ring closest to the pith corresponded to the year of activation of the lateral bud, which corresponded to the year of the beaver browsing (Figure 2b). However, in the case of beaver browsing during summer or autumn (i.e., after growth was initiated for that year), the ring closest to the pith corresponded to the first year after browsing.

2.4. Data Analysis

To visually describe the similarity of occupation over time of the pair of beaver lodges, we ran classical multidimensional scaling (MDS) analysis using the number of browsed stems per year in each beaver lodge as a dependent variable. Data were grouped in classes of two years to increase the accuracy of our results because we did not determine the browsed season of studied stems using cross-dating methods (our method precision is ±1 year). MDS illustrates the similarity and dissimilarity between two data sets (each of the two lodges of a water body) by representing them on a 2Dplot [47]. The dissimilarity between two datasets is represented by the Euclidean distance, which is the distance separating the two data points [47]. The distance between the data points enables us to determine whether the pair of lodges on the same water body are used in a similar manner. Pairs of lodges showing a Euclidian distance of 30 or more were considered dissimilar. This value was estimated based on the mean Euclidian value among all the studied lodges. Since dissimilarity does not mean alternation, the Euclidian distance criteria, combined with the occupation histograms (Figure 3), enables us to confirm the alternating occupation of the lodges or not. We performed these analyses only for browsed stem data after 2007 as we lacked data from some bodies of water prior to 2007. Data analyses were performed using the 3.5.2 version of R environment, using the package "vegan" [48,49].
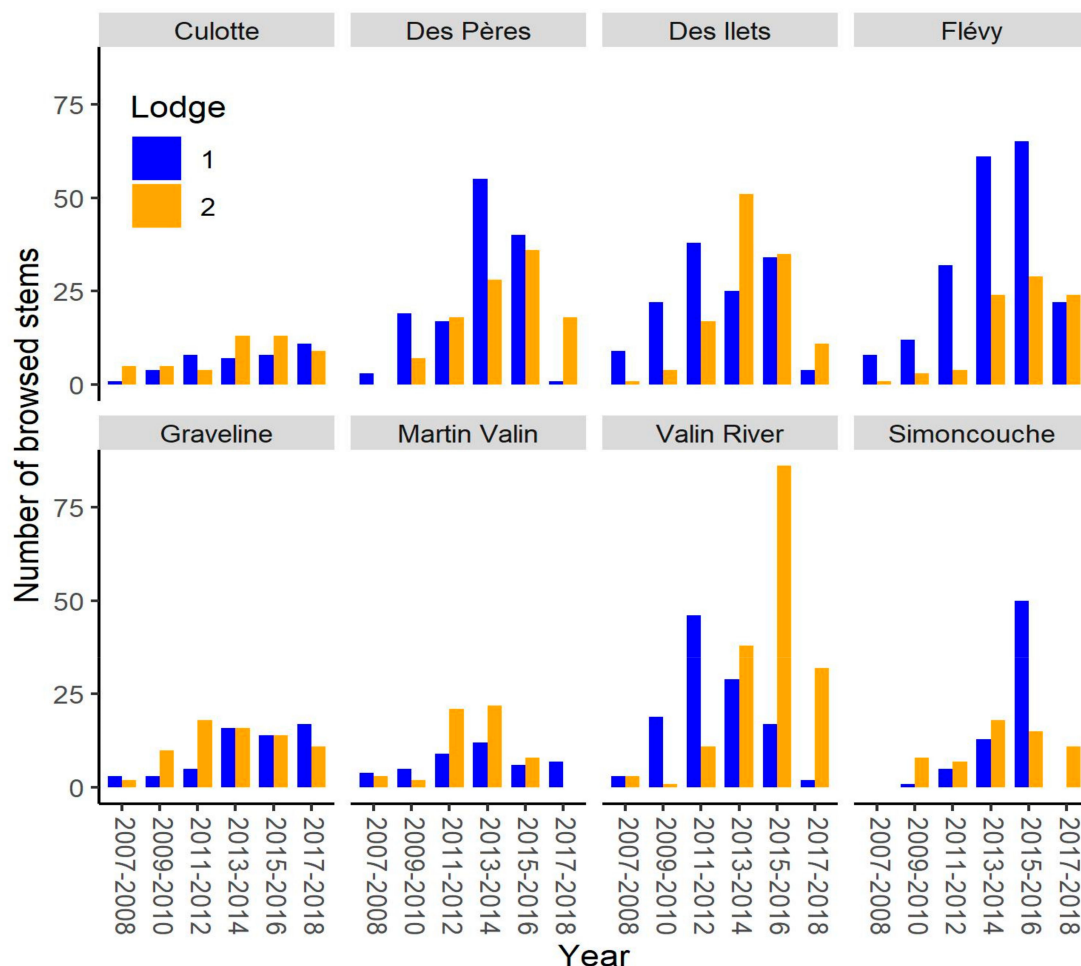
Figure 3. Number of stems browsed by beaver during 2007–2018 for each of the pair of lodges sampled on each of the eight studied water bodies.

3. Results

We observed various patterns in the temporal use of the lodges by beavers: alternation, no alternation, and unclear but potential alternation. Of the studied water bodies, three (37.5% of sample

sites) showed an alternating occupation of lodges, which is demonstrated by the changes on the temporal pattern (increase-peak-decrease) from one lodge to another (Figure 3, Des Îlets and Flévy lakes, and the Valin River). For these three water bodies, a decreasing number of browsed stems around one lodge was synchronous with an increasing number of browsed stems around the second lodge. To illustrate this pattern, Lodge #1 of Des Îlets Lake reached a maximum of browsed stems in 2011–2012; this amount decreased by 35% the year that Lodge #2 attained its maximum number of browsed stems in 2013–2014. A similar pattern was registered for Flévy Lake, where Lodge #1 had a maximum number of browsed stems in 2015–2016 followed by a striking a 65% decrease in 2017–2018 when Lodge #2 reached near its maximum value. We observed a decrease for Lodge #1 of the Valin River after reaching its maximum number of browsed stems in 2011–2012, followed by a 63% reduction for 2015–2016 when Lodge #2 reached its maximum.

We found three (37.5% of sample sites) of the studied water bodies (Figure 3, Culotte, Martin-Valin, Graveline lakes) did not have an alternating occupation in the use of the two lodges. In these cases, we observed no marked differences in the use of the respective two lodges over time. Finally, two of the studied water bodies (25% of sample sites) presented an unclear pattern (Figure 3, Des Pères and Simoncouche lakes) with no alternation observed.

MDS method was able to visualize the patterns of the temporal use of two lodges for all studied water bodies (Figure 4).The MDS results, combined with the occupation histograms showed in the Figure 3, confirm if two lodges are used in alternation or not. Based on this, the Valin River (▼) had two lodges presenting the most different temporal use, and we observed marked differences in the temporal use of the two lodges at Des Pères (●), Flévy (+), Des Îlets (×), and Simoncouche (∗) lakes. The two respective lodges of Culotte (▲), Martin-Valin (■), and Graveline (♦) lakes only showed minor differences in their temporal use (Figure 4).
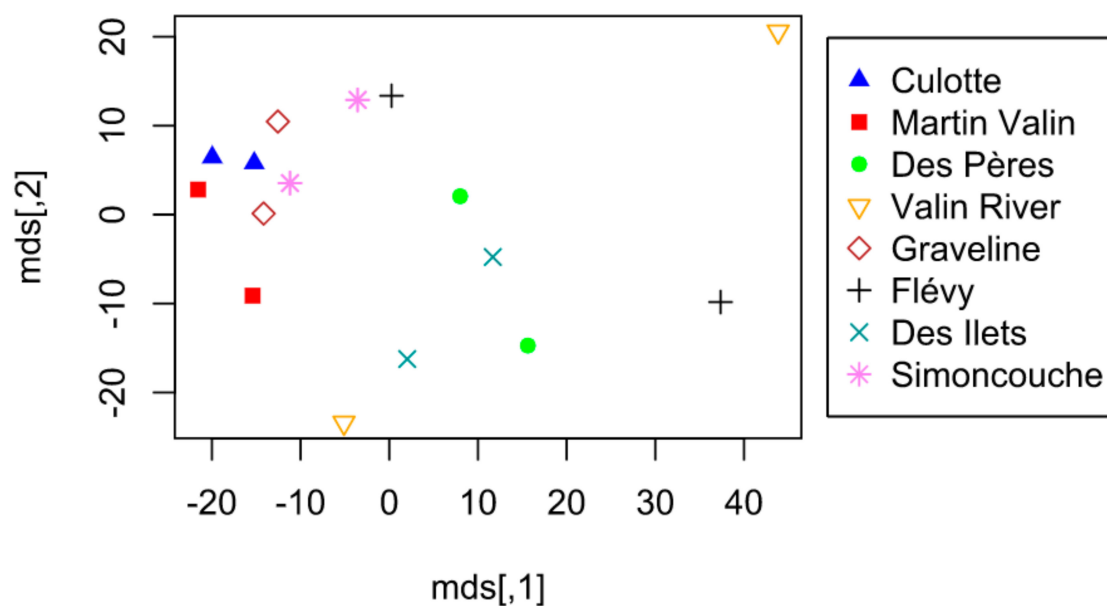
Figure 4. Multidimensional scaling (MDS) based on Euclidean distance comparing the temporal use of pairs of lodges on each of the studied water bodies.

4. Discussion

As ecosystem engineers, North American beavers modify their environment by building dams and lodges to make their habitat more suitable for their survival [15]. This has important consequences on the surrounding biodiversity, human infrastructure, and forest management plans [9]. Despite these major effects, the spatial use of habitat by beavers is poorly documented. Our research provides a novel dendroecological approach to study the occupation of lodges by beavers as well as a better

understanding of these dynamics. Thus, our results add important information for forest management and damage prevention, as they indicate the time a colony has been established on a water body, and whether or not the territory is prone to future disturbances by a newly established colony.

4.1. Alternation of Lodge Use

The majority of beaver colonies have more than one lodge on a single territory (lake or river), and the use of these multiple lodges over time is not well known [30]. In our study, a pattern of alternating use of a pair of lodges on a single lake or river over time was found in 37.5% of the studied water bodies (Valin River, Des Îlets and Flévy lakes). For these three water bodies, the alternation seen on Figure 3 were confirmed by the results of the MDS, showing a Euclidian distance greater than 30. Therefore, our results support the hypothesis that beavers alternate in their occupation of lodges on a single water body over time for these sites. Bluzma et al. [29] also found similar patterns over 13 years for beaver sites in Europe; in their study, colonies alternated their lodge use every two to three years. The MDS method determined whether or not two lodges are occupied in a similar pattern (Figure 4). Those results, combined with the alternation seen on the Figure 3, confirm if two lodges are use in alternation or not. However, our experimental design incorporated a single pair of lodges on each body of water. Due to the associated lack of replication, we were unable to perform additional statistical analyses to confirm dissimilarity between the occupations of those lodges. Thus, we suggest developing a future study with enough replication to confirm this question.

In our study, the pattern of alternating use of lodges approximates a two- to three-year pattern (Figure 3) [29] that could be explained by the depletion of the food resources around an occupied lodge. The quantity of available food around a lodge decreases as a beaver colony harvests the trees and shrubs over consecutive years [29]. The colony must migrate to another lodge while food resources regenerate around the previously occupied lodge. This alternating pattern continues as food resources deplete over two to three years at the 'new' lodge, and the colony migrates back to the old lodge [29]. Even though we were able to determine patterns of lodge use, our method (Section 2.3) for dating of browsed stems had a precision of ±1 year. To determine the actual year that browsing occurred, samples must be cross-dated [50]. The browsed stems were grouped in two years classes to solve it. Thus, we recommend using a cross-dating method to estimate with high resolution the date of beaver browsing disturbances in future studies.

4.2. Other Observed Patterns

The use of beaver habitat is clearly a complex phenomenon because not all of the studied lakes and rivers showed identical patterns. Three water bodies (Martin-Valin, Graveline, and Culotte lakes) did not show any alternating pattern (Figure 3) or any important dissimilarity in the use of the pair of lodges (Figure 4). Many factors, such as the water level fluctuations, the specific tree species surrounding the water bodies, the size of the beavers' territories, the density of beaver, and the number of lodges on each water body could explain these results.

To protect against any potential predator, beavers tend to keep their lodge's entrance underwater [13]. As the water level fluctuates naturally among seasons, the beaver colony might select a different lodge having an entrance that remained underwater even as water levels fluctuate. For example, Bloomquist et al. [30], found that some beaver colonies used different lodges seasonally, probably because of the seasonal water level fluctuations. Thus, in our study area, multi-annual alternating use of lodges could be complicated by an alternating pattern dictated by seasonal water level fluctuations.

The Culotte and Martin-Valin lakes are both located at higher elevations than the other water bodies, and both are surrounded predominantly by black spruce and balsam fir (Table 1). These two conifer species are not used by beaver as food [13]. Thus, the food resources around the lodges of these two lakes were poorer relative to the other studied water bodies where deciduous species were more abundant. As both lakes are located at higher elevations, and thus zones having slower tree

productivity [51], the regeneration of food resources may take longer at these higher altitude sites. Graf et al. [26] found that poor or depleted food resources led to more movement of a beaver colony within its territory. Therefore, food resources of poorer quality and quantity combined with longer regeneration times may favour a faster alternation in lodge selection for these two lakes. For future studies, we recommend considering food quality (species composition, site productivity, tree density) as key factors in determining the beaver's use of the territory.

Even if all beaver colonies do not have the same territory size, Campbell et al. [27] suggested that territory size is influenced by the regional population density of beavers, habitat quality, and the number of members of the beaver colony. As territories are not always the same size, we could not confirm that a single beaver colony was found on each studied water body. This is particularly true for Martin-Valin Lake, one of our largest study lakes that also had one of the highest number of lodges (8) in this study (Table 1). In the case where more than one colony is present in a water body, it is possible that the two studied lodges are not used by the same colony. This would render it impossible to observe an alternating pattern in the use of these lodges given that more than one beaver colony used the lodges. For future studies, we recommend considering the size of the water bodies as a variable that can affect the distribution of the beaver colonies, as well as territorial use by beavers.

Some lakes, such as Martin-Valin, Culotte, and Graveline lakes, had more than two lodges along their shores (Table 1). Studying the alternating occupation of two lodges on a single water body can produce uncertain results when there are more than two lodges on the water body. In these cases, the alternating pattern might be split between more than two lodges. However, this factor was omitted from our study. Thus, we recommend in future studies to study a higher number of (or all) lodges found on a given lake. Furthermore, we suggest developing a similar research study in the Abitibi-Témiscamingue region where the highest beaver densities in Quebec exist, estimated at approximately 5.50 colonies/10 km^2, as well as the highest dam densities, 4.01–6.22 dams/10 km^2 [52].

5. Conclusions

This pilot study improves our understanding of the dynamics of the North American beaver as a natural agent of disturbance. Using a new, simple, and effective dendroecological approach, our study investigated the poorly known dynamics of lodge occupation. Based on the assumption of the temporal pattern of browsed stems will change with the use of beaver lodges (among lodges), we were able to identify an increase of the number of browsed stems around a single lodge during a few years (from 2 to 4), until it reached a peak value and then started to decrease. When the patterns were different between paired lodges, an alternating use of beaver lodges was confirmed. Based on these assumptions and methods, we found that in 37.5% of our study sites, beavers alternated in their use of different (paired) lodges within a water body; this alternating pattern was most likely linked to food resource availability. This method is efficient and simple while still in a development stage and some weakness in our pilot study need to be considered (short temporal scale, few plot replications, only two lodges sampled etc.). Even with these limitations, we were nonetheless able to determine the local spatial dynamics of North American beavers. This new contribution could thus be integrated into boreal forest management strategies and included within the projected scenarios of climate change. Our future studies in reconstructing long-term beaver dynamics will include a greater diversity of forest stands and water bodies, as well as using complementary telemetry and cameras monitoring to validate the use of beaver lodges. Given the lack of research regarding this topic, we invite the scientific community to develop future research avenues to better understand the factors controlling beaver dynamics and identify the implications of beaver behaviour over the long-term.

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