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Article

Can the Impact of Gravel Roads on Organic Layer Thickness Explain the Distribution of *Populus tremuloides* along Road Networks in the Boreal Forest of Eastern Canada?

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Abstract: Roads are known to alter environmental conditions and the composition of road edge plant communities, particularly when exogenous materials are used as road surfacing. In this study, we evaluate the impact of gravel roads on the organic layer thickness (OLT) and aspen distribution in a boreal forest landscape of Eastern Canada. The OLT and aspen distribution were compared at different distances from the roads (0 m, 10 m, and >10 m) to determine whether a reduction in the OLT along the roads could explain the distribution of aspen along the road network, and in particular the role of the roads as habitat corridors. In addition, germination tests were carried out to determine whether mineral soil from the roads could promote aspen establishment, by comparing the germination rate of substrates consisting only of mineral soil or mosses, and substrates consisting of mosses covered with 0.5 cm or 2 cm of mineral soil. The presence of aspen in the study landscape is limited by thick organic deposits (≥50 cm). However, the thickness of these deposits is reduced to approximately 10 cm at the edges of gravel roads, in part by the transport of mineral soil from the roads. This reduction in the OLT facilitates the establishment of aspen and helps explain its distribution along the road network.

Keywords: *Populus tremuloides*; gravel roads; road edges; habitat corridors; organic layer thickness; boreal forest

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1. Introduction

Roads are one of the most widespread forms of natural landscape modification, with numerous ecological impacts on ecosystems [1]. Their construction is accompanied in particular by the creation of edge habitats with environmental characteristics and plant communities that differ from adjacent habitats [2,3]. In forest ecosystems, opening up the canopy through road construction and maintenance modifies habitat conditions by altering wind and light regimes and microclimatic conditions [4–6]. These open and frequently disturbed road edge habitats favor the establishment of pioneer plant species, which are intolerant of shade and adapted to disturbance [7]. The use of exogenous materials with properties different from those of existing forest soils as road surfaces also contributes to the alteration of habitat conditions and species composition along roads [8–10]. These effects are particularly pronounced in acidic, nutrient-poor environments, where the frequent use of alkaline materials, such as gravel, increases the soil pH and nutrient availability, making conditions unsustainable for acidophilic species [11–13]. In addition, these impacts can spread to many adjacent habitats via particle transport by wind, road traffic, and run-off water [14,15].

Although the ecological impacts of roads are well documented, e.g., [16–19], few studies have examined their impact on native tree species, exceptions being [20–22], particularly in the boreal forest [23]. In the Canadian boreal forest, trembling aspen (*Populus tremuloides* Michx., hereafter referred to as aspen) appears to be particularly effective in using edge habitats [24]. Aspen is the most widely distributed native tree species in North America [25], reflecting its adaptation to a wide variety of environmental conditions. It is also a fast-growing, shade-intolerant pioneer species, capable of establishing massive stands in newly disturbed environments [26–29] via abundant reproduction by seed and suckering [30–33]. Aspen also has an excellent dispersal capacity due to its small seeds, which can be carried by the wind over several kilometers [34,35]. According to Andrews [16], species with excellent dispersal abilities and the ability to invade disturbed habitats are "attracted" to edge habitats. In the boreal forest of Eastern Canada, the aspen distribution does indeed appear to be influenced by road edge habitats. For example, east of James Bay (Quebec, Canada), the aspen distribution is concentrated near anthropogenic infrastructures such as roads [36]. South of James Bay in the Clay Belt of Quebec and Ontario, aspen is densely present along the road network and can colonize road edges even when the surrounding habitat matrix is unsustainable for it [37].

In the Clay Belt of Quebec and Ontario, the aspen distribution seems to be partly constrained by edaphic conditions, particularly by the thickness of the organic layer [38,39]. The Clay Belt is a region prone to paludification because the cold climate, flat topography, relatively long fire cycle, and abundance of fine-textured deposits favor the accumulation of a thick layer of organic matter on the forest soils [40]. This accumulation of organic matter affects edaphic conditions, forest productivity, and plant community composition [41,42]. As organic matter has a low thermal conductivity, its accumulation leads to a drop in the soil temperature, which consequently decreases decomposition and nutrient availability [43]. The accumulation of organic matter is also accompanied by a rise in the water table, due to the increased bulk density of the soil, which induces high capillarity and low hydraulic conductivity [44]. The rising water table creates anoxic conditions [45], which reduce the rate of decomposition of organic matter [44] and can lead to tree death. The accumulation of organic matter is also maintained by facilitation processes during the succession of bryophyte communities [46,47]. These changes in edaphic conditions induced by the accumulation of organic matter create unsustainable environments for aspen, which is intolerant to flooded conditions and cold soils [48,49]. The region's forests thus tend to converge on open peatlands dominated by sphagnum moss (*Sphagnum* spp.) and black spruce [50], which are more tolerant to these conditions.

The main objective of this study was to evaluate the impact of gravel roads on the organic layer thickness and aspen distribution in a coniferous boreal forest landscape located on the Clay Belt (Quebec, Canada). Despite the strong development of the forest road network since the 1970s in the Province of Quebec, few studies have focussed on their ecological impacts [51]. Between 2017 and 2021, nearly 20,300 new kilometers of forest roads were constructed, reaching a total length of 479,243 km [52,53]. In our study landscape, the road network extends for almost 10,500 km, with approximately 3500 km of this network being gravel roads. Bryophyte-dominated communities, such as those found in the Clay Belt, are known to be particularly susceptible to dust from these roads [15,54] and to edge effects [24,55,56]. At the same time, the edges of these roads can provide a favorable habitat for aspen [57,58]. In a previous study [37], we demonstrated that roads sometimes acted as habitat corridors for aspen, enabling it to establish in unfavorable habitat matrices, generally characterized by the presence of thick organic deposits. In this study, we further assess the relationships between the organic layer thickness, aspen distribution, and the presence of roads by answering the following questions:

1. Does the thickness of the organic layer (hereafter OLT) have an impact on the distribution of aspen in the study landscape?
2. Do forest roads have an impact on the OLT via the transport of mineral particles from the roads, thus promoting the establishment of aspen?
3. Can the impact of roads on OLT explain the distribution of aspen along the road network, and in particular, the role of roads as habitat corridors?

We hypothesize 1. that thick organic deposits >30 cm, cf. [38] limit the presence of aspen in our study landscape; 2. that mineral soil transport from roads reduces the OLT along roads and consequently favours aspen establishment; 3. that the reduction in the OLT along roads explains their role as habitat corridors for aspen.

2. Materials and Methods

2.1. Study Area

The study area (49°–49°50′ N; 78°–79°30′ W) covers an area of 10,930 km^2. It is located in the Quebec–Ontario Clay Belt, which was created during the drainage of proglacial Lake Ojibway about 8000 years ago [59]. The topography is flat with the main types of surface deposits being organic (45%), clays (35%), and till (12%). The climate is subpolar, subhumid continental [60]. Average annual precipitation is 909 mm, of which 29% falls as snow. The mean annual temperature is 0 °C (±2.9 °C) (data from the Joutel meteorological station for the period 1981–2010 [61]). The study area is located in the bioclimatic domain of the black spruce–feather moss forest of western Quebec, which corresponds to the Mesoboreal bioclimatic subdivision of the Canadian boreal biome [62]. The vegetation is largely dominated by black spruce (*Picea mariana* (Mill.) BSP.). Jack pine (*Pinus banksiana* Lamb.) and aspen are also abundant, forming pure stands or mixed stands with black spruce. Severe stand-replacing crown fires are the main natural disturbance, although fire activity is relatively low [63,64]. Large-scale industrial forestry activities, notably mechanized clear-cutting, began in the 1970s. Logging is mainly focused on conifers, which account for over 75% of the forest potential, while poplars (*Populus* spp.) represent around 20% [65].

2.2. Organic Layer Thickness and Aspen Distribution

Before determining whether the distribution of aspen along the road network, and more specifically, the role of roads as habitat corridors can be explained by the reduced thickness of the organic layer (OLT) along roads, we first sought to confirm that thick organic deposits limit the presence of aspen in our study landscape, by performing a logistic regression of aspen presence as a function of OLT.

2.2.1. Databases

Aspen presence/absence data were obtained from the forest information system per tessera (SIFORT) [66]. This database is made up of polygonal units (i.e., tesserae) that each cover an area of around 14 ha. The tesserae contain, among other things, information on the composition of forest stands. This information is derived from the forest maps that have been produced by the Quebec government since 1970, as part of the decennial forest inventory program. Although the forest composition data are generalized to the entire area of the tesserae (14 ha), they actually represent the composition of the stand located at the central point of each tesserae on the forest maps.

Only the most recent SIFORT data (i.e., 4th forest inventory) were used to establish the distribution of aspen [66]. Aspen was noted as "present" in observations where the forest composition was identified as "PT" (i.e., trembling aspen, "peuplier faux-tremble" in French) or "PE" (i.e., poplar, "peupliers" in French). The "PE" grouping corresponds to the presence of trembling aspen and balsam poplar (*Populus balsamifera* L.). Aspen, on the other hand, was noted as "absent" in observations where the forest composition was identified as "FI" (i.e., intolerant hardwoods, "feuillus intolérants" in French). The "FI" group corresponds to forest compositions that may or may not include aspen, i.e., stands of white birch (*Betula papyrifera* Marsh.) and aspen, or stands of white birch and balsam poplar [67]. Considering that aspen is absent in these observations, its presence is potentially underestimated. However, as only 567 observations were identified as "FI" out of the 77,935 observations contained in our database (0.7%), we conclude that assigning "absent" to "FI" observations had little impact on the data analysis.

Organic layer thickness (OLT) data were obtained from the soil paludification map created by Mansuy et al. [68]. Succinctly, the authors created a predictive map of OLT for a 180,000 km^2 region located in the black spruce–feather moss forest of western Quebec, from a database containing 13,944 georeferenced measurements of organic layer thickness, with a resolution of 30 m. As our study landscape falls entirely within the study area of Mansuy et al. [68], all OLT data were obtained from their map. However, only data intersecting the center of the tesserae were extracted, to respect the punctual nature of the SIFORT database.

2.2.2. Data Analyses

In order to determine whether the presence of aspen is limited by the thickness of the organic layer at the scale of our study landscape, a logistic regression was performed in the Stats library of the R software (version 4.3.1, R Foundation for Statistical Computing, Vienna, Austria) [69]. Our database initially contained 77,935 observations, but the logistic regression was performed on 61,267 observations. All observations corresponding to non-forest land (e.g., lakes, gravel pits, anthropogenic infrastructures), making up 3013 in total, were excluded from our database. In addition, all observations corresponding to stands less than 7 m tall were excluded (13,655 observations), as it is not mandatory to assign a composition to them as part of forest inventories [67]. Once all this data had been excluded, only 156 observations identified as "FI" remained in our database (0.3%).

2.3. Organic Layer Thickness and Aspen Distribution

After determining whether thick organic deposits limit the presence of aspen in our landscape, we determined whether gravel roads induce a reduction in OLT by comparing OLT at different distances from roads in 27 stands. We then determined whether the reduction in OLT along roads could explain the distribution of aspen along the road network by comparing OLT at different distances from roads in habitat corridors, aspen stands (i.e., favourable habitat), and control stands (i.e., unfavourable habitat).

2.3.1. Stand Sampling

Road network data were obtained from AQréseau+ [70]. The methodology used to select aspen stands is detailed in Marchais et al. [37]. Briefly, 19 aspen stands were randomly selected from a vegetation inventory carried out along the road network in 2018 (Figure 1). The ecological characteristics of the stands are described in Table S1. In each stand, a 10 m × 100 m transect was placed parallel to the road and a second perpendicular to it. The starting point of the two transects corresponded to the center of the stand, thus creating an L-shaped transect. Each transect was subdivided into 10 plots of 10 m × 10 m. In each plot, the thickness of the organic layer (OLT) was measured using an Edelman hand auger (i.e., soil sampler probe) to a maximum depth of 120 cm. Where a ditch was present on transects parallel to the roads, OLT measurements were taken before the ditch in order to be able to observe the effect of the roads on OLT. In addition, a stand containing no aspen (i.e., a control stand) was sampled using the same methodology for each portion of road playing the functional role of habitat corridor for aspen, for a total of 8 stands (Figure 1, Table S1). Finally, soil profile descriptions were carried out to a depth of 50 cm in 4 stands where roads acted as habitat corridors (Table S1) to determine whether mineral soil had been transported from the roads. The soil profiles are described in Table S2 and follow the Canadian System of Soil Classification [71]. In each of these 4 stands, a first description was made at a distance of 5 m from the road, with a second being made at a distance of 25 m.

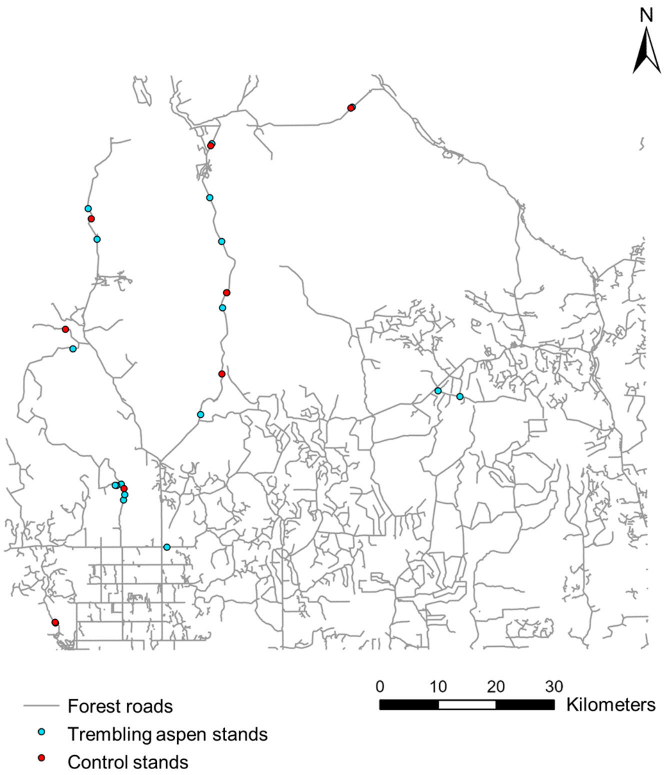

Figure 1. Location of forest roads and sampled stands in the study landscape. The stands sampled include 19 aspen stands located along roads, as well as 8 stands containing no aspen as control stands.

2.3.2. Data Analyses

The impact of roads on OLT was assessed by comparing OLT at different distances from roads using a Friedman test. For this analysis, data from transect T17B-3300 were excluded, as OLT was not systematically measured before the ditch in the transect parallel to the road. Data from parallel transects were grouped into a single distance class (0 m), while data from perpendicular transects were divided into two distance classes (10 m and >10 m). These distance classes were used as the effect of roads on aspen abundance extends over 10 m in our study area [37]. We therefore presume that if OLT is the limiting factor for aspen establishment away from roads, the effect of roads on organic layer thickness should also extend over 10 m. An exact post hoc test [72] with Holm correction was then performed to determine between which distance classes OLT varied significantly. Analyses were performed in the rstatix and PMCMRplus libraries (respectively, version 0.7.2 and 1.9.7) [73,74] of the R software (version 4.3.1, R Foundation for Statistical Computing, Vienna, Austria).

To determine whether the influence of roads on OLT can explain the distribution of aspen along the road network, OLT according to distance from roads was compared between 3 habitat types: (1) habitats where roads play no functional role (NFR) and which correspond to stands where aspen is present both near and far from roads; (2) habitat corridors (HC), which correspond to stands where aspen is present near roads, but is rare or absent far from roads; (3) control habitats (C), which correspond to stands where aspen is absent both near and far from roads. To simplify the interpretation of the results, the 0 and 10 m distance classes were combined into a single distance class of less than 10 m for this analysis (<10 m). The comparison of OLT according to distance from roads between the 3 habitat types was carried out using a linear mixed model, followed by an ANOVA. To meet the assumptions of these analyses, a logarithmic transformation was used on the OLT data. The homogeneity of variance and normality of residuals were checked using Levene's and Shapiro–Wilk tests, respectively. A Tukey's post hoc test was then performed to determine between which habitat types (NFR, HC, C) and distance classes (<10 m,

>10 m), OLT varied significantly. Analyses were performed in the lme4, car, and emmeans libraries (respectively, version 1.1-34, 3.1-2 and 1.8.8) [75–77] of the R software (version 4.3.1, R Foundation for Statistical Computing, Vienna, Austria).

In the 4 stands where soil profile descriptions were made to determine whether mineral soil had been transported from the roads, a Student's paired samples test was used to compare mean organic layer thickness at 5 m and 25 m from the roads. These stands include transect T17B-3300, which was retained for this analysis. As we suppose that OLT is lower at 5 m than at 25 m from the roads, a one-tailed test was preferred to a two-tailed test in order to increase the power of the test. The organic layer thickness data were transformed using a logarithmic function, to meet the assumptions of the Student's paired-samples test. Differences were tested for normality using a Shapiro–Wilk test. Analyses were performed in the rstatix library (version 0.7.2) [74] of the R software (version 4.3.1, R Foundation for Statistical Computing, Vienna, Austria).

2.4. Mineral Soil and Germination of Aspen: Experimental Setup

After determining whether gravel roads induce a reduction in OLT via the transport of mineral particles from the roads, we finally investigated whether this mineral soil allows aspen to establish along roads. To this end, an experimental setup designed to test the effect of substrate type on aspen germination was set up at the Lake Duparquet Research Station (LDRS) during the summer of 2021 (Figure S1). The experimental setup included 4 substrate types (i.e., treatments):

1. Mineral soil only;
2. Mosses covered with 2 cm of mineral soil;
3. Mosses covered with 0.5 cm of mineral soil;
4. Mosses only.

The first treatment corresponds to a "positive control", because the mineral soil is known to be a good germination bed for aspen. The fourth treatment corresponds to a "negative control", because mosses are known to be an unfavorable germination bed for aspen [78]. Finally, treatments two and three correspond to situations where mineral soil would have been transported to the edges of forest roads, on the moss which constituted the substrate initially present.

Mineral soil was collected from the edges of forest roads, while live mosses were collected from stands adjacent to the roads, in three different stands located on organic deposits. Each of the 4 treatments was replicated 21 times. Twelve aspen seeds were sown on 18 August, in each of the 84 pots of our experimental setup. Germination was monitored until 21 September. Aspen seeds were obtained from the National Tree Seed Centre (NTSC). They were collected in 2018 from 9 different trees in the Acadia Research Forest (ARF) in New Brunswick. The viability of aspen seeds was estimated at 96.7% in 2021 before the experimental scheme was set up. The number of germinations was statistically compared between treatments using a Kruskal–Wallis test, and a Dunn post hoc test with Holm correction. These analyses were performed in the GmAMisc library (version 1.2.0) [79] of the R software (4.0.5, R Foundation for Statistical Computing, Vienna, Austria).

3. Results

3.1. Organic Layer Thickness and Aspen Distribution

At the scale of the study landscape, the logistic regression demonstrated that the probability of aspen presence varies with the organic layer thickness (X^2 = 12.332, $p < 0.001$; Figure 2). The model indicates that the probability of aspen presence is of the order of 80% for an organic layer thickness (OLT) equal to 0 cm, 40% for an OLT equal to 20 cm, 10% for an OLT equal to 40 cm, and 0% for an OLT equal to 60 cm. The model's 95% confidence intervals are nevertheless very wide for organic layer thicknesses below 50 cm (Figure 2), indicating a poor model fit. However, our model reliably indicates that the probability of aspen presence is practically zero when the organic layer is 50 cm or more thick.

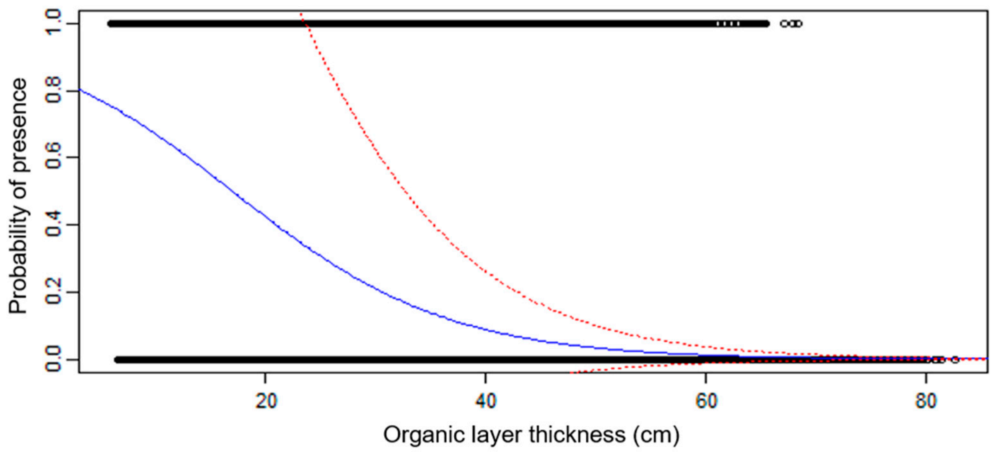

Figure 2. Probability of aspen presence according to organic layer thickness. The blue line represents the logistic regression curve. Red lines represent 95% confidence intervals. Circles represent aspen presence/absence observations.

3.2. Forest Roads and Organic Layer Thickness

In the 27 roadside stands sampled, the Friedman's test showed that the thickness of the organic layer (OLT) varied significantly with the distance from the road ($X^2 = 13.2$, df = 2, $p = 1.39 \times 10^{-3}$). The thickness of the organic layer is lower near the roads than far from them (Figure 3). The median value for the organic layer thickness is around 14 cm at 0 and 10 m from the roads, compared with 28.7 cm at more than 10 m (distance class >10 m).

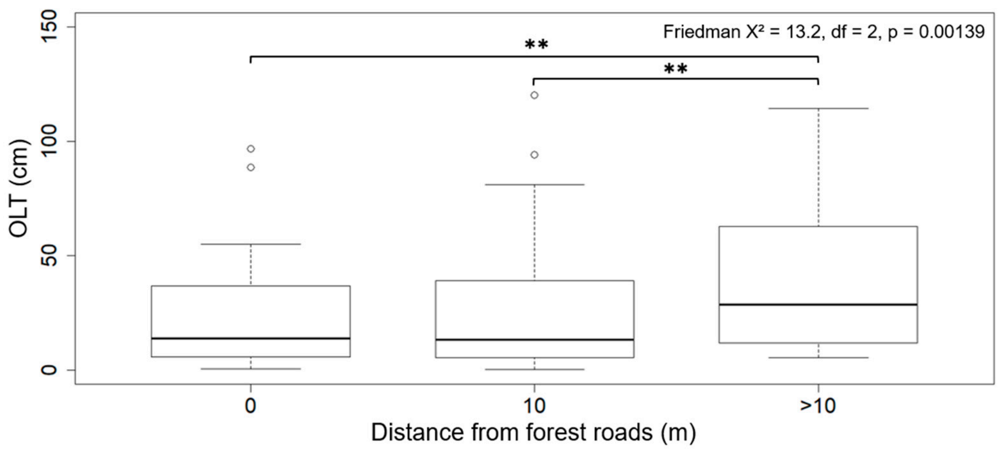

Figure 3. Thickness of organic layer (OLT) according to distance from forest roads. Transects parallel to roads form a single distance class (0 m). Transects perpendicular to roads are divided into two distance classes (10 m and >10 m). The results of the Friedman test are shown. The symbol ** indicates significant differences between distance classes according to the results of the post hoc exact test with Holm correction ($p < 0.01$).

Significant differences in the OLT according to the distance from the roads ($X^2 = 37.8$, df = 5, $p = 4.16 \times 10^{-7}$; Figure 4) were also identified by the ANOVA performed on the habitats where the roads play no functional role (NFR), where they constitute habitat corridors (HC), and control habitats (C). Furthermore, the OLT appears to explain the distribution of aspen along the road network. Thus, the OLT does not vary significantly with the distance from the roads for the NFR habitats where aspen is present both near and far from the roads (Figure 4). The mean OLT value for these habitats is around 10 cm, which, according to our logistic regression model, corresponds to a probability of aspen presence of over 60%. Similarly, the OLT does not vary significantly with the distance from the roads for the C habitats, where aspen is absent. The mean OLT value for these habitats is around 50 cm, corresponding to an almost zero percent probability of aspen presence (Figure 2). The OLT, on the other hand, varies significantly with the distance from the roads in the HC habitats (Figure 4), where aspen is abundant close to the roads, but scarce or absent far from them. In these habitats, the mean OLT value within 10 m of the roads is 10 cm and does not differ significantly from the OLT values in the NFR habitats. At more than 10 m from the roads, the mean OLT value is 35 cm and does not differ significantly from the C habitats (Figure 4).

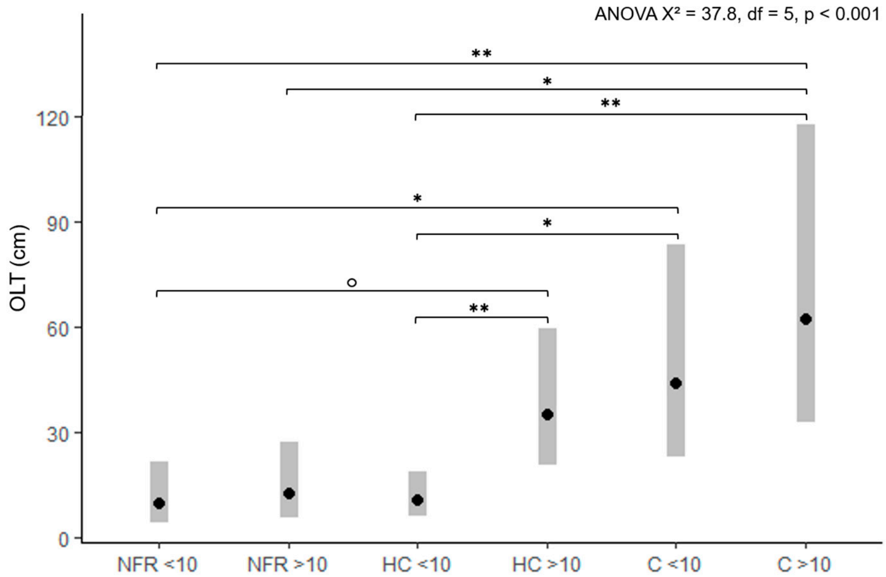

Figure 4. Organic layer thickness (OLT) according to distance from forest roads estimated by the mixed linear model for habitats where roads play no functional role (NFR), where they play the role of a habitat corridor (HC), and for control habitats (C). For each habitat type, the distance to roads is divided into two classes (<10 m and >10 m). The gray bars represent the 95% confidence intervals estimated by the model. ANOVA results are shown. The symbols °, *, and ** indicate significant differences between groups according to the results of Tukey's post hoc test ($p < 0.1$, $p < 0.05$, and $p < 0.001$, respectively).

The soil profile descriptions carried out in the four HC stands (Table S2) confirmed the presence of mineral soil transported from the roads and its influence on the organic layer thickness. The results of the Student's paired samples test indicate a statistically significant difference in the organic layer thickness according to the distance from the roads (T = 2.47, df = 3, $p = 4.51 \times 10^{-2}$). The organic layer is thinner close to the roads than far from them (Figure 5). The average thickness of the organic layer at 5 m from the roads is 6.8 cm (±3), compared with 41 cm (±7) at 25 m from the roads. These values are in line with the average OLT values measured in the HC stands (Figure 4). The reduction in the OLT near the roads is due to the transport of mineral soil from the roads. A layer of mineral soil ranging from 1 to 7 cm thick was observed in the four stands sampled (Table S2).

3.3. Mineral Soil and Aspen Germination

The experiment results from the Lake Duparquet Research Station showed a significant effect of the substrate type (i.e., treatment) on aspen germination (Kruskal–Wallis: H = 47.97, df = 3, $p = 2.16 \times 10^{-10}$). The mineral soil-only treatment led to higher aspen germination than all the other treatments (Figure 6). The average germination rate for this treatment was 64.7%. The aspen germination was also higher when a 2 cm layer of mineral soil covered the mosses than when the substrate consisted solely of mosses (Figure 6). On the other hand, the aspen germination did not differ between the treatment with only mosses and the treatment with mosses covered with 0.5 cm of mineral soil. The average germination rate for the 2 cm mineral soil treatment was 25%, compared with 8.3% and 5.2% for the 0.5 cm mineral soil and mosses only treatments, respectively.

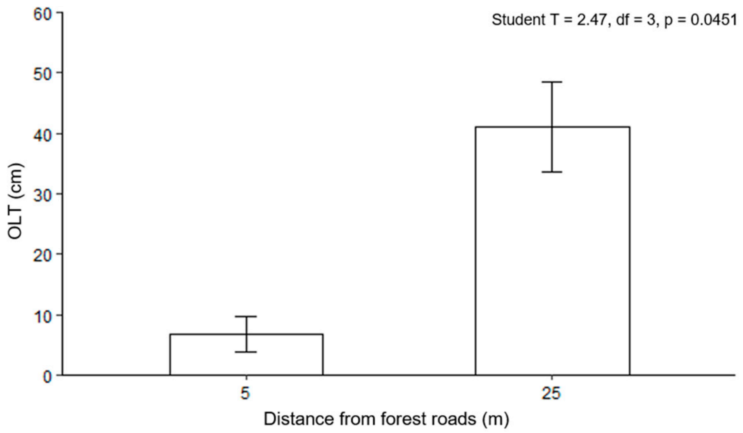

Figure 5. Average organic layer thickness (OLT) at 5 m and 25 m from forest roads based on the soil profiles of 4 stands where roads act as functional habitat corridors. Error bars represent standard errors. Results of the Student's paired-sample test are shown.

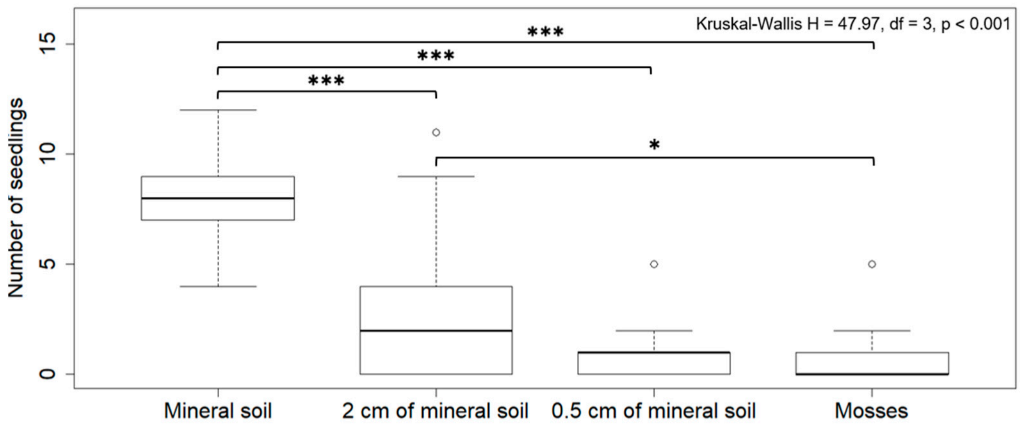

Figure 6. Number of aspen seedlings by substrate type (i.e., treatment). The results of the Kruskal–Wallis test are shown. The symbols * and *** indicate significant differences between treatments according to the results of Dunn's post hoc test with Holm correction ($p < 0.05$ and $p < 0.001$, respectively).

4. Discussion

4.1. Organic Layer Thickness and Aspen Distribution

As we hypothesized, thick organic deposits limit the presence of aspen in our study landscape (Figure 2). In the Clay Belt of Quebec and Ontario, a thick layer of organic matter tends to accumulate on forest soils over time [46]. This accumulation of organic matter is accompanied by a drop in the soil temperature and nutrient availability, as well as a rise in the water table [41,43,80], creating unfavorable conditions for aspen establishment and growth [38,39]. In particular, temperatures of 5 °C can inhibit root growth and reduce photosynthesis and water uptake by seedlings [81,82], while temperatures of 8 °C and below inhibit sucker emergence and growth [49]. Furthermore, while aspen can survive for several weeks on water-saturated soil [83], it has poor resistance to flood conditions due to its inability to form adventitious roots [48,84].

According to our results, the distribution of aspen in our study landscape extends over a gradient of organic layer thicknesses ranging from 1 to 60 cm (Figure 2). Our gradient values are more extensive than those reported by Gewehr et al. [38]. These authors showed that the aspen distribution at the landscape scale in the Quebec Clay Belt was limited to an organic layer thickness gradient between 1 and 30 cm. The results of Gewehr et al. [38]

are similar to those of Lafleur et al. [39], with both showing that an organic layer thicker than 25 cm strongly limits aspen establishment by seed and suckering. The wider organic layer thickness gradient observed in our study probably reflects the poor fit of our logistic regression model for organic layer thicknesses below 50 cm.

There are two main reasons for the poor fit of our model. First, Mansuy et al.'s [68] model shows a poor performance in predicting organic layer thicknesses between 0 and 20 cm and between 20 and 40 cm, compared with predictions above 40 cm thickness (R^2 = 0.041, R^2 = 0.209, and R^2 = 0.793, respectively). These limitations likely increased the maximum value of our gradient, as well as the upper value of the confidence interval. Second, the absence of aspen may be related to factors other than the organic layer thickness, such as the type of surface deposits or stand age [50]. Thus, the absence of aspen in stands with a thin organic layer, due to confounding factors, probably increased the lower value of our model's confidence interval.

4.2. Forest Roads and Organic Layer Thickness

Forest roads have an impact on the thickness of the organic layer. The organic layer thickness is lower near the roads (<10 m) than far from them (>10 m) (Figures 3 and 5), due to soil disturbance during road construction [2] and mineral soil transport from the roads (Table S2). Gravel roads, such as those in our study area, are known to have a chronic and cumulative impact on adjacent ecosystems through the deposition of particulate matter [15,85]. In acidic and nutrient-poor environments, mineral soil transported from roads increases the nutrient availability and soil pH and tends to reduce the soil moisture due to its lower water retention capacity compared to organic soil [11,13,86,87]. Environmental conditions thus become less sustainable for acidophilic mosses such as sphagnum mosses (*Sphagnum* spp.), the abundance of which is greatly reduced along roadsides [88–90]. Conversely, conditions become more favorable for aspen, which grows best in slightly acidic or neutral soils rich in nutrients, especially calcium and nitrogen [91–93]. Road edges are also characterized by higher soil temperatures [7,94], which should help increase the rate of organic matter decomposition and aspen growth [11,49]. Furthermore, once established, aspen can exert positive feedback on its environment by accelerating nutrient cycling, via a change in the soil macrofauna composition and an increase in the litter quality [95,96] and by limiting the sphagnum cover [46]. Thus, aspen itself contributes to limiting the thickness of the organic layer [97] and facilitates its subsequent establishment along roads.

The impact of gravel roads on the thickness of the organic layer extends to around 10 m in our study area (Figures 3 and 5). These results are in line with those reported in the literature. In Alaska, Walker and Everett [90] estimated that 70 to 75% of particle deposition occurred within 10 m of gravel roads. Similarly, Spatt and Miller [89], Meininger and Spatt [98], and Ackerman and Finlay [99] noted an exponential decrease in dust deposition rates with distance from the road. In North Dakota, Creuzer et al. [100] also observed a higher particle load at 10 m than at 80 m from gravel roads, a trend that is exacerbated by traffic intensity. Finally, in Sweden, Tamm and Troedsson [101] also noted a sharp drop in particle deposition beyond 10 m from gravel roads.

4.3. Mineral Soil and Aspen Germination

Mineral soil transported from forest roads may favor the establishment of aspen by seed (Figure 6). These results support the observations of Ackerman and Breen [57] in four aspen stands on roads and gravel fills, beyond the species' northern limit in Alaska. They hypothesized that the presence of aspen was because the gravel provided islands of substrate favorable to their establishment and growth. Mineral soil or a fine layer of organic matter are indeed known to make good germination beds, e.g., [102]. Conversely, a thick layer of organic matter limits aspen establishment, e.g., [39]. This difference in substrate quality is due in particular to differences in the soil humidity [103], the most critical factor for germination and seedling survival [78,104,105]. Organic matter tends to exhibit greater moisture fluctuations than mineral soil [106], due to its greater porosity [107]. Aspen seedlings are sensitive to moisture variations in the surface layer [78,105], because the slow development of radicles makes them particularly vulnerable to desiccation [108]. Thus, seed germination can be inhibited in the absence of sufficient and continuous moisture, with seedling survival and growth also being severely hampered [78,109].

4.4. Aspen Distribution along the Road Network

The reduction in the thickness of the organic layer (OLT) at road edges by the addition of mineral particles helps to explain their role as habitat corridors for aspen. In our study area, roads constituting habitat corridors are generally located in matrices characterized by the presence of thick organic deposits [37]. However, the OLT along these roads is equivalent to that found in habitats favourable to aspen (Figure 4). The combined effects of opening the forest canopy, disturbing the soil, and adding mineral soil during road construction must have altered the environmental conditions and reduced OLT, making conditions unsustainable for acidophilic mosses [11], but favorable for aspen [37]. In particular, the mineral soil transported from the roads must have created islands of substrate, enabling the initial establishment of aspen by seed along the roads constituting habitat corridors (Figure 6; ref. [57]), since it is rare in thick organic deposits (Figure 2; ref. [110]). However, once established, aspen was able to spread quickly along the road network by suckering, because it can produce suckers as early as 1 or 2 years of age [25,111]. Given that the impact of roads on the OLT extends over only 10 m (Figures 3 and 5) and that thick organic deposits prevent aspen establishment by seed and suckers in adjacent habitats (Figure 4; ref. [39]), its distribution is channeled along roads [37]. Since a layer of mineral soil lower than that generally found in stands is sufficient to favor aspen establishment (i.e., 2 cm vs. 5 cm on average; Figure 6, Table S2), we can suggest that a large portion of the road network in our study area constitutes a habitat favorable to aspen. This could explain its strong presence and abundance along the road network [37].

The distribution of aspen along gravel roads could promote the invasion of adjacent habitats, particularly if silvicultural treatments aimed at limiting paludification are employed. As the aim of these treatments is to better reproduce the effect of severe fire on soils, they tend to reduce the thickness of the organic layer, and increase soil temperature and aeration [112–114], thus creating conditions favorable to aspen establishment [78,115]. As aspen abundance has already greatly increased in the study landscape as a result of logging [110], the ability of aspen to colonize road edges should be considered in silvicultural strategies and road network development planning, so as not to risk inducing further expansion.

5. Conclusions

The distribution of aspen in our study landscape is constrained by the thickness of the organic layer, with an almost zero probability of presence for deposits 50 cm or more thick. The mineral soil transported from gravel roads does, however, tend to reduce the thickness of this organic layer along the roads, thus favouring the establishment of aspen. This reduction in organic layer thickness seems to explain the distribution of aspen along the road network, and in particular, the role of the roads as habitat corridors.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f15020298/s1, Table S1: Ecological characteristics of sampled stands based on information from the 4th provincial inventory forest map and the functional role of roads for trembling aspen based on the results of Marchais et al. [37]; Table S2: Description of soil profiles in 4 aspen habitat corridor stands. The names of soil order follow the Canadian System of Soil Classification [71]; Figure S1: Forest peatlands in the Clay Belt of Quebec (A), gravel road acting as habitat corridor for trembling aspen (*Populus tremuloides*) (B), soil profile in a stand where the road acted as habitat corridor (C), and germination test carried out at the Lake Duparquet Research Station (D).

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Data Availability Statement: The datasets generated for this study are available on request to the corresponding author.

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