



## Article

# Long-Term Impacts of Forest Management Practices under Climate Change on Structure, Composition, and Fragmentation of the Canadian Boreal Landscape

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**Abstract:** Forest harvesting and fire are major disturbances in boreal forests. Forest harvesting has modified stand successional pathways, which has led to compositional changes from the original conifer-dominated forests to predominantly mixed and hardwood forests. Boreal fire regimes are expected to change with future climate change. Using the LANDIS-II spatially explicit landscape model, we evaluated the effects of forest management scenarios and projected fire regimes under climate change in northeastern Canadian boreal forests, and we determined the subsequent alteration in stand- and landscape-level composition, succession, and spatial configuration of boreal forests. We observed that, in contrast to successional pathways that followed fire, successional pathways that followed forest harvesting favored mixed forests with a prevalence of shade-intolerant hardwoods for up to 300 y after harvesting. This trend was exacerbated under climate change scenarios where forests became dominated by hardwood species, particularly in ecoregions where these species were found currently in low abundance. Our results highlight the failure of existing forest management regimes to emulate the effects of natural disturbance regimes on boreal forest composition and configuration. This illustrates the risks to maintaining ecosystem goods and services over the long term and the exacerbation of this trend in the context of future climate change.

**Keywords:** ecological modeling; ecosystem-based management; LANDIS-II; landscape ecology; mixedwood boreal forest; successional pathways

## 1. Introduction

In boreal forest ecosystems, stand-replacing disturbances, such as wildfires and insect outbreaks, determine the dynamics, structure, and composition of forests [1–3]. Mechanized harvesting has also been a major anthropogenic disturbance that affected the dynamics within boreal forests [4,5]. This form of harvesting (clear-cut) for timber production has attempted to emulate major disturbance regimes (such as fire) in terms of frequency and severity at the landscape scale to reduce the ecological differences between natural and managed landscapes [6,7].

Mechanized forest harvesting is an imperfect surrogate of fire disturbance, and its impacts on both successional dynamics and landscape characteristics can vary markedly. For example, pioneer species that require fire to regenerate were disadvantaged after harvesting compared with species that regenerated in the absence of fire; the result was an alteration of forest composition and successional dynamics because coniferous pioneer species were more dependent on fire than hardwood species [8]. The impact of forest harvesting on boreal landscapes was difficult to predict because it primarily targeted stands of sufficient age and market value following contiguous spatial patterns [4,9,10]. Thus, this disturbance caused important changes in forest structure and composition, decreased and fragmented the area of old-growth forests, and produced a large-scale shift from coniferous to mixed and hardwood stands [8,10–14]. These alterations in composition, structure, and biomass had negative implications for timber supply and value chains [15–17]. Overall, conifers are preferred over hardwoods by the industry due to the quality and type of products that can be manufactured [18].

Under future warming scenarios, the Quebec boreal region is expected to experience increases in both precipitation and temperature [19,20]. Nonetheless, the fire frequency for boreal stands is expected to be greater because higher temperatures will concentrate the precipitation in some short periods that will result in drier conditions during long periods of the year. Thus, this increased fire activity will affect the structure, composition, and functioning of forest landscapes markedly by promoting the recruitment of early-successional hardwood species and some conifers, such as jack pine (*Pinus banksiana*) [21]. Therefore, the presence of hardwood or mixed forests will expand at the landscape level, which will exacerbate the effects of forest harvesting on the composition and structure of the forest [18,22–25].

Forestry intensification (i.e., short rotation and increasing harvest rate) has been proposed often as a possible solution to reduce carbon emissions into the atmosphere [26,27] and minimize the risks related to an enhanced fire regime [28,29]. However, depending on forest conditions, there is considerable uncertainty associated with the effectiveness of such a strategy to prepare forests for climate change [30,31]. Intensification also increases the already significant human pressure (i.e., harvesting and mining) on these forest ecosystems and favors their further degradation [32].

A balance must be found between the contribution of forests toward climate change mitigation and the maintenance of the many ecosystem services that forests provide. Projections of future forest changes—over decades and centuries—may help guide the selection of appropriate forest management strategies to anticipate the sustainability of wood production within the boreal ecosystem under climate change. Nevertheless, insight into forest dynamics and recovery patterns in managed forests under future climate change are lacking [33,34].

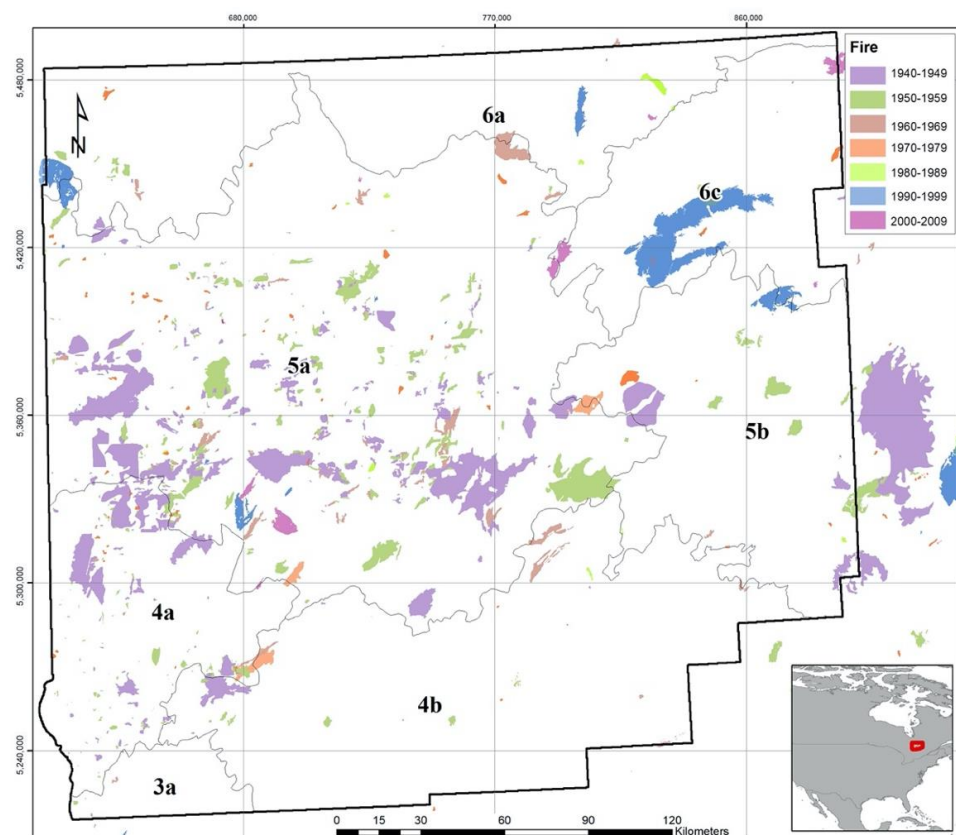
Advances in landscape modelling may be able to simulate and help understand the long-term and combined impacts of climate change and forest harvesting [35]. Thus, species composition and dynamics and their response to forest harvesting and climate change in North American boreal forests are key factors that need to be monitored [18,35]. The northeastern boreal forest of Canada (Abitibi plain) already exhibits evidence of the impact of forest management [4,12]. However, for a significant part of eastern Canada's boreal forest, mechanized forest harvesting only began recently [4]. Therefore, an assessment of the long-term effects of this harvesting, which include possible climate change-related modifications to the fire regime, is necessary to evaluate the sustainability of the forest industry. Here, we aim to evaluate the feasibility of maintaining wood production based on the composition, successional attributes, and spatial configuration of the boreal mixedwood forest under future climate change conditions. Because forest management generally leads to increasing dominance of non-fire-adapted species and smaller and more fragmented forest patches, we hypothesize that (i) forest harvest will have a greater impact on species dominance and composition under climate change scenarios compared with wildfires,

and (ii) the long-term impacts of harvesting will modify the spatial landscape structure profoundly and compromise wood supply for the industry in the next three centuries.

## 2. Materials and Methods

### 2.1. Study Area

This study covered an area of 67,600 km<sup>2</sup> of boreal forest in northeastern Canada (Abitibi plain) that presented a clear north–south climate gradient [36]. The area included specific types of vegetation that encompassed portions of six ecological regions as defined by the Quebec’s Ministère de la Forêt, de la Faune et des Parcs du Québec (Ministry of Forest, Wildlife and Parks (MFFP)) [37] (Figure 1, Table 1). In the northern part of the study area, average annual temperature was 1.2 °C and annual precipitation was 917 mm (La Sarre meteorological station). In the southern part of the study area, the average annual temperature was 3.4 °C, and the average annual precipitation was 831 mm (Ville-Marie meteorological station) [38]. In the south, the temperate mixedwood forests (balsam fir–yellow birch bioclimatic domain, ecological regions 4a and 4b) were dominated by mixed stands of yellow birch (*Betula alleghaniensis*) and conifers like balsam fir (*Abies balsamea*). The boreal mixedwood forests (balsam fir–white birch bioclimatic domain, ecological regions 5a and 5b) in the center of the study area were dominated by hardwood and mixed stands with shade-intolerant taxa, such as the hardwood species trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) and the coniferous jack pine. The result was a relatively heterogeneous (less aggregated) landscape. In the north, the boreal stands (spruce-fermoss bioclimatic domain, ecological regions 6a and 6c) were dominated by conifer stands of black spruce (*Picea mariana*) with occasional balsam fir distributed across the relatively homogeneous landscape of mature stands [12,39].



**Figure 1.** Study area in the Boreal Forest of Quebec with the ecoregions and historical fires classified by decade. The black line corresponds to the delimitation of the ecological regions 4a, 4b, 5a, 5b, 6a, and 6c. Ecological regions 4a and 4b (temperate mixedwood forests), 5a and 5b (boreal mixedwood forests), 6a and 6c (boreal conifer forests). See Table 1 for the detailed descriptions of the ecological regions.

**Table 1.** Characteristics and fire regime of the ecoregions within the study area in the Boreal Forest of Quebec.

Bioclimatic Subdomain	Ecological Region		Dominant Forest Cover	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)	Growth Season (Days)	Area (km <sup>2</sup> )	Studied Area (%)	Current Burn Rate (%)	Fire Return Interval— <i>k</i>
Balsam fir–yellow birch domain	4a	Simard Lake plains and hills	Mixed stands of yellow birch and conifers	2.5	800–1000	160–170	5943	79	0.048	2083
	4b	Cabonga watershed slopes		0–2.5	1000–1100	160–170	27,429	52	0.036	2778
Balsam fir–white birch domain	5a	Abitibi plains	Hardwood species or mixed stands with shade-intolerant hardwood species (trembling aspen, white birch) and jack pine	2.5	800–900	160	26,842	89	0.258	388
	5b	Gouin watershed slopes	Balsam fir and white spruce stands mixed with white birch	2.5	900–1100	150–160	15,758	51	0.048	2083
Spruce-moss domain	6a	Matagami Lake plains	Black spruce with scattered balsam fir	−2.5 to 0	700–900	140–160	48,842	18	0.239	418

Over the last 20 y, the study area experienced a reduction of about 20% in the allowable cut quota due to restrictions on the harvesting of fir, spruce, jack pine, and larch (*Larix* sp.) species [40]. The occurrence of wildfires in the study area was not uniform, and it showed a higher burn rate in the northern and western regions and a lower burn rate in the southeastern portion [41] (Figure 1, Table 1). The fire regime of each ecological region was described by the *k* parameter, which determined the return interval based on the rate of accumulation of combustible materials at a site (Table 1). A low value of *k* represented a rapid accumulation of fuel and a short interval. The values of *k* were adjusted from the current burning rate defined by Bergeron et al. [41].

## 2.2. Simulations of Succession after Fire and Harvesting under Different Scenarios of Climate Change

LANDIS-II is a spatially explicit forest landscape model that simulates forest dynamics at multiple spatial and temporal scales [42]. Thus, this model simulates forest stand processes, such as tree competition, establishment, and growth, and landscape processes, such as dispersal of tree species and disturbances, and it captures the successional pathways result of forest management and climate change [43]. LANDIS-II has been demonstrated to be a useful tool for conducting controlled experiments to predict the response of boreal ecosystems to spatial changes at stand and landscape levels, especially in southeastern Canada [13,44,45]. This model has been used widely to evaluate the impacts on forest composition and landscape heterogeneity after forest management after considering different climate change scenarios in southeastern Canada [13,46,47]. We used LANDIS-II to simulate forest dynamics at multiple spatial and temporal scales [42]. To identify the future spatial distribution and changes of stand types, we conducted 300 y simulations after fire under climate change and forest management scenarios (see details in Molina et al. [24]). The model simulated forest carbon (C) dynamics in response to different wildfire scenarios and anthropogenic interactions under projected climate warming [42,48]. The stocks of aboveground biomass (AGB) by species and by pixel were simulated for the entire study area [49].

The model was fed with the following four data sets scaled at 4 ha pixel size (200 m × 200 m): (1) An ecological region layer that divided the landscape on the basis of the similarity of soil and climatic conditions that followed the delimitation defined by the Quebec MFFP (ecological regions 4a, 4b, 5a, 5b, 6a, and 6c, see Table 1), (2) the life-history

traits (i.e., fire adaptation, shade tolerance, and composition) of the most dominant species (13 taxa) found in the study area (Table 2) [42,50–53], (3) an initial community layer that represented the current distribution of species by age across the study area, which was elaborated from the available fourth decennial forest inventory map of Quebec [54], and (4) a species-specific establishment probability by ecoregion estimated according to the proportion of the area occupied by each species by ecological region, which was obtained from the fourth decennial forest inventory of Quebec [54].

**Table 2.** Life-history attributes for the 17 species included in this study.

Specie	Longevity (Years)			Sexual Maturity (Years)			ST	FT	ED (m)		MD (m)		VRP	VRP	VRP	RPF
	Min	Mean	Max	Min	Mean	Max			Min	Max	Min	Max		Min Age (Years)	Max Age (Years)	
Gray birch	20	20	20	8	8	8	1	1	60	60	80	100	0.5	2	16	Sprout
Yellow birch	150	225	300	20	40	70	2	1	213	250	400	400	0	0	0	None
White birch	80	110	140	15	15	40	1	2	60	100	5000	5000	1	40	125	Sprout
White spruce	100	211	250	15	30	40	3	3	64	100	200	400	0	0	0	None
Black spruce	150	180	250	10	20	30	4	2	50	80	150	300	0	0	0	Serotiny
Red spruce	250	350	400	20	30	40	4	1	50	50	61	100	0	0	0	None
Tamarack	150	180	230	15	30	40	1	3	14	21	40	60	0	0	0	None
Eastern white pine	200	200	450	10	20	30	4	3	60	60	210	210	0	0	0	None
Jack pine	75	140	200	5	10	15	1	4	20	40	60	100	0	0	0	Serotiny
Red pine	200	300	400	15	25	50	2	4	12	12	275	300	0	0	0	None
Balsam fir	80	150	200	20	25	30	5	1	25	60	100	160	0	0	0	None
Red maple	80	100	150	4	10	10	4	1	100	100	200	1000	1	10	150	Sprout
Sugar maple	300	400	500	30	40	60	4	1	15	15	100	200	0.5	40	240	Sprout
Balsam poplar	120	140	150	8	10	20	1	2	200	1000	5000	5000	1	0	100	Sprout
Largetooth aspen	50	70	100	10	15	20	1	1	200	200	5000	10,000	1	7	56	Sprout
Trembling aspen	60	130	200	10	15	20	1	2	500	1000	5000	10,000	1	0	100	Sprout
Eastern white-cedar	300	350	400	6	30	35	4	1	45	45	60	60	0	0	0	None

ST: Shade tolerance, FT: Fire tolerance, ED: Effective seed dispersal distance in meters, MD: Maximum seed dispersal distance in meters, VRP: Vegetative reproduction probability, RPF: Post-fire regeneration. Vegetative reproduction minimum and maximum values were estimated as 10% and 80% of the mean longevity, respectively.

We used the Biomass Succession extension to project the changes in biomass over time [55]. We used the results of Boulanger et al. [47] to adapt the parameters of climate change to the species growth model under the same climate change and harvesting scenarios. Boulanger et al. [47] used the PICUS model to simulate the dynamics of individual trees across forest stand areas, which accounted for the population dynamics due to stress and age-related mortality that included forest fire and forest harvesting [47,56]. PICUS generated the inputs used to feed the Biomass succession extension in LANDIS-II that included species establishment probabilities by ecoregion according to the proportion of the area occupied by each species by ecological region from the fourth decennial forest inventory of Quebec (Table 3), net primary productivity, and aboveground biomass.

We used a baseline scenario “Baseline” of the 2010 annual burn rate and forest harvest (i.e., between 0.048% and 0.239% of the study area burned annually [41] and a forest harvest allowance of around 1% per year) [57]. The minimum age for harvesting conifers and hardwood species was set at 70 y and 50 y, respectively, which was observed in the study area (Table 2).

Fire was simulated using the extension Base-Fire [58]. The extension Base-Fire, which simulated stochastic fire events based on the annual area burned, fire occurrence, and mean fire size, was calibrated using a layer that compiled the historical forest fire events (1941–2006), which was registered by the Quebec forest fire agency (Société de Protection des Forêts Contre le Feu, SOPFEU), and the burn rate and ignition probability for the study area, estimated by Bergeron et al. [41]. Climate change is expected to affect fire frequency and severity in the study area [59]. We followed the representative concentration pathways (RCPs) climate change scenario 8.5 (hereafter, “RCP 8.5”). RCP 8.5 represented a low mitigation scenario with an increase of 7.0 °C in temperature and 7% in average precipitation

by 2100 (compared with the baseline) [60]. We selected this scenario because it represented some of the most potentially severe climate change impacts on boreal landscapes. To model how the fire regime affected forest composition, succession, and spatial configuration of boreal forests under the RCP 8.5 scenario, the changes in fire intensity were simulated according to Bergeron et al. [61], where they found an increase in the burn rate and in the fire return interval.

**Table 3.** Species establishment probability.

Specie	Ecoregion					
	4a	4b	5a	5b	6a	6c
Gray birch	1.73	0.54	1.45	1.47	7.40	0.84
Yellow birch	2.88	14.17	0.08	0.87	0.00	0.00
White birch	36.93	59.67	27.09	43.83	15.40	12.13
White spruce	2.00	1.60	1.50	0.54	1.91	2.78
Black spruce	36.13	37.25	52.35	57.14	57.41	80.71
Red spruce	21.30	25.48	0.14	5.87	0.03	0.01
Tamarack	2.76	1.24	5.56	1.99	0.44	0.17
Eastern white pine	2.37	2.13	0.03	0.00	0.00	0.00
Jack pine	15.11	14.04	21.65	27.24	30.30	30.29
Red pine	0.90	0.16	0.01	0.00	0.00	0.00
Balsam fir	24.93	17.78	15.68	19.25	11.11	12.77
Red maple	4.85	12.54	0.42	1.49	1.30	0.05
Sugar maple	0.20	2.02	0.01	0.02	0.00	0.01
Balsam poplar	24.59	9.66	21.68	8.53	18.08	4.65
Large-tooth aspen	24.32	9.65	21.67	8.53	18.08	4.65
Trembling aspen	35.17	14.09	32.08	12.53	28.74	8.46
Eastern white cedar	1.64	4.37	0.17	0.03	0.00	0.00

Forest harvest was simulated using the extension Base-Harvest [48]. To model future annual harvesting, we used 14 forest management units (FMU) that covered the study area, which was defined according to the MFFP in which specific harvesting prescriptions were planned [62]. For each forest management unit, we defined a forest management scenario on the basis of the maximum area that could be harvested under the current annual allowable cut (AAC) volume that was calculated for 2013–2018 Quebec’s chief forester, [57] and the minimum tree age for harvesting conifer and hardwood species. Our high-intensity scenario represented a 2% harvest ratio, the maximum forest area that could be harvested annually, and the minimum age for harvesting conifers and hardwood species was set at 50 y and 30 y, respectively. Thus, there was no tree size restriction to be harvested when the stands exceeded these age thresholds. We labeled this high-intensity scenario with an enhanced fire regime and harvest rate scenario as “RCP 8.5 5030\_2%”, where RCP 8.5 represented a low climate change mitigation scenario and 5030\_2% represented the high-intensity harvest ratio.

### 2.3. Successional Pathways after Fire and Forest Harvesting

To account for the variability among simulations, we performed five repetitions for each model simulation (Baseline and RCP 8.5 5030\_2%), each run for 300 y (2010–2310) at a 20 y time step, and 200 m resolution (4 ha) to meet the minimum sample number required for statistical analysis [63]. Then, to evaluate how forest management emulated fire disturbance in terms of forest composition and landscape structure, we created successional pathway curves that relied on the AGB accumulated by species and year for each individual pixel disturbed by fire or harvested at the beginning of the disturbance event. For each disturbance (fire or forest harvesting), five disturbed pixels were selected randomly from each of the six ecological regions, which followed the two scenarios that we described, Baseline and RCP8.5 5030\_2% (other simulated scenarios are available in Molina et al. [24]). We also grouped the 13 tree species (Table 2) according to their functional characteristics: (1) Fire

adaptation (adapted or not adapted), (2) shade tolerance (intolerant, moderately tolerant, tolerant, or very tolerant), and (3) functional composition (conifer or hardwood species). For the three groups of species' functional characteristics (fire adaptation, shade tolerance, and composition), we created successional pathways curves that used the summed biomass of all species that comprised each functional characteristic group by combining and averaging the biomass according to the initial disturbance.

#### 2.4. Spatial Patterns and Landscape Metrics of the Study Area

Spatial projection maps that covered a 300-y period were created using the AGB accumulated by pixel to identify the main changes according to the functional characteristics of the species (see details in Molina et al. [24]). For the fire-adapted group, pixels were classified as fire-adapted when  $\geq 70\%$  of the AGB corresponded to fire-adapted species. A non-fire-adapted classification was given when  $\geq 70\%$  of the AGB corresponded to non-fire-adapted species, and a mixed classification was applied when the AGB was classified neither as adapted nor as non-adapted. For shade tolerance, pixels were classified as intolerant when  $\geq 70\%$  of the AGB corresponded to shade-intolerant species, moderately tolerant when  $\geq 70\%$  of the AGB corresponded to species having moderate tolerance to shade, and shade tolerant when  $\geq 70\%$  of the AGB corresponded to shade-tolerant species. The classification of very tolerant was given when  $\geq 70\%$  of the AGB corresponded to very shade-tolerant species. The third group, composition, was classified as hardwoods or conifers if  $>70\%$  of the species in the stand were hardwoods or conifers. We excluded pixels that did not meet any of the above conditions.

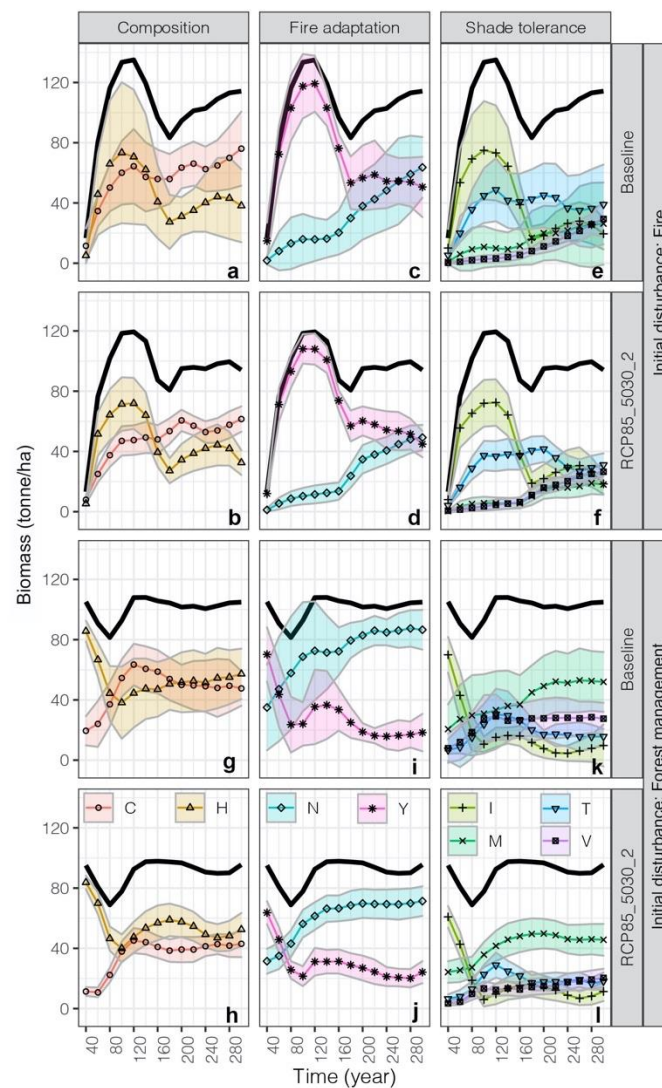
Furthermore, a metric analysis of the forest maps generated by the spatial projection was performed with the software FRAGSTAT v.4.2 [64] to determine the maximum difference between scenarios over time (Baseline and RCP 8.5 5030\_2%). Spatial variability was described using three metrics: The AGB of the area (mean area "AREA"), shape (perimeter-area ratio "PARA"), and aggregation (aggregation index "AI"). AREA described the mean stand area in hectares by class. PARA was a simple measure of shape complexity by dividing the perimeter by the area. PARA was equal to 1 when the shape was a square and increased as the form became less regular or more sinuous. The value increased with a greater border effect and smaller core area. AI showed the frequency with which different pairs of patch types appeared side-by-side on the map, which measured the level of aggregation of each class stand [64].

### 3. Results

#### 3.1. Post-Fire and Post-Harvest Successional Pathways

The results of the Baseline successional simulations were generally consistent with current observations of the successional pathways in the study area. Moreover, simulated current biomass ( $t = 0$ ) was consistent with the actual biomass reported in the NFI forest cover maps [47,65].

After a fire within the Baseline scenario, hardwood species increased in AGB to ca. 75 tonne/ha for ca. 100 y and then decreased thereafter by about 60% until the end of the simulation (Figure 2a). Over the same period, conifer AGB increased rapidly to ca. 60 tonne/ha after about 120 y. Conifer AGB then remained relatively stable until the end of the simulation. Under the most extreme climate change and harvest scenario (RCP 8.5 5030\_2%), AGB followed a similar trajectory to Baseline, although at lower values. AGB reached ca. 60 tonne/ha and 30 tonne/ha for conifer and hardwood species, respectively, by the end of the simulation period (Figure 2b).



**Figure 2.** (a–l) Successional pathways of aboveground biomass (AGB, tonne/ha) in the Boreal Forest of Quebec of the functional characteristics groups of tree species in relation to fire and forest management over the simulation period for the Baseline and RCP 8.5 5030\_2% scenarios. Left column: Species composition; H, group of hardwood species and C, group of conifer species (see hardwood species and conifer species considered in Table 2). Middle column: Species fire adaptation; Y, group of species with fire adaptations; and N, group of species without fire adaptations. Right column: Species shade tolerance; I, group of shade-intolerant species; M, group of species with moderate shade tolerance; T, group of shade-tolerant species; and V, group of very shade-tolerant species. The solid black line represents the total AGB (tonne/ha). Shaded areas around the mean AGB over time for the various functional characteristic groups correspond to the mean standard error.

The post-fire AGB of the fire-adapted species in the Baseline scenario increased for ca. 120 y to reach a maximum of 120 tonne/ha, which was followed by a rapid decline of 58% at about 180 y. AGB remained relatively stable thereafter to the end of the simulation. In contrast, AGB of non-fire-adapted species in the Baseline scenario increased slowly but steadily during the simulation and reached 60 tonne/ha at the end of the simulation (Figure 2c). Under the RCP 8.5 5030\_2% scenario, AGB of the fire-adapted species increased for ca. 120 y to a maximum of 110 tonne/ha and then decreased rapidly to approximately half by the end of the simulation period. AGB of non-fire-adapted species in the RCP 8.5 5030\_2% scenario increased slowly but steadily throughout the simulation and reached 50 tonne/ha after 300 y (Figure 2d). In both the Baseline and RCP 8.5 5030\_2% scenarios,



shade-intolerant species showed similar trends as fire-adapted taxa, whereas moderately tolerant species and very shade-tolerant species followed a pattern that was similar to that of the non-fire-adapted trees. In the latter scenarios, AGB of shade-tolerant species increased for approximately 100 y and then stabilized at about 40 tonne/ha for approximately 100 y (until 200 y in the simulation); thereafter, AGB of shade-tolerant species experienced a decrease (Figure 2e,f). In almost all considered cases, total AGB in the RCP 8.5 5030\_2% scenario was about 25% lower than that of Baseline (Figure 2a–f).

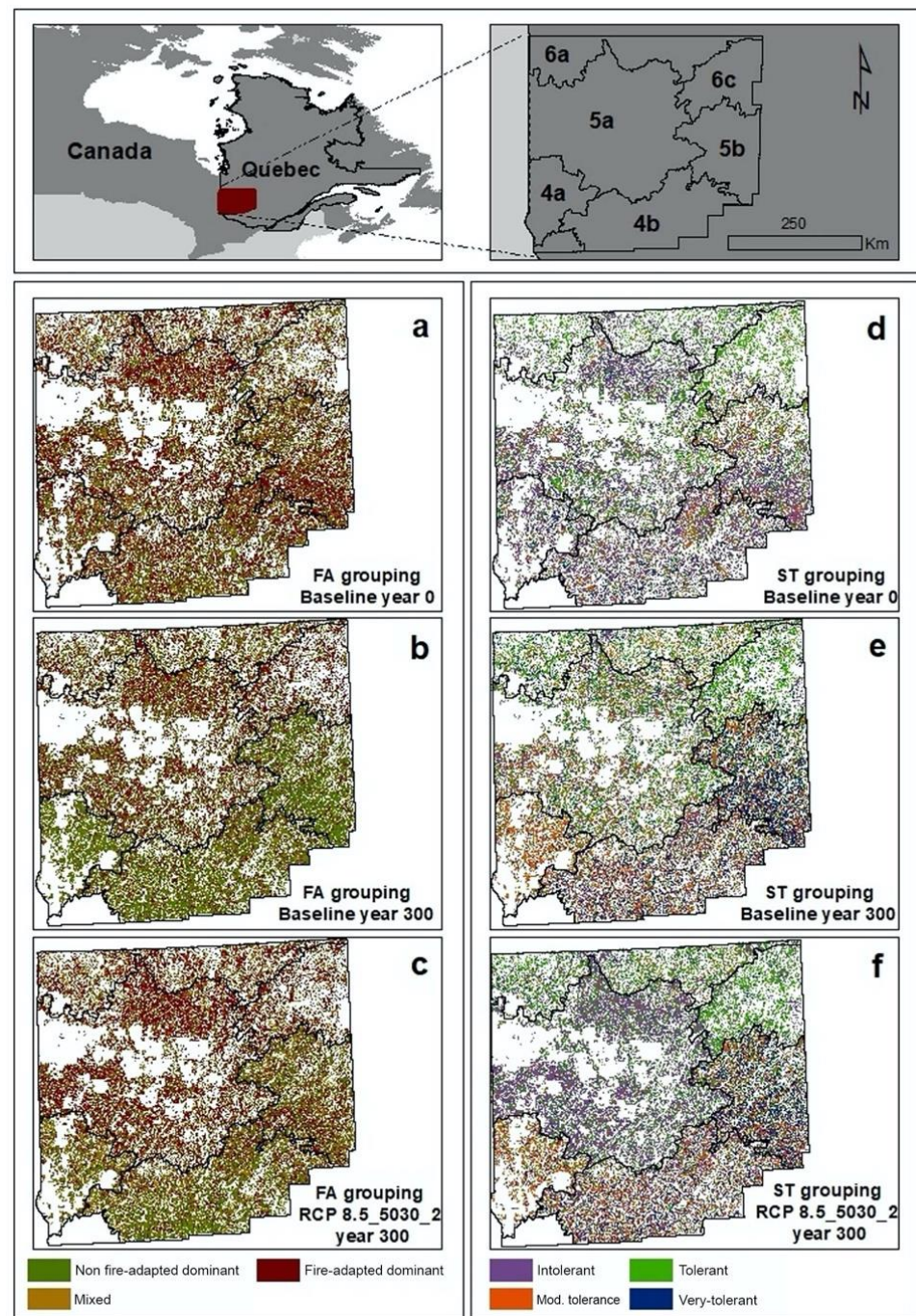
Post-harvest AGB patterns in Baseline and RCP 8.5 5030\_2% were similar at the beginning of the simulation. In both, AGB of hardwood species declined continuously over the first 100 y of simulation to ca. 40 tonne/ha and then stabilized. Conifer AGB increased steadily to reach levels near that of hardwood species after 120 y. Conifer AGB then remained stable around 40–45 tonne/ha (Figure 2g,h). In contrast to the post-fire successional patterns of the Baseline and RCP 8.5 5030\_2% scenarios, forest management favored an increasing AGB for non-fire-adapted species over the simulation period. AGB of non-fire-adapted species increased steadily to reach a maximum of approximately 90 tonne/ha at the end of the simulation for the Baseline scenario and approximately 70 tonne/ha under the RCP 8.5 5030\_2% scenario (Figure 2i,j). Post-forest management in both the Baseline and RCP 8.5 5030\_2% scenarios had, at the end of the simulation period, moderately shade-tolerant species that dominated over shade-intolerant, shade-tolerant, and very shade-tolerant species with an AGB of ca. 50 tonne/ha (Figure 2k,l). The post-forest management AGB was higher in the Baseline than in the RCP 8.5 5030\_2% scenario. However, the difference between scenarios was only about 10% (Figure 2g,l).

### 3.2. Spatial Changes in the Successional Pathways under Climate Change and Forest Management Scenarios

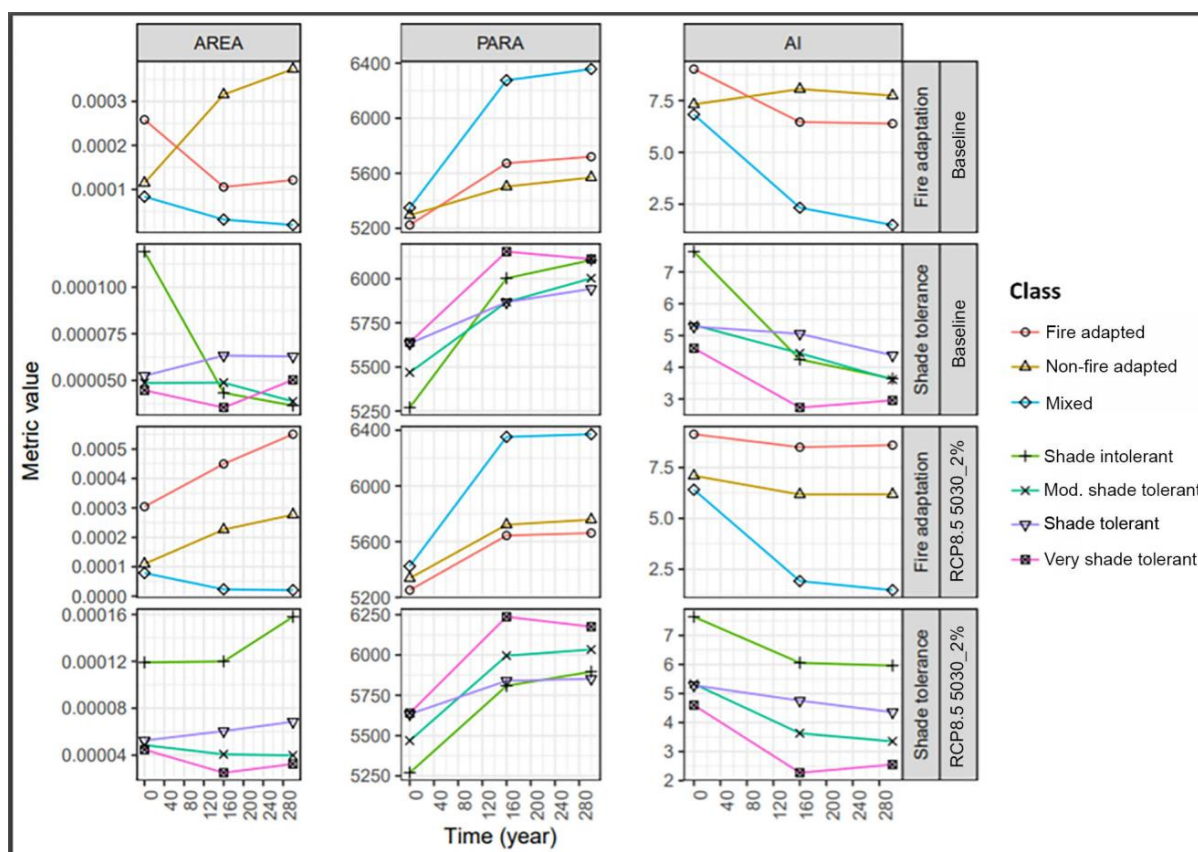
At the beginning of the simulation period (year 0), stands were dominated by fire-adapted species (Figure 3a). After 300 y in the baseline and the RCP 8.5 5030\_2% scenarios, the proportion of stands dominated by non-fire-adapted species had increased in the southern portion of the study area (ecological regions 4a, 4b, and 5b), whereas the proportion of stands dominated by fire-adapted species had increased in the north (ecological regions 5a, 6a, and 6c) (Figure 3b,c). This trend was exacerbated under the most extreme climate change and greater forest harvesting scenarios (RCP 8.5 5030\_2%) relative to the Baseline scenario (Figure 3c).

The southern and eastern regions of the study area had a higher proportion of shade-intolerant species at the beginning (year 0), whereas the northern part contained a higher proportion of stands dominated by shade-tolerant and very shade-tolerant species, which revealed the forest management pressure and dominant species in those regions (Figure 3d). However, the proportion of stands dominated by shade-intolerant and moderately shade-tolerant species in the Baseline scenario increased in the south (ecological regions 4a, 4b, and 5b) after 300 y (Figure 3e). We noted a similar response for shade-tolerant species in the northern portion of the study area (ecological regions 5a, 6a, and 6c) after the 300-y simulation. A higher proportion of stands dominated by shade-intolerant species was observed in the southern and central regions of the study area (ecological regions 4a, 4b, 5a, and 5b) under the most extreme climatic and harvesting scenarios (RCP8.5 5030\_2%), whereas the northern part of the study area remained dominated by shade-tolerant trees (ecological regions 5a, 6a, and 6c) (Figure 3f).

The landscape metrics showed that the stands dominated by non-fire-adapted species increased in mean area (AREA) over time, whereas the stands dominated by mixed and fire-adapted species decreased under the Baseline scenario (Figure 4). We also noted a simultaneous increase in shape complexity (PARA), which indicated an increase of border area and a decreased stand aggregation (AI). Metrics for the shade tolerance functional group showed that stands dominated by shade-intolerant species decreased in mean area (AREA) until the year 160. After this time, all shade tolerance classes (I, M, T, and V) remained more or less constant.



**Figure 3.** Simulations of fire adaptation (FA) and shade tolerant (ST) functional groups of trees in the Boreal Forest of Quebec under the Baseline and RCP 8.5 5032\_2% scenarios at the beginning (year 0) and at the end of the simulation (year 300) for the study area. (a) Fire adaptation functional group in the Baseline scenario at the beginning of the simulation period, (b) fire adaptation functional group in the Baseline scenario at the end of the simulation period, (c) fire adaptation functional group in the RCP 8.5 5030\_2% scenario at the end of the simulation period, (d) shade-tolerant functional group in the Baseline scenario at the beginning of the simulation period, (e) shade-tolerant functional group in the Baseline scenario at the end of the simulation period, (f) shade-tolerant functional group in the RCP 8.5 5030\_2% scenario at the end of the simulation period. White areas on the map represent agricultural areas or water bodies.



**Figure 4.** Landscape metrics from Figure 3 for the functional species groups of trees in the Boreal Forest of Quebec. (1) Fire adaptation and (2) shade tolerance under the baseline modeling scenario and the most severe climate change and forest management scenario RCP 8.5 5030\_2%. Landscape metrics: AREA (mean patch area), PARA (measure of shape complexity), and AI (patch aggregation measurement).

Stands dominated by fire-adapted and non-fire-adapted species increased slightly in mean area over the simulation, whereas mixed stands (i.e., stands where the proportion of fire-adapted or non-fire-adapted species was <70%) decreased in mean area under the extreme climate change and forest harvesting scenarios (RCP8.5 5030\_2%) by almost 100% (Figure 4). In addition, shape complexity (PARA) increased for both evaluated functional groups (shade tolerance and fire adaptation), but especially for mixed-species stands. AI presented a contrasting trend to that of shape complexity. Shade-intolerant stands under the most severe climate change scenario had a mean stand area (AREA) that increased over the simulation period, which was a trend that was opposite to that observed in the Baseline scenario for shade-intolerant stands. Similar to the Baseline scenario, PARA increased over time by about 20%, whereas stand aggregation (AI) decreased by 25%–80%, which depended on the shade tolerance class (Figure 4, RCP 8.5 5030\_2%).

#### 4. Discussion

Our study demonstrated that the initial type of disturbance (i.e., fire or harvest) had a much greater impact on forest successional dynamics than the landscape disturbance type, which supported our first hypothesis. Based on our simulations, forest management has not been able to emulate natural post-fire succession and landscape configuration. Thus, contrary to post-fire successional pathways, forest management favored non-fire-adapted species in the early-successional stages, which led to the prevalence of mixed forests after 300 y.

At the landscape scale, the combination of an enhanced fire regime due to climate change and the intensification of the cutting rate led to a more heterogeneous landscape

with more complex shapes, disaggregated stands, and smaller stand areas. Shade-intolerant and generally fire-adapted species generally were dominant over the simulation period under a climate change scenario, which supported our second hypothesis. Nevertheless, even the Baseline scenario showed marked changes in landscape structure and tree species composition after 300 y. These results indicate that even without the influence of climate change, current management strategies will cause significant changes in boreal landscape characteristics eventually. Severe climate change and forestry intensification will exacerbate the current effects of forest management.

As reported in many boreal forests, our model showed that fire-induced changes in stand composition over time generally depicted a successional pathway from hardwoods or mixed stands to a mixture of hardwoods and some conifer species (mixedwoods) and, finally, to conifer-dominated stands [66,67]. However, multiple pathways are possible depending on pre-fire stand composition and the specific local site conditions [1,66,68].

Similarly, at the final successional stage, shade-intolerant and fire-adapted species can still be present to a limited degree [69,70]. Secondary disturbances showed a large gradient of severity in the mixedwood boreal forest, from the tree to a landscape scale [69,71,72]. In this context, variability in the severity of secondary disturbance allows the regeneration of early-successional species even if forests are several centuries old but in a much smaller proportion than late-successional species. Therefore, the congruence between our results based on LANDIS-II simulations and actual observations in old-growth forests highlights the ability of this model to accurately describe forest structural changes over long timescales. It is noteworthy that LANDIS-II could not simulate possible fires that started from outside the study area and that spread to the study area [73,74], which may have affected the simulation of the conditions of the boundary of forest landscapes.

In contrast to fire, forest management may favor the pre-established regeneration of shade-tolerant conifers, regardless of their fire adaptation [75,76]. We observed similar results for both the Baseline and climate change scenarios. In general, in the early-successional stages after post-forest harvesting, residual trees or shade-tolerant species that were already established under the canopy held an advantage over shade-intolerant species, which began to emerge in the canopy at the end of the early-successional stages or during the intermediate successional stages [77–79]. Thus, depending on pre-disturbance stand composition and the type of disturbance, stands may return to their initial successional stage because the protected regeneration contains a larger proportion of conifers [8]. This scenario may lead hardwood species such as aspen, which dominated or co-dominated stands due to its competitive advantage over conifers, to colonize open areas [80,81]. For instance, aspen-dominated, mixed, and conifer-dominated stands are likely to respond differently to partial cutting and clearcutting. Overall, these results underscored those successional dynamics following harvest markedly differed from post-fire dynamics, which was independent of harvesting and climate change scenarios.

Interestingly, the studied scenarios differed minimally regarding the successional process for the same initial disturbance; however, they showed an important divergence at the landscape scale. Forest management has increased stand fragmentation when compared with forest fire disturbance and will accelerate this trend in the future (Figure 4). In particular, the landscape of northwestern Quebec has become progressively more heterogeneous since the beginning of forest management [8,12]. This fragmentation has produced more complex patch shapes, smaller core areas, and more isolated patches that have changed the landscape composition and affected the relative abundance of the conifer-dominated, mixedwood, and hardwood-dominated stands [12]. The expected higher burn rate of boreal stands in the future would be advantageous for forests dominated by shade-intolerant and fire-adapted species, especially in ecoregions where these taxa are currently at a lower abundance (central and northern portions of the study area). For example, more frequent fires will favor the recurrence of stands dominated by jack pine or birch, in which jack pine may be present with or without black spruce [82]. Molina et al. [24] emphasized that the impacts of climate change and forestry intensification were additive but did not interact

within this study area. Hence, climate change will mainly exacerbate the effects of forest management, which will produce more sinuous forest shapes and more fragmented areas at the landscape level [83]. Our study, however, considered only the effects of climate change as a function of the changes in fire frequency. It is also possible that boreal species may be less adapted to the new climatic conditions in the study area and may be replaced by temperate forest species. However, the rate of change for this species replacement remains uncertain [84,85]. Nevertheless, given the heightened fire and logging regimes, it is likely that the ecological traits of the new species that will become established in the study area would be similar to those of the boreal species favored by each scenario.

It is also important to note that even the Baseline scenario modified the study area markedly after 300 y of simulation. In contrast to post-fire successional pathways, forest management favored the development of a mixed forest with a higher prevalence of hardwood-dominant stands even after 300 y (Figures 2 and 3). This change in forest composition—with an increase of non-fire-adapted and hardwood species compared with fire-related changes—suggests that there will be a modification of the two key attributes of biodiversity and biological legacies, such as remnant old-growth trees and deadwood, which contribute to the resilience and resistance of this forest ecosystem [11,21]. This alteration of species composition and landscape heterogeneity implies a lower ecosystem redundancy, which is a trait necessary for responding to disturbances and stresses [6]. Similarly, the spatial structure of the study area was altered markedly over the simulation, which resulted in greater fragmentation and smaller core areas after 300 y. This shift implies that even if climate change and increasing forest harvest pressure change the boreal landscapes markedly in the future, the forthcoming impacts of existing forest management strategies are also non-negligible. These results are consistent with many previous studies that have highlighted the important discrepancy between the impacts of harvest and fire in boreal landscapes, e.g., [10,24,86,87].

Since 2013, the province of Quebec has aimed to apply ecosystem-based management within its public forests, with the objective of bringing management closer to natural disturbance dynamics [6]. It is likely, however, that the combination of (i) the specific successional pathway that characterizes harvested stands compared with burned stands, (ii) a harvest rate greater than the fire rate, and (iii) the use of clearcuts at a relatively early stand age that truncated forest succession, produced the changes in landscape characteristics observed after 300 y in the Baseline simulations. This observation underlines that current management strategies—without the added influence of climate change—cannot be enough to maintain the forest characteristics of the study area that are observed currently.

#### *4.1. Implications for Forest Management*

Existing forest management practices are not sufficient to emulate the post-fire successional pathways in terms of stand composition and landscape configuration. The increased harvest of forest areas under current practices decreases the abundance of species typical of mid- and late-successional stages [88] because these are the most sought-after species for the timber industry. Among the consequences of these management practices will be a decrease in the abundance of species of higher economic value, whereas the abundance of species of lower economic value, such as birch and aspen, may increase. Current forest management practices seek to harvest species for timber, principally balsam fir, spruce, pine, and larch [89]. However, under the RCP 8.5 5030\_2% scenario, most of these desired species are expected to become less abundant. This projection implies that the timber industry will likely have to access a higher proportion of less valuable species and be forced to find alternatives for ensuring sustainable revenue.

To mitigate the depletion of conifer timbers, Kruhlov et al. [90] recommended changing the abundance of species at the landscape scale by taking into consideration a changing climate and landscape gradients by enriching the understory with the desired species to ensure the appearance of conifers in early- and mid-successional stages. Regeneration enrichment with conifers will shorten the time for conifers to appear within the stands—

a scenario not simulated in our study—and allow them to dominate in mid- and late-successional stages, which is a period in which post-fire stands are generally dominated by conifers [91]. In addition, alternative silvicultural interventions (e.g., various forms of partial cutting) need to be developed at a reasonable cost to better emulate secondary disturbances, such as wind and insects, rather than simply attempting to emulate the effects of wildfire disturbance. These alternatives must aim to maintain both the pre-industrial forest characteristics of composition and age class distribution and a coniferous forest cover [92,93]. Additionally, because of the economic impacts of such alternatives, improved solutions must integrate fire risk into the timber supply within a decision support framework [29].

#### 4.2. Model Limitations and Uncertainties

Climate change influences forest landscapes in different ways, such as tree species growth, mortality, and dispersal [94], nutrient cycles, shifts in the atmospheric concentration of CO<sub>2</sub> and soil nitrogen deposition and their fertilizing effect [95,96], changes in natural disturbance regimes, such as fires [97] and insect outbreaks [98], and variations in seasonal weather patterns—(e.g., the timing of spring thaw) [99] that introduced a lot of uncertainty in the model that is not estimated. All those variables have a direct effect on the structure and composition of forests. However, our simulations were consistent with current observations of the successional pathways in the study area. Although satisfactory simulations under current conditions do not guarantee consistent landscape projections under climate change [100], we were looking for the direction of trends rather than the exact magnitude of the changes. This model included several phenomenological components. However, other natural disturbances, such as insect outbreaks, may also have some impact on forest structure and composition [98], and their impact may increase in the future with increasing fire regimes under climate change [101]. Regardless of the potential importance of secondary natural disturbances, changes in the fire regimes within the study area were only incorporated in our modeling to determine the exact role of climate and management on forest structure and composition at the landscape scale.

Moreover, despite the possible uncertainties in the landscape dynamics model due to model formulations, LANDIS-II simulations have been used in many studies, and its validity has been reported widely for boreal forests worldwide [13,46,47,55,83,102,103]. Boulanger et al. [44] used many model approaches to project the performance of tree species under future climate change in boreal forests of Quebec, Canada, and they found that despite the different assumptions among models, they were reliable in predicting species responses under high forcing due to climate change.

### 5. Conclusions

Our simulations indicated that current forest management practices have an impact on the long-term structure, composition, and patch characteristics of stands at the landscape level. The result will be less resilient forest ecosystems. Moreover, the intensive management practices under future climate warming scenarios, along with an increase in wood demand, show important changes in forest composition with implications for the wood supply chain. Thus, our results highlighted the limitation of current forest management practices in emulating natural post-fire succession. This demonstrates the need to look for new silvicultural practices that are inspired by natural forest dynamics to maintain economic and social sustainability, in particular, in the context of future climate change. LANDIS-II modeling, which relied on our current understanding of the ecological processes that structure boreal forests and landscapes, proved very useful for conducting controlled experiments to discover general trends of boreal ecosystem response to several long-term spatial changes at both the stand and landscape levels.

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**Conflicts of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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