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Resilience of natural forests can jeopardize or enhance plantation productivity

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A R T I C L E I N F O

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A B S T R A C T

The demand for wood products continues to increase globally. Productivity of forest plantations can be greater than that of naturally regenerated forests. Plantation forestry could thus be employed to meet up to 75% of global wood supply by 2050. The resilience of natural forests could jeopardize plantation productivity. If the plantation scenario is not oriented in the same direction as the natural successional trajectories that are driven by resilience, then naturally regenerating tree species could recover to the detriment of planted species. Unproductive plantations will likely generate sustainability issues, as they must provide ecosystem services (e.g., wood fiber production) while being economically viable for forest management to be sustainable. Our general objective of our study was to assess whether resilience of natural forests can jeopardized plantation productivity. We studied successional trajectories in recent, young and old black spruce plantations that are located within the balsam fir ecological region on balsam fir ecological site types. To compare with a plantation scenario that was more susceptible to aiming in the same direction as resilience-driven successional trajectories, we also studied successional trajectories in recent, young and old black spruce plantations that are not only located within the balsam fir ecological region, but on black spruce ecological site types. Successional trajectories on balsam fir ecological site types pointed towards recovery of balsam fir and white birch, to the detriment of black spruce. Successional trajectories on black spruce ecological site types pointed towards the recovery of black spruce. Thus, we showed that resilience of natural forests could jeopardize plantation productivity when the plantation scenario is not oriented in the same direction as resilience-driven successional trajectories. It also can enhance plantation productivity when the regime is oriented in the same direction as resilience-driven successional trajectories. To ensure that plantations are economically viable and promote sustainability, forest managers should thus favor plantation scenarios that point in the same direction as resilience-driven successional trajectories. Finally, we suggest adopting such scenarios, and stress that it would also be necessary to develop regimes that would promote sustainability in the context of alternative successional trajectories that will undoubtedly arise because of global changes.

1. Introduction

The demand for wood products continues to increase globally (FAO, 2010). Productivity of forest plantations can be greater than the productivity of naturally regenerated forests (Paquette and Messier, 2010). Plantation forestry, therefore, could be employed to meet up to 75% of global wood supply by 2050 (FAO, 2010) and are expected to dominate future industrial wood supply (Carle and Holmgren, 2008). Yet, the very resilience of natural forests could jeopardize plantation productivity (Seidl et al., 2016; Mori et al., 2017; Barrette et al., 2019). Resilience refers to the capacity of a system to absorb a disturbance and reorganize so that the same structure and functions are essentially recovered, e.g., a natural forest recovering to a forest of similar composition, structure and function after clearcutting (Holling, 1973, Gunderson, 2000). Consequently, if the plantation scenario is not oriented in the same direction as the natural successional trajectories that are driven by resilience, then naturally regenerating tree species could recover and exert significant competition to the detriment of planted species with impacts on stand structure and productivity. Unproductive plantations will generate sustainability issues, as they must provide ecosystem services (e.g.,

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wood fiber production) while being economically viable for forest management to be sustainable (Kneeshaw et al., 2000; Barrette et al., 2014a; Köhl et al., 2015). Usual goals of plantation scenarios are to manage density, distribution and composition to minimize competition and maximize productivity of a desired tree species (Bell et al., 2006; Thiffault et al., 2013). But even when the main objective of plantation establishment is not focused on fiber production only (see Paquette and Messier, 2010), planted trees must survive and grow adequate so reforestation efforts can help respond to the global challenges of conservation of biodiversity and natural capital, climate mitigation, and poverty alleviation (Neves Silva et al., 2019).

Canada's forests make up about 9% of the world's total forest area and Quebec accounts for 22% of the national wood supply of the country (National Forestry Database, 2020). About 120 M seedlings are planted every year in this province only (Delisle, 2020). Black spruce (*Picea mariana* (Miller) B.S.P.) plantations frequently occur on balsam fir (*Abies balsamea* (L.) Miller) ecological site types within the balsam fir ecological region (Fig. 1; MFFP, 2018). Black spruce has higher economic value and is less vulnerable to eastern spruce budworm (*Choristoneura fumiferana*) than fir. Ecological site types are a land classification unit that is determined by climate, superficial deposits, soil texture, slope, drainage and understory indicator species, and which predicts natural successional trajectories (Grondin et al., 2013; Robitaille et al., 2015; Prach et al., 2016). On balsam fir ecological site types, natural successional trajectories that are driven by resilience point toward the recovery of balsam fir and birch species (Barrette et al., 2019). Although planting black spruce on balsam fir ecological site types is widespread within the balsam fir ecological region, we do not know whether the productivity of these plantations could be jeopardized by the resilience of balsam fir forests. Moreover, plantations in this region of North America are established under an ecosystem-based management paradigm and under extensive silviculture regimes, which entail minimal vegetation management treatments and precludes the use of herbicides (Thiffault and Roy, 2011). Indeed, forest management in general, and plantation silviculture in particular, must now address new societal challenges so that the so-called "licence to operate" in the development or extraction of natural resources can be maintained (Moffat et al., 2015). Hence, the productivity of these plantations is especially vulnerable to the resilience of balsam fir forests.

Our general objective was to assess whether resilience of natural forests can jeopardize plantation productivity. To determine if naturally regenerating tree species recovered to the detriment of black spruce, we studied successional trajectories (Buma and Wessman, 2011, Hidding et al., 2013, Ghazoul et al., 2015). We analyzed species composition of saplings and trees in recent, young and old black spruce plantations that are located within the balsam fir ecological region on balsam fir ecological site types (Fig. 1). To compare with a plantation scenario that is more susceptible to aiming in the same direction as resilience-driven successional trajectories, we analyzed species composition of saplings and trees in recent, young and old black spruce plantations that are also located within the balsam fir ecological region, but on black spruce ecological site types (Fig. 1). We predicted that successional trajectories on balsam fir ecological site types would point towards the recovery of naturally regenerating species, notably balsam fir and white birch (*Betula papyrifera* Marshall), to the detriment of the desired black spruce. We also predicted that successional trajectories on black spruce ecological site types would point towards the recovery of naturally regenerating tree species, notably black spruce, to the benefit of the desired species.

2. Materials and methods

2.1. Study area

Our study area is in the balsam fir ecological region that is located in eastern Canada (Fig. 1; Grondin et al., 2007). Mean annual precipitation is 1101 mm, mean annual temperature is 2 °C, and mean annual number of frost-free days is 110 (Grondin et al., 2007). This ecological region is

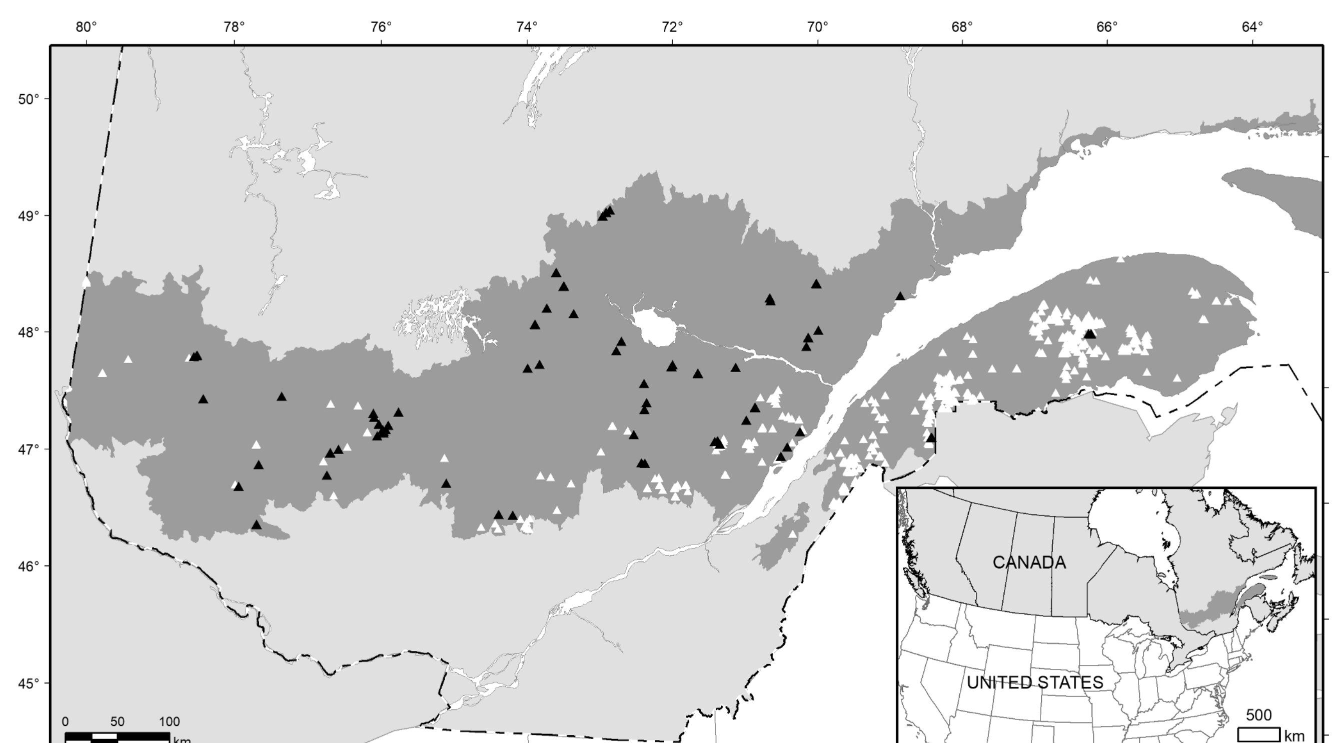

Fig. 1. Location of sample plots from the provincial governmental Forest Inventory Program in eastern Canada. We used data from plots that were established from 1953 to 2016 within the balsam fir ecological region (dark gray area), in black spruce plantations on balsam fir ecological site types (white triangles; n = 881) and in black spruce plantations on black spruce ecological site types (black triangles; n = 83).

disturbed by insect outbreaks (e.g., Eastern Spruce Budworm) blowdowns and fire (Grondin et al., 2007; MRN, 2013). Common tree species are balsam fir, white or paper birch, yellow birch (*B. alleghaniensis* Britton), black spruce, white spruce, red spruce (*Picea rubens* Sargent), jack pine (*Pinus banksiana* Lambert), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), northern white cedar (*Thuja occidentalis* (L.), eastern larch or tamarack (*Larix laricina* (Du Roi) K. Koch), sugar maple (*Acer saccharum* Marshall), red maple (*A. rubrum* L.), balsam poplar (*Populus balsamifera* L.) and trembling aspen (*P. tremuloides* Michaux) (MRN, 2013).

2.2. Data

We used sample plots of the Forest Inventory Program of the provincial government of Quebec (MRNF, 2006a, 2006b). To monitor forest growth and compostitional change, plots were spread across the forest area in a stratified random manner. We selected plots that were identified as black spruce plantations, in the balsam fir ecological region, on balsam fir (n = 881) or on black spruce (n = 83) ecological site types according to the Eco-Forest Stand Map (Fig. 1; MRNF, 2009). Plantations were established historically according to provincial guidelines. This particular silvicultural regime includes clearcutting followed by mechanical site preparation, planting of about 2 000 nursery seedlings per hectare and mechanical release during sapling development. Plots were located on mesic sites (balsam fir sites, 96%; black spruce sites, 84%), sub-hydric (3%; 11%) or xeric sites (1%; 5%; MRNF, 2009). Trees (diameter at breast height, DBH ≥ 9.1 cm) were counted by species and by 2-cm DBH classes in either 400-m^2 circular plots (forest height ≥ 7 m) or 100-m^2 circular plots (forest height < 7 m). Saplings (DBH 1.1–9.0 cm) were counted by species and by 2-cm DBH classes in concentric 40-m^2 circular subplots. Planted black spruce was not distinguished from naturally regenerated black spruce during the inventories.

2.3. Data analysis

We studied successional trajectories in black spruce plantations, by analyzing sapling and tree species composition in recent, young and old plantations that were located in the balsam fir ecological region on balsam fir or black spruce ecological site types (Fig. 1). Available plantations were divided in age groups of equal range, i.e., recent (0–13 years; n = 94 on balsam fir site types; 22 on black spruce site types), young (14–26 years; n = 648; 36) and old (27–40 years; n = 119; 25) plantations. Since a number of species were too infrequently encountered to enable us to do valid analyses, we formed functional groups (Table 1).

We used a linear mixed-effects models (PROC MIXED; SAS Institute, 2003) with ecological site types, age groups and species groups, and their interactions, as fixed effects, and plots as a random effect, to analyze sapling density and tree basal area. We verified differences between means by performing pairwise Tukey tests and used $\alpha = 0.05$ as a significance threshold. We log-transformed the data to meet normality requirements. However, we present data at their original scales, for the sake of clarity.

3. Results

3.1. Successional trajectory of trees in black spruce plantations

The successional trajectory in black spruce plantations that were established on black spruce ecological site types diverged from the successional trajectory of trees in black spruce plantations that were established on balsam fir ecological site types (Fig. 2A and C). On black spruce ecological site types, mean tree basal area of black spruce was three times higher in old than in young plantations (Table 2; Fig. 2A; $t_{8,3752} = 5.76$, $p < 0.001$); likewise, it was three times higher in young plantations than in recent plantations ($t_{8,3752} = 4.33$, $p = 0.006$). Mean tree basal area of balsam fir and other conifers was similar in old and young plantations ($t_{8,3752} = 2.23$, $p = 0.921$); likewise, it was similar in young plantations and in recent plantations ($t_{8,3752} = 2.05$, $p = 0.972$). Mean tree basal area of all other species groups was low in all ecological site type × age group combinations. In recent and young plantations, mean tree basal area of black spruce was similar to mean tree basal area of balsam fir and other conifers ($t_{8,3752} = 0.39$, $p = 1.000$; $t_{8,3752} = 2.51$, $p = 0.776$). In old plantations, mean tree basal area of black spruce was three times higher than that of balsam fir and other conifers ($t_{8,3752} = 5.82$, $p < 0.001$).

On balsam fir ecological site types, mean tree basal area of black spruce was three times higher in old plantations than in young plantations (Table 2; Fig. 2C; $t_{8,3752} = 13.72$, $p < 0.001$), while its value was not different than zero in recent plantations ($t_{8,3752} = 0.51$, $p = 0.610$). Mean tree basal area of balsam fir and other conifers was four times higher in old than in young plantations ($t_{8,3752} = 20.20$, $p < 0.001$) while it was similar in young plantations and in recent plantations ($t_{8,3752} = 2.12$, $p = 0.955$). Mean tree basal area of all other species groups was low in every combination, except for white birch and other intolerant hardwoods, which was slightly higher in old plantations. More specifically, in recent plantations, mean tree basal area of black spruce was two-fold lower than balsam fir and other conifers ($t_{8,3752} = 3.78$, $p = 0.045$). In young plantations, mean tree basal area of black spruce was slightly lower than mean tree basal area of balsam fir and other conifers ($t_{8,3752} = 4.80$, $p = 0.001$). In old plantations, mean tree basal area of black spruce was two times lower than mean tree basal area of balsam fir and other conifers ($t_{8,3752} = 7.79$, $p < 0.001$).

Finally, between ecological site types, mean tree basal area of black spruce was almost two-fold higher in old plantations on black spruce ecological site types than in old plantations on balsam fir ecological site types ($t_{8,3752} = 5.68$, $p < 0.001$). Further, mean tree basal area of balsam fir and other conifers was three-fold lower in old plantations on black spruce ecological site types than in old plantations on balsam fir

Table 1
Mean (±1 SE) proportion of stems (diameter at breast height ≥ 1.1 cm) of each species forming the functional groups in black spruce plantations on black spruce ecological site types and on balsam fir ecological site types.

	Proportion of stems (%)			
	Black spruce site type		Balsam fir site type	
Yellow birch and other tolerant hardwoods				
Betula alleghaniensis	0		54	±5
Acer saccharum	0		41	±6
Fraxinus nigra	0		3	±2
Acer nigrum	0		2	±2
White birch and other intolerant hardwoods				
Betula papyrifera	56	±7	73	±2
Populus tremuloides	38	±8	12	±1
Acer rubrum	6	±3	13	±1
Populus balsamifera	0		2	±1
Non-commercial hardwoods				
Prunus pensylvanica	23	±10	48	±4
Sorbus americana	15	±10	13	±3
Salix sp.	37	±12	15	±3
Acer spicatum	0		10	±2
Alnus sp.	16	±10	6	±2
Viburnum cassinoides	9	±8	0	
Amelanchier sp.	0		4	±1
Corylus cornuta	0		3	±1
Acer pensylvanicum	0		1	±1
Balsam fir and other conifers				
Abies balsamea	49	±6	80	±1
Larix larinina	14	±4	0	
Picea glauca	2	±1	16	±1
Picea rubens	0		3	±1
Pinus banksiana	31	±6	0	
Pinus strobus	4	±2	0	
Thuja occidentalis	0		1	±1

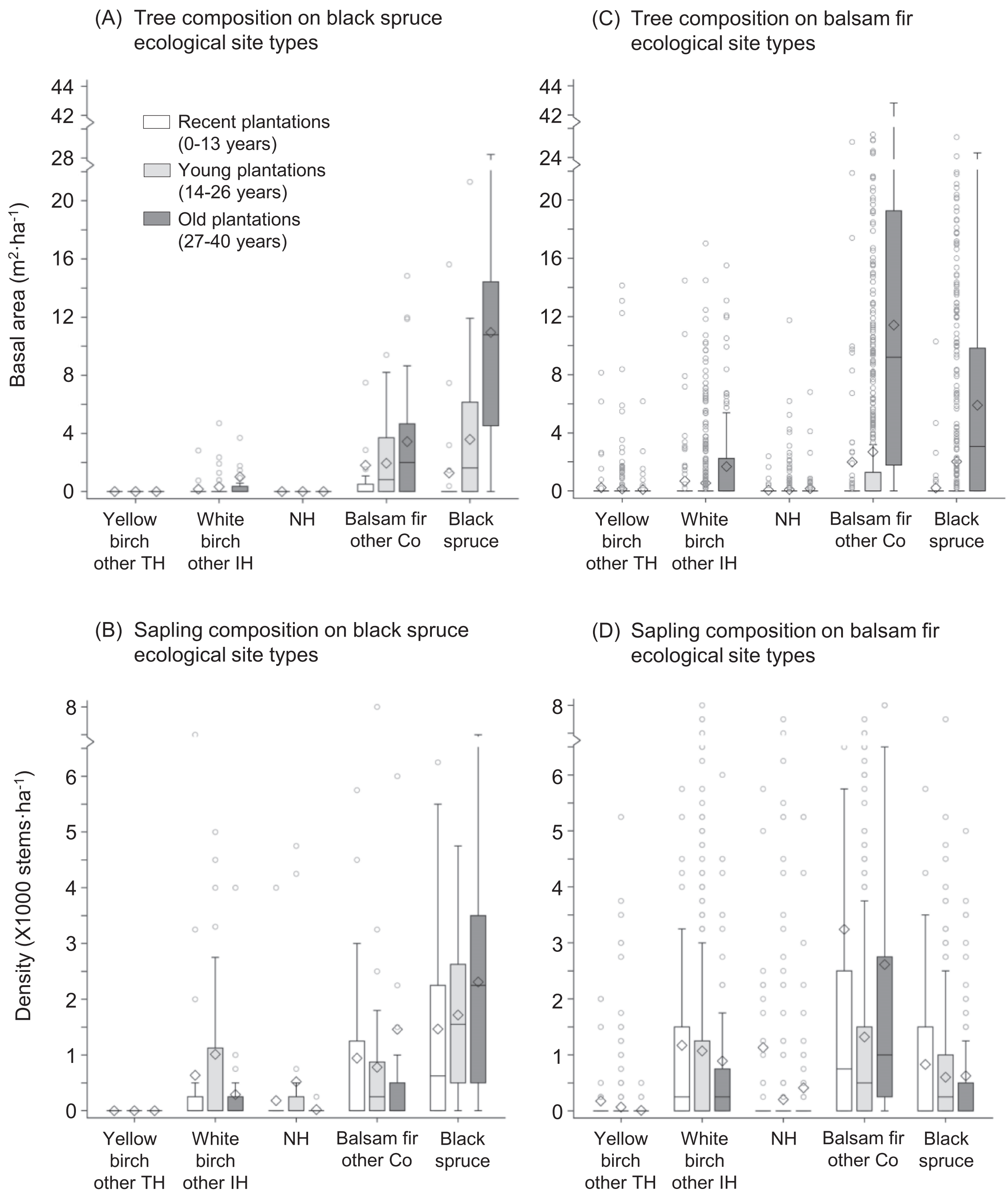

Fig. 2. Distribution of tree basal area (diameter at breast height [DBH] ≥ 9.1 cm) and sapling density (DBH: 1.1–9.0 cm) for each functional species group in black spruce plantations on black spruce ecological site types (n = 83) and in black spruce plantations on balsam fir ecological site types (n = 881). Diamonds and horizontal lines in each box represent means and medians, respectively. Boxes enclose the 25th and 75th percentiles (the interquartile range; whiskers enclose minimum to maximum values, excluding outliers. Circles beyond the whiskers are outliers (>1.5 × IQR). TH: Tolerant Hardwoods, IH: Intolerant hardwoods, NH: Non-commercial Hardwoods, Co: Conifers.

ecological site types ($t_{8,3752} = 4.81$, $p = 0.001$).

3.2. Successional trajectory of saplings in black spruce plantations

The successional trajectory of saplings in black spruce plantations that were established on black spruce ecological site types diverged from that of saplings in black spruce plantations that were established on balsam fir ecological site types (Fig. 2B and D).

On black spruce ecological site types, mean sapling density of black spruce was similar in recent, young and old plantations (Table 2; Fig. 2B; $t_{8,3752} < 2.35$, $p > 0.871$). Mean sapling density of balsam fir and other conifers was also similar in recent, young and old plantations ($t_{8,3752} < 0.894$, $p = 1.000$). Likewise, mean sapling density of white birch and other intolerant hardwoods was similar in recent, young and old plantations ($t_{8,3752} < 0.576$, $p > 0.956$). Mean sapling density of all other species groups always remained very low. More specifically in recent plantations, mean sapling density of black spruce, of balsam fir and other conifers and of white birch and other intolerant hardwoods were similar ($t_{8,3752} < 0.232$, $p > 0.225$). However, in young plantations, mean sapling density of black spruce was twice as high as mean sapling density of balsam fir and other conifers ($t_{8,3752} = 4.05$, $p = 0.017$) and than mean sapling density of white birch and other intolerant

Table 2
Analysis of variance and associated probabilities (P > F) for mean tree basal area and mean sapling density. Degrees-of-freedom (df) of the denominator are 3752.

Sources of variation	df num.	*F*-value	*p*
Tree basal area			
Ecological site type (E)	1	0.41	0.524
Age group (A)	2	44.36	< 0.001
Species group (Sp)	4	154.42	< 0.001
A × Sp	8	28.93	< 0.001
A × E	2	2.37	0.094
Sp × E	4	21.99	< 0.001
A × Sp × E	8	4.55	< 0.001
Sapling density			
Ecological site type (E)	1	1.22	0.270
Age group (A)	2	0.42	0.657
Species group (Sp)	4	103.58	< 0.001
A × Sp	8	1.56	0.133
A × E	2	7.94	< 0.001
Sp × E	4	27.05	< 0.001
A × Sp × E	8	1.78	0.075

hardwoods ($t_{8,3752} = 4.40$, $p = 0.004$). Likewise, in old plantations, mean sapling density of black spruce was 1.6 times higher than mean sapling density of balsam fir and other conifers ($t_{8,3752} = 4.47$, $p = 0.003$) and eight times higher than mean sapling density of white birch and other intolerant hardwoods ($t_{8,3752} = 6.46$, $p < 0.001$).

On balsam fir ecological site types, mean sapling density of black spruce was similar in recent, young and old plantations (Table 2; Fig. 2D; $t_{8,3752} < 0.804$, $p > 0.858$). Mean sapling density of balsam fir and other conifers was twice as high in old plantations than in young plantations ($t_{8,3752} = 14.21$, $p < 0.001$), while it was twice as low in young plantations than in recent plantations ($t_{8,3752} = 15.84$, $p < 0.001$). Mean sapling density of white birch and other intolerant hardwoods was similar in recent, young and old plantations ($t_{8,3752} < 0.294$, $p > 0.992$). Mean sapling density of all other species groups always remained very low. More specifically in recent plantations, mean sapling density of black spruce was four-fold lower than mean sapling density of balsam fir and other conifers ($t_{8,3752} = 5.46$, $p < 0.001$), while it was similar to mean sapling density of white birch and other intolerant hardwoods ($t_{8,3752} = 0.97$, $p = 1.000$). In young plantations, mean sapling density of black spruce was two times lower than mean sapling density of balsam fir and other conifers ($t_{8,3752} = 5.70$, $p < 0.001$), while it was similar to mean sapling density of white birch and other intolerant hardwoods ($t_{8,3752} = 0.27$, $p = 1.000$). In old plantations, mean sapling density of black spruce was four times lower than mean sapling density of balsam fir and other conifers ($t_{8,3752} = 8.30$, $p < 0.001$), while it was similar to mean sapling density of white birch and other intolerant hardwoods ($t_{8,3752} = 1.13$, $p = 1.000$).

Finally, between ecological site types, mean sapling density of black spruce was almost four times higher in old plantations on black spruce ecological site types than in old plantations on balsam fir ecological site types ($t_{8,3752} = 6.67$, $p < 0.001$). Further, mean sapling density of balsam fir and other conifers was almost two times lower in old plantations on black spruce ecological site types than in old plantations on balsam fir ecological site types ($t_{8,3752} = 3.97$, $p = 0.023$).

4. Discussion

As predicted, successional trajectories on balsam fir ecological site types pointed towards recovery of naturally regenerating tree species, namely balsam fir and white birch, to the detriment of the desired planted species. After 40 years, basal area of black spruce trees was half that of balsam fir and other conifers. Furthermore, density of black spruce saplings was one-quarter of balsam fir and other conifer saplings, but was similar to the density of white birch saplings. Since recovering species were not the same as the planted species, resilience most likely induced competitive interactions with undesired species. Such interactions could have prevented the plantation scenario from fully attaining its goals, which are to manage density, distribution and composition to minimize competition and maximize productivity of a desired species, in our case, black spruce (Bell et al., 2006; Thiffault et al., 2013). Competitive interactions were most probably exacerbated by the extensive silviculture regimes, which entail minimal vegetation management treatment and preclude the use of herbicides (Thiffault and Roy, 2011).

Resilience of natural forests jeopardized productivity of black spruce plantations on balsam fir ecological site types, essentially because regeneration processes of balsam fir and birch are more effective than regeneration processes of black spruce on these site types (Barrette et al., 2019). Given that they drive successional trajectories, regeneration processes are a key mechanism of natural forest resilience (Buma and Wessman, 2011; Hidding et al., 2013; Barrette et al., 2014b). Balsam fir usually produces very dense and persistent seedling banks on diverse substrates (i.e., >60 000 seedlings·ha^{-1}), which are shade-tolerant and can rapidly fill canopy openings (Côté and Bélanger, 1991; McCarthy and Weetman, 2007). Birch species can establish and fill canopy openings promptly from annual seed production and pre-established seed banks (Foster and King, 1986; Bélanger et al., 1993; MRN, 2013; Gauthier et al., 2016). However, on balsam fir ecological sites types where fires are infrequent, establishment of black spruce can be dependent upon other factors, such as availability of coarse woody debris for seedling establishment (Simard et al., 1998; Barrette et al., 2014b; Dumais and Prévost, 2016). Thus, establishment of black spruce can be hindered, especially when coarse woody debris are removed or destroyed by mechanical site preparation usually performed prior to planting (MRN, 2013). Therefore, on balsam fir ecological site types, regeneration processes of black spruce usually produce fewer seedlings than regeneration processes of balsam fir and birch species (Côté and Bélanger, 1991; MRN, 2013; Barrette et al., 2014b; Barrette et al., 2019).

Resilience of natural forests has enhanced plantation productivity when the plantation scenario is aimed in the same direction as resilience-driven successional trajectories. Also as predicted, successional trajectories on black spruce ecological site types have pointed towards the recovery of naturally regenerating tree species, mainly black spruce, to the benefit of the desired tree species, i.e., black spruce. Indeed, after a continuous increase during the 40-year period, basal area of black spruce trees was three times higher than basal area of balsam fir and other conifers, which were the only other tree species present in significant numbers. Moreover, after having remained relatively stable throughout the 40-year period, the density of black spruce saplings was higher than for any other sapling species. Finally, basal area and density of black spruce trees and saplings were both at least two times higher on black spruce ecological site types than on balsam fir ecological site types. Since the recovering species was the same as the planted species, resilience apparently did not induce competitive interactions with undesired species, enabling the plantation scenario to reach its goals (Bell et al., 2006; Thiffault et al., 2013).

Resilience of natural forests enhanced productivity of black spruce plantations on black spruce ecological site types, probably because regeneration processes of black spruce are more effective than those of balsam fir and birch species on these ecological site types. Typically, black spruce ecological site types are more poorly drained or more rapidly drained than balsam fir ecological site types. On less well-drained sites, black spruce can regenerate much better than can balsam fir by layering of the former, while semi-serotinous cones enable black spruce to better regenerate after fire on more rapidly drained sites (Veilleux-Nolin and Payette, 2012; MRN, 2013).

5. Forest management implications

We have shown that resilience of natural forests can jeopardize plantation productivity when the plantation scenario is not oriented in the same direction as the natural successional trajectories that are driven by resilience. However, we also showed that resilience of natural forests can enhance plantation productivity when the plantation scenario is aimed in the same direction as resilience-driven successional trajectories. To ensure that plantations are economically viable and promote sustainability, forest managers should thus favor plantation scenarios inspired by successional trajectories. In northeastern North America, such regimes could be to plant black spruce and jack pine, alone or in mixtures, on black spruce ecological site types (Barrette et al., 2018) or to plant only balsam fir on balsam fir ecological site types (Brousseau et al., 2017). Further research is needed to determine plantation scenarios that will not only promote sustainability in the context of natural successional trajectories, but also in the context of alternative successional trajectories that will undoubtedly arise because of global change (Price et al., 2013).

CRediT authorship contribution statement

Martin Barrette: Conceptualization, Methodology, Writing - original draft. **Nelson Thiffault:** Methodology, Writing - review & editing. **Isabelle Auger:** Software, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Barrette, M., Leblanc, M., Thiffault, N., Paquette, A., Lavoie, L., Bélanger, L., Bujold, F., Côté, L., Lamoureux, J., Schneider, R., Tremblay, J.-P., Côté, S., Boucher, Y., Deshaies, M.-È., 2014a. Issues and solutions for intensive plantation silviculture in a context of ecosystem management. For. Chron. 90 (6), 748–762.
Barrette, M., Bélanger, L., De Grandpré, L., Ruel, J.-C., 2014b. Cumulative effects of chronic deer browsing and clear-cutting on regeneration processes in second-growth white spruce stands. For. Ecol. Manag. 329, 69–78.
Barrette, M., Tremblay, S., Auger, I., 2018. Commercial thinning that maintained species diversity of a mixed black spruce–jack pine stand enhanced productivity. Scan. J. For. Res. 33, 756–763.
Barrette, M., Thiffault, N., Tremblay, J.-P., Auger, I., 2019. Balsam fir stands of northeastern North America are resilient to spruce plantation. For. Ecol. Manag. 450, 117504.
Bélanger, L., Allard, D., Meek, P., 1993. Dynamique d'établissement d'un peuplement bi-étagé de bouleau blanc et de sapin baumier en zone boréale. For. Chron. 69 (2), 173–177.
Bell, F.W., Douglas, G.P., Wester, M.C., 2006. Is intensive forest management a misnomer? An Ontario-based discussion of terminology and an alternative approach. For. Chron. 82 (5), 662–674.
Brousseau, M., Thiffault, N., Beguin, J., Roy, V., Tremblay, J.-P., 2017. Deer browsing outweighs the effects of site preparation andmechanical release on balsam fir seedlings performance: implications to forest management. For. Ecol. Manag. 405, 360–366.
Buma, B., Wessman, C.A., 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2 (5), 1–13.
Carle, J., Holmgren, P., 2008. Wood from planted forest: a global outlook 2005–2030. Forest Prod. J. 58 (12), 6–18.
Côté, S., Bélanger, L., 1991. Variations de la régénération préétablie dans les sapinières boréales en fonction de leurs caractéristiques écologiques. Can. J. For. Res. 21 (12), 1779–1795.
Delisle, J.F., 2020. Ressources et industries forestières du Québec. Portrait statistiques 2019. Ministère des Forêts, de la Faune et des Parcs. 136p.
Dumais, D., Prévost, M., 2016. Germination and establishment of natural red spruce (*Picea rubens*) seedlings in silvicultural gaps of different sizes. For. Chron. 92 (1), 90–100.
FAO (Food and Agriculture Organization of the United Nations), 2010. Global Forest Resources Assessment. Rome.
Foster, D.R., King, G.A., 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (Birch) forest development in relation to fire history and physiography. J. Ecol. 74 (2), 465–483.
Gauthier, M.-M., Lambert, M.-C., Bédard, S., 2016. Effects of harvest gap size, soil scarification, and vegetation control on regeneration dynamics in sugar maple-yellow birch stands. For. Sci. 62 (2), 237–246.
Ghazoul, J., Burivalova, Z., Garcia-Ulloa, J., King, L.A., 2015. Conceptualizing forest degradation. Trends Ecol. Evol. 30 (10), 622–632.
Grondin, P., Noël, J., Hotte. D., 2007. Atlas des unités homogènes du Québec méridional selon la végétation et ses variables explicatives. Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière. Québec, Canada. 138p.
Grondin, P., Gauthier, S., Borcard, D., Bergeron, Y., Noël, J., 2013. A new approach to ecological land classification for the Canadian boreal forest that integrates disturbances. Lands. Ecol. 29, 1–16.
Gunderson, L.H., 2000. Ecological resilience—in theory and application. Annu. Rev. Ecol. Syst. 31, 425–439.
Hidding, B., Tremblay, J.-P., Côté, S.D., 2013. A large herbivore triggers alternative successional trajectories in the boreal forest. Ecology 94 (12), 2852–2860.
Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1–23.
Kneeshaw, D.D., Leduc, A., Drapeau, P., Gauthier, S., Paré, D., Carignan, R., Doucet, R., Bouthillier, L., Messier, C., 2000. Development of integrated ecological standards of sustainable forest management at an operational scale. For. Chron. 76, 481–493.
Köhl, M., Lasco, R., Cifuentes, M., Jonsson, O., Korhonen, K., Mundhenk, P., de Jesus Navar, J., Stinson, G., 2015. Changes in forest production, biomass and carbon, results from the 2015 UN Global Forest Resources Assessment. For. Ecol. Manag. 352, 21–34.
McCarthy, J.W., Weetman, G., 2007. Stand structure and development of an insect-mediated boreal forest landscape. For. Ecol. Manag. 241 (1–3), 101–114.
MFFP (Ministère des Forêts, de la Faune et des Parcs), 2018. Cartographie du 5e inventaire écoforestier du Québec méridional — Méthodes et données associées, Ministère des Forêts, de la Faune et des Parcs, Secteur des forêts, Direction des inventaires forestiers, 111p. https://mffp.gouv.qc.ca/forets/inventaire/pdf/carto_5E_methodes_donnees.pdf.
Moffat, K., Lacey, J., Zhang, A., Leipold, S., 2015. The social licence to operate: a critical review. Forestry cpv044. https://doi.org/10.1093/forestry/cpv044.
Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems, a research agenda for applied forest ecology. J. Appl. Ecol. 54, 12–27.
MRN (Ministère des Ressources Naturelles), 2013. Le guide sylvicole du Québec, Tome 1. Les fondements biologiques de la sylviculture. Ouvrage collectif sous la supervision de B. Boulet et M. Huot, Les Publications du Québec, Québec, Canada. 1044p.
MRNF (Ministère des Ressources Naturelles et de la Faune), 2006a. Normes d'inventaire forestier; placettes échantillons permanentes. Forêt Québec, Direction des inventaires forestiers. Québec, Canada.
MRNF (Ministère des Ressources Naturelles et de la Faune), 2006b. Normes d'inventaire forestier; placettes échantillons temporaires. Forêt Québec, Direction des inventaires forestiers. Québec, Canada.
MRNF (Ministère des Ressources Naturelles et de la Faune), 2009. Norme de cartographie écoforestière; troisième inventaire écoforestier. Forêt Québec, Direction des inventaires forestiers. Québec, Canada.
National Forestry Database, 2020. Provincial and Territorial Profiles. Available from http://nfdp.ccfm.org/ (accessed 10 December 2020).
Neves Silva, L., Freer-Smith, P., Madsen, P., 2019. Production, restoration, mitigation: a new generation of plantations. New For. 50, 153–168.
Paquette, A., Messier, C., 2010. The role of plantations in managing the world's forests in the Anthropocene. Front. Ecol. Environ. 8 (1), 27–34.
Prach, K., Tichý, L., Lencová, K., Adámek, M., Koutecký, T., Sádlo, J., Bartošová, A., Novák, J., Kovář, P., Jírová, A., Šmilauer, P., Řehounková, K., 2016. Does succession run towards potential natural vegetation? An analysis across seres. J. Veg. Sci. 27, 515–523.
Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., McKenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J.A., Venier, L.A., 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. Environ. Rev. 21, 322–365.
Robitaille, A., Saucier, J.-P., Chabot, M., Côté, D., Boudreault, C., 2015. An approach for assessing suitability for forest management based on constraints of the physical environment at a regional scale. Can. J. For. Res. 45, 529–539.
SAS Institute, 2003. The SAS System for Windows, version 9.1. SAS Institute Inc., Cary, NC, USA.
Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016. Searching for resilience, addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53, 120–129.
Simard, M.J., Bergeron, Y., Sirois, L., 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci. 9, 575–582.

Thiffault, N., Roy, V., 2011. Living without herbicides in Québec (Canada): historical context, current strategy, research and challenges in forest vegetation management. Eur. J. For. Res. 130, 117–133.

Thiffault, N., Roy, V., Ménétrier, J., Prégent, G., Rainville, A., 2013. Chapitre 11 –La plantation, dans Ministère des Ressources Naturelles, Le guide sylvicole du Québec, Tome 2 – Les concepts et l'application de la sylviculture, ouvrage collectif sous la supervision de C. Larouche, F. Guillemette, P. Raymond et J.-P. Saucier, Les Publications du Québec, pp. 196–225.

Veilleux-Nolin, M., Payette, S., 2012. Influence of recent fire season and severity on black spruce regeneration in spruce-moss forests of Quebec. Canada. Can. J. For. Res. 42, 1316–1327.