Modeling tolerant hardwood sapling density and occurrence probability in the Acadian forests of New Brunswick, Canada: Results 14 years after harvesting

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ABSTRACT

Natural forest regeneration after natural or anthropogenic disturbance is difficult to predict given its high variability. The process is poorly documented for commercial northern hardwood species in the Acadian forest of eastern Canada. Our objective was to identify the silvicultural, environmental, and ecological factors that best explain the variability in sapling density and occurrence of two commercial tolerant hardwood species in New Brunswick: American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.). Forty-three permanent sample plots were established in 2002 and measured before harvesting in 2004. Sapling density and occurrence were measured 14 years after harvesting. The results showed that the interactions between the species and the residual merchantable basal area and between the species and the percent of hardwoods in the original stand best explained the sapling density and occurrence variation of tolerant hardwoods. The sapling density of sugar maple increased with increasing merchantable residual basal area. However, the effect of this variable was not significant for the density of American beech saplings. The density and occurrence of tolerant hardwood saplings both increased along with the percent of hardwoods in the original stand. These results provide an improved understanding about tolerant hardwood regeneration dynamics in New Brunswick forests.

Keywords: Acadian forest, tolerant hardwoods, sapling density, occurrence probability, regeneration modeling

RÉSUMÉ

Il est difficile de prévoir la régénération naturelle de la forêt à la suite d'une perturbation d'origine anthropique puisqu'elle est hautement variable. Le processus est mal documenté dans les essences feuillues des forêts commerciales de la forêt acadienne de l'est du Canada. Nos travaux avaient pour but de trouver les facteurs sylvicoles, environnementaux et écologiques qui permettraient d'expliquer la variabilité de la présence et de la densité des gaules chez deux essences de feuillus tolérants commerciaux au Nouveau-Brunswick : le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) et l'érable à sucre (*Acer saccharum* Marsh.). En 2002, nous avons donc établi quarante-trois placettes permanentes et les avons mesurées avant l'opération de récolte 2004. Quatorze ans après cette coupe, nous sommes retournés mesurer la densité et la présence des gaules. Les résultats nous indiquent que ce sont la relation entre l'essence et la surface terrière résiduelle, et celle liant l'essence au pourcentage de feuillus du peuplement original qui expliquent le mieux les variations dans la densité et la présence de gaules de feuillus tolérants. La densité des gaules d'érable à sucre avait tendance à augmenter avec une augmentation de la surface terrière marchande. Toutefois, l'effet de cette variable ne s'est pas avéré significatif pour la densité des gaules de hêtre à grandes feuilles. La densité et la présence des gaules de feuillus tolérants ont toutes les deux crû avec le pourcentage de feuilles dans le peuplement original. Ces résultats ont permis d'améliorer nos connaissances sur la dynamique de la régénération chez les feuillus tolérants dans les forêts du Nouveau-Brunswick.

Mots-clés: Forêt acadienne, feuillus tolérants, densité des gaules, probabilité de présence, modélisation de la régénération

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Introduction

Regeneration is an important process shaping forest dynamics because it directly influences the future composition and productivity of forest stands (MacDonald and Thompson 2003; MacDonald *et al.* 2004; Man *et al.* 2010). The forest regeneration process is the ability of a stand to renew spontaneously after natural or anthropogenic disturbance (Carle and Holmgren 2003) by establishing new cohorts. This process is difficult to predict, given its high variability (Li *et al.* 2011) and the influence from several factors such as the physiological characteristics of the species, ecological and soil conditions, and disturbances (Kozlowski 2002; MacDonald *et al.* 2004; Bataineh *et al.* 2013; Nelson and Wagner 2014). Some studies have proposed various models for regeneration predictions based on one or several predictor variables such as disturbance intensities, stand basal area (before and after harvesting), environmental conditions of the site, seed dispersal and parent tree location, and the initial composition of the stand (Ribbens *et al.* 1994; Liu and Ashton 1998; Hanson *et al.* 2011; Klopcic *et al.* 2012; Danyagri *et al.* 2017, 2019). However, these models have some limits related to their low accuracy and their inability to explain the complexity of the regeneration process (Hanson *et al.* 2011; Klopcic *et al.* 2012), and in some cases, related to limited data availability (Hanson *et al.* 2011).

In the Acadian forest region of North America, understanding the factors that determine the density and occurrence of regeneration of tolerant hardwood species in space and time has always been a concern for forest managers. The patterns of forest regeneration for commercial northern hardwood species (Li *et al.* 2011; Nelson *et al.* 2013) represent an important knowledge gap, and this situation will continue and perhaps worsen, given the anticipated climate change that will bring an additional share of uncertainty and complexity. Modifications in the patterns of temperature, precipitation, and the occurrence and intensity of extreme weather events are expected (Dullinger *et al.* 2004; Dore 2005; Kirilenko and Sedjo 2007). For Atlantic Canada's forests, these climate changes will likely affect the regeneration of tree species. The distribution of native tree species in this region is expected to shift with climate change as it lies in the transition zone between the temperate and the boreal biomes (Chapin *et al.* 2004; Williamson *et al.* 2009). Furthermore, the Acadian Forest Region of Canada might face a temporary decrease in forest growth and wood supply by the end of the 21st century due to climate change (Taylor *et al.* 2017). In addition to such predictions, some studies showed that harvest intensity influences the composition of regeneration in hardwood forests (Danyagri *et al.* 2017). For example, in hardwood stands, partial harvesting is preferred to clearcutting since it favours the regeneration of tolerant species (Jenkins and Parker 2001; Angers *et al.* 2005) and allows for the production of good quality saw timber (Leak and Sendak 2002). Edaphic conditions may also influence the composition of the regeneration in hardwood stands (Coates and Burton 1997), although the effects of partial harvesting on soils are variable (Beaudet *et al.* 2002).

Tolerant hardwood species such as sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) often grow together and they count among the most common hardwood species in the Acadian forest region (Seymour *et al.* 2002). In this region, the stands dominated by tolerant hardwoods have important ecological and economic interests, since they contribute to ecosystem complexity at the landscape scale, provide habitat for many wildlife species and supply a variety of forest products (Betts *et al.* 2003; Etheridge *et al.* 2005). Nevertheless, the current economic value of American beech is much lower than that of sugar maple, which is managed for the production of high value appearance wood products used in flooring, furniture and cabinetmaking (Havreljuk *et al.* 2014). In addition, increasing American beech abundance might perpetuate beech bark disease in forest stands and substantially reduce its economic and ecological values (Griffin *et al.* 2003; Hane 2003; Loo and Ives 2003). With climate change, it is expected that the percent of American beech and red maple (*Acer rubrum* L.) will increase to the detriment of sugar maple (Taylor *et al.* 2017).

Arguably, predicting regeneration dynamics is one of the most complex tasks in forest modeling (Spence and MacLean 2012; Danyagri *et al.* 2017). After decades of research, it remains challenging to predict the impact of several factors on forest regeneration in the Acadian forest of North America (Li *et al.* 2011; Salmon *et al.* 2016). Predicting the effects of silvicultural, environmental and ecological factors on sapling density of tolerant hardwoods is a challenging task due to the complexity of the processes involved and the limited availability of data in this region. Adequate wood supply calculations requires the prediction of sapling dynamics of commercial hardwood species in order to practice sustainable forest management (Beyeler 2002; Bose *et al.* 2014).

The objective of this study was to identify the silvicultural, environmental, and ecological factors that best explain variations in sapling density and occurrence probability of two commercial tolerant hardwood species (American beech, sugar maple) in New Brunswick, Canada. We first predicted that the variation in sapling density and occurrence probability is best explained by treatment intensity expressed as the percent of merchantable basal area removed during harvesting. We also predicted that sapling density and occurrence of sugar maple were favoured by the highest treatment intensity, contrary to the sapling density and occurrence of American beech.

Materials and methods

Study area

The study area is located in the Black Brook District (~ 200 000 ha) owned by J.D. Irving Limited in northwestern New Brunswick, Canada (Fig. 1). The regional climate (Central Uplands Ecoregion) is cold with relatively abundant precipitation (Zelazny *et al.* 2007). The mean annual precipitation is 1104 mm; mean annual temperature is 3.5 °C and mean growing degree days above 5 °C is 1532.6 (Environment and Climate Change Canada 2020). The forest stands in the study area have complex structures and are composed of a mixture of hardwood and softwood species (Hennigar *et al.* 2016). They are dominated by American beech, sugar maple and yellow birch (*Betula alleghaniensis* Britt.). Other hardwood species such as red maple, white birch (*Betula papyrifera* Marsh.) and poplar (*Populus spp.*) are found in low proportions. The most common softwood species in these stands are balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea*

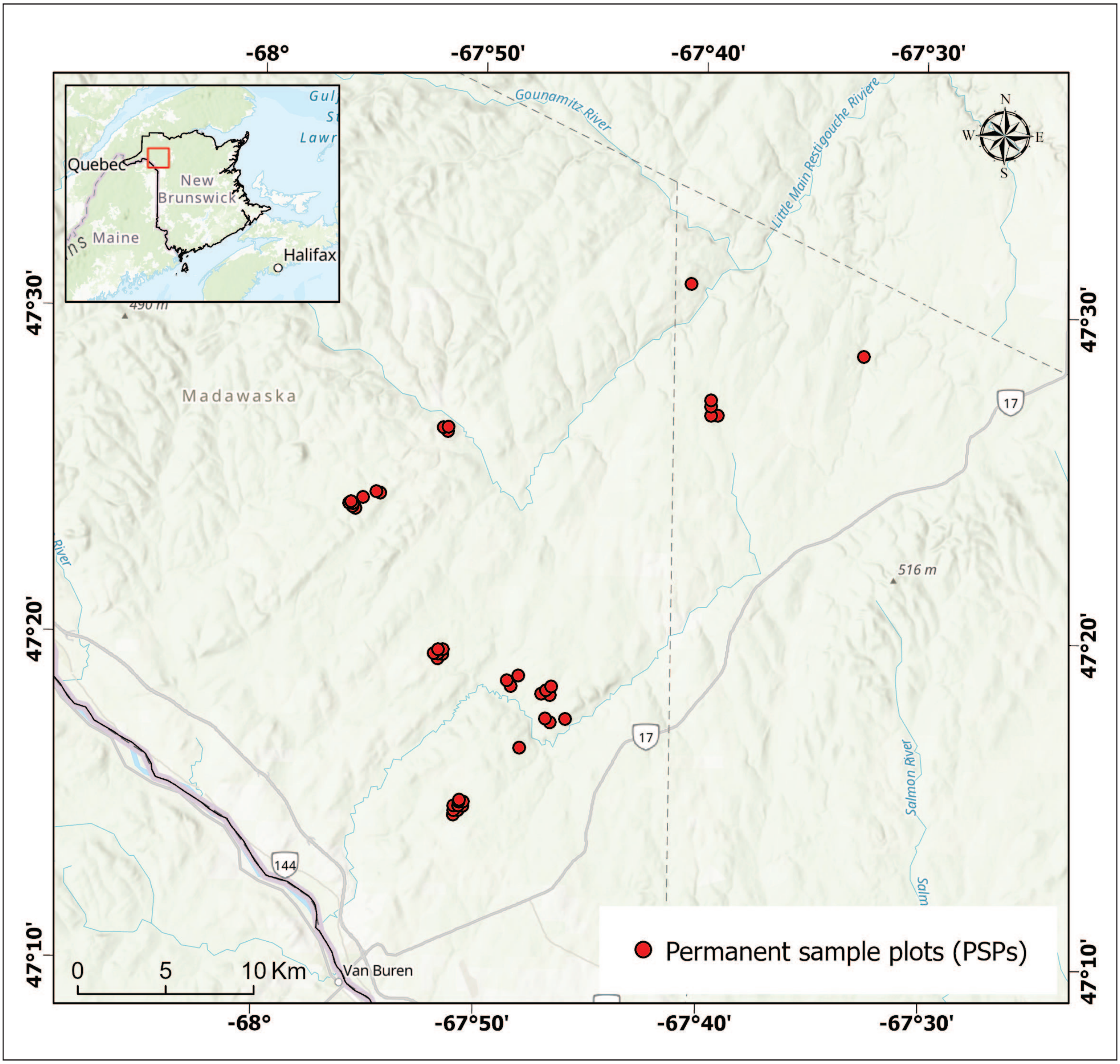

Fig. 1. Location of the study area (red square) in Eastern Canada and distribution of the permanent sample plots (PSPs) within the study area.

glauca (Moench) Voss) and red spruce (*Picea rubens* Sarg.). These species are found in proportions and associations that vary according to the local climate, soil fertility, topography and local disturbances (Erdle and Pollard 2002).

Experimental design and data collection

We used data collected in 43 permanent sample plots (PSPs) of 0.05 ha randomly distributed in the Black Brook District (Fig. 1). These PSPs are part of a network of plots that have been used in several studies to evaluate the regeneration rates of commercial tree species before and after different harvest treatments (Maclean *et al.* 2010; Dracup and MacLean 2018). The PSPs were established and measured in 2002 before harvesting. The merchantable cohort in the original stands was dominated by softwoods, with a density of merchantable trees (DBH > 9.1 cm) ranging between 20 and 3720 trees ha^{-1} (Fig. S1, Appendix 1). However, the merchantable basal area of sugar maple, ranging from 0.82 to 40.18 m^2 ha^{-1} (mean = 17.33 m^2 ha^{-1}), was higher than other species or group of species (Fig. S2, Fig. S3, Appendix 1).

In 2004, the study area was treated using different harvest intensities expressed as the percent of merchantable basal area removed in each plot ranging between 11.6% and 95.8%. Four categories of harvest intensity were created from the four quantiles of the percent of merchantable basal area removed data, low (basal area removed ≤ 25%), medium

(25% basal area removed ≤ 50%), high (50% basal area removed ≤ 67%) and very high (67% basal area removed ≤ 96%). Balsam fir was heavily targeted by these harvest treatments in order to emulate a spruce budworm (*Choristoneura fumiferana* Clem.) outbreak and to create gaps in the stand. In the residual stands (after harvesting), the merchantable tree density and basal area of sugar maple (ranging from 20 to 740 trees ha^{-1}, and from 0.24 to 31.78 m^2 ha^{-1}, respectively), were higher than softwood and other commercial hardwood tree density (Fig. S1, Fig. S2, Fig. S3, Appendix 1). Tolerant hardwoods (American beech, sugar maple) were the most dominant in the original and residual stands compared to other hardwood species or groups (Fig. S1, Fig. S2, Fig. S3, Appendix 1).

In 2018, 14 years after harvesting, the density of commercial hardwood saplings (stems ha^{-1}, regeneration with diameter outside bark at breast height (DBH; 1.3 m above ground) – between 1 cm and 9 cm) was measured in each PSP. We conducted a complete census of saplings in each PSP. Silvicultural and ecological variables were collected or calculated for each PSP from existing inventory data. Environmental variables were extracted from geographical information system layers for each plot (all data from the Northern Hardwoods Research Institute, New Brunswick, Canada).

Silvicultural and ecological variables

All silvicultural and ecological variables were summarized for pre- and post-harvest stands. The silvicultural variables included the percent of merchantable basal area removed after the first harvest, the residual merchantable basal area (m^2 ha^{-1}), the percent of softwoods in the residual merchantable basal area, the percent of hardwoods in the residual merchantable basal area, and the quadratic mean diameters (QMD, cm) of the removed and residual merchantable trees after the first harvest. The ecological variables were associated with the original stand characteristics (before harvest). These variables included the total basal area of the original stand (m^2 ha^{-1}), the QMD of merchantable trees in the original stand before harvest, and the percent of the following species group in the merchantable basal area of the original stand: percent of softwood, hardwoods, tolerant hardwoods (American beech, sugar maple), mid-tolerant hardwoods (yellow birch, red maple) and intolerant hardwoods (white birch, trembling aspen).

Environmental variables

The environmental variables included forest ecosite, namely a stand-scale ecological classification unit that includes a series of site conditions influencing forest productivity in Acadian and maritime-boreal forests (Zelazny *et al.* 2007). The ecosite is an ecological basis used to group vegetation and soil types (Yang *et al.* 2017), depth of the water table (DWT, m), slope inclination (%) and aspect, elevation (m) and topographic index (TPI), soil type, biomass growth index (BGI, kg^{-1} ha^{-1} yr^{-1}). BGI is a forest productivity site index in the Acadian forest region (Hennigar *et al.* 2016). BGI values were extracted from a BGI map of the Acadian forest region in New Brunswick (data from the Northern Hardwoods Research Institute, New Brunswick, Canada).

Statistical analyses

To identify the silvicultural, ecological and environmental variables that best explained variations in sapling density and occurrence of tolerant hardwood species (American beech and sugar maple saplings), we compared a series of zero-inflated negative binomial (ZINB) models (function “zeroinfl”, package “pscl” in R) (Jackman 2008; Zeileis *et al.* 2008). Several authors recommend using ZINB models for over-dispersed count data (e.g., sapling density) with extra zeros (Thomas *et al.* 2018; Aldirawi *et al.* 2019; Wang *et al.* 2020). In this case, the ZINB distribution is more appropriate for modeling count data compared to the commonly used Poisson distribution (Aldirawi *et al.* 2019). In addition, we used ZINB models because they can simultaneously predict the density and the occurrence probability of saplings, while modeling nonlinear effects of silvicultural, environmental, and ecological factors. A ZINB model relies on the joint distribution that combines a negative binomial probability mass function (PMF) and a binomial PMF. The former predicts the sapling count whereas the latter accounts for the excess of zero values. The means of the two PMFs are modelled through link functions (McCullagh and Nelder 1989) so that the predictors can enter the model linearly. More specifically, a logit link function was used in the binomial PMF whereas the negative binomial PMF implemented a log link function. This analytical approach has been used in several studies, notably in horticultural research, wildlife inventorying, and forest ecology to predict tree recruitment (Hall 2000; Cunningham and Lindenmayer 2005; Ripley *et al.* 2005; Fortin and DeBlois 2007).

A series of 104 candidate models were fitted in accordance with our research objectives (ecological concerns) and to provide silvicultural guidance to forest managers. The candidate models included different combinations of the predictors (silvicultural, ecological and environmental variables) and relevant interactions between these predictors. All candidate models are shown in Table S1, Appendix 1. In addition, we checked the goodness-of-fit for each model by examining the fitted values against actual values.

We selected the ZINB model that best explained variations in sapling density and occurrence probability using the second order Akaike Information Criterion (AICc) for small sample size (Burnham *et al.* 2011). We report the parameter estimates and their 95% confidence intervals (95% CIs) obtained with the model that best fitted variations in sapling density and occurrence probability, namely the one with a ΔAICc < 2 (Burnham *et al.* 2011). We conducted all analyses in the R statistical environment (v. 3.5.1, R Core Team 2018) and used $P = 0.05$ as a threshold for significance.

Results

The model, including the interaction between the regenerating tolerant hardwood species and the residual merchantable basal area (m^2 ha^{-1}) of the stand (after harvesting), as well as the interaction between the regenerating tolerant hardwoods and the percent of hardwoods in the original stand (before harvesting), was the best to explain variations in sapling density (stems ha^{-1}) and occurrence probability variation of American beech and sugar maple (Table 1; Table S2, Appendix 1).

Table 1. Model selection for the prediction of the density and occurrence probability of tolerant hardwood saplings in New Brunswick, Canada. The list of models includes the 20 best models selected. The best model (#8) is shown in bold with the lowest AICc and ΔAICc value. The AICc and ΔAICc values of all selected candidate models are mentioned in Table S2, Appendix 1

Model #	Model variables	AICc	ΔAICc
Model 8	**Sps^{1} * BA residual stand^{2} + Sps * % HWD original stand^{3}**	**690.96**	**0**
Model 59	Sps * % HWD original stand	694.51	3.55
Model 9	Sps + % HWD original stand + QMD original stand^{4}	695.80	4.83
Model 71	Sps * BA original stand^{5} + Sps * % IHWD original^{6} stand + Sps * % HWD original stand	696.36	5.40
Model 7	Sps + BA original stand + % HWD original stand	696.41	5.45
Model 70	Sps * BA original stand + Sps * % MHWD original stand^{7} + Sps * % HWD original stand	696.53	5.57
Model 69	Sps * BA original stand + Sps * % THWD original stand^{8} + Sps * % HWD original stand	696.77	5.81
Model 45	Sps + % BA removed trees^{9} + % HWD original stand	697.05	6.09
Model 60	% HWD original stand	697.14	6.18
Model 58	Sps + % HWD original stand	697.41	6.44
Model 46	Sps * % BA removed trees + Sps * % HWD original stand	697.48	6.52
Model 27	Sps + % HWD original stand + Elevation	699.73	8.77
Model 28	Sps * % HWD original stand + Sps * Elevation	700.66	9.70
Model 21	Sps + % HWD original stand + TPI^{10}	701.35	10.39
Model 91	Sps + % BA removed trees + % MHWD original stand + % HWD original stand	701.39	10.43
Model 90	Sps + % BA removed trees + % THWD original stand + % HWD original stand	701.54	10.58
Model 92	Sps + % BA removed trees + % IHWD original stand + % HWD original stand	701.72	10.76
Model 22	Sps * % HWD original stand + Sps * TPI	702.82	11.86
Model 30	Sps * QMD original stand + Sps * Elevation	703.34	12.38
Model 95	Sps * % BA removed tree + Sps * % IHWD original stand + Sps * % HWD original stand	703.71	12.75

[1]Species; [2]Residual merchantable basal area (m^{2} ha^{-1}); [3]Percent of hardwoods in the original stand; [4]Quadratic mean diameter of merchantable trees in the original stand before harvest (cm); [5]Total basal area of the original stand (m^{2} ha^{-1}); [6]Percent of intolerant hardwoods in the original stand; [7]Percent of mid-tolerant hardwoods in the original stand; [8]Percent of tolerant hardwoods in the original stand; [9]Percent of merchantable basal area removed; [10]Topographic index.

Sapling density

We observed a significant effect of the residual merchantable basal area on sugar maple sapling density, but the effect was not significant for American beech (Table 2). The sapling density of sugar maple increased with increasing merchantable residual basal area, which ranged from 1 to 32 m^{2} ha^{-1} across the PSPs (Fig. 2), corresponding respectively to 4% and 88% of the total merchantable basal area. Although there appeared to be a declining trend for American beech for these sample data (Fig. 2), this was not significant.

We also observed a significant effect of the percent of hardwoods in the original stand on sugar maple and American beech sapling density (Table 2). Sapling density increased with the percent of hardwoods in the original stand (Fig. 3). However, sapling density of American beech was higher than those of sugar maple in original stands dominated by hardwoods before harvesting, especially in original stands with a percent of hardwoods greater than 75% (Fig. 3).

Sapling occurrence probability

We found a significant effect of the percent of hardwoods in the original stand on the occurrence probability of tolerant hardwood saplings (Table 2). The occurrence probability increased as the percent of hardwoods in the original stand rose (Fig. 4). The occurrence probability of American beech saplings was higher than sugar maple occurrence probability, independent from percent of hardwoods in the original stand (Fig. 4). However, we did not detect any significant effect of the residual merchantable basal area on occurrence probability of sugar maple and American beech saplings (Table 2).

Discussion

Several studies of the Acadian forest of New Brunswick have found that the partial opening of the canopy after harvesting and the percent of hardwoods in the stand can influence processes underlying forest dynamics such as the recruitment of stems into the merchantable cohort (Forget *et al.* 2007; Li *et al.* 2011; Baral *et al.* 2016). In fact, our analyses showed that sapling density and occurrence probability of tolerant hardwood saplings increased with the initial proportion (before harvesting) of hardwoods in the plot. In addition, the density of sugar maple saplings increased slightly with the residual merchantable basal area (after harvesting). These results partially confirm our first prediction that the variation in sapling density and occurrence would be best explained by treatment intensity (via the residual merchantable basal area). Contradictory to our second prediction though, American beech saplings were more abundant than sugar maple in plots with low basal area after harvesting. We discuss in turn the implications of our results for the density and occurrence probability, respectively, of tolerant hardwood saplings.

Sapling density

Despite the shade tolerance of sugar maple, several studies have reported that the establishment of this species is favored by partial opening of the canopy through harvesting; its density generally increases with light availability (Forget *et al.* 2007; Baral *et al.* 2016). Here, we observed that the sapling density of sugar maple increased with increasing merchantable residual basal area of the stand after harvesting. This suggests that, within the range of harvesting intensities

Table 2. Summary and coefficient (Coef.) estimates for the density (log link function) and the occurrence probability (logit link function) of saplings obtained with the best predictive model for tolerant hardwood species in New Brunswick, Canada

Predictors	Coef. estimates	SE	t-value	p-value[3]
Sapling density				
Intercept	0.470	0.807	0.583	0.560
American beech × Residual BA[1]	-0.023	0.022	-1.020	0.307
Sugar maple × Residual BA	0.072	0.027	2.675	**0.007**
American beech × % HWD original stand[2]	0.049	0.009	5.387	< **0.001**
Sugar maple × % HWD original stand	0.031	0.008	3.812	< **0.001**
Occurrence probability of saplings				
Intercept	1.338	1.079	1.240	0.214
American beech × Residual BA	0.065	0.051	1.263	0.206
Sugar maple × Residual BA	0.077	0.043	1.792	0.073
American beech × % HWD original stand	-0.044	0.016	-2.710	**0.006**
Sugar maple × % HWD original stand	-0.031	0.014	-2.274	**0.022**

[1] Residual merchantable basal area (m^2 ha^{-1})

[2] Percent of hardwoods in the original stand (%)

[3] Values in bold type indicate significance at $P = 0.05$

included in our database, canopy opening was sufficient to trigger a positive response in sapling establishment. The increase in basal area might have reduced light levels in the understory such that the growth of fast-growing competing species could have been limited (Thiffault *et al.* 2015). However, no significant effect was observed for the sapling density of American beech. Hence, several studies recommend the application of partial harvest in stands with an abundance of pre-established sugar maple regeneration in order to increase their abundance after harvesting (Nyland *et al.* 2006; Kershaw *et al.* 2012). Under these conditions, the density of sugar maple saplings can exceed that of American beech (Nolet *et al.* 2008; Danyagri *et al.* 2019).

Also, we observed a positive effect of increasing percentage of hardwoods in the original stand on sapling density, especially on sapling density of American beech. The percentage of hardwoods in the stands can have a direct influence on the regeneration of tolerant hardwoods as it can influence light availability reaching the understory by influencing the canopy cover (Nyland 2016). Due to its high shade-tolerance, the density of American beech saplings is more strongly influenced by canopy closure (Nolet *et al.* 2008, 2015), particularly in stands with a high percentage of hardwoods. Indeed, American beech has a higher growth rate (high leaf display efficiency) and more efficient reproduction than sugar maple under a closed canopy characterized by low light availability (Canham 1988). Under these conditions, the density of American beech saplings exceeds that of sugar maple (Nolet *et al.* 2015).

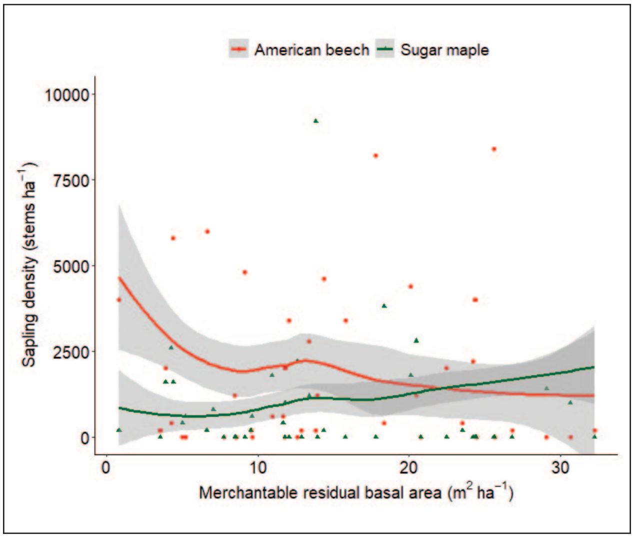

Fig. 2. Sapling density of tolerant hardwoods (stems ha^{-1}) as a function of merchantable residual basal area (m^2 ha^{-1}). Raw values for each species and plots are shown along with the curves and their 95% confidence intervals predicted by the best-fitting model for each species.

Sapling occurrence probability

Although the probability of occurrence of tolerant hardwood saplings increased with increasing percentage of hardwoods in the original stand, the occurrence probability of American beech saplings was higher than that of sugar maple. Previous studies have reported that the difference between species in the response of sapling occurrence is related to several factors, especially the ecological and physiological requirements of each tolerant hardwood species (Nyland *et al.* 2006; Nyland 2016), site environmental conditions (Grime and Hunt 1975; Walters and Reich 1996) such as fertility, light availability, and the presence of interspecific competition within the stand (Seymour 1992). In general, sugar maple saplings are frequent on fertile sites with a partial canopy opening that increases light availability, and less frequent under dense forest cover (Forget *et al.* 2007; Nolet *et al.* 2008; Baral *et al.* 2016). However, American beech saplings are more frequent under dense forest cover due to their higher tolerance to shade (Canham 1988; Beaudet *et al.* 1999; Nolet

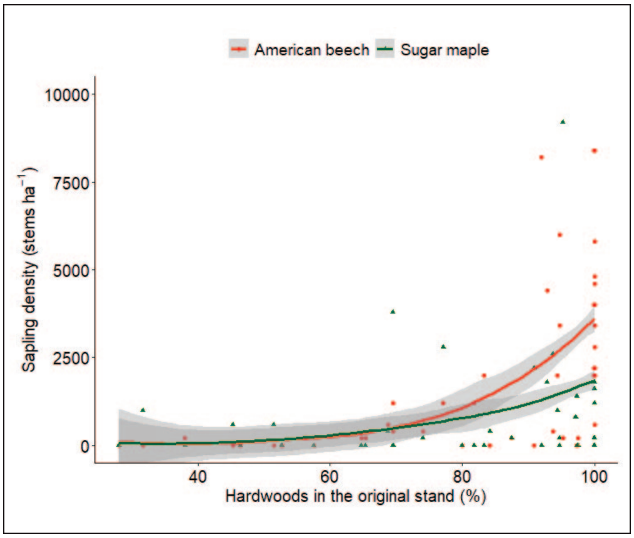

Fig. 3. Sapling density of tolerant hardwoods (stems ha^{-1}) as a function of the percent (%) of hardwoods in the original stand. Raw values for each species and plots are shown along with the curves and their 95% confidence intervals predicted by the best-fitting model for each species.

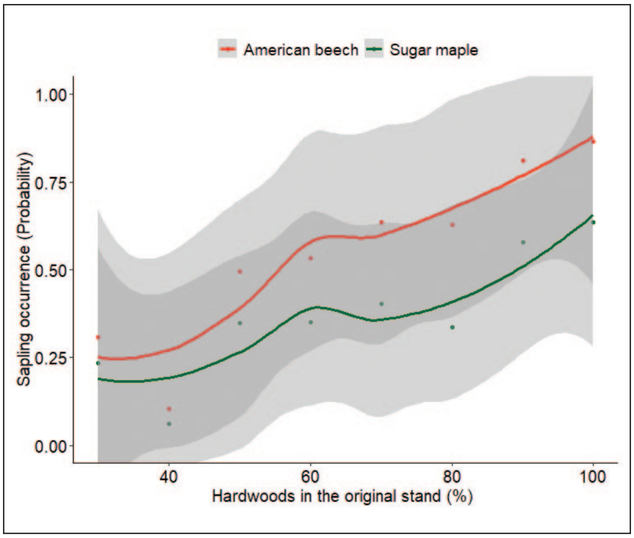

Fig. 4. Occurrence probability of tolerant hardwood saplings as a function of the percent classes (30% to 100%) of hardwoods in the original stand. Occurrence probability values for each percent classes are shown along with the curves and their 95% confidence intervals predicted by the best-fitting model for each species.

et al. 2008, 2015). The occurrence of tolerant hardwood regeneration can also be influenced by other factors not addressed in this study, such as browsing by large herbivores (Bose *et al.* 2017).

Study limitations

Our study was limited by its small sample size (n = 43), which restricts the inference potential of the results compared to studies based on more extensive sampling designs (Bataineh *et al.* 2013; Nolet *et al.* 2015; Bose *et al.* 2017). This limits our capacity to identify the factors driving regeneration success across a large gradient of conditions. We therefore recommend increasing the number of sample plots to confirm the patterns found for each species and reach more comprehensive conclusions about the most important factors explaining variations in density and occurrence of tolerant hardwood saplings.

In spite of these limitations, our study addresses the response of tolerant hardwood saplings 14 years after harvest. For future research, it would be useful to evaluate the response of saplings over shorter periods, notably two, five and 10 years after harvest through continuous regeneration monitoring. This information would improve our understanding of the regeneration dynamics of tolerant hardwoods after harvest over short-, medium- and long-terms. It also would be relevant to evaluate the density and occurrence of other species groups such as mid-tolerant hardwoods (yellow birch, red maple), intolerant hardwoods (white birch, trembling aspen) and softwood species. These species groups could have a commercial interest to forest managers and, at the same time, may compete with tolerant hardwoods for site resources (e.g., light, nutrients) and influence their density and occurrence (Tubbs 1973; Burns and Honkala 1990; Hane 2003; Hane *et al.* 2003).

Conclusion

In this study, we examined the effects of silvicultural, environmental, and ecological factors on sapling density and occurrence variability of two commercial tolerant hardwood species in New Brunswick: American beech and sugar maple. Despite its limitations, our study demonstrated that the variation in density and occurrence probability was best explained by treatment intensity expressed as merchantable residual basal area (after harvesting), and by the percent of hardwoods in the original stand. Also, in contradiction to our predictions, we found that American beech saplings seemed more abundant than sugar maple in plots with low basal area after harvesting (plots with low harvesting intensity).

The regeneration of tolerant hardwood stands is an important issue in the management of the Acadian forests of eastern North America which provide a range of economic, environmental and social services (Loo and Ives 2003; Weaver *et al.* 2009). Improving our understanding of the factors influencing the regeneration and productivity of these forests is essential to optimize their services and ensure their sustainability (Loo and Ives 2003; Salonius 2007). Future research should focus on evaluating the effects of site fertility and the degree of interspecific competition between tolerant hardwoods and other hardwood groups co-existing in the stand on density and occurrence variability. Efforts also should be invested in evaluating the regeneration dynamics of tolerant hardwoods after harvest in the short-, medium- and long-term.

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Table S1. List of 104 candidate models for AICc selection used for predicting the density and occurrence of tolerant hardwood saplings

Model#	Model variables and interactions
Null model	-
Global model	Sps[1] + BA residual stand[2] + % BA removed trees[3] + % HWD original stand[4] + TPI[5] + % THWD original stand[6] + % MHWD original stand[7] + % IHWD original stand[8] + Elevation + % HWD residual stand[9] + QMD original stand[10] + QMD removed trees[11] + BA original stand[12]
Model 1	Sps + BA residual stand + % BA removed trees + % HWD residual stand
Model 2	Sps * BA residual stand + Sps * % BA removed trees + Sps * % HWD residual stand
Model 3	Sps + BA residual stand + % BA removed trees + QMD removed trees
Model 4	Sps * BA residual stand + Sps * % BA removed trees + Sps * QMD removed trees
Model 5	Sps + QMD removed trees + % HWD residual stand
Model 6	Sps * QMD removed trees + Sps * % HWD residual stand
Model 7	Sps + BA original stand + % HWD original stand
Model 8	Sps * BA residual stand + Sps * % HWD original stand
Model 9	Sps + % HWD original stand + QMD original stand
Model 10	Sps * % HWD residual stand + Sps * QMD residual stand[13]
Model 11	Sps + DWT[14]
Model 12	Sps * DWT
Model 13	Sps + BGI[15]
Model 14	Sps * BGI
Model 15	Sps + TPI + Elevation
Model 16	Sps * TPI + Sps * Elevation
Model 17	Sps + Aspect + Slope
Model 18	Sps * Aspect + Sps * Slope
Model 19	Sps + BA original stand + TPI
Model 20	Sps * BA original stand + Sps * TPI
Model 21	Sps + % HWD original stand + TPI
Model 22	Sps * % HWD original stand + Sps * TPI
Model 23	Sps + QMD original stand + TPI
Model 24	Sps * QMD original stand + Sps * TPI
Model 25	Sps + BA original stand + Elevation
Model 26	Sps * BA original stand + Sps * Elevation
Model 27	Sps + % HWD original stand + Elevation
Model 28	Sps * % HWD original stand + Sps * Elevation
Model 29	Sps + QMD original stand + Elevation
Model 30	Sps * QMD original stand + Sps * Elevation
Model 31	Sps + BA residual stand + % BA removed trees
Model 32	Sps * BA residual stand + Sps * % BA removed trees
Model 33	Sps + BA residual stand
Model 34	Sps * BA residual stand
Model 35	Sps + % BA removed trees
Model 36	Sps * % BA removed trees
Model 37	Sps + % BA removed trees + Slope
Model 38	Sps * % BA removed trees + Sps * Slope
Model 39	Sps + % BA removed trees + TPI
Model 40	Sps * % BA removed trees + Sps * TPI
Model 41	Sps + % BA removed trees + Elevation
Model 42	Sps * % BA removed trees + Sps * Elevation
Model 43	Sps + % BA removed trees + BGI
Model 44	Sps * % BA removed trees + Sps * BGI
Model 45	Sps + % BA removed trees + % HWD original stand
Model 46	Sps * % BA removed trees + Sps * % HWD original stand
Model 47	Sps + % BA removed trees + BA original stand
Model 48	Sps * % BA removed trees + Sps * BA original stand
Model 49	Sps + % BA removed trees + QMD original stand
Model 50	Sps * % BA removed trees + Sps* QMD original stand
Model 51	Sps + Slope
Model 52	Sps * Slope
Model 53	Sps + Elevation
Model 54	Sps * Elevation
Model 55	Sps * QMD original stand
Model 56	Sps * QMD removed trees
Model 57	Sps * QMD original stand
Model 58	Sps + % HWD original stand
Model 59	Sps * % HWD original stand
Model 60	% HWD original stand
Model 61	Sps
Model 62	Sps + Soil
Model 63	Sps * Soil
Model 64	Sps + Ecosite
Model 65	Sps * Ecosite
Model 66	Sps + BA original stand + % THWD original stand
Model 67	Sps + BA original stand + % MHWD original stand

Model#	Model variables and interactions
Model 68	Sps + BA original stand + % IHWD original stand
Model 69	Sps * BA original stand + Sps * % THWD original stand + Sps * % HWD original stand
Model 70	Sps * BA original stand + Sps * % MHWD original stand + Sps * % HWD original stand
Model 71	Sps * BA original stand + Sps * % IHWD original stand + Sps * % HWD original stand
Model 72	Sps + % THWD original stand + % HWD residual stand + QMD residual stand
Model 73	Sps + % MHWD original stand + % HWD residual stand + QMD residual stand
Model 74	Sps + % IHWD original stand + % HWD residual stand + QMD residual stand
Model 75	Sps * % THWD original stand + Sps * % HWD residual stand + Sps * QMD residual stand
Model 76	Sps * % MHWD original stand + Sps * % HWD residual stand + Sps * QMD residual stand
Model 77	Sps * % IHWD original stand + Sps * % HWD residual stand + Sps * QMD residual stand
Model 78	Sps + % THWD original stand + % HWD original stand + TPI
Model 79	Sps + % MHWD original stand + % HWD original stand + TPI
Model 80	Sps + % IHWD original stand + % HWD original stand + TPI
Model 81	Sps * % THWD original stand + Sps * % HWD original stand + Sps * TPI
Model 82	Sps * % MHWD original stand + Sps * % HWD original stand + Sps * TPI
Model 83	Sps * % IHWD original stand + Sps * % HWD original stand + Sps * TPI
Model 84	Sps + % THWD original stand + % HWD original stand + Elevation
Model 85	Sps + % MHWD original stand + % HWD original stand + Elevation
Model 86	Sps + % IHWD original stand + % HWD original stand + Elevation
Model 87	Sps * % THWD original stand + Sps * % HWD original stand + Sps * Elevation
Model 88	Sps * % MHWD original stand + Sps * % HWD original stand + Sps * Elevation
Model 89	Sps * % IHWD original stand + Sps * % HWD original stand + Sps * Elevation
Model 90	Sps + % BA removed trees + % THWD original stand + % HWD original stand
Model 91	Sps + % BA removed trees + % MHWD original stand + % HWD original stand
Model 92	Sps + % BA removed trees + % IHWD original stand + % HWD original stand
Model 93	Sps * % BA removed trees + Sps * % THWD original stand + Sps * % HWD original stand
Model 94	Sps * % BA removed trees Sps * % MHWD original stand + Sps * % HWD original stand
Model 95	Sps * % BA removed tree + Sps * % IHWD original stand + Sps * % HWD original stand
Model 96	Sps + % THWD original stand
Model 97	Sps + % MHWD original stand
Model 98	Sps + % IHWD original stand
Model 99	Sps * % THWD original stand
Model 100	Sps * % MHWD original stand
Model 101	Sps * % IHWD original stand
Model 102	% THWD original stand
Model 103	% MHWD original stand
Model 104	% IHWD original stand

[1] Species
[2] Residual merchantable basal area ($m^2 ha^{-1}$)
[3] Percent (%) of merchantable basal area removed
[4] Percent (%) of hardwoods in the original stand
[5] Topographic index
[6] Percent (%) of tolerant hardwoods in the original stand
[7] Percent (%) of mid-tolerant hardwoods in the original stand
[8] Percent (%) of intolerant hardwoods in the original stand
[9] Percent (%) of hardwoods in the residual stand
[10] Quadratic mean diameter of merchantable trees in the original stand before harvest (cm)
[11] Quadratic mean diameter of the removed merchantable trees after the first harvest (cm)
[12] Total basal area of the original stand ($m^2 ha^{-1}$)
[13] Quadratic mean diameter of the residual merchantable trees after the first harvest (cm)
[14] Depth of the water table (m)
[15] Biomass growth index

Table S2. The AICc and ΔAICc values of all selected candidate models used for the prediction of the density and occurrence of tolerant hardwood saplings in New Brunswick, Canada. The best model (#8) is shown in bold with the lowest AICc and ΔAICc value.

Model #	AICc	ΔAICc	df
Model 8	**690.96**	**0**	**11**
Model 59	694.51	3.55	7
Model 9	695.80	4.83	9
Model 71	696.36	5.40	15
Model 7	696.41	5.45	9
Model 70	696.53	5.57	15
Model 69	696.77	5.81	15
Model 45	697.05	6.09	9
Model 60	697.14	6.18	5
Model 58	697.41	6.44	7
Model 46	697.48	6.52	11
Model 27	699.73	8.77	9
Model 28	700.66	9.70	11
Model 21	701.35	10.39	9
Model 91	701.39	10.43	11
Model 90	701.54	10.58	11
Model 92	701.72	10.76	11
Model 22	702.82	11.86	11
Model 30	703.34	12.38	11
Model 95	703.71	12.75	15
Model 85	704.27	13.31	11
Model 84	704.50	13.54	11
Model 86	704.83	13.8	11
Model 5	705.69	14.73	9
Model 80	705.87	14.91	11
Model 79	706.24	15.27	11
Model 78	706.29	15.30	11
Model 89	706.56	15.59	15
Model 56	706.7	15.78	7
Model 55	707.05	16.08	7
Model 57	707.05	16.08	7
Model 93	707.38	16.42	15
Model 94	707.43	16.47	15
Model 83	707.95	16.99	15
Model 23	708.10	17.14	9
Model 99	708.18	17.22	7
Model 54	709.11	18.14	7
Model 49	709.17	18.21	9
Model 6	709.55	18.59	11
Model 29	709.94	18.98	9
Model 10	709.98	19.02	11
Model 87	710.30	19.34	15
Model 88	710.32	19.36	15
Model 96	710.49	19.50	7
Model 66	710.89	19.93	9
Model 53	710.98	20.01	7
Model 61	711.36	20.40	5
Model 64	712.02	21.06	13
Model 24	712.23	21.27	11
Model 81	712.37	21.41	15
Model 19	712.60	21.64	9
Model 102	712.65	21.69	5
Model 33	712.65	21.69	7
Model 25	712.79	21.83	9
Model 82	713.00	22.03	15
Model 15	713.00	22.04	9
Model 50	713.15	22.19	11
Model 26	713.17	22.21	11
Model 42	713.70	22.74	11
Model 16	713.89	22.93	11
Model 35	713.99	23.03	7
Null model	714.01	23.05	3
Model 1	714.07	23.11	11
Model 12	714.17	23.21	7
Model 34	714.18	23.22	7
Model 67	714.21	23.25	9
Model 47	714.26	23.30	9
Model 41	714.45	23.49	9
Model 77	714.55	23.59	15
Model 68	714.62	23.66	9
Model 75	715.12	24.16	15
Model 98	715.15	24.19	7
Model 3	715.15	24.19	11
Model 13	715.19	24.23	7
Model 72	715.27	24.31	11
Model 17	715.35	24.39	9
Model 11	715.39	24.43	7
Model 97	715.52	24.55	7
Model 14	715.67	24.71	7
Model 51	715.77	24.81	7
Model 36	715.81	24.85	7
Model 39	716.23	25.26	9
Model 20	716.92	25.96	11
Model 31	717.07	26.11	9
Model 104	717.41	26.45	5
Model 74	717.45	26.49	11
Model 2	717.48	26.52	15
Model 52	717.52	26.56	7
Model 73	717.67	26.71	11
Model 62	717.83	26.87	15
Model 103	717.90	26.94	5
Model 43	718.08	27.12	9
Model 37	718.69	27.73	9
Model 100	718.72	27.76	7
Model 48	718.72	27.76	11
Model 101	719.90	28.94	7
Model 40	720.53	29.57	11
Model 76	720.89	29.93	15
Model 32	721.10	30.14	11
Model 18	721.61	30.65	11
Model 44	722.43	31.47	11
Model 4	724.12	33.16	15
Model 38	725.24	34.28	11
Global model	747.37	56.41	29
Model 63	2825.90	2134.94	27

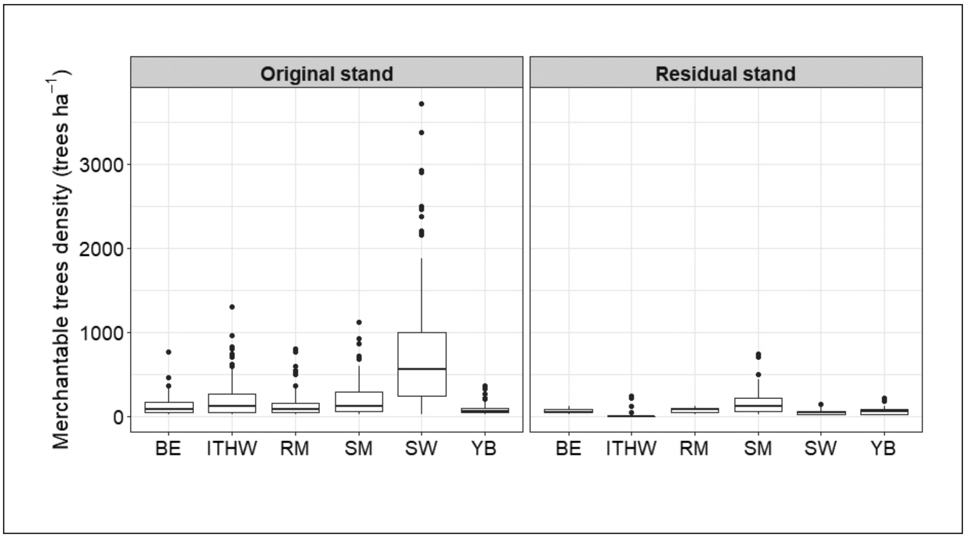

Fig. S1. Box plots showing the variation of trees density (trees ha^{-1}) by species or group of species in the original (before harvesting) and residual stands (after harvesting). BE: American beech; ITHW: intolerant hardwoods (white birch, trembling aspen); RM: red maple; SM: sugar maple; SW: softwood; YB: yellow birch.

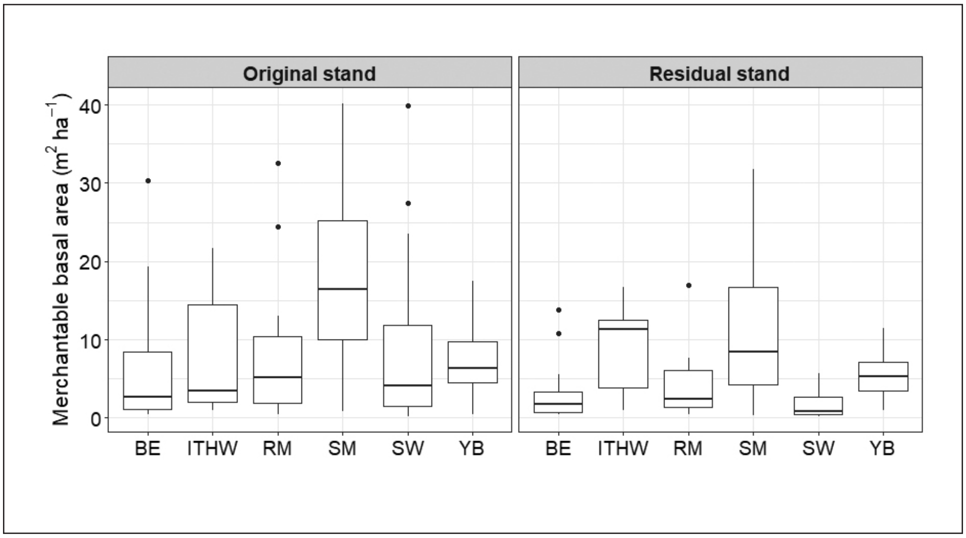

Fig. S2. Box plots showing the variation in merchantable basal area (m^2 ha^{-1}) by species or group of species in the original (before harvesting) and residual stands (after harvesting). BE: American beech; ITHW: intolerant hardwoods (white birch, trembling aspen); RM: red maple; SM: sugar maple; SW: softwood; YB: yellow birch.

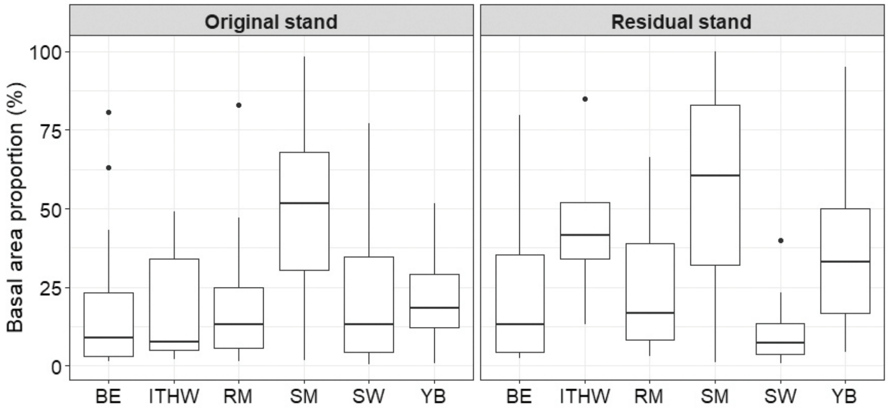

Fig. S3. Box plots showing the variation in the proportion of basal area (%) for each species or group of species in original (before harvesting) and residual stands (after harvesting). BE: American beech; ITHW: intolerant hardwoods (white birch, trembling aspen); RM: red maple; SM: sugar maple; SW: softwood; YB: yellow birch.