Forest Ecology and Management 455 (2020) 117649

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Comparing the predictions of gap model with vegetation and disturbance data in south-eastern Canadian mixed forests

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ABSTRACT

The lack of long term independent historical data constitute a major impediment to the further improvement and validation of forest simulation models. In this study, we evaluate the degree to which the gap model ZELIG-CFS realistically predicts the long term stand development of mixed forests in southeastern Quebec when disturbance history is considered. An early 1930 forest inventory and disturbance data were used to evaluate model simulation performance over the 1930–2013 period. ZELIG-CFS well predicted the basal area of balsam fir in simulations with and without disturbances. When disturbances were simulated, the predictions for white spruce and white birch were more realistic than in the simulation without disturbances. At the same time, deciduous species that contributed the most to the compositional changes observed during the 20th century in mixed forests (red maple, sugar maple, and trembling aspen) were systematically underestimated by the model. Several improvement avenues are suggested: (1) A better integration of regeneration strategies of tree species, especially the integration of a probability of vegetative reproduction for sprouting species like red maple, sugar maple, trembling aspen and northern white cedar, (2) Coupling gap models with a stand risk model to better simulate natural and human disturbance probability as a source of exogenous mortality.

1. Introduction

Forest gap models are a class of semi mechanistic, individual-tree forest dynamics models that have wide applications, but need further developments to improve their capacity to simulate forest ecosystem dynamics. They have been developed over the last few decades to study succession pathways in forest ecosystems (Botkin, 1993; Peng et al., 2006; Larocque, 2016) and landscapes (Urban et al., 1991), and have also been applied to study past vegetation dynamics using fossil pollen data (Solomon and Shugart, 1984). Their strength resides in their realism at emulating basic vegetational processes which make them reliable tools to explore forest dynamics (Solomon, 1986; Shugart and Smith, 1996; Keane et al., 2001; Norby et al., 2001; Price et al., 2001; Wullschleger et al., 2001). Some authors have also suggested that they have the potential to replace empirical growth and yield models in policy and forest management planning (Landsberg, 2003; Taylor et al., 2009). Suggested improvements of gap models concern the simulation of processes inducing mortality (Lindner et al., 1997; Keane et al., 2001; Pabst et al., 2008; Larocque et al., 2011) and regeneration (Price et al., 2001; Wehrli et al., 2007). The effects of temperature response functions on growth rate have also been discussed in several studies and reviews (Sirois et al., 1994; Loehle and LeBlanc, 1996; Schenk, 1996; Monserud, 2003; Portner et al., 2010).

Several simulation studies emphasize the importance of the explicit consideration of natural and human forest disturbances as an exogenous source of mortality (Schumacher and Bugmann, 2006; Seidl et al., 2011). Simulated species composition can differ when mortality caused by specific disturbances like fire, harvest, browsing, grazing by mammals, and insect outbreaks was taken into account (Dale et al., 1986; Kienast and Kräuchi, 1991; Prentice et al., 1993; Lexer and Hönninger, 1998; Jorritsma et al., 1999; Miller and Urban, 1999; Keane et al., 2001; Seagle and Liang, 2001; Pabst et al., 2008). Disturbances are important drivers of forest dynamics and would eventually affect the successional trajectory of a forest stand (Smith and Urban, 1988; White and Jentsch, 2001; Frelich, 2002). For example, mixed forests in eastern North America have experienced a shift in disturbance regime following European colonisation due to settlement fires and intensive industrial logging (Foster et al., 1998; Lorimer, 2001; Blanchet, 2003; Friedman and Reich, 2005; Terrail et al., 2019; Elzein et al., submitted for publication). These novel disturbances represent an increasing risk of large scale mortality compared to preindustrial background levels (Canham et al., 2013; Trumbore et al., 2015). Furthermore, mortality caused by different disturbance types such as fires, insect outbreaks, and logging varies across species, size classes and vigor classes and also affect the regeneration processes through the modification of light conditions and soil humidity (Price et al., 2001; White and Jentsch, 2001).

One of the difficulties that limits the further improvement and

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https://doi.org/10.1016/j.foreco.2019.117649
Received 26 July 2019; Received in revised form 19 September 2019; Accepted 20 September 2019
Available online 12 November 2019
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Table 1
Species characteristics in ZELIG-CFS.

Species	Maximum age (years)	Maximum dbh (cm)	Maximum height (m)	Growth rate scaling coefficient	Growing degree-days		Shade[a] tolerance class	Maximum[b] drought tolerance	Fertility[c] class
					Species characteristics in ZELIG	Species characteristics in ZELIG			
Abies balsamea	200	65	30	69	250	2404	1	1	3
Acer pensylvanicum	75	22	15	150	889	5500	1	2	3
Acer rubrum	150	80	30	176	1260	6601	2	3	3
Acer saccharum	300	110	44	89	1204	3200	1	2	2
Acer spicatum	50	18	9.5	150	889	5500	1	2	3
Betula alleghaniensis	250	150	45	100	1420	3084	3	2	2
Betula papyrifera	140	70	30	160	700	2500	4	3	3
Picea glauca	200	64	30	132	447	1929	2	3	3
Picea mariana	250	40	20	70	265	1929	2	3	3
Pinus strobus	450	150	37	68	1500	3183	4	2	3
Populus tremuloides	125	75	37	158	889	5556	5	3	2
Fraxinus americana	300	100	40	75	1225	2279	3	1	1
Thuja occidentalis	400	100	29	55	1000	2188	2	4	3

*Adapted from Larocque, G.R., Archambault, L., Delisle, C., 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222, 2570–2583.

[a] Rank: 1 = very shade-tolerant; 5 = very shade intolerant.

[b] Rank: 1 = very drought intolerant; 5 = very drought tolerant.

[c] Rank: 1 = nutrient stress intolerant; 3 = nutrient stress tolerant

validation of gap models is the limited availability of long-term, independent historical data to evaluate the realism of models simulations (Botkin et al., 1972; Smith and Urban, 1988; Shugart and Smith, 1996; Lindner et al., 1997; Bugmann, 2001; Larocque et al., 2016). Yet, gap models have well been tested against long-term independent historical data (Dale et al., 1986; Liu and Ashton, 1995; Lindner et al., 1997; Makela et al., 2000; Yaussy, 2000; Badeck et al., 2001; Risch et al., 2005; Larocque et al., 2006; Pabst et al., 2008; Didion et al., 2009; Larocque et al., 2011; Holm et al., 2012; Rasche et al., 2012; Shuman et al., 2014; Foster et al., 2017). An example of gap model validation with long-term independent data is a study conducted by Larocque et al. (2006) in the mixed forests of eastern Canada which highlighted the critical lack of knowledge on the dynamics of regeneration, which resulted in poor predictions for some species like yellow birch. In the case of this paper, the quantitative nature of the vegetation database and the spatially explicit disturbance data represent an additional opportunity to further test the predictions of gap models and validate the role of disturbances in the simulations. Furthermore, many modellers have used gap models to study forest changes over long time periods (100–500 years), whereas some authors suggest that their accuracy should be evaluated for time scales < 100 years (Yaussy, 2000).

The objective of this study was to evaluate the degree to which the gap model ZELIG-CFS (Larocque et al., 2011) realistically predicted the long term stand development of mixed forests using a detailed historical dataset of forest composition and disturbance. The observation dataset consisted of a spatially explicit 1930 stand inventory data coupled with a detailed disturbance database (1935–2005) in south eastern Canadian mixed forests. We specifically aimed at using the model in a mixed forest region and to identify biases in model performance with or without exogenous mortality caused by disturbances.

2. Material and methods

2.1. Study area

The study area (2564 km^2) is located in the Lower Saint Lawrence region (LSL) in the province of Quebec, Canada (47° 92′–48° 91′ N and 66° 84′–68° 86′ W). It is characterized by low elevation hills with moderate slopes. The mean and maximum elevations are 350 and 910 m, respectively. Underlying geology is characterized by the sedimentary bedrock of the Appalachian geological formation. Meteorological data from weather stations at Rimouski and Trinité-des-Monts between 1981 and 2010 showed that mean annual temperature varied between 4.4 and 2.5 °C, respectively, and mean annual total precipitations varied between 959 and 1100 mm, 30% of which fall as snow (EnvironmentCanada, 2019).

The vegetation zone is at the northern limit of the Great Lakes-St. Lawrence mixed forests (Rowe, 1972) at the transition between the temperate deciduous and the boreal coniferous forests. Balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), yellow birch (*Betula alleghaniensis*), white birch (*Betula papyrifera*) are abundant in mesic sites. Sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*), are at their northern range limit and generally occupy hill tops, while Black spruce (*Picea mariana*) and northern white cedar (*Thuja occidentalis*) generally occupy organic deposits mostly next to water courses (Robitaille and Saucier, 1998).

Forests in the study area have been shaped by extensive logging and anthropogenic settlement fires during the 20th century (Elzein et al., submitted for publication). Prior to extensive industrial logging at the beginning of the century, the forest in the region was dominated by old growth (> 100 years old) coniferous stands in the lowlands, while mixed and deciduous stands represented less than 40% of the landscape and occupied hill tops (Boucher et al., 2009). Intensive logging gave place to a fragmented landscape, that is nowadays a mosaic of plantations, regenerating deciduous stands, and young even-aged forests with a few patches of unmanaged mature forests (Boucher et al., 2009; Dupuis et al., 2011; Elzein et al., submitted for publication). The post-industrial landscape has been also structured by anthropogenic fires, which increased the abundance of trembling aspen (*Populus tremuloides*) (Terrail et al., 2019; Elzein et al., submitted for publication).

2.2. ZELIG-CFS structure and function

ZELIG-CFS (Larocque et al., 2011) is a modified version of ZELIG (Urban and Shugart, 1992), which has its roots in JABOWA and FORET simulation models (Urban, 1990). Like ZELIG, it simulates individual-tree growth, regeneration and mortality. Individual-tree growth is computed by estimating maximum potential growth rate in an annual time step and then constrains it through limiting ecological factors based on light interception by competitors, soil moisture, a soil fertility factor and ambient temperature. The effect of temperature on species-specific growth rate is modelled by a parabolic equation constrained by

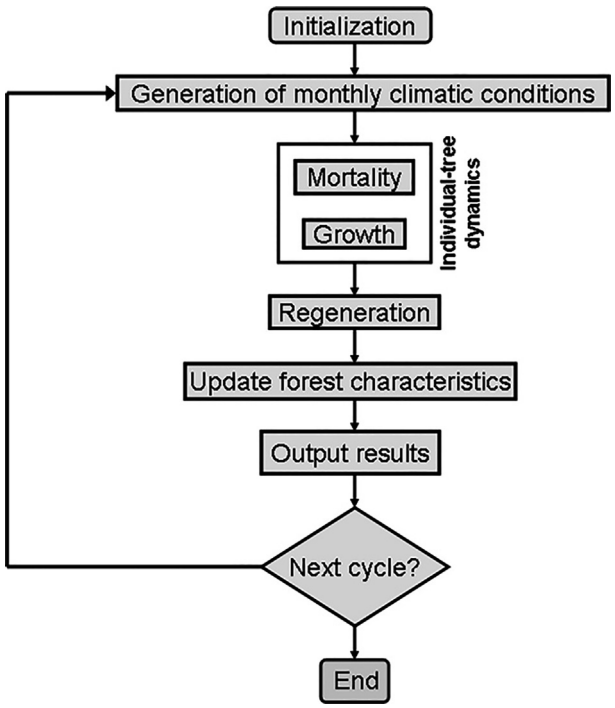

Fig. 1. Basic conceptual diagram of ZELIG-CFS gap model (from Larocque et al. (2011)).

the species' minimum and maximum growing degree-days within its entire geographical range (Table 1).

ZELIG-CFS is an advanced simulation model based on ZELIG (Smith and Urban, 1988). Compared to other gap models, new algorithms for crown interaction effects and prediction of species-specific mortality rate and regeneration were developed in ZELIG-CFS. In particular, mortality rate functions based on DBH and DBH growth rate were developed (Larocque et al., 2011). Then, a random value is computed to determine if a tree dies or not depending on its probability of survival. The consideration of species-specific crown shape allows interaction between individual trees instead of modelling the forest as a matrix of gap sized squares variably filled leaf area as in the original version of ZELIG. Modelling of the available light growing factor (ALGF) and crown recession rate influence radial growth of the stems. Mortality rate in ZELIG-CFS is computed by taking into consideration species-specific degree of tolerance to slow growth rate as a function of DBH and radial growth rate (Larocque et al., 2011), estimated from empirical data. Furthermore, ZELIG-CFS accounts for spatial heterogeneity of seedling distribution by using a species-specific stocking factor that is provided as input. The stocking factor adjusts the potential number of seedlings that can germinate under the prevailing site conditions, species ecological requirements, and competition. ZELIG-CFS randomly introduces a pre-established number of seedlings per species each year of the simulation based on empirical observations, and simulates the shade tolerance of species as the sensitivity to light conditions in the understorey. Ecological characteristics of different species are described in ZELIG-CFS using 5 shade tolerance classes, 3 stress tolerance classes in response to soil fertility, and 5 drought tolerance classes in response to soil moisture (Table 1).

ZELIG-CFS functioning includes several steps. Simulations are initialized with site physical data, monthly mean temperature and precipitation values, species' functional traits, potential seed establishment values and individual tree DBH data. The annual changes are then computed as follow: generation of random fluctuations of monthly climatic conditions, prediction of individual-tree mortality and growth, prediction of seedling establishment and sapling development, update of characteristics such as basal area and leaf area index, and recording of the main state variables. These computations are repeated for the number of annual cycles determined in the initialization phase (Fig. 1). Many individually simulated forest patches can be aggregated to depict vegetation succession at the landscape level.

2.3. Initializing ZELIG-CFS

To initialize ZELIG-CFS, we used data from a detailed forest inventory conducted by the Price Brothers & Company between 1930 and 1931 (hereafter referred to as the 1930 inventory) in 457 rectangular plots of 0.1 ha each. Individual stems (DBH > 3 in.; ~7.6 cm) were then tallied by tree taxa and 2-inches DBH classes. In order to validate ZELIG-CFS simulations with observations, the same plots were resampled in the summers of 2012 and 2013 (2013 inventory). The plots selected for this study represent naturally regenerated stands and do not include any plantations that are commonly found in the region. In 1930 these plots were known to be mature forests that had not been disturbed between 1895 and 1935 according to our disturbance data base (Elzein et al., submitted for publication). In the historical data base, some taxa were grouped such as birches, poplars, maples and spruces. Because some species were aggregated in genera in 1930 database, we attributed the proportional abundance of species belonging to each genera in 2013 to the 1930 database. This permitted us to identify these genera in the 1930 database to the species level, information necessary to initiate simulations in ZELIG-CFS. The simulations were made per plot. Tree DBHs in the 1930 sample plots were entered for model initialization. Regeneration density (potential number of seedlings/m^2) and stocking (proportion) per species were determined using values from the literature (Table 2). Spatially explicit disturbance history was reconstructed for each plot per 10 year interval between 1935 and 2005 using historical and modern forest maps (Elzein et al., submitted for publication). The reconstructed disturbances were classified as fires,

Table 2
Regeneration density and stocking values used in the simulation.

Species		Density	Stocking	References
Abies balsamea	Balsam fir	2.12	0.84	Roy et al. (2000)
Acer pensylvanicum	Striped maple	0.03	0.05	Larocque et al. (2006)
Acer rubrum	Red maple	2.37	0.83	Roy et al. (2000)
Acer saccharum	Sugar maple	5.00	0.80	Archambault et al. (2009)
Acer spicatum	Mountain maple	1.00	0.75	Archambault et al. (1997)
Betula alleghaniensis	Yellow birch	1.00	0.30	Bolton and D'Amato (2001)
Betula papyrifera	White birch	0.03	0.04	Archambault et al. (1997)
Picea glauca	White spruce	0.03	0.08	Archambault et al. (1997)
Picea mariana	Black spruce	0.14	0.20	Roy et al. (2000)
Pinus strobus	White pine	0.01	0.02	Larocque et al. (2006)
Populus tremuloides	Trembling aspen	1.00	0.50	Roy et al. (2000)
Fraxinus americana	American ash	0.02	0.05	Larocque et al. (2006)
Thuja occidentalis	Northern white cedar	0.30	0.44	Roy et al. (2000)

Table 3
Simulated percentage of basal area removed per species for each disturbance type.

Disturbances	SAB	ERP	ERR	ERS	ERE	BOJ	BOP	EPB	EPN	PIB	PET	SOA	THO
Fire (1935–2005)	100	100	100	100	100	100	100	100	100	100	100	100	100
Partial Logging (1935–1965)	75	0	0	0	0	0	0	75	75	0	0	0	50
Partial Logging (1965–2005)	50	50	50	50	50	50	50	50	50	50	50	50	50
Total Logging (1965–2005)	100	100	100	100	100	100	100	100	100	100	100	100	100
Moderate spruce budworm outbreak (1975–2005)	25	0	0	0	0	0	0	25	0	0	0	0	0
Severe spruce budworm outbreak (1975–2005)	75	0	0	0	0	0	0	75	0	0	0	0	0

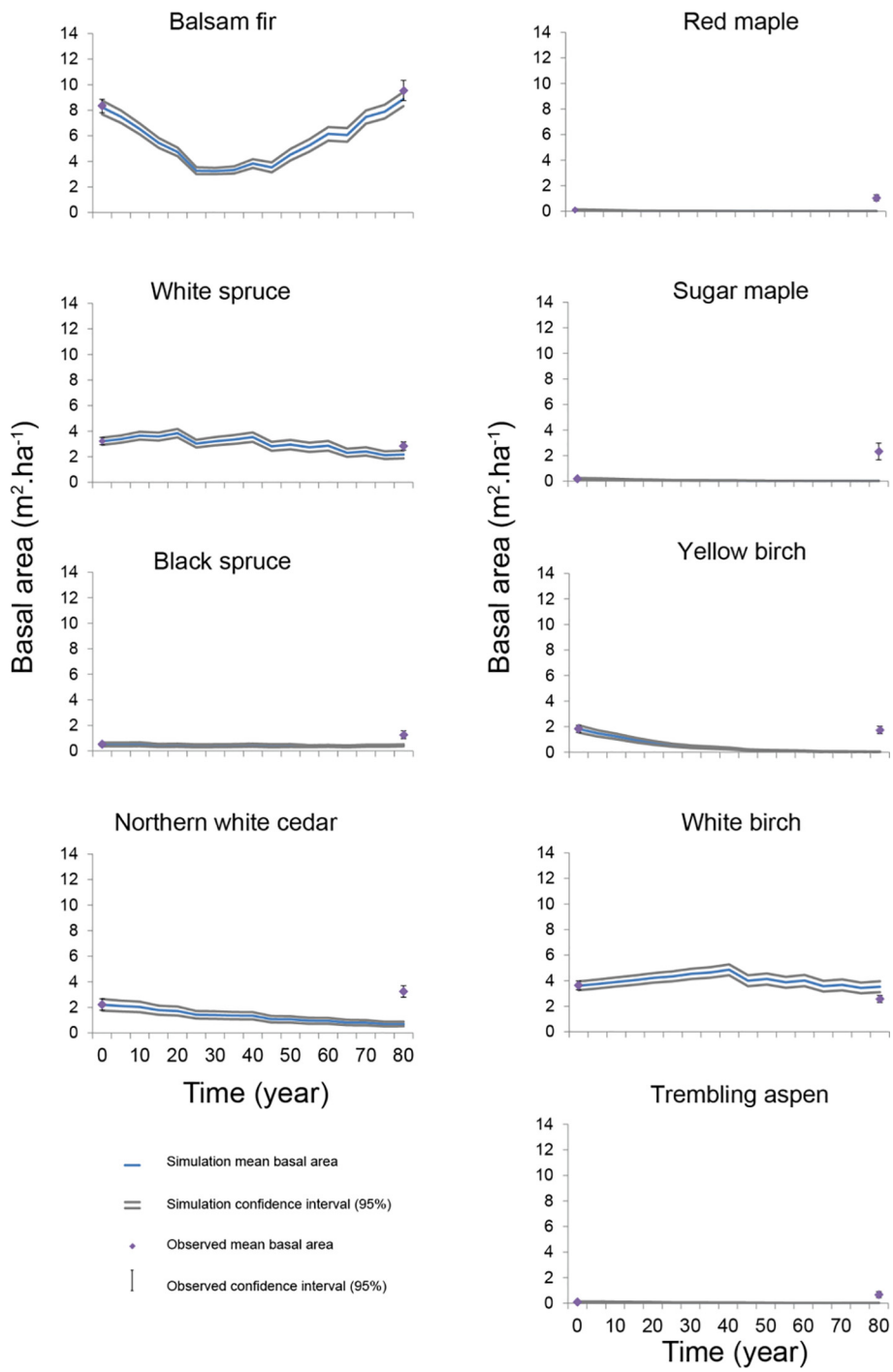

Fig. 2. Mean simulated and observed basal area ($m^2.ha^{-1}$) for species using regeneration density and stocking values of Table 1 and disturbance history for each sampling plot. N = 457.

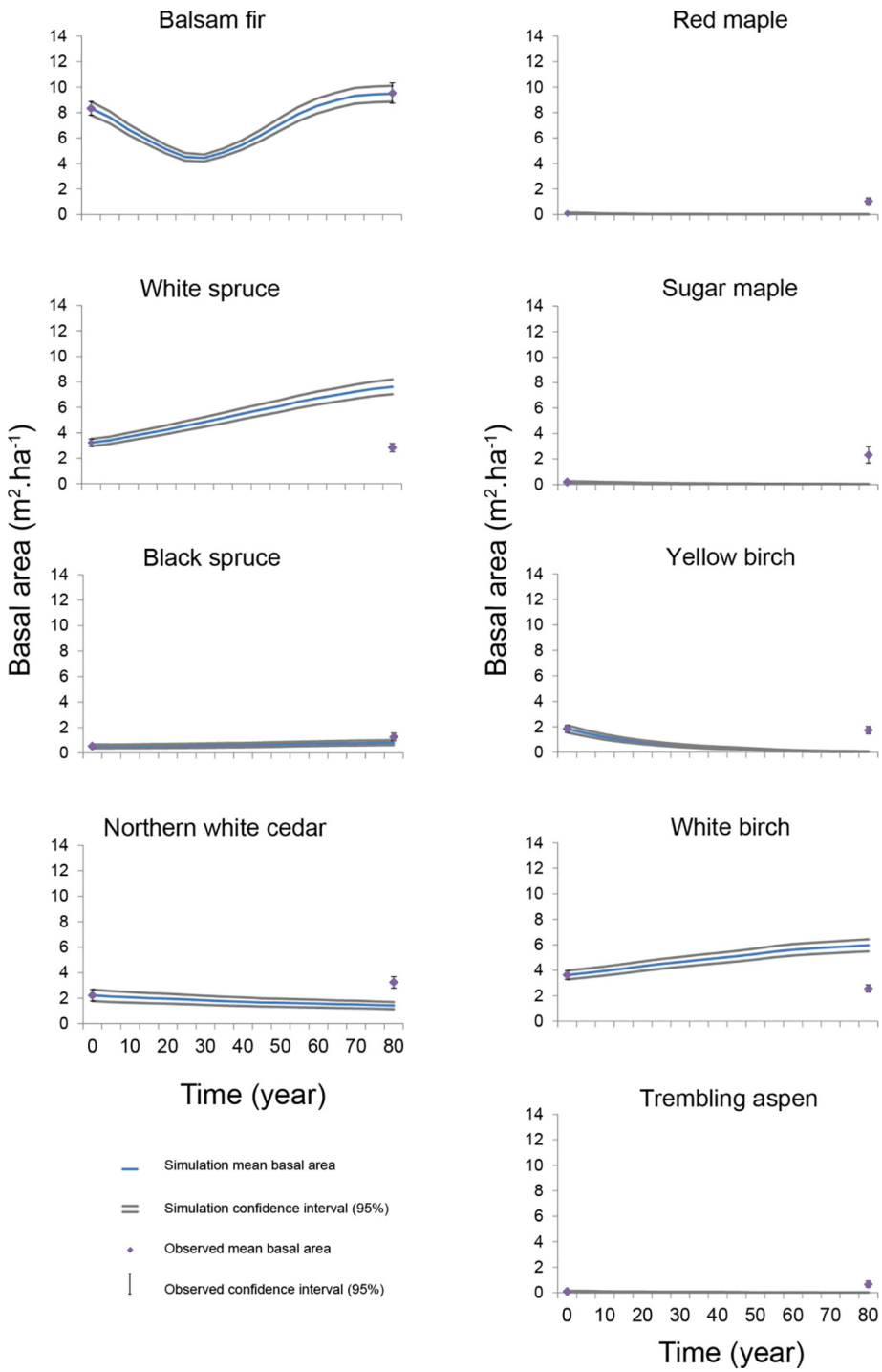

Fig. 3. Mean simulated and observed basal area ($m^2.ha^{-1}$) without disturbances for species using regeneration density and stocking values of Table 1. N = 457.

logging, and a 1970 s Spruce Budworm outbreak. Logging includes three categories: partial logging (1935–1965), partial logging (1965–2005), and total logging (1965–2005). On the Price Brothers & Company historical maps, logging polygons between 1935 and 1965 were identified as Cut Over zones, without a precise logging type. However, these cut over zones were most likely diameter limit partial logging operations, based on written accounts of logging practices at that time (Price Brothers & Company Limited, 1944; Fortin et al., 1993) and an analysis of forest diameter structure in logged vs. unlogged plots subsequently surveyed in 1930–1931 (Elzein et al., submitted for publication). Logging polygons for the period 1965–2005 were classified as partial cuts (logging severity varying from 25% to 75% of basal area) or total cuts (more than 75% basal area removal) based on Quebec's department of forests decadal inventories. Species' traits to be entered in ZELIG-CFS include maximum age (years), maximum DBH (cm), maximum height (m), growth rate scaling coefficient, minimum and maximum growing degree days in species' range, shade tolerance class, drought tolerance class, and crown shape. Site Fertility class is also parametrized in the model (Larocque et al., 2011).

We adapted ZELIG-CFS for our study area by providing the relevant environmental parameters, including longitude (°), latitude (°), altitude (m), plot area (m^2), soil type (qualitative variable based on texture), soil fertility factor (mg/ha/year), and monthly mean temperatures (°C) and precipitations (mm), along with corresponding standard deviations.

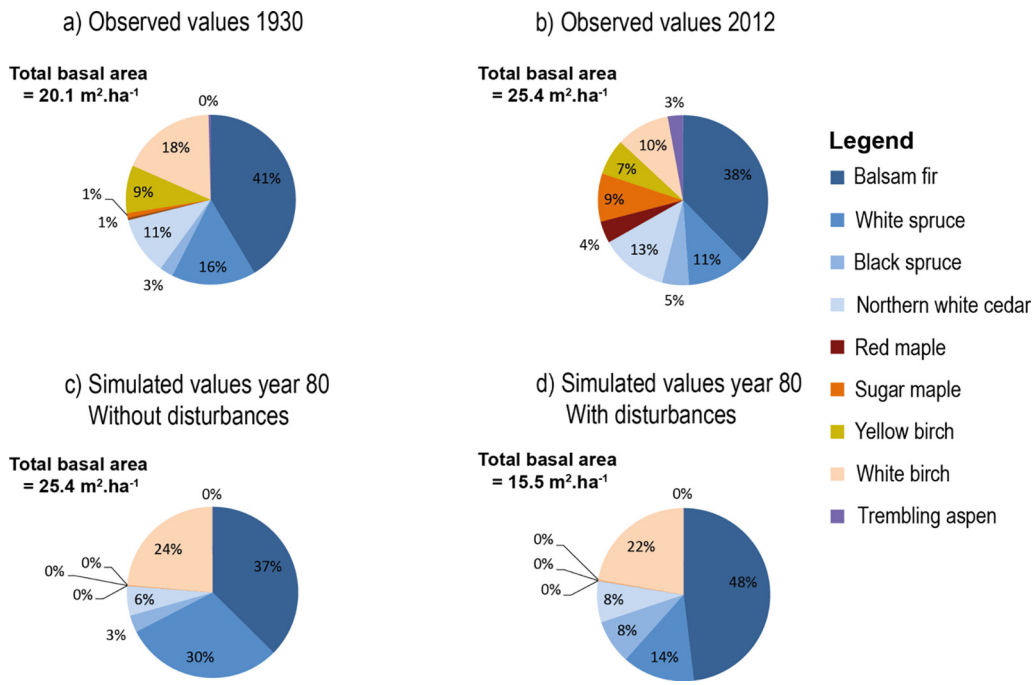

Fig. 4. Total basal area ($m^2.ha^{-1}$) and species relative basal area (proportion) for a) observed values of 1930, b) observed values of 2012, c) Simulated values of year 80 without disturbances, and d) simulated values of year 80 with disturbances.

Soil fertility factor is expressed in terms of the maximum megagrams per hectare of aboveground biomass that a site can produce in a year and is used to determine potential competition for nutrients per forest type. Soil type per plot was inferred using drainage classes from the fourth decadal inventory map produced by the Quebec's department of forests. The Sandy soil type was attributed to drainage classes 0.1, and 2, sandy loam to class 3, loam to class 4, silt loam to class 5, and clay loam to class 6. The 457 sampled plots were classified into four compositional types (Yellow birch-Red maple, White birch-Balsam fir, Balsam fir-Spruce, and Northern white cedar-Spruce) by cluster analysis of the main species basal area in 1930. Soil fertility factor for each forest type was then calculated using DBH values from one representative plot whose total basal area was closest to the mean value of all plots belonging to a particular forest type. Finally, monthly temperatures and precipitations for each sampling plot were obtained from BioSim 11 (https://cfs.nrcan.gc.ca/projects/133), based on available Canada-USA daily climatic data for the periods 1951–1980 and 1981–2013. BioSim 11 forecasts are based on regional air temperature and precipitation interpolated from nearby weather stations, adjusted for elevation and location differentials with regional gradients. Plots adjusted growing degree days (GDD) are calculated in ZELIG-CFS from mean monthly temperatures generated per plot by BioSim 11 for the growing season (May to September) using the following formula:

$$\mathrm{GDD} = (\textit{Mean Monthly Temprature} - 5.56) \times \textit{Number of days in the month}$$

GDD varied between 884 and 1218 in our study area, with 15% of our plots with values greater than 1204.

2.4. ZELIG-CFS performance and evaluation

To evaluate the degree to which ZELIG-CFS realistically predicts the long term stand development of mixed forests two sets of simulations were performed, with and without disturbances. For each set, each plot was simulated for 80 years and outputs were generated at 5 year intervals. For simulation with disturbance, each known disturbance event was simulated in the year and plots it actually occurred (Elzein et al., submitted for publication). During each disturbance event, randomly selected individual trees were removed to account for a determined percentage of basal area removal per species per disturbance type (Table 3). These percentages were estimated according to the known results of each disturbance on stand basal area in our study area. Depending on its disturbance history, each plot could be subjected to one or several disturbances in various years of the simulations. 169 out of the total 457 simulated plots have been subjected to 100% biomass removal and were grown from scratch at various stages of the simulation to account for stand replacing disturbances like clear cuts and/or fires.

ZELIG-CFS performance was evaluated by plotting the trajectory of simulated basal area per species and comparing the results of the last simulation year (year 80) to observed values in 2013. For simulations with disturbances, five groups of plots were considered depending on the presence/absence of each disturbance into each plot during the simulation period. We plotted the trajectory of simulated basal area values and compared the last simulated year value to observed values in each group. In this latter analysis, plots with more than one disturbance type were selected more than once.

3. Results

ZELIG-CFS is sensitive to disturbance regime. It performed better in the simulation with disturbances than without disturbance (Figs. 2 and 3). It has well estimated the basal area of balsam fir, white spruce, white birch and black spruce by the end of the simulation period in the simulation with disturbances (Fig. 2), while white spruce and white birch were overestimated in the simulation without disturbances (Fig. 3). Relative to observations, both simulations with and without disturbances under-predicted the basal area increase for red maple, sugar maple, trembling aspen, yellow birch and northern white cedar in 2013 as compared to 1930. During the 1930–2013 time interval, relative basal area of trembling aspen, red maple and sugar maple increased from less than 1% to 3%, 4%, and 9%, respectively (Fig. 4). Yet, at the end of simulations with or without disturbances relative basal areas of these three taxa were near 0% (Fig. 4). Conversely, the model over-estimated the relative basal area of softwood tree species other than cedar. The basal area of these taxa decreased from 71% to 67% in

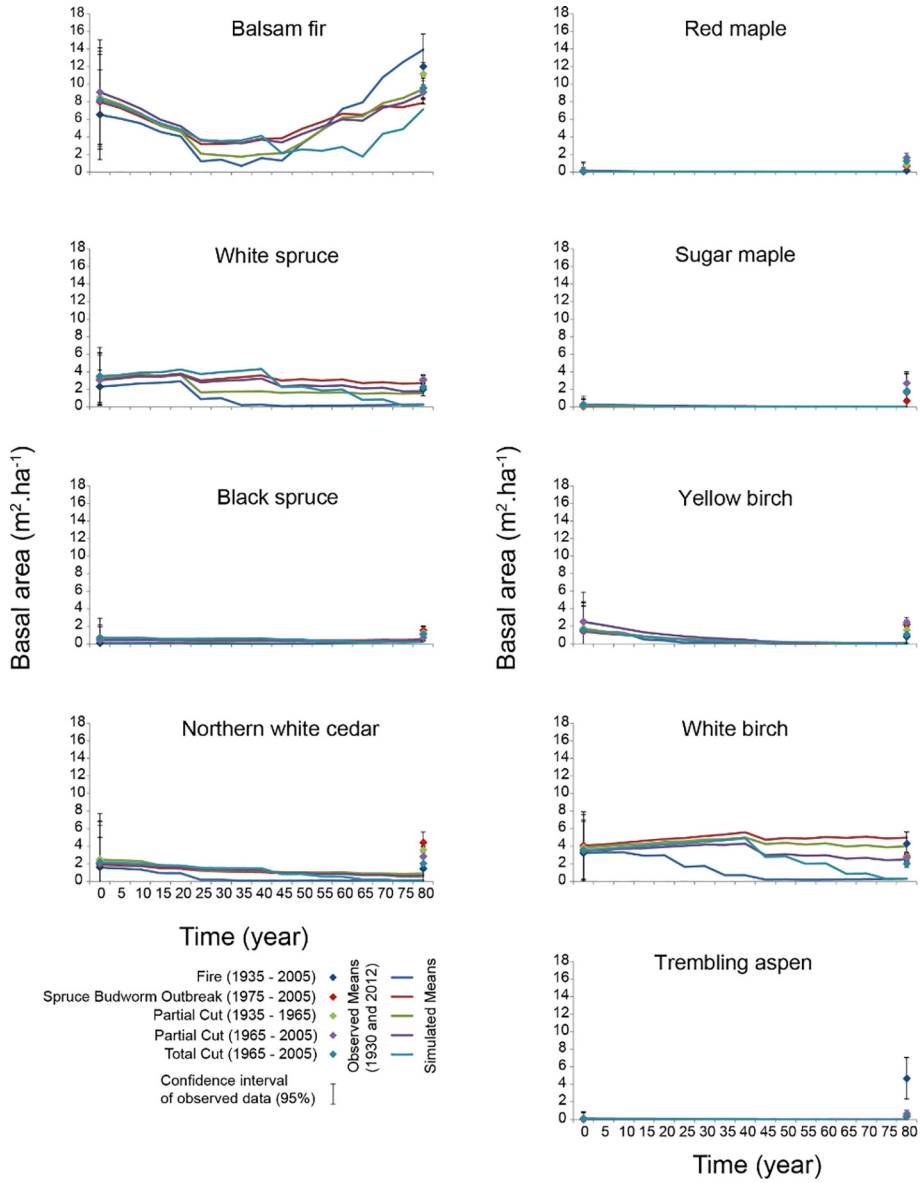

Fig. 5. Mean simulated and observed basal area ($m^2.ha^{-1}$) for species per disturbance group using regeneration density and stocking values of Table 1 and disturbance history for each sampling plot. Fire (1935–2005): N = 31; Spruce Budworm outbreak (1975–2005): N = 201; Partial logging (1935–1965): 201; Partial logging (1965–2005): N = 160; Total logging (1965–2005): 157.

plots over the 1930–2013 time interval, yet it increased to 76% and 78% in simulations with and without disturbances respectively (Fig. 4). Differences were particularly pronounced for sugar maple, yellow birch, and northern white cedar.

When disturbance types were simulated separately, the simulated mean basal area per species was relatively similar among disturbance types, except for fire and total logging (1965–2005) (Fig. 5). For all disturbance types, mean basal area decreased during the simulation for white spruce, white birch and northern white cedar. For balsam fir, mean basal area for fire and total logging (1965–2005) groups decreased and then started to increase again. The simulated basal areas for all disturbance types were underestimated for red maple, sugar maple, yellow birch and black spruce. Trembling aspen basal area was slightly underestimated for all disturbance types, except for fire where it was largely underestimated.

Simulated diameter distributions diverged compared to observed values for some species (Fig. 6). In simulations with and without disturbances, white spruce and white birch simulated mean basal area at year 80 was mostly concentrated in large diameter individuals, while the observed values indicated a more homogeneous distribution across DBH classes. This indicates a lower simulated mortality rate in larger individuals compared to observations. Similarly, balsam fir diameter distribution at year 80 was mostly concentrated in small DBH while observed values were more homogenous across DBH classes. For sugar maple and yellow birch, individuals in large diameter classes were under-estimated by the model suggesting higher levels of mortality compared to observations. All diameter classes for northern white cedar were underestimated by the simulations compared to observed values.

The observed and simulated prevalence (frequency of occurrence) differed according to species. White spruce and white birch were present in 60% of simulated plots with disturbances at year 80, while observed prevalence in 2013 was 80% for white spruce and 90% for white birch (Fig. 7). For balsam fir, prevalence was about 90% in observed and simulated plots. For sugar maple, red maple, yellow birch,

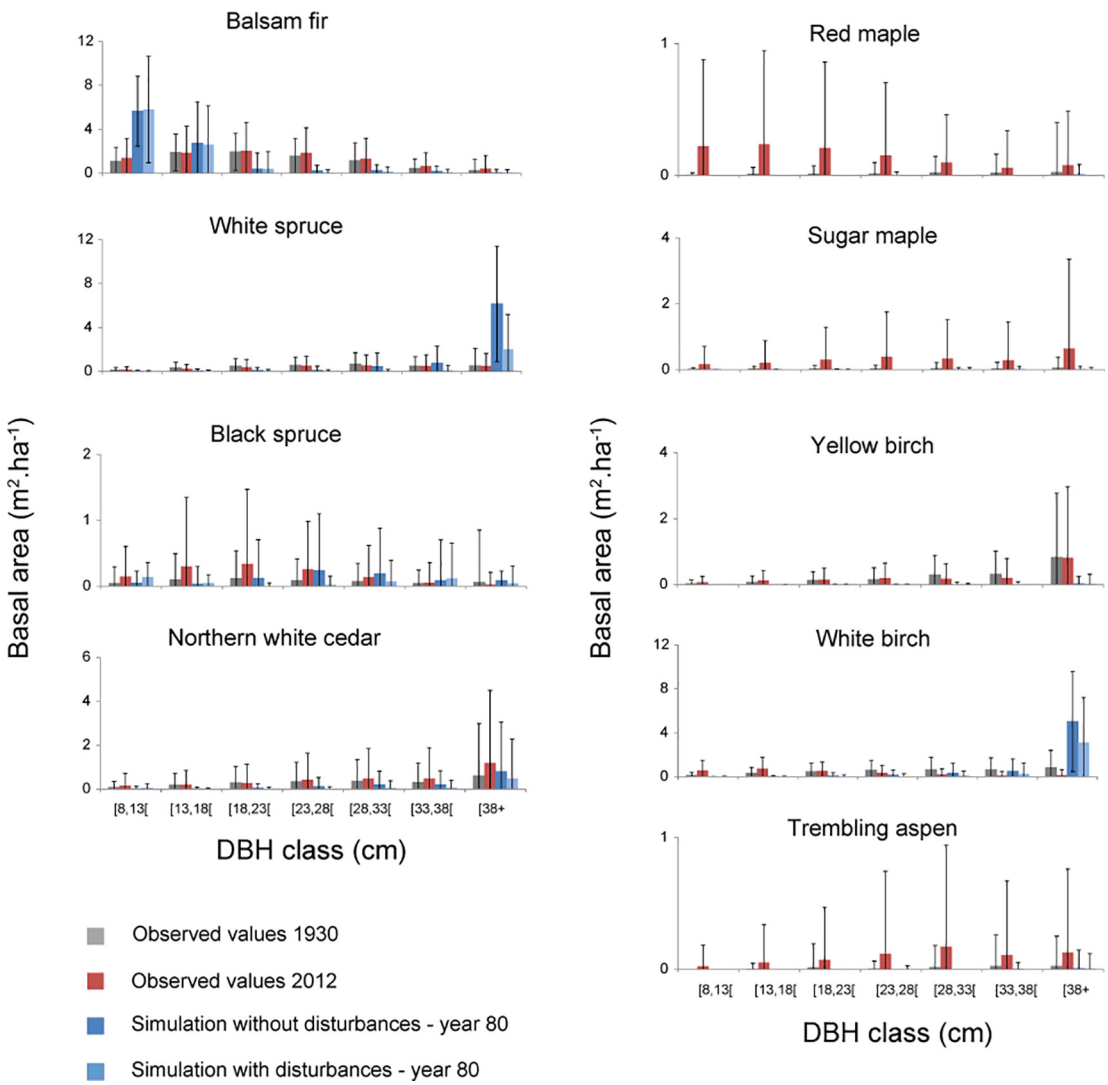

Fig. 6. DBH structure per species for observed values (1930 and 2012) and simulated values at year 80 for simulations without and with disturbances. Bars represent standard deviation. N = 457.

and trembling aspen, prevalence showed a drastic low (near 0%) in simulated plots compared to observed values of 22%, 38%, 47%, and 16%, respectively (Fig. 7). Northern white cedar prevalence was sensibly the same for simulated and observed plots. On the other hand, black spruce prevalence in the simulated plots is 66%, compared to the 36% observed prevalence.

Balsam fir, white spruce and white birch showed a balance between the number of plots where basal area was overestimated and under-estimated (Fig. 8). There was a systematic under-estimation of the mean basal area in the simulated plots for red maple, sugar maple, yellow birch and trembling aspen. Black spruce and northern white cedar mean basal areas were more frequently under-estimated than over-estimated.

4. Discussion

In the context of the intensified 20th century anthropogenic disturbances (Foster et al., 1998; Foley et al., 2005; Elzein et al., submitted for publication), the simulations with disturbances resulted in more realistic predictions of the dynamics of mixed forests. When disturbances were simulated (Fig. 2), ZELIG-CFS performed well for the three most dominant species in 1930 (Balsam fir, White birch and white spruce) (Fig. 4), while without disturbances white spruce and white birch were over estimated by the simulation (Fig. 3). On the other hand, for deciduous species (red maple, sugar maple and trembling aspen) that had low relative basal areas in 1930 (Fig. 4), the model could not reproduce their observed expansion and densification in 2013 (Figs. 4 and 7). These expanding taxa were systematically underestimated in the simulations with and without disturbances (Figs. 2 and 3). The increase of red maple, sugar maple and trembling aspen is a generalised phenomenon contributing to the observed post-industrial mixed forests compositional change in eastern North America (Whitney, 1994; Foster et al., 1998; Fuller et al., 1998; Dupuis et al., 2011; Fisichelli et al., 2014; Danneyrolles et al., 2019). Many studies have discussed factors responsible of this compositional change in mixed forests, notably climate change and anthropogenic disturbances (Nowacki and Abrams, 2015; Pederson et al., 2015; Danneyrolles et al., 2019).

Our study area is located at the northern range limits of sugar maple and red maple. In the simulation, the growth rate of these two species was likely reduced compared to their growth in the middle of their geographic range, thus increasing the probability of stress-related mortality (Reich et al., 2015). Indeed, the parabolic growing-degree-day function in ZELIG-CFS underlying assumption is that the minimum and maximum temperature tolerances for a species are the values observed at the northern and southern boundaries of its geographic distribution, respectively (Shugart and Smith, 1996). Despite our assumption of a constant climate throughout our simulations, the 20th

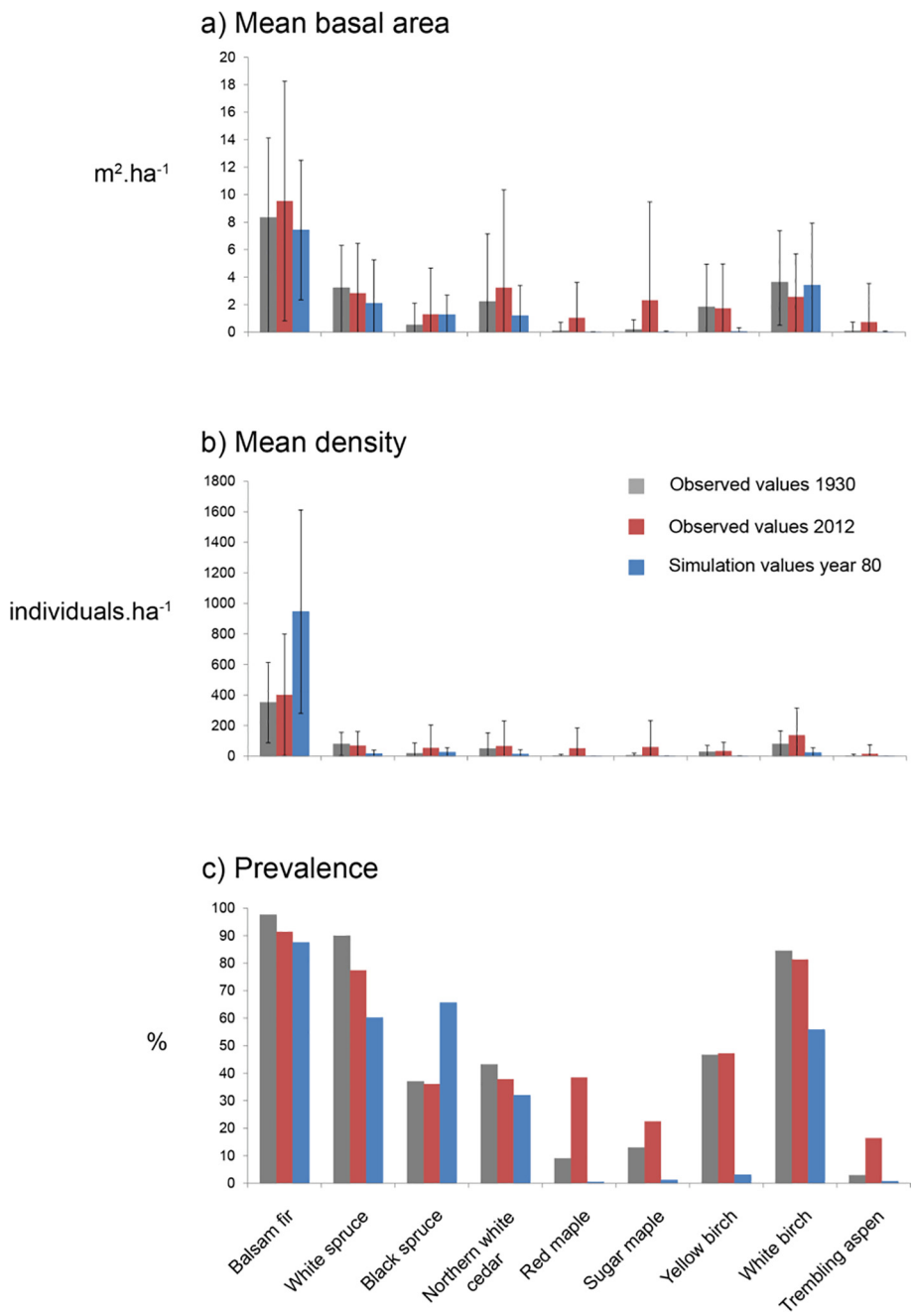

Fig. 7. Mean basal area ($m^2.ha^{-1}$), mean density ($individuals.ha^{-1}$) and prevalence (%) per species for observed values in 1930, 2012 and simulated values at year 80. Bars represent standard deviation. N = 457.

century has been warmer than the 19th century in North America (Anchukaitis et al., 2017; Gennaretti et al., 2017) and precipitations have increased (IPCC, 2013). Many empirical studies have linked the increase in sugar and red maples in temperate forests to rising temperatures (Tremblay et al., 2002; Goldblum and Rigg, 2005; Fei and Steiner, 2008; Fisichelli et al., 2014; Boisvert-Marsh et al., 2019). Simulations with higher temperatures (or degree-days) would have likely improved sugar maple and red maple growth rate and survival (El-Bayoumi et al., 1984).

Anthropogenic disturbances of the 20th century are also considered as an important contributor to the observed forest compositional changes (Nowacki and Abrams, 2015; Danneyrolles et al., 2019). Some processes related to anthropogenic disturbances, not simulated by ZELIG-CS, might explain the underestimation of maples and poplars. Red maple and sugar maple are often considered shade tolerant species (Table 1); therefore large disturbance-induced canopy openings would disfavour their recruitment (Dansereau, 1944; Parker et al., 1985). Yet, these species produce a large quantity of seeds, have good germination rates, and can grow rapidly when exposed to light (Fei and Steiner, 2008; Nolet et al., 2008). Their shade tolerance class in the model might have been detrimental to them when stand replacing disturbances were simulated (Table 3). Furthermore, vegetative reproduction is not simulated by ZELIG-CFS and the model may have underestimated the ability of sprouting and layering species, like red maple, northern white cedar and trembling aspen to recover and expand following disturbances (Oliver and Larson, 1996; Price et al., 2001). Early successional trembling aspen increase (Fig. 7) has been associated with fire activity in the study area (Boucher et al., 2017; Terrail et al., 2019; Elzein et al., submitted for publication). Indeed, fires consume litter and modify temperature conditions and nutrient availability, favouring

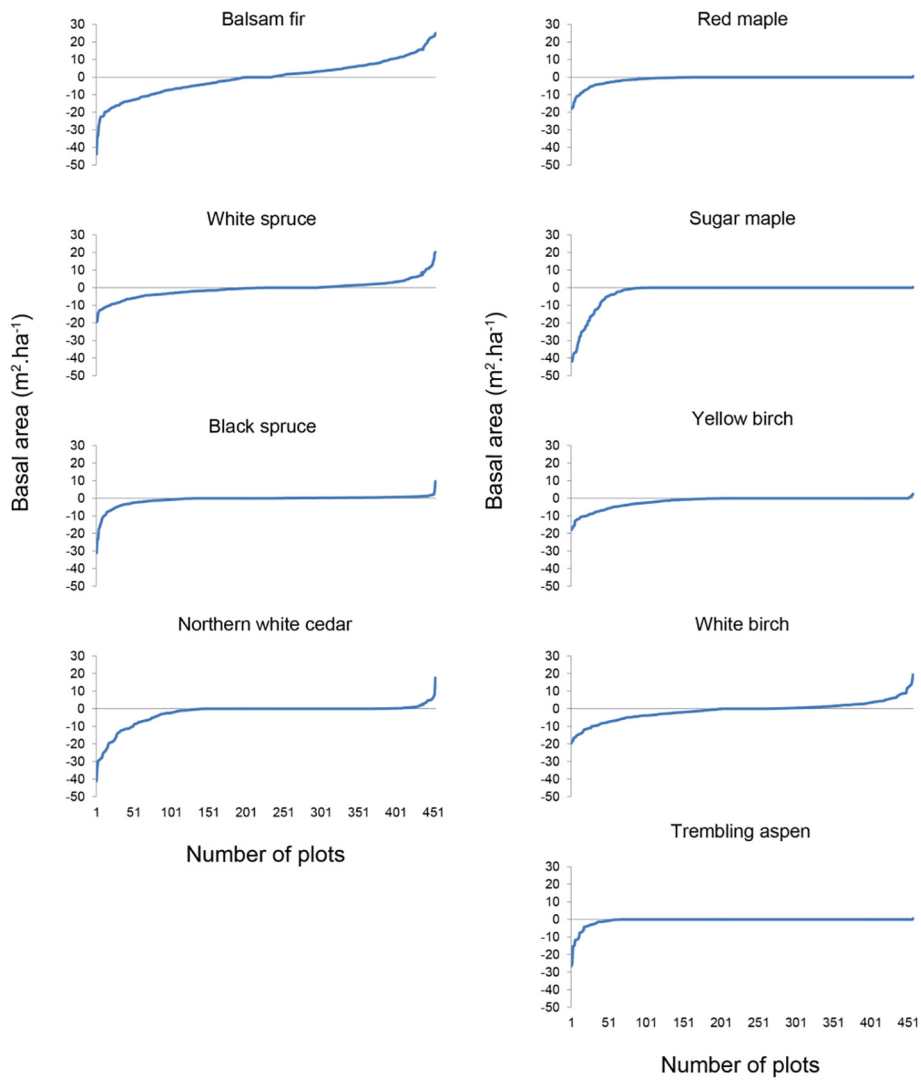

Fig. 8. Comparison between observed and simulated basal area values per species for each sampling plot. N = 457.

seedlings establishment and sprouting of fire-prone trembling aspen (Johnstone et al., 2010; Bowman et al., 2015; Johnstone et al., 2016). On the other hand, fire preventive measures (Blanchet, 2003) could have favoured the expansion of maples (Hutchinson et al., 2008).

For northern white cedar, layering as well as the interaction between partial disturbances and advanced regeneration (Danneyrolles et al., 2017), might explain why its increase observed in our study region was not simulated by the model (Fig. 7).

In the absence of disturbances, the model overestimated white spruce and white birch basal area at year 80 (Fig. 3). Moreover, their simulated basal area is concentrated among large individuals when disturbances are removed (Fig. 6). This may reflect the fast growth rate coefficient of these two species compared to the other species (Table 1) as well as the fact that they are located in the middle of their distribution range in our study area, thus, their growth is optimal.

There is considerable room for debate regarding the level of details that should be included in gap models to simulate forest processes (Bonan and Sirois, 1992; Bugmann and Martin, 1995; Fischlin et al., 1995; Loehle and LeBlanc, 1996; Schenk, 1996; Deutschman et al., 1999; Didion et al., 2009). The results of this study provide some possible avenues to improve the realism of gap models at simulating different types of disturbances: (1) A better integration of regeneration strategies of tree species, especially the integration of a probability of vegetative reproduction for sprouting and layering species like red maple, sugar maple, trembling aspen and northern white cedar, (2) Coupling gap models with a stand risk model to better simulate natural and human disturbance probability as a source of exogenous mortality across species and stem size classes, especially in the context of anthropogenic disturbance regime shift. For example, integrating the probability of presence of pyrophiles species like trembling aspen with fire activity and modifying red maple and sugar maple shade tolerance classes to better adapt fast growth in zones with stand replacing disturbances like total cuts.

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.

Acknowledgments

This work was financed by Quebec's Nature and Technology Research Fund (FRQ-NT) and the Research Chair of the Inhabited Forest (Chaire de recherche sur la forêt habitée) of the University of Quebec in Rimouski (UQAR).

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