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Millennial stocks and fluxes of large woody debris in lakes of the North American taiga

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Summary

1. Large woody debris (LWD) is an important cross-boundary subsidy that enhances the productivity of lake ecosystems and the stability of aquatic food webs. LWD may also be an important carbon sink because LWD pieces are preserved for centuries in the littoral zone of lakes and rivers. However, a long-term analysis of LWD stocks and fluxes in lakes, coupled with the reconstruction of past disturbances at the site level, has never been attempted.

2. Large woody debris was sampled in five lakes of the Quebec taiga. Actual LWD stocks were described and residence time of the LWD pieces was established using tree-ring and radiocarbon dating. LWD losses by decomposition and burial and other factors influencing LWD residence time were investigated using linear regressions.

3. Impacts of wildfires on LWD fluxes during the last 1400 years were reconstructed separately for the five lakes using piecewise regression models. Fire years at each site were identified from the recruitment dates of charred LWD pieces.

4. Large woody debris volume ranged between 0.92 and 1.57 m^3 per 100 m of shoreline, and extrapolating these results to the landscape scale, it was concluded that LWD littoral carbon pools represent a minimal portion of boreal carbon storage.

5. Large woody debris residence time in boreal lakes was confirmed to be very long. Tree-ring dates of 1571 LWD pieces, mainly black spruce (*Picea mariana* (Mill.) BSP.), spanned the last 1400 years, while LWD specimens of older floating chronologies were preserved from decomposition for up to five millennia. The most influential variables explaining the variation in LWD residence time were the degree of burial and the distance from the shore.

6. Large woody debris recruitment rates averaged 5.8 pieces per century per 100 m of shoreline. Fourteen wildfires were the primary cause for changes in the rates of tree establishment in the riparian forests and of LWD recruitment in the lakes.

7. *Synthesis*. Interactions between terrestrial and aquatic ecosystems in northern boreal regions are strongly influenced by wildfires whose effects can last for centuries due to the slow large woody debris decay rate. Actual LWD stocks and carbon pools are a legacy of the past fire history.

Key-words: carbon storage, coarse woody habitat, cross-boundary subsidy, dendrochronology, fire ecology, land–water interaction, littoral zone, palaeoecology and land-use history, *Picea mariana*, Quebec's boreal forest

Introduction

Ecosystems are rarely closed systems, and movements of nutrients, detritus and preys and predators are extremely common between adjacent habitats. These movements can influence the structure of ecosystems, the quantity of available resources, the stability of trophic networks and the dynamics of existing communities and populations (Polis, Anderson & Holt 1997). For instance, the trophic networks of lakes can be, in part, considered as spatially subsidized food webs supported by allochthonous resources, such as the remains of trees, branches and leaves from the riparian vegetation falling into the littoral zone (Schindler & Scheuerell 2002; Doi 2009).

Among these subsidies, large woody debris (hereafter 'LWD') can supply aquatic ecosystems with a large amount

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of organic matter and can increase the spatial heterogeneity of the littoral zone (Gurnell *et al.* 2002; Webb & Erskine 2003; Collins *et al.* 2012). LWD represents the ideal habitat for many communities of microorganisms (Tank & Webster 1998; Vadeboncoeur & Lodge 2000; Collier, Smith & Halliday 2004), invertebrates (Lester, Wright & Jones-Lennon 2007; Scealy, Mika & Boulton 2007; Hrodey, Kalb & Sutton 2008; Glaz, Nozais & Arseneault 2009) and fish (Fausch & Northcote 1992; Everett & Ruiz 1993; Hrodey & Sutton 2008).

Large woody debris in aquatic environments may also play an important role in the long-term sequestration of carbon at the landscape scale (Guyette, Dey & Stambaugh 2008) because dead wood resides longer in water than in terrestrial habitats (Guyette *et al.* 2002; Harmon *et al.* 2004). Carbon storage in LWD can be relevant especially in landscapes where lakes and rivers are very common, such as in the boreal forest. Although many studies have examined the amount of carbon stored in forest ecosystems and soils (Dixon *et al.* 1994; Nabuurs & Mohren 1995), little is known regarding the portion of carbon sequestered in aquatic environments or about the causes of its temporal and spatial variability (but see Guyette *et al.* 2002; Buffam *et al.* 2011). Considering the long residence time of LWD, its quantity and distribution in lakes has to be examined in order to establish accurate carbon budgets.

Large woody debris stocks in the littoral zone of lakes reflect the balance between inputs from the riparian forest and losses through decomposition and burial by sediments. In anthropogenic landscapes, LWD stocks are strongly dependent on the history of human disturbances, such as logging or residential development, that influence dead wood production in the riparian environment (Guyette & Cole 1999; Marburg, Turner & Kratz 2006; Glaz, Nozais & Arseneault 2009). In the northern boreal forest, where human activities are less intensive, wildfire is the main disturbance affecting terrestrial and aquatic environments (Payette *et al.* 1989; Marchand, Prairie & del Giorgio 2009; Boulanger *et al.* 2012). It has been established that wildfires have major impacts on LWD stocks and recruitment rates in boreal streams and lakes (Chen, Wei & Scherer 2005; Arseneault, Boucher & Bouchon 2007; Arseneault *et al.* 2013).

Very few studies have documented the dynamics of LWD in lakes. In North America, LWD stocks and their short-term (decadal) variability have been documented in lakes of the northern temperate zone (Marburg, Turner & Kratz 2006; Marburg *et al.* 2009) and dendrochronology has allowed dating of LWD in lakes of the northern temperate and northern boreal forests (Guyette & Cole 1999; Guyette *et al.* 2002; Glaz, Nozais & Arseneault 2009; Arseneault *et al.* 2013). However, no studies have combined dendrochronology with exhaustive LWD sampling to reconstruct the long-term dynamics of LWD stocks in lakes.

The objectives of this research are (i) to document the stocks of LWD in five lakes situated in the unmanaged boreal forest of eastern Canada with an exhaustive sampling of a portion of their littoral zone, (ii) to use dendrochronology in order to reconstruct LWD transfers across the forest–lake interface, the impacts of wildfires on such transfers and LWD losses through decomposition and burial over the last millennia and (iii) to identify the factors influencing residence time and decomposition of LWD in the littoral zone. In order to allow and improve the tree-ring dating, we deliberately sampled sites with large stocks of LWD. Subsequently, we discuss how these stocks could decrease as a result of disturbances and site conditions.

Materials and methods

STUDY AREA

The study area is located in the northern taiga of Quebec, Canada, between latitudes 53°50′N and 54°35′N and longitudes 70°15′W and 72°25′W (Fig. 1). This area is situated at the transition between the spruce-lichen woodland and the forest-tundra and is characterized by a continental subarctic climate with short mild summers and long cold winters.

The vegetation of the region reflects mostly the topography and the past fire history. Forests are strongly dominated by black spruce (*Picea mariana* (Mill.) BSP.), which is well adapted to various fire frequencies. Its semi-serotinuous cones shed seeds after fires, thus allowing rapid post-fire recovery, while its ability to form layers (i.e. to propagate vegetatively through the rooting of the lower branches that are touching the ground) allows stands to persist in the absence of fires (Black & Bliss 1980). Black spruce canopy height and density vary according to the time since the last fire, the severity of the fire and the topographic position of a given stand (Morneau & Payette 1989; Payette 1993; Lavoie & Sirois 1998; Girard, Payette & Gagnon 2008). Other less-abundant tree species include balsam fir (*Abies balsamea* L.) and tamarack (*Larix laricina* (Du Roi) K. Koch).

The study area is located in a remote region where significant human influence is sparse and only recent (last 40 years). Lakes of various sizes are extremely abundant, covering about 25% of the landscape. A portion of the littoral zone of each of the five lakes was selected for this study (Fig. 1, Table 1) according to the criteria developed by Arseneault *et al.* (2013) in order to identify sites of high potential for developing millennial tree-ring chronologies. The selected littoral segments possess features that maximize LWD recruitment (an abrupt forest–lake interface on the leeward side of the

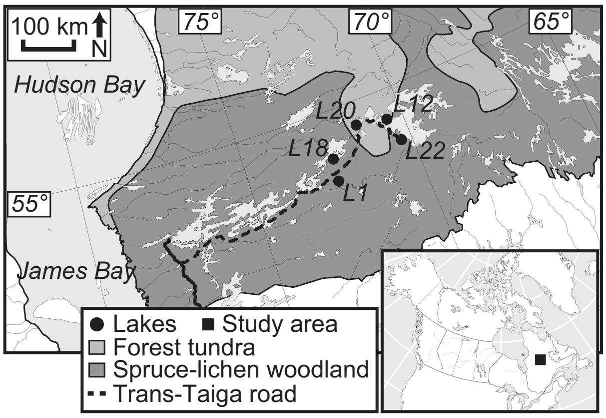

Fig. 1. Location of the study area in the northern boreal forest of Quebec, eastern Canada.

Table 1. Description of the sampled lakes and large woody debris (LWD) pieces

Lake	L1	L12	L18	L20	L22	All sites
Surface area (ha)	13.4	43.1	44.8	35.1	665.6	
Length of sampled shore (m)	360	540	1150	1010	270	3330
No. of LWD pieces	267	273	627	850	177	2194
Species abundance (%; spruce/tamarack/fir)	93/7/0	96/2/2	95/4/1	91/2/7	92/2/6	93/3/4
LWD pieces with roots (%)	1.5	3.7	1.0	0.1	3.4	1.2
LWD oriented perpendicularly to the shore (%)	58.0	50.8	54.7	60.0	56.5	56.9
No. of charred (trunk/branch tips)	0/1	0/2	4/12	0/3	2/4	6/22
No. of cross-dated to the calendar year	178	219	426	613	135	1571
No. of cross-dated into floating chronologies	20	4	9	39	1	73
Average no. of tree-rings per dated LWD piece (mean ± SD)*	121 ± 37	118 ± 35	115 ± 38	116 ± 39	108 ± 38	116 ± 38
LWD mean residence time (mean ± SD; years)*	505 ± 451	514 ± 341	472 ± 365	588 ± 547	557 ± 308	535 ± 452
Oldest tree-ring cross-dated to the calendar year (year AD)	639	569	594	651	648	569

*Including LWD samples of the floating chronologies.

lake and an old-growth riparian forest) and LWD preservation (presence, near the shoreline, of a talus at least 1 m deep and, on its bottom, of fine sediments).

LWD STOCKS AND DATING

The five sites were exhaustively sampled during several summer field campaigns between 2005 and 2011. Any exposed (i.e. laying on the bottom of the lake) or buried logs with a diameter equal or >4 cm, which makes dendrochronological dating possible, were collected by a diver aided by two to three assistants, as described by Arseneault *et al.* (2013). Most logs were pulled to the shore, although a few heavy or stuck logs were partially cleared of sediments, measured and cut with a hand saw in the water. Buried specimens were located as loose sediments can be systematically probed by hand. Only LWD pieces buried in less than about 20 cm of sediments could be extracted. Once on the shore, LWD pieces were mapped with a total station and their length and maximum diameter were measured in order to calculate the LWD number and volume per 100 m of shoreline, which are two metrics that characterize LWD stocks. The volume of each LWD piece was estimated as the volume of a cylinder multiplied by a form factor of 0.6. The form factor was based on more detailed measurements on a subset of 1626 LWD pieces from this study (i.e. minimum and maximum diameters and their position on each LWD piece). LWD specimens were also examined to detect the presence of charcoal on the trunk and the branch tips and the presence of main roots still connected or not. A stem cross-section was sampled from each LWD piece so as to maximize the number of measurable tree-rings for dendrochronological dating.

In the laboratory, tree species were identified from wood anatomy (Hoadley 1990). Two radii were then scanned at 6400 DPI on each cross-section of spruce and fir in order to measure tree-ring widths using the OSM3 software (SCIEM, Austria). Individual series (i.e. average of two radii) were cross-dated to the calendar year using local master chronologies as a reference (Arseneault *et al.* 2013) and sequences of light rings as an additional dating tool (Arseneault & Payette 1998). Cross-dating was performed using COFECHA (Holmes 1983) and PAST4 (SCIEM, Austria) softwares. All floating chronologies older than the master chronology and comprising at least two tree-ring series of different LWD pieces, not necessarily from the same lake, were AMS (accelerator mass spectrometry) radiocarbon dated. To do this, wood samples from the innermost tree-rings of selected LWD pieces were sent to the Centre for Northern Studies (CEN) radiochronology laboratory (Université Laval, QC, Canada). Conventional radiocarbon ages were calibrated using CALIB 6.0 (Stuiver & Reimer 1993) and the IntCal09 calibration curve.

LWD RESIDENCE TIME AND LOSSES

To determine the residence time in the lake of each LWD piece that could be cross-dated to the calendar year or into a floating chronology, we estimated its recruitment date in the water from its outermost tree-ring date (hereafter 'recruitment date'). The residence time was then determined as the time since the LWD recruitment (2012 minus recruitment date), even if this measure can be overestimated by a few years to a few decades due to the decomposition of outermost tree-rings. Similarly, the pith date of each LWD piece was used to estimate the date at which the corresponding former tree in the riparian forest had reached the height needed to develop an upper stem portion that later became recruited and conserved as a LWD piece (hereafter 'establishment date').

To quantify the rate at which LWD pieces are lost from the littoral stocks by abiotic and biotic decomposition and burial, we identified distinct reference time intervals of negligible losses for exposed and buried specimens. First, the cumulative numbers of exposed and buried LWD samples were plotted separately according to residence time. Samples of all lakes were plotted together in order to smooth out the impact of local disturbances (see Fig. 3a). Secondly, in the range of observed residence times, for each sequential time interval of 400 years lagged backward in time by 1 year, a linear regression model was fitted on the exposed and buried series until at least two LWD specimens could be included (the number of available specimens decreases backward in time). The successive slopes of these regression models allow the comparison between time intervals as their values depend on the LWD recruitment into the exposed or buried groups during the corresponding time interval and on the cumulated losses. Higher recruitment rates would produce more negative slopes, and higher losses would produce less negative slopes. With constant recruitment and no losses, the slopes would be constant. Thirdly, for the exposed and buried series, the time interval with the more negative slope was considered as a reference state with no losses as it displayed a very good linear fit to the data (see Fig. 3a). Indeed, exposed specimens reside for some time in water before being lost through decomposition or superficial burial, whereas buried specimens, after the time needed for burial, reside for some time in superficial sediments before being lost through decomposition or deep burial (i.e. at depth >20 cm). Last, assuming that recruitment of exposed and buried specimens is approximately constant through time when several lakes are averaged, the percentage of LWD losses for each 400-year time interval and each burial category was calculated as: [losses = 100 – (S_i/S_{ref}) * 100]. In the equation, s_i is the slope of the regression on the residence time interval of 400 years centred in year i and s_{ref} refers to the corresponding reference slope.

In addition, the proportion of the exposed LWD pieces that has been eventually buried relative to the proportion that has been lost through decomposition before burial was estimated from the ratio of the two reference slopes (buried over exposed). We also used the slopes of the most recent time intervals of each burial category to compute the average rate of LWD recruitment across all studied lakes (number of LWD pieces per 100 years per 100 m of shoreline computed as the summation of the two slopes × 100 years × 100 m, divided by a total of 3330 m of sampled shoreline).

FACTORS INFLUENCING LWD RESIDENCE TIME

Factors influencing LWD residence time in the lakes were analysed using black spruce LWD samples cross-dated to the calendar year or into floating chronologies at sites L18 and L20, where most LWD samples were collected. Residence time was log-transformed to reduce skewness and kurtosis. Multiple linear regressions were then performed with the residence time entered as the dependent variable. The independent variables tested were the minimum depth in the water of each LWD piece (feet), its minimum distance from the shore (cm), its orientation relative to the shoreline (perpendicular = 3; parallel = 2; inverted = 1), its burial type (completely buried = 3; partly buried = 2; exposed = 1), the type of underlying substratum (fine sediments = 5; sand = 4; gravel = 3; stones = 2; wood = 1), the aspect of the corresponding littoral zone (from 0 to 2) and the exposure to the wave action of the littoral zone (cm). The computations used to obtain these independent variables and the samples used in the regression models are described in the Appendix S1 in the Supporting Information.

Models were fitted to data in the R environment, and all the possible models from the different combinations of the independent variables were ranked according to their Akaike information criterion (AIC). Because models with smaller AIC are better fitted, only models with a delta AIC (Δi = AICi–AICmin) smaller than two were retained (Burnham & Anderson 2002). The selected models were checked for normality and homogeneity of variance of the residuals and absence of multicollinearity to verify that the assumptions of regression were met. For each lake, the relative contribution of the independent variables that were significant in all the alternative best models was estimated by an analysis of variance (ANOVA).

WILDFIRE IMPACTS ON LWD FLUXES

Impacts of wildfires on LWD fluxes during the last 1400 years were reconstructed separately for the five selected lakes using piecewise regression models. Due to their longer sampled shore distances and more complex fire history in comparison with the other lakes, L18 and L20 were divided into three different segments and the results of only two segments are shown here for each lake, while the other segment is shown in Fig. S1.

For each site or shore segment, piecewise regression models were fitted to the cumulative number of LWD pieces according to their establishment and recruitment date using the 'segmented' package of the R software (Muggeo 2008). Piecewise regressions allow identifying patterns in data using a set of linear regressions linked by breakpoints (see Appendix S2 for technical aspects). The slopes of the piecewise regression segments were then used to estimate the recruitment rates of LWD pieces into the littoral zones (hereafter 'recruitment rates') and the establishment rates in the riparian forests of upper stem portions that later generated LWD pieces (hereafter 'establishment rates').

Past fires were dated at each site from the recruitment dates of charred LWD pieces (Appendix S2). Breakpoints from the piecewise regressions were then associated with a wildfire date on the condition that they coincided with either (i) the limits of a period of reduced establishment or recruitment around a fire date; (ii) the beginning of a period of increased establishment or recruitment after a fire; or (iii) the limits of a massive LWD recruitment event due to a fire. We used these breakpoints, along with associated fire dates and segment's slopes, to compute three metrics of past fire impacts on establishment and recruitment rates (see Table 5). First, the time needed for the normalization of the establishment rate was computed as the length of the time interval between a fire and the following breakpoint marking increasing establishment rate. Secondly, the time needed for the normalization of the recruitment rate was computed as the length of the time interval between a fire and the breakpoint after the subsequent reduction in recruitment or massive recruitment (a massive recruitment was defined as an input >20 LWD pieces per 100 years per 100 m of shoreline over <50 years). Thirdly, the fire-induced recruitment reduction (%) was computed using the following formula: [recruitment reduction = ((S_a–S_b)/S_b) * 100]. In the equation, S_a is the slope of the segment following the fire and S_b is the slope of the segment preceding the fire.

Results

LWD STOCKS AND DATING

A total of 2194 LWD pieces were sampled along 3330 m of shoreline in the five lakes (Table 1). A very large proportion of these LWD specimens had no roots, confirming that they represent the upper stem portions of former riparian trees (Table 1). Most samples were black spruce with minor components of balsam fir (4%) and tamarack (3%). Exposed LWD pieces were more abundant than buried ones (62% vs. 38%), although buried specimens had higher diameters, lengths and volumes than exposed ones at all lakes, except L1 (Table 2). LWD number varied among lakes at between 50.6 and 84.2 specimens per 100 m of shoreline, whereas LWD volume ranged between 0.92 and 1.57 m^3 per 100 m of shoreline (Table 2).

Tree-ring dating was very successful with 72% of all LWD pieces being cross-dated to the calendar year (Table 1). LWD recruitment dates were nearly continuous during the last 1400 years (Fig. 2). The oldest tree-rings cross-dated to the calendar year ranged between AD 569 and AD 651 depending on the site (Table 1). An additional 3% of all LWD pieces were cross-dated into seven floating chronologies, each comprising from 2 to 51 pieces and spanning from 143 to 460 years (Tables 3). Radiocarbon dating indicated that 68 out of the 73 LWD pieces that compose these chronologies fell in the water between the 7th century BC and the 6th century AD, whereas five LWD pieces were even older and have

Table 2. Large woody debris (LWD) stocks in the littoral zone of the five studied lakes. Buried LWD includes completely buried and partly buried specimens. LWD pieces correspond to wood pieces with a maximum diameter equal or >4 cm

Lake	Burial	*N*	Average no. of tree-rings (mean ± SD)	Average diameter (mean ± SD; cm)	Average length (mean ± SD; cm)	Average volume (mean ± SD; m^3)	No. per 100 m of shore	Volume per 100 m of shore (m^3)
L1	Buried	69	112.3 ± 40.3	8.8 ± 2.3	331.8 ± 193.7	0.0142 ± 0.0149	19.2	0.2729
	Exposed	198	116.6 ± 36.6	9.1 ± 3.0	359.7 ± 186.2	0.0175 ± 0.0246	55.0	0.9649
	Total	267	115.5 ± 37.6	9.0 ± 2.8	352.5 ± 188.6	0.0167 ± 0.0225	74.2	1.2378
L12	Buried	124	114.6 ± 35.2	10.8 ± 3.0	441.4 ± 210.0	0.0265 ± 0.0216	23.0	0.6078
	Exposed	149	116.3 ± 37.7	10.3 ± 2.9	374.8 ± 176.2	0.0211 ± 0.0194	27.6	0.5834
	Total	273	115.5 ± 36.5	10.5 ± 2.9	405.0 ± 195.5	0.0236 ± 0.0206	50.6	1.1913
L18	Buried	190	94.4 ± 40.5	9.1 ± 3.1	424.6 ± 243.3	0.0196 ± 0.0216	16.5	0.3241
	Exposed	437	102.2 ± 42.3	8.4 ± 2.8	340.4 ± 216.9	0.0156 ± 0.0317	38.0	0.5931
	Total	627	99.9 ± 41.9	8.6 ± 2.9	365.9 ± 228.5	0.0168 ± 0.0291	54.5	0.9172
L20	Buried	389	107.8 ± 39.5	9.6 ± 2.9	406.8 ± 236.3	0.0211 ± 0.0247	38.5	0.8124
	Exposed	461	105.4 ± 42.4	8.8 ± 3.4	364.3 ± 194.6	0.0166 ± 0.0245	45.6	0.7558
	Total	850	106.5 ± 41.1	9.2 ± 3.2	383.8 ± 215.8	0.0186 ± 0.0247	84.2	1.5681
L22	Buried	68	109.0 ± 50.0	9.9 ± 2.9	368.1 ± 199.4	0.0188 ± 0.0184	25.2	0.4746
	Exposed	109	90.1 ± 31.2	9.5 ± 3.3	336.0 ± 176.3	0.0183 ± 0.0220	40.4	0.7383
	Total	177	97.3 ± 40.4	9.7 ± 3.2	348.3 ± 186.2	0.0185 ± 0.0207	65.6	1.2129
Total	Buried	840	106.1 ± 40.7	9.6 ± 3.0	406.6 ± 230.3	0.0208 ± 0.0227	25.2	0.5249
	Exposed	1354	105.8 ± 40.9	8.9 ± 3.2	354.8 ± 198.5	0.0170 ± 0.0266	40.7	0.6928
	Total	2194	106.0 ± 40.8	9.2 ± 3.1	374.7 ± 212.9	0.0185 ± 0.0252	65.9	1.2180

been preserved from decomposition for 4 or 5 millennia (Table 3).

LWD RESIDENCE TIME AND LOSSES

Large woody debris mean residence time in the five lakes varied between 472 and 588 years (Table 1). As expected, exposed specimens had shorter mean residence time than buried ones (386 ± 287 vs. 794 ± 556 years, considering all lakes). All exposed LWD specimens had residence times shorter than 1700 years compared to more than 5000 years for buried ones (Fig. 3a).

For residence times of <650 years, the decrease in the cumulative number of LWD pieces with increasing residence time was much faster for exposed specimens than for buried ones, indicating a greater recruitment rate into the exposed group (Fig. 3a, b). In fact, buried LWD pieces increased in abundance with residence times up to and including the 400- to 600-year residence time class (Fig. 3d, e), pointing out that exposed LWD was transferred to the buried compartment, where sedimentary conditions were favourable for burial, only after an average residence time of about 500 years. Furthermore, the ratio of the two reference slopes (Fig. 3a, b) indicated that only about 46% of the exposed pieces eventually become buried, whereas 54% decay before burial.

Losses of exposed LWD pieces were much faster than those of buried ones. The method based on the reference states estimated that 50% of the exposed pieces have been lost through decomposition or burial in <612 years, while 50% of the buried specimens have been lost through decomposition or deep burial after a residence time of 1044 years (Fig. 3c). Moreover, about 8% of the buried specimens resided in surficial sediments for more than 1500 years and up to 5 millennia (Fig. 3a). Because buried LWD pieces were generally older and larger than exposed ones (Fig. 3a and Table 2), their relative importance increased with residence time, especially when LWD volume was considered (Fig. 3f). The lower number of tree-rings confirmed the faster decomposition of exposed LWD pieces as compared to buried ones. The quartiles of the number of measurable tree-rings per residence time classes of 200 years were always lower for exposed than for buried LWD samples, except for the most recent class (Fig. 4). Based upon linear trends calculated on the median numbers of tree-rings, exposed and buried LWD pieces lost through decomposition an average of 3.16 ± 0.57 and 0.92 ± 0.75 rings per century (mean ± SE), respectively.

FACTORS INFLUENCING LWD RESIDENCE TIME

The results of the linear regression models retained to explain LWD residence time as a function of multiple variables at L18 and L20 were similar. Total variance explained ranged between 42% and 50% (Table S1) with burial type (26–35% of the variance explained) and distance from the shore (15–10%) being the most significant variables (Table 4). Although the remaining variables retained in the models differed between lakes L18 and L20, these variables explained only a tiny fraction of the total variance (<2% per each variable; Table 4). Exposure to wave action was significant at L18, but the sign of its coefficient opposed our expectation. Depth in the water, orientation and substratum were significant only at L20 (Table S1).

WILDFIRE IMPACTS ON LWD FLUXES

At least 14 wildfires influenced the LWD fluxes across the forest–lake interface in the five selected lakes during the last 1400 years, but no fire occurred after AD 1848 (Figs 2 and 5). The number of fires per shore segment varied between zero

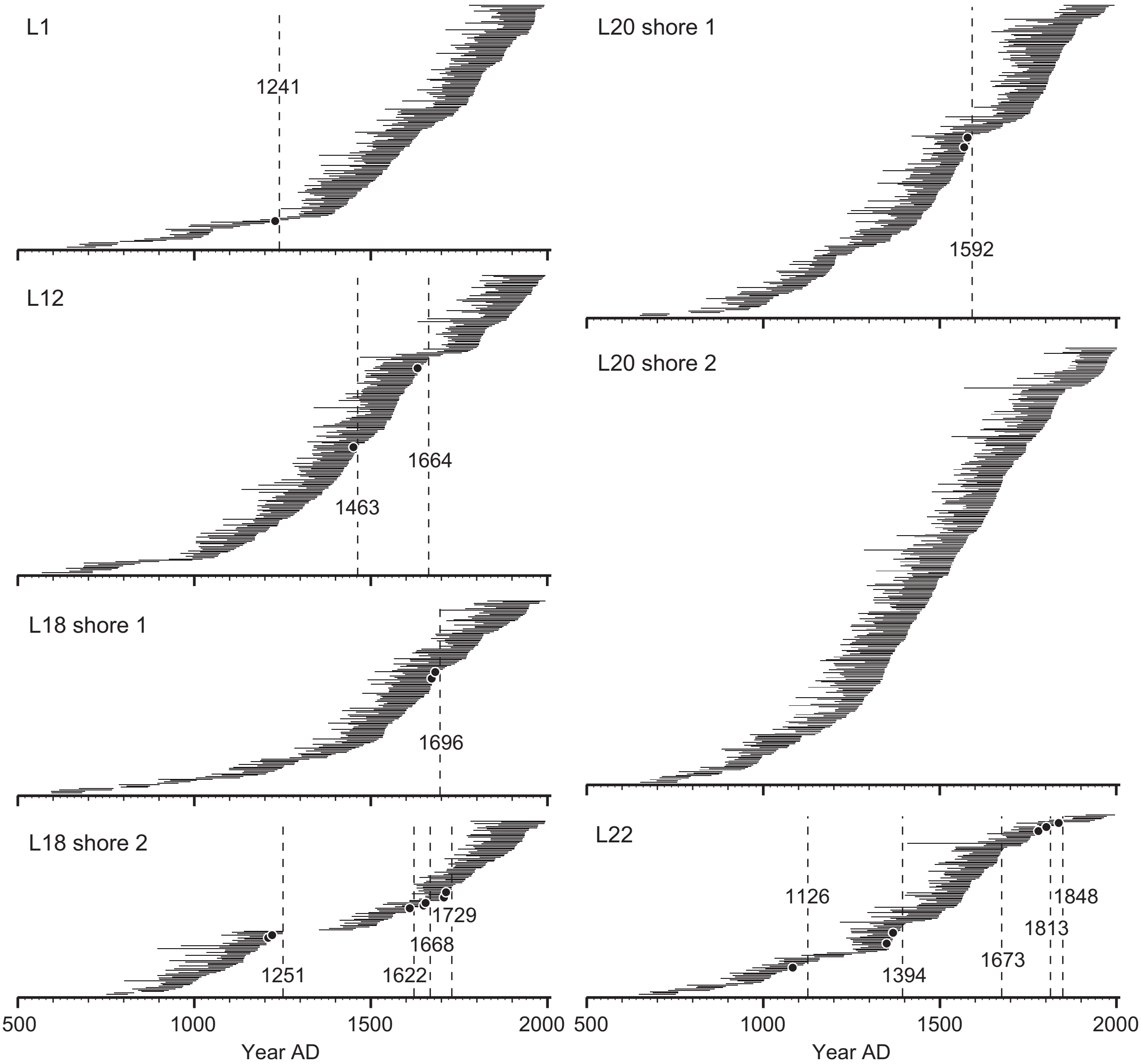

Fig. 2. Life spans of large woody debris (LWD) samples from the study sites cross-dated to the calendar year. Each horizontal black line refers to one LWD piece, and its length indicates the number of tree-rings in the sample. Vertical dashed lines are estimated wildfires dates. Black dots show the end of the life span of charred LWD pieces.

Table 3. Description of the floating chronologies

ID	No. of LWD pieces	Time span (years)	No. of AMS dates	Calibrated age range of the chronology end (years AD/BC)*
CF1	51	460	6	AD 578/AD 592
CF8	9	266	2	AD 164/AD 240
CF14	2	178	1	185 BC/27 BC
CF17	2	192	1	614 BC/388 BC
CF9	4	186	2	608 BC/401 BC
CF12	2	143	1	1938 BC/1848 BC
CF7	3	172	1	3187 BC/2942 BC

*Determined from the overlap of the two sigma confidence intervals once shifted to the end of their respective chronology.

(L20 shore 2) and five (L22). Shore 2 at L20, the only site that has escaped fire over the last 1400 years, displayed a very regular recruitment rate of 13.4 LWD pieces per 100 years per 100 m of shoreline over about 600 years (AD 1254–1834; Figs 5 and 6, Table S2). The remaining sites were characterized by generally lower, but highly variable, recruitment rates that were dependent on their respective fire histories (Fig. 6). Recruitment rates during the last 500 years that were characterized by low LWD losses by decomposition and deep burial varied from 0.5 LWD pieces per 100 years per 100 m during AD 1668–1768 at L12 to 23.7 pieces per 100 years per 100 m during AD 1722–1731 at shore 2 of L18 (Table S2). Recruitment rates averaged 5.8 LWD pieces per 100 years per 100 m across all sites (computed from the slopes of the most recent time intervals of 400 years for each burial category; Fig. 3b).

Piecewise regressions models were efficient in reconstructing wildfire impacts on LWD fluxes. From the 14 wildfires identified from charred LWD specimens, 10 and 9 corresponded to breakpoints in the recruitment and establishment

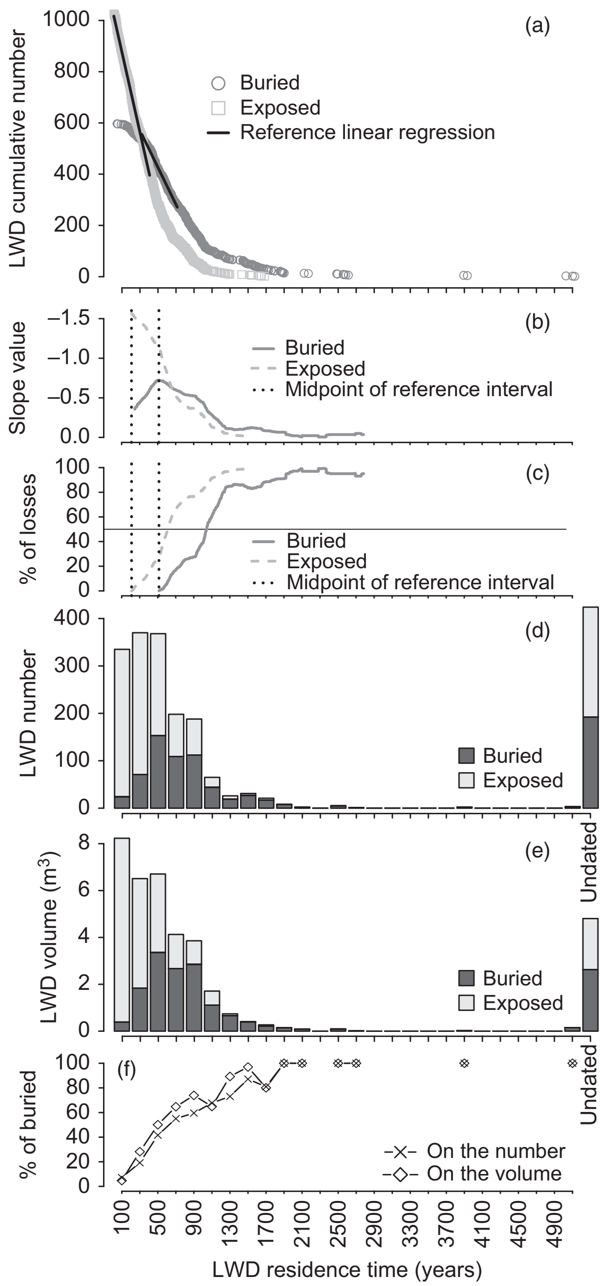

Fig. 3. Decay of large woody debris (LWD) abundance according to residence time in lakes: (a) cumulative distributions of buried and exposed LWD pieces; (b) slopes of linear regression models fitted to the cumulative distributions on consecutive residence time intervals of 400 years; (c) percentage of LWD losses by decomposition and burial; (d) number and (e) volume of LWD specimens per residence time classes of 200 years; and (f) percentage of buried specimens. Computations are based on black spruce LWD specimens from all lakes (cross-dated into floating and master chronologies). Buried LWD samples include completely buried and partly buried specimens.

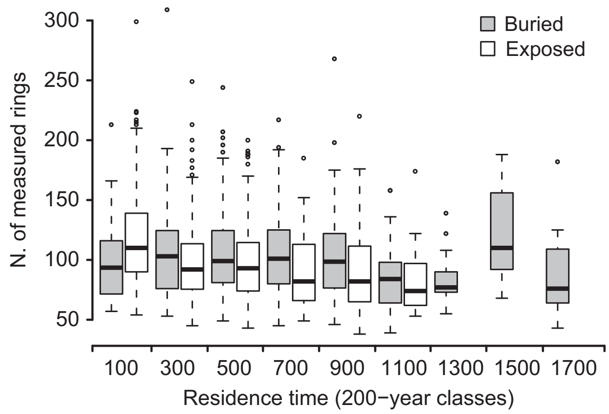

Fig. 4. Boxplot of the number of measured tree-rings per large woody debris (LWD) specimen according to residence time classes of 200 years. For each class, quartiles (central bar and box limits), extreme values within 1.5 interquartile ranges from the boxes (whiskers) and outliers (circles) are represented. All dated black spruce specimens from all lakes (master and floating chronologies) are considered, but time classes with <10 specimens are excluded. Buried LWD samples include completely buried and partly buried specimens.

data, respectively (Tables 5 and S2). Conversely, 54% and 58% of the breakpoints in the recruitment and establishment data, respectively, could be associated with a fire date (Table S2). Fire events often caused a typical response, including the presence of charred LWD pieces, along with the reduction and subsequent normalization of the establishment and recruitment rates (Figs 5 and 6, Table 5). Most fire events caused large reductions in LWD recruitment rates, varying from −46 to −94%, and many years were sometimes required for the normalization of the LWD fluxes (Table 5). For example, the AD 1126 fire at L22 caused a recruitment reduction by −65% for 225 years (Table 5). However, only two fires, the AD 1729 fire at shore 2 of L18 and the presumed AD 1673 fire at L22 (not confirmed by charred LWD), generated massive LWD recruitments (i.e. more than 20 LWD pieces per 100 years per 100 m in <50 years; Figs 5 and 6, Table 5). Furthermore, an increasing establishment rate of upper stem portions on the shores was often observed with a post-fire delay ranging from 0 to 143 years (Table 5). The duration of the time periods needed for the normalization of the establishment and recruitment rates after fires was intercorrelated ($r = 0.84$; $P < 0.01$) because the first trees to establish in the riparian forest after a fire were generally the first to be subsequently recruited as LWD pieces. Finally, heterogeneity of fire effects increased with the length of the sampled shore, as shown by the contrasting recruitment trends between shore sections at L18 and L20 (Figs 2 and 5).

Discussion

RESIDENCE TIME, DECOMPOSITION AND BURIAL OF LWD PIECES

Once they enter in the littoral ecosystem, tree trunks may accumulate and form stocks spending a long residence time outside of sediments as exposed LWD (mean residence time of 386 years in our sites; Fig. 7). The slow decomposition of wood in a lake littoral environment is related to several factors: first, the low oxygen concentration compared to terrestrial environments that restricts microbial colonization of LWD pieces; secondly, the absence of wood-boring organisms that is a peculiarity of freshwater habitats; thirdly, the lower physical

Table 4. ANOVA table for the selected regression models with large woody debris residence time (log-transformed) as dependent variable

Lake	Source of variation	d.f.	Sum square	*F* value	Variance explained
L18	Burial type	1	13.57	105.68***	0.259
	Distance from the shore	1	7.92	61.68***	0.151
	Exposure to wave action	1	0.78	6.11*	0.015
	Residuals	235	30.18	NA	0.575
L20	Burial type	1	14.43	291.12***	0.353
	Distance from the shore	1	4.15	83.76***	0.102
	Depth in the water	1	0.77	15.45***	0.019
	Orientation	1	0.58	11.77***	0.014
	Substratum	1	0.53	10.66**	0.013
	Residuals	412	20.43	NA	0.500

*P-value < 0.05, **P-value < 0.01 and ***P-value < 0.001.

fragmentation caused by flowing water compared to streams and rivers (Harmon *et al.* 2004). Furthermore, our study area in the northern taiga of Quebec is characterized by a continental subarctic climate and carbon decomposition is limited by low temperatures (Davidson & Janssens 2006). For all these reasons, decomposition of exposed LWD in this region appears to occur mainly on the outer surface of wood pieces, leaving their interior relatively unaltered (Savard *et al.* 2012). This pattern is also suggested by the smaller number of measurable tree-rings of exposed as compared to buried specimens of similar residence times (Fig. 4). This centripetal pattern of wood decomposition depends on the action of physical agents such as waves and ice, as well as of biotic agents such as bacteria, fungi and algae that form biofilms on the surface of exposed LWD (Tank & Webster 1998; Collier, Smith & Halliday 2004; Guyette, Dey & Stambaugh 2008). However, the long residence time of exposed LWD pieces implies that LWD stocks are resistant to riparian disturbances as they would continue to structure littoral ecosystems over several centuries even after complete deforestation of the riparian environment (Fig. 7).

Marburg, Turner & Kratz (2006) found that areas with low exposure to wind and waves are important sites of littoral LWD accumulation within lakes in Wisconsin, USA. In our models, no strong relationship was obtained between the LWD residence time and the aspect of the littoral zone or its exposure to wave action (Table 4). Exposure was significant only at L18, but the sign of its coefficients did not correlate with our expectations and it only explained a small fraction of the total variance (Tables 4 and S1). Three hypotheses can explain this contrasting result. First, the exposure of the littoral zone may be important for the LWD accumulation, but does not influence the length of the LWD residence time. Secondly, this result may depend on our sampling design that focused on the most important LWD stocks of our study area which almost systematically occur along shoreline segments protected from dominant winds (Arseneault *et al.* 2013). This design was necessary in order to develop the master tree-ring chronologies needed for cross-dating the LWD samples to the calendar scale. Thirdly, LWD pieces are not significantly redistributed in our lakes contrary to what happens in the lakes studied by Marburg, Turner & Kratz (2006). This is shown by the relatively high proportion of specimens oriented perpendicularly to the lake shore with their base towards the riparian forest at all our sites (Table 1). The stability of the LWD stocks is also revealed by the contrasting LWD recruitment trends between consecutive shore sections with different fire histories at L18 and L20 (Figs 2 and 5, Table S2).

About half of the LWD pieces that enter the littoral zone of our lakes eventually become buried (Fig. 7). Even if we did not assess the decay rate of littoral wood in terms of density lost per unit of time, we conclude that buried LWD specimens are much more persistent than exposed ones. This is confirmed by their slower losses (Fig. 3c), longer residence time (Fig. 7), greater diameter, length and volume (Fig. 3f and Table 2) and greater number of measurable tree-rings (Fig. 4). Superficially buried specimens have formed relatively dense LWD stocks, which are similar to the exposed stocks on a volume basis (Fig. 7). Burial type and distance from shore have been the most influential factors for the long-term LWD preservation at the studied sites (Table 4). This result suggests that the upper stem portions of the tallest trees growing near the shore are more likely to generate persistent LWD. In comparison with shorter trees, upper portions of tall trees have better chances of falling at greater distances from the shoreline where sediment accumulation and burial are faster. The process of wood decomposition in sediments is poorly known but its slow rate probably reflects pronounced anoxic conditions, which suggests that buried trees are mostly decayed through abiotic hydrolyses (Guyette, Dey & Stambaugh 2008). Although deeply buried stocks (i.e. more than 20 cm deep) could not be quantified (Fig. 7), we estimate that they are much less important than superficial stocks. This is suggested by the discontinuous occurrence of deep loose fine sediments in the littoral zone, along with the occurrence of LWD pieces more than five millennia old in the superficial sediment layer (Fig. 3a).

Some studies have already reported that tree trunks buried in lake and river sediments can be several millennia old (Hyatt & Naiman 2001; Eronen *et al.* 2002; Guyette, Dey & Stambaugh 2008). In our lakes, about 8% of the buried LWD pieces resided in superficial sediments for more than 1500 years and up to five millennia (Fig. 3a). Since our study area was deglaciated about 7000 years ago (Dyke 2004), it is likely that the superficial sediment layer still comprises some of the first trees that colonized the region. Although these

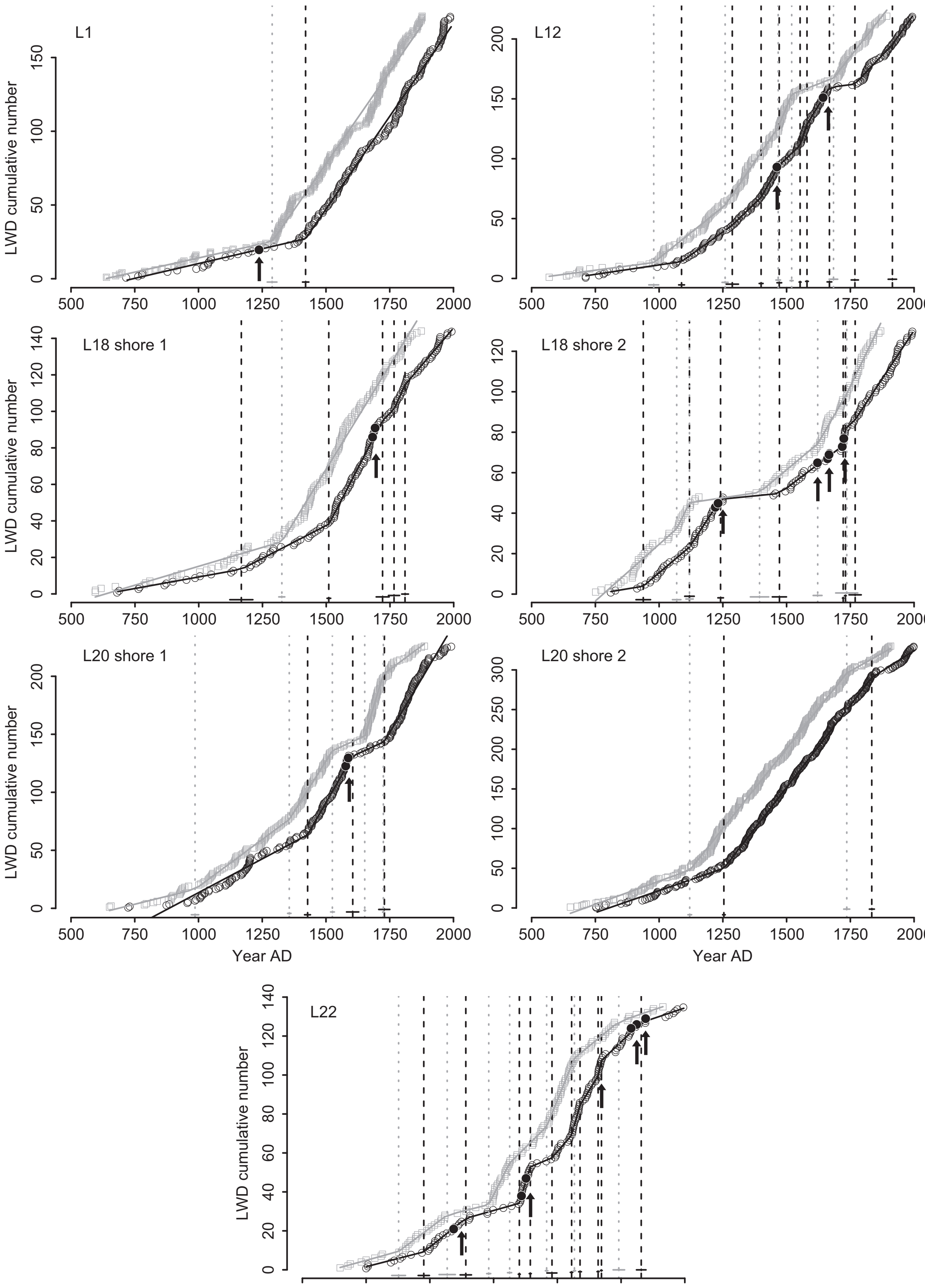

Fig. 5. Cumulative number of large woody debris (LWD) specimens cross-dated to the calendar year versus their recruitment (black circles) and establishment (grey squares) dates. Piecewise regression models fitted to the recruitment (black solid line) and establishment (grey solid line) data are also shown, as well as corresponding breakpoint dates (vertical dashed or dotted lines), 95% confidence intervals for the breakpoints (horizontal lines at the base of the dashed or dotted lines), estimated wildfire dates (vertical arrows) and recruitment dates of charred LWD pieces (black dots).

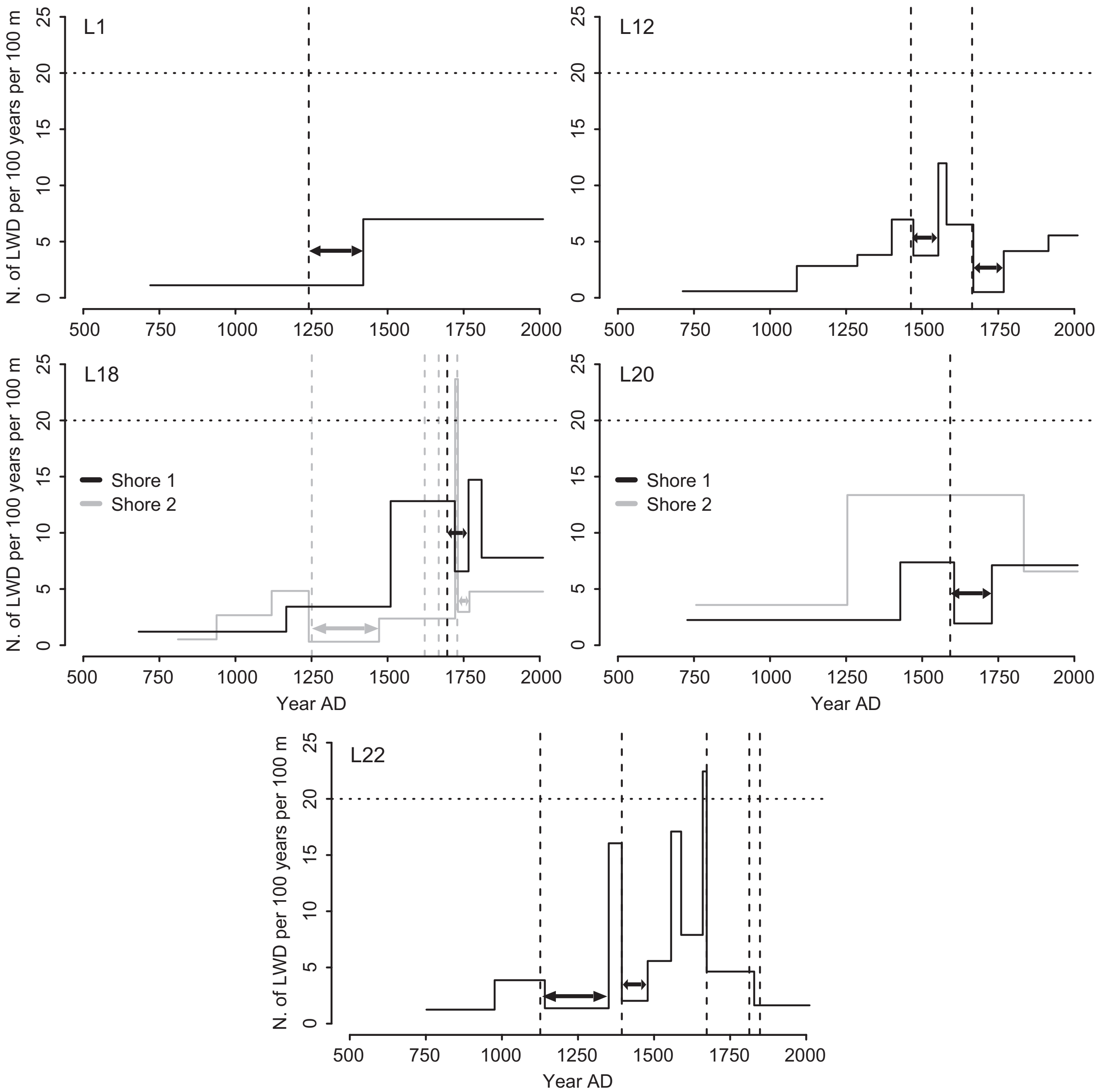

Fig. 6. Large woody debris (LWD) recruitment rates in the five littoral zones during the last 1400 years as reconstructed through piecewise regressions. Vertical dashed lines are estimated wildfires dates. The horizontal dotted line indicates the chosen threshold for a massive recruitment. Horizontal arrows show the time needed for the normalization of the recruitment rate after a fire.

buried specimens probably only played a minor ecological role, they nevertheless form an important deposit of highly valuable material for developing millennial tree-ring chronologies. Such chronologies would be useful for reconstructing long-term climate change and millennial forest dynamics. The old age of some LWD pieces also suggests that several of the undated specimens (25% of all sampled LWD pieces) could not be cross-dated because they are older than the master chronology. As these specimens are probably scattered in time over several centuries or even millennia, they would not have contributed significantly to our computations of LWD fluxes (Figs 5 and 6, Table S2) or losses (Fig. 3c).

FIRE RECURRENCE VS. LWD FLUXES

Our study highlights the important role of wildfires in regulating interactions between terrestrial and aquatic ecosystems in boreal landscapes. Despite the fact that we deliberately located our sampling sites within an area of relatively low fire occurrence (Boulanger *et al.* 2012) and selected shore segments with old forests, all sites possessed at least one shore segment that burned at least once and at least 14 wildfires occurred at our sites during the last 1400 years. These fire events were the main disturbances of the LWD fluxes across the forest–lake interfaces (Figs 2 and 5).

Table 5. Effects of wildfires prior to AD 1750 on the fluxes of large woody debris (LWD) across the forest–lake interface at the studied sites. Two more recent fires at L22 are excluded because their effects on the LWD fluxes are still ongoing (Fig. 5)

Littoral zone	Fire year	Normalization of establishment rate (years)	Normalization of recruitment rate (years)	Post-fire recruitment reduction (%)	Massive recruitment
L1	1241	48	179*	NA	No
L12	1463	4	90	−46.1	No
L12	1664	20	104	−92.2	No
L18 shore 1	1696	NA	70	−48.7	No
L18 shore 2	1251	143	221	−93.6	No
L18 shore 2	1622	0	NA	NA	No
L18 shore 2	1668	NA	NA	NA	No
L18 shore 2	1729	7	40	−87.5	Yes
L20 shore 1	1592	60	137	−73.8	No
L22	1126	105	225	−64.6	No
L22	1394	64	85	−87.4	No
L22	1673†	NA	0	−79.4	Yes

NA indicates that no value could be calculated because piecewise regressions failed in detecting a corresponding breakpoint.
*The calculation was made because an increased LWD recruitment rate was observed after this wildfire even if it did not cause a recruitment reduction (Fig. 5).
†Wildfire deduced from the pattern of recruitment even if no charred LWD pieces were found.

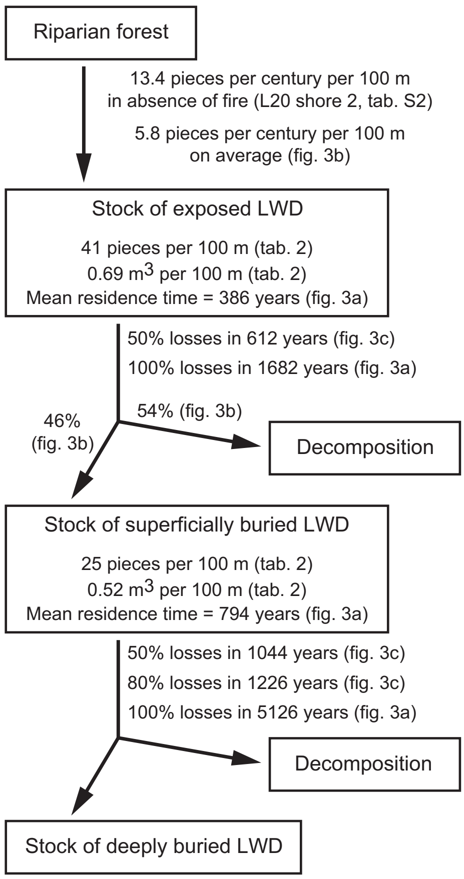

Fig. 7. Relative importance of large woody debris (LWD) stocks and fluxes in the studied lakes. The sources of the data are in parentheses.

The observed variability of the fire impacts (Table 5) most likely reflects varying fire severity. Depending on the fire severity (i.e. proportion of fire-killed trees), fire impacts on LWD fluxes would vary from almost unnoticeable (no charred LWD pieces, absence of massive recruitments, short normalization periods) to very important (charred LWD pieces, massive LWD recruitments, long normalization periods; Figs 5 and 6, Table 5). A similar long-term pattern of varying fire severity and associated LWD recruitment rate has already been observed along a small boreal stream (Arseneault, Boucher & Bouchon 2007). Varying fire severity along the shoreline probably explains the contrasting histories of the LWD recruitment rate between consecutive shore sections at L18 and L20 (Figs 2 and 5).

Some empirical and simulation studies have shown that severe natural disturbances such as fire and insects outbreaks trigger massive LWD recruitments into adjacent aquatic ecosystems (Bragg 2000; Chen, Wei & Scherer 2005). However, the millennial perspective provided by our study indicates that the net result of disturbances in riparian forests is to reduce the long-term LWD recruitment rates relative to values measured in absence of disturbances (Figs 2 and 7). Indeed, riparian trees have to reach a minimum height before being available to generate LWD pieces from their upper stem portions. Consequently, any disturbance resetting height growth to the ground level would interrupt the transfer of LWD pieces across the forest–lake interface and would reduce the long-term LWD recruitment rate, despite the possible short-term massive recruitment of disturbance-killed trees. Although black spruce seedlings generally establish massively during the first few post-fire years (Sirois 1995), complete stand recovery is slow (Auclair 1985; Morneau & Payette 1989) and several decades are needed for the recovering stand to reach the minimum height to generate LWD pieces. This explains the long time periods observed in our sites for the post-fire normalization of the establishment and recruitment rates (Table 5).

Stand-replacing wildfire is the main natural disturbance in the unmanaged boreal forest of northern Quebec, with annual burn rates that decrease eastward from the extremely high rate of 2.5% per year along the James Bay coast to about 0.2% per year in our study area (Payette *et al.* 1989; Boulanger *et al.* 2012). The time needed for the post-fire normalization of the LWD recruitment rate has a mean value of 115 years at our sites (Table 5). Comparing these durations to the supra-regional fire occurrence gradient, we conclude that fire is a major factor limiting LWD stocks and recruitment rate at large spatial and temporal scales. LWD recruitment in boreal lakes would cease almost completely if a severe wildfire occurs every 100 years, as is currently the case to the west of our study area. A preliminary survey of some lakes in this fire-prone region revealed to us almost non-existent LWD stocks in littoral ecosystems. By the same line of reasoning, the anticipated increase in fire frequency and total area burned in the North American boreal forest (Girardin & Mudelsee 2008; Balshi *et al.* 2009) would imply a progressive large-scale decrease in future LWD stocks in boreal lakes.

Our method, based on piecewise regressions fitted to establishment and recruitment data, was powerful enough to detect changes in LWD fluxes due to past fire disturbances. Piecewise regression can be a useful tool for identifying ecological thresholds and discontinuities in data (Toms & Lesperance 2003). In our analysis, most fires were detected by the piecewise regressions (Fig. 5, Table 5) and the majority of the breakpoints could be explained by the occurrence of fires (Table S2). However, not all wildfires corresponded to breakpoints and not all breakpoints depended on wildfires. Impacts of low-severity fires (e.g. AD 1696 fire at L18 shore 1; Fig. 5, Table 5), of fires recurring with short time intervals among them (e.g. AD 1622, 1668 and 1729 fires at L18 shore 2; Fig. 5, Table 5) and of recent wildfires (e.g. AD 1813 and 1848 fires at L22; Fig. 5) have been more difficult to detect. On the other hand, breakpoints may also have occurred in response to alternative disturbances (e.g. windstorms or changes in lake water level) as well as to continuous LWD losses related to physical and biochemical decomposition or deep burial (Fig. 3c).

CARBON STORAGE IN BOREAL LITTORAL LWD

Stocks of littoral LWD may represent an important, but poorly studied carbon sink at the landscape scale because of their slow decay rate (Guyette *et al.* 2002; Guyette, Dey & Stambaugh 2008). Our exhaustive sampling of large stocks of LWD at several sites allows for the estimation of the maximum amount of carbon stored in aquatic LWD in boreal lakes, considering separately stocks of exposed and superficially buried LWD. First, we can estimate the wood density of each LWD piece (kg m^{-3}) according to its residence time in water (years) by using the equation developed by Guyette & Stambaugh (2003): [density = 1000 * Exp(ln (0.41)–0.00011 * residence time)]. In the equation, 0.41 is the specific gravity of black spruce wood (Forest Products Laboratory 2010), and for undated LWD pieces, we used the mean residence time of the corresponding burial category (386 and 794 years for exposed and buried LWD pieces, respectively). Secondly, multiplying the volume of each LWD piece by its wood density and considering that the mass of softwood is about 52.1% carbon (Birdsey 1992), LWD volume can be transformed to LWD biomass and LWD carbon storage. The results suggest that the LWD biomass in our lakes is 470 kg per 100 m of shoreline (273 and 197 kg per 100 m of shoreline for exposed and buried specimens, respectively) and that the corresponding LWD carbon storage is 245 kg C per 100 m of shoreline (142 and 103 kg C per 100 m of shoreline for exposed and buried specimens, respectively).

In our study area, an average of 2.68 km of lake shore is found per km^2 of landscape (value calculated in a GIS). Based on the observation that mature riparian trees tend to fall in the direction of the dominant winds (Arseneault *et al.* 2013), about half of the total shoreline length would allow LWD accumulation in the littoral zone. Multiplying the obtained total (exposed plus buried) LWD volume, biomass and carbon content per km of shore length by 1.34, the maximal LWD volume in the region can be estimated at 16.32 m^3 per km^2, with maximal LWD biomass at 6294 kg per km^2 and maximal LWD carbon storage at 3279 kg C per km^2. Although these values are rough estimates and are not considering deeply buried LWD stocks, they are based on lakes with an exceptional amount of LWD and thus reveal that the maximum amount of carbon that can be sequestered by LWD stocks in the littoral zone of boreal lakes is extremely low. Despite the extreme abundance of lakes in our study area and the long residence time of LWD pieces, the associated carbon storage in littoral areas represents <0.05% of the total amount of carbon sequestered in boreal black spruce forest ecosystems on a per area basis (Kane & Vogel 2009). It has been recently pointed out that all boreal carbon stocks must be urgently quantified and preserved because the boreal forest corresponds to about one-third of the global forests and comprises roughly 30% of the stored terrestrial carbon (Bradshaw, Warkentin & Sodhi 2009). Even if large amount of carbon can be sequestered in boreal wetlands and lake sediments (Buffam *et al.* 2011), our results indicate that the LWD littoral carbon pools represent a negligible portion of the boreal carbon storage.

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Data accessibility

All data from the manuscript are archived in 'Figshare': http://dx.doi.org/10.6084/m9.figshare.826213 (Gennaretti, Arseneault & Begin 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Samples and variables used in the regression models to determine the factors influencing large woody debris residence time.

Appendix S2. Technical aspects of computing piecewise regressions models and of dating past fires.

Table S1. Linear regression models explaining the variation in large woody debris residence time at sites L18 and L20.

Table S2. Description of piecewise regression models.

Figure S1. Wildfire impacts on large woody debris fluxes at the shore 3 of L18 and the shore 3 of L20.