CONSERVATION ECOLOGY - ORIGINAL RESEARCH

Temperate forest fragments maintain aboveground carbon stocks out to the forest edge despite changes in community composition

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Abstract Edge effects are among the primary mechanisms by which forest fragmentation can influence the link between biodiversity and ecosystem processes, but relatively few studies have quantified these mechanisms in temperate regions. Carbon storage is an important ecosystem function altered by edge effects, with implications for climate change mitigation. Two opposing hypotheses suggest that aboveground carbon (AGC) stocks at the forest edge will (a) decrease due to increased tree mortality and compositional shifts towards smaller, lower wood density species (e.g., as seen in tropical systems) or, less often, (b) increase due to light/temperature-induced increases in diversity and productivity. We used field-based measurements, allometry, and mixed models to investigate the effects of proximity to the forest edge on AGC stocks, species richness, and community composition in 24 forest fragments in southern Quebec. We also asked whether fragment size or connectivity with surrounding forests altered these edge effects. AGC stocks remained constant across a 100 m edge-to-interior gradient in all fragment types, despite changes in tree community composition and stem density consistent with expectations of forest edge effects. We attribute this constancy primarily to compensatory effects of small trees at the forest edge; however, it is due in some cases to the retention of large trees at forest edges, likely a result of forest management. Our results suggest important differences between temperate and tropical fragments with respect to mechanisms linking biodiversity and AGC dynamics. Small temperate forest fragments may be valuable in conservation efforts based on maintaining biodiversity and multiple ecosystem services.

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Introduction

Forest fragmentation is ubiquitous, and is one of the predominant ways human activity alters biodiversity and ecosystem processes (Gonzalez et al. 2011). While the outcomes of forest fragmentation take many forms, one of the primary mechanisms by which fragmentation can change the diversity and function of a forest landscape is through edge effects (Murcia 1995; Ries et al. 2004; Harper et al. 2005). The establishment of forest edges during fragmentation and the ensuing alteration in microclimate affect both plant and animal populations. The exposure of organisms to dry, windy, high-light conditions that differ considerably from the dark, humid forest interior (Chen et al. 1993, 1995; Laurance and Curran 2008) can bring about shifts in the composition of tree species communities (Matlack

1994; Tabarelli et al. 2008), changes in population viability and recruitment (Cadenasso and Pickett 2000; McEuen and Curran 2004), altered species interactions (Chalfoun et al. 2002), and the degradation of various ecosystem processes (Laurance et al. 2002).

Despite an extensive body of research on forest edge effects (Ries et al. 2004; Harper et al. 2005; Nascimento and Laurance 2004), relatively few studies have focused specifically on the ways in which edge effects can alter the link between biodiversity and ecosystem functions occurring within temperate forest fragments. Instead, most research focuses primarily on the effects of forest fragmentation and edge exposure on particular species, or on summary metrics such as species diversity and richness. However, as edge effects are often linked to changes in diversity, it is likely that these changes will translate to differences in function, as recent research on forest biodiversity and ecosystem function shows that the two are linked (Paquette and Messier 2011; Ziter et al. 2013, but see Magnago et al. 2014). For example, ecosystem functions such as primary production and carbon (C) storage are predicted to change with proximity to forest edges via both changes in plant diversity and species composition as well as increased mortality due to high physiological stress on trees at the forest edge as result of increased wind and temperatures (Laurance et al. 2006b; Dantas de Paula et al. 2011).

Carbon storage is a function of particular interest in forest fragments, as it is likely to be altered by the increased prevalence of forest edges in fragmented systems. Forests contribute to climate regulation through the uptake of carbon dioxide (CO_2) from the atmosphere and the storage of C in biomass and soils. Fragmentation can alter this process by changing the uptake and emission of CO_2 (Numata et al. 2011). However, we lack a complete understanding of how forest fragmentation and the accompanying edge effects will impact C storage. This is especially true in temperate forests, where there is a dearth of large-scale field studies in fragmented systems compared to their tropical counterparts. In the tropics, alterations in aboveground tree biomass in fragmented forests occur primarily due to increased mortality of large, emergent (i.e., above the canopy) trees at fragment edges; a result of microclimatic stressors (Laurance et al. 2000; DAngelo et al. 2004; Nascimento and Laurance 2004). This tree loss contributes to sharp declines in standing aboveground carbon (AGC) storage in tropical fragments, with some edge habitats storing as little as one-third of the AGC held in interior forests (Dantas de Paula et al. 2011). Secondarily, this large-tree mortality occurs concomitantly with a shift in community composition towards light-demanding, early-successional pioneer species that are typically smaller, with lower wood density, than the trees they are replacing (Laurance et al.

2006a, b; Tabarelli et al. 2008), leading to further C loss at forest edges.

Studies investigating effects of forest fragmentation on landscape-level C storage have also found the spatial arrangement of forest patches to be important (Smithwick et al. 2003; Robinson et al. 2009). In a modeling study of wind-induced tree mortality and light limitations on temperate forest C dynamics, Smithwick et al. (2003) noted decreases in C stocks at forest edges for both live tree C stocks and total C stocks (including live and dead C pools, above and belowground), as well as non-additive consequences at the landscape level (i.e., C dynamics could not be measured in homogeneous patches and summed to predict dynamics at larger scales), with the spatial arrangement of patches affecting C storage. Robinson et al. (2009) also noted the sensitivity of temperate AGC stocks to fragmentation patterns (including fragment size, shape, and landscape configuration), and concluded that both within-patch and landscape heterogeneity should be accounted for in order to improve AGC estimation. Contrary to the majority of fragmentation studies, the authors noted an increase in AGC stocks in fragmented landscapes, which they attributed to the positive influences of increased temperature at the forest edge on vegetation growth. This assumption is supported by other studies that show shifts in species composition, and corresponding increases in growth rates for at least some temperate tree species at the forest edge (Matlack 1994; McDonald and Urban 2004; Harper et al. 2005).While these studies provide valuable insight into how forest fragmentation may alter temperate AGC storage at the landscape level, the extent to which these largely model-based insights will occur in the field remains unclear (e.g., Numata et al. 2011).

Thus, the literature supports the existence of a gradient in aboveground carbon stocks with proximity to the forest edge and with changes in fragment size, shape, and location; however, there is uncertainty about the hypothesized mechanisms and even the direction of this gradient. There are two alternative hypotheses regarding the mechanisms by which edge effects influence aboveground biomass and AGC stocks. The first hypothesis (H1) suggests that AGC stocks will be lower at fragment edges compared to the interior; H2 suggests that AGC stocks will be higher at fragment edges compared to the interior. Lower forest-edge carbon stocks are predicted as a result of increased mortality of trees at the forest edge due to wind-throw and other abiotic stressors, and/or as a result of the lower wood density and smaller maximum size of many early-successional tree species that colonize forest edges (e.g., Biological Dynamics of Forest Fragments Project, Laurance et al. 2002). Higher carbon stocks are predicted at the edge compared to the interior as a result of increased diversity and productivity resulting from increased sunlight and temperature at the forest edge (e.g., Robinson et al. 2009).
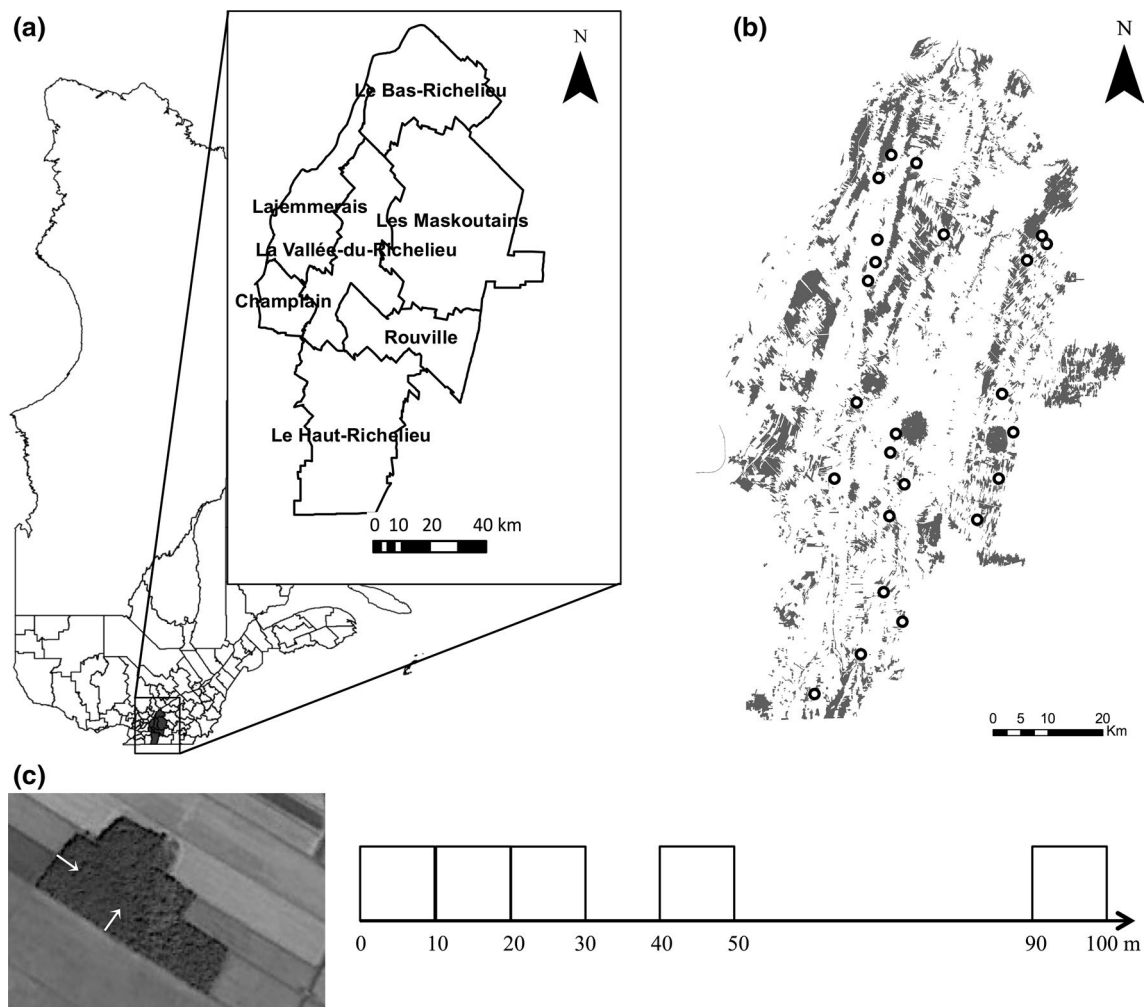
Fig. 1 a Administrative boundaries of the study area within Montérégie, QC, and **b** forest fragments ($n = 1,702$) within the study area. *Circles* indicate site locations. **c** Example of field sampling design in a small forest fragment; *white arrows* indicate locations of transects

Here, we address the effects of forest fragmentation on tree community composition and AGC stocks (including standing live and dead trees, and downed woody debris) in a highly fragmented temperate forest region in southern Quebec. We tested our alternative hypotheses and investigated the effects of proximity to the forest edge on AGC stocks, species richness, and community composition in small forest fragments, as well as whether fragment size or level of isolation altered these forest edge effects.

Materials and methods

Study area and site selection

The Montérégie is an administrative region of Quebec, including the area to the south and east of the Island of

Montreal, from the south shore of the St. Lawrence River to the US–Canada border. Home to over 1.4 million people, the Montérégie is typical of many of Canada's peri-urban regions that comprise a mix of agricultural lands, protected areas, private and public green spaces, and urban development. The region is characterized in large part by fragmented, secondary-growth forest dispersed throughout a soy-corn agricultural matrix. The current study is restricted to an area of approximately 4,700 km^2 surrounding the Vallée du Richelieu regional county municipality (Fig. 1, adapted from Ziter et al. 2013).

Study sites were chosen based on fragment size and connectivity level. A total of 24 individual forest fragments were analyzed: six each of small isolated, small connected, large isolated, and large connected. The study took place on privately owned land, with permission obtained from all landowners prior to the start of field surveys (Ziter et al. 2013).

In order to ensure sites were representative of the greater region in terms of forest characteristics, all fragments within the study region were first screened with respect to three forestry attributes: forest population type (deciduous, mixed, or coniferous), drainage, and age class. Data for these three attributes were obtained from Système d'information écoforestière (SIEF, a forest database from the Quebec Ministry of Natural Resources, MRNFP 2004), and values for all polygons within each distinct forest fragment were averaged to arrive at a single value of each attribute for each fragment (ArcGIS version 9.3.1). Potential sites were restricted to those fragments demonstrating forest population type and drainage criteria consistent with those most prevalent within the region, and were required to meet a minimum age cutoff to ensure tree maturity. Specifically, all fragments considered for this study met the following conditions: >70 % deciduous forest cover; >70 % satisfactory/moderate drainage class; and a minimum age class of 41−60 years.

Remaining fragments within the study extent were then classified into small (~10 ha, range 7−13 ha) and large (~100 ha, range 75−165 ha) fragments using FRAGSTATS (version 3.3, McGarigal et al. 2002). Size classes were chosen to reflect the forest fragmentation patterns in the region, where over 90 % of fragments are <100 ha and 53 % are <10 ha, and to be consistent with previous fragmentation studies (e.g., see Laurance et al. 2011; Ewers et al. 2011). From each of these size classes, the fragments with the highest and lowest connectivity levels, relatively, were chosen as "connected" and "isolated." Connectivity levels were based firstly on FRAGSTATS patch proximity metrics (PROX, an index accounting for the number, size, and distance of forest fragments within a given buffer; PROX measures are computed as the sum, over all patches with edges within a set radius of the focal patch, of each patch size divided by the square of its distance from the focal patch) using a buffer of 150 m, and secondarily on the Euclidean nearest neighbor (ENN) distance in the event that PROX measures were equal (see Ziter et al. 2013 for further details). Sites bisected by major roads or waterways were discarded. Small fragments chosen had a mean of 10.3 ha (SE ± 0.65), and large fragments had a mean of 107.8 ha (SE ± 8.78). Isolated sites had a FRAGSTATS PROX measure of 0, with a mean ENN of 514 m (SE ± 98), and connected sites had a mean PROX of 2,504 (SE ± 947.9) and a mean ENN of 84 m (SE ± 4.9).

Field methods

Within each of the 24 forest fragments, we established two 100-m long transects. Transects originated from the southwest (SW) and northwest (NW) facing edges towards the interior at a randomly chosen entrance point a minimum distance of 50 m from any fragment corners (following Robinson et al. 2009), but ≥100 m when possible. Anthropogenic disturbances such as small cabins or trails are common in this region, and were avoided (by shifting the entrance point, at random, either to the right or left of the disturbance) to the extent possible when determining the location of transects. As edge effects are predicted to be stronger on the southern edge of a fragment (in the Northern Hemisphere), we chose two different transect directions to account for potential differences with respect to aspect (Fig. 1c). Due to the typical forest fragment orientation in the Montérégie (along a NE–SW axis, a result of agricultural field orientation), directions were modified from south and north to SW and NW (compass bearings) to ensure that the majority of the transects were established perpendicular to the forest edge. SW and NW were chosen as opposed to SE and NE due to increased site accessibility.

Along each transect, we established five 10 × 10 m sample plots at distances of 0−10, 10−20, 20−30, 40−50, and 90−100 m from the forest edge, with plots placed closer together near the edge in anticipation of stronger ecological gradients with edge proximity (Fig. 1c). Irregularity in fragment shape resulted in omission of the fifth plot in five of the 48 established transects due to a total fragment width of less than 200 m, such that transects never crossed the midpoint of a fragment. We discarded one transect from the analysis due to an observed lack of mature trees, leaving a total of 47 transects.

Within each 10 × 10 m plot, we surveyed all live woody plants (including both trees and large shrubs, hereafter simply "trees") and standing dead wood (hereafter "snags") ≥1 cm diameter at breast height (DBH, measured at 1.3 m) and ≥1.5 m tall. DBH was recorded for all adult trees (trees ≥9 cm DBH), with sapling DBH (trees <9 cm DBH) recorded by DBH class (1−3, 3−5, 5−7, 7−9 cm DBH, following Quebec MRNF size classes, Boudreau and Philibert 2011). All live trees were identified to species; we recorded the species ID for snags where possible. We also surveyed fine and course downed woody debris (DWD) within each plot using a modified version of the Van Wagner (1968) method (Bruederle and Stearns 1985), following Hooper et al. (2001). Within each plot, we established a 10-m transect in a random compass direction, with the diameter at point of intersection recorded for each piece of DWD ≥ 1 cm diameter, as well as the decay class (two decay classes, adapted from USDA recommendations; Harmon et al. 2008), for details see Appendix A of Ziter et al. 2013).

Aboveground carbon stocks

We calculated the total aboveground carbon stocks for each plot, comprising C stored in live trees, snags, and downed

woody debris (hereafter, "AGC" refers to carbon in all three of these pools unless otherwise specified). For live trees, DBH measurements were converted to aboveground biomass using generalized allometric regression equations developed by Jenkins et al. (2003, 2004). Based on a compilation of 2,640 equations from the literature, Jenkins' equations generate aboveground biomass predictions for ten species groups. All species in our study region were sorted according to species group, and the corresponding equation was applied to determine aboveground dry-weight biomass (see Appendix A of Ziter et al. 2013 for details). As per the standard in the field, C stocks were estimated at 50 % of the dry-weight biomass (Schlesinger 1997; Intergovernmental Panel on Climate Change 2006).

Snags identifiable to species in the field were treated as above. For all unidentifiable snags (due to leaf and/or bark loss), we assumed that snag community composition was equivalent to live tree community composition within the same 10×10 m sample plot, with species group allometric equations used to calculate an average biomass for each snag based on the distribution of species groups in the surrounding community of live trees. Biomass of all snags was adjusted for the gradual loss of leaves and branches from dead trees using a biomass reduction factor of 0.8874 (modified from UNFCCC recommendations, UNFCCC 2010). Snag C stocks were estimated at 50 % of this adjusted biomass.

Biomass of DWD was derived from plot DWD volume (calculated following Hooper et al. 2001). DWD was split into fine woody debris (FWD, $1-10$ cm diameter) and coarse woody debris (CWD, ≥ 10 cm diameter), and differentiated by decay class (modified from USDA recommendations, Harmon et al. 2008, to account for changes in wood density as decomposition progresses). Volume was converted to biomass using density values from the literature for each size and decay class (see Appendix A of Ziter et al. 2013 for details). Biomass from each category was summed to determine the total DWD biomass per plot, and DWD C stocks were estimated at 50 % of this biomass value.

Analysis

We used linear mixed effects models (both general and generalized, using R's "(g)lmer" in the "lme4" package) to analyze within-transect (forest edge to interior) trends in AGC stocks, species richness, and stem density (total number of live trees), with plots nested within transects as a random effect (R Core Team 2012). Models included both a random slope and intercept term. While transects are also nested within sites (i.e., there are two transects within each individual forest fragment), we did not include site in the random effect structure, as its inclusion explains very little

variance at the transect level in our study region (see Ziter et al. 2013).

Model residuals were checked for normality using diagnostic plots and the Shapiro–Wilk test. Log transformations were performed as appropriate to improve normality. We used general linear mixed effects models to test the effect of proximity to the forest edge on AGC stocks and stem density, and generalized linear mixed effects models with a Poisson distribution to test the effect of proximity to the forest edge on tree species richness. We also tested whether connectivity, fragment size, or aspect affected the relationships of our dependent variables with proximity to the forest edge. We performed model comparisons using likelihood ratio tests, which generate P values using a chi-square test (see Table 1A of the Electronic supplementary material, ESM, for a summary of all mixed model analyses and results).

Multivariate analysis was used to compare differences in tree community composition within transects. Specifically, multivariate ordination techniques were used to visualize differences in tree community composition at the forest edge ($0-10$ m) vs the interior ($90-100$ m). We ordinated sites using nonmetric multidimensional scaling (NMDS) (McCune and Grace 2002) with a Bray–Curtis dissimilarity index, a non-Euclidean distance measure that is useful for analyzing species abundance data (using R's "metaMDS" in the "Vegan" package, Oksanen et al. 2013). We calculated 95 % confidence ellipses of the group centroids, based on the standard error of the average of the axis scores (using Vegan's "ordiellipse") to assess differences between tree species communities at forest edge and interiors.

We also categorized trees by size classes to investigate the relative contribution of each class to live tree C stocks: <10 cm DBH; $10-15$ cm; $15-20$ cm; $20-25$ cm; $25-30$ cm; $30-35$ cm; $35-40$ cm; >40 cm. The percentage of each size class to total C stocks in live trees was plotted in order to visualize the effects of forest structure on C stocks.

Results

Aboveground carbon stocks remained constant over the distance gradient, with no effect of proximity to the forest edge on AGC stocks ($\chi^2(1) = 0.0071$, $P = 0.93$) (Fig. 2a). Neither connectivity, fragment size, nor transect aspect significantly influenced the relationship between proximity to the forest edge and AGC stocks. Carbon stocks in live trees displayed the same pattern as total AGC stocks.

There was a significant quadratic effect of proximity to the forest edge on stem density ($\chi^2(5) = 99.008$, $P = <0.001$), with edge plots ($0-10$ m) containing over twice the number of individuals as any further plot
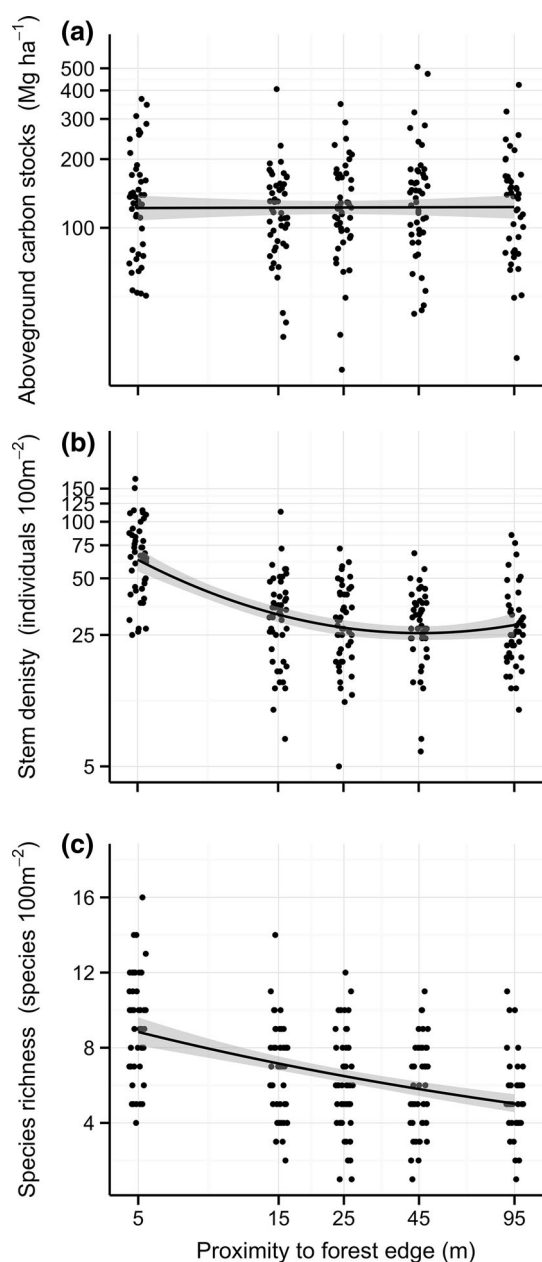
Fig. 2 The effect of proximity to the forest edge on **a** aboveground carbon stocks (in standing live and dead trees, and downed woody debris), **b** stem density, and **c** species richness in Montérégie, QC. Data points are from 10 × 10 m sample plots in 47 forest transects from fragments of varying size and connectivity; *lines* and *shading* indicate the smoothed conditional mean and 95 % confidence interval for the mean, respectively

(0−10 m, mean stem density per 100 m^2 = 71 (±4.6 SE); plots from 10−100 m, mean stem density per 100 m^2 = 32 (±1.1 SE)) (Fig. 2b). There was a significant effect of fragment size on the model intercept ($\chi^2(1) = 13.422$, $P = <0.001$) but not the model slope, with stem densities approximately ten individuals greater in larger fragments. There was no significant effect of proximity to the forest

edge on basal area (mean basal area 40 m^2/ha (±1.1 SE)). This relationship held across all fragment types.

Species richness ranged from 1 to 16 tree species within a single 100 m^2 plot. There was a significant effect of proximity to the forest edge on plot species richness ($\chi^2(1) = 44.41$, $P = <0.001$), with an approximately 20 % drop in species for each one unit increase in log(distance from the forest edge). Thus, the average species richness drops from ~9 species 10 m from the forest edge (9.2 ± 0.40 SE) to 5−6 species per 100-m^2 plot at distances farther than 20 m (6.1 ± 0.38 at 20−30 m; 5.9 ± 0.34 at 40−50 m; 5.3 ± 0.31 at 90−100 m) (Fig. 2c). Neither fragment connectivity nor size nor transect aspect significantly influenced the relationship between proximity to the forest edge and species richness.

NMDS results (dimensions = 2, stress = 0.275) show differences in tree community composition at the forest edge (0−10 m) vs. interior (90−100 m) that are consistent with expectations based on ecological preferences for light vs. shade (Fig. 3). Edge plots cluster towards shade-intolerant species, for example birch species (*Betula populifolia* and *papyrifera*), trembling aspen (*Populus tremuloides*), buckthorn (*Rhamnus cathartica*), and willow species (*Salix* spp). Interior plots cluster towards shade-tolerant and intermediate shade-tolerant species such as red and sugar maple (*Acer rubrum* and *saccharum*), ironwood (*Ostrya virginiana*), and American elm (*Ulmus americana*).

Averaged across all fragments, C stocks in live trees were relatively evenly distributed between size classes at the forest edge, with larger size classes making up a greater percentage of the total live tree C pool towards the forest interior (Fig. 4a). Despite the overall constancy in AGC stocks (and live tree C stocks), substantial variation was observed in the structural distribution of live tree C among fragments. In many fragments, the contribution of smaller size classes increased towards the forest edge and the contribution of larger size classes decreased (e.g., Fig. 4b). In others, the structural distribution remained constant across the gradient, with large trees contributing the majority of the C stocks from edge to interior (e.g., Fig. 4c).

Discussion

Contrary to our expectations, we found that proximity to the forest edge does not influence AGC stocks in forest fragments. Within our study fragments, AGC stocks remained constant across a 100-m edge to interior gradient, regardless of fragment size and connectivity or transect aspect. These results do not confirm either of the prevailing hypotheses regarding the influence of edge effects on forest biomass and C storage. The most prevalent hypothesis predicts a decrease in C stocks as a result of abiotic

Fig. 3 NMDS of tree community composition in the Montérégie, QC. *White and gray filled symbols* indicate forest-edge (0−10 m) and interior (90−100 m) plots, respectively. The *white* and *gray ellipses* represent the 95 % confidence interval for the group centroid in edge fragments and interior fragments, respectively
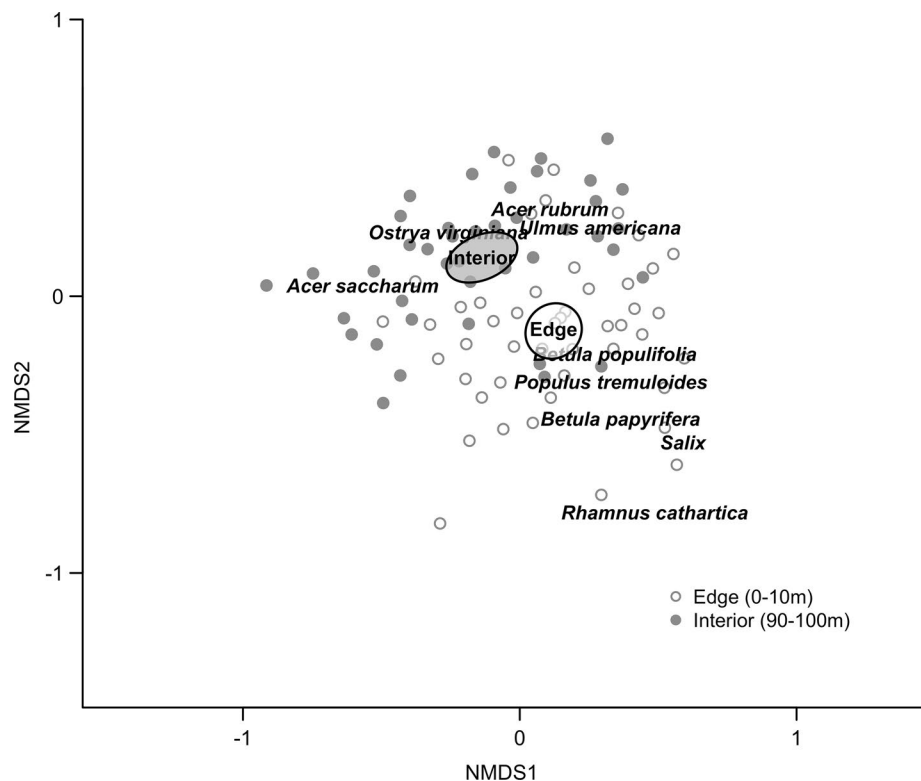
effects at the forest edge (Laurance et al. 2000; Smithwick et al. 2003; Laurance and Curran 2008; Dantas de Paula et al. 2011), or compositional shifts towards low wood density species (Matlack 1994; Harper et al. 2005; Laurance et al. 2006a) (H1). Less commonly, C stocks are predicted to increase at the forest edge due to high productivity and increased growth rates driven by increased temperature and light availability (H2) (McDonald and Urban 2004; Robinson et al. 2009).

A proposed explanation for the absence of a C gradient is that forest fragments in our study are too small to have a true interior (i.e., they are "all edge"), precluding edge effects of the magnitude observed in studies of larger forest fragments. However, our study fragments are consistent in size with previous studies (Laurance et al. 2011; Ewers et al. 2011), and we also found that the changes in community structure along fragment transects were consistent with knowledge of forest edge effects (Murcia 1995; Ries et al. 2004; Harper et al. 2005). For example, we observed a significant increase in stem density with proximity to fragment edges, likely a consequence of increased temperature and light availability. An increase in tree species richness at fragment edges was also observed, as well as shifts in forest community composition consistent with a species' physiological tradeoff for light vs. shade. Forest edges were dominated by shade-intolerant, fast-growing pioneer species such as birch and aspen, as compared to the more shade-tolerant maple, ironwood, and elm species that dominated

the fragment interiors. These trends were true of fragments of both 10 and 100 ha, which showed only very minor differences in the attributes measured and no dependence on transect direction. These effects were strongest in the first 10 m, indicating that edge effects on species composition fade relatively rapidly in our system. The presence of marked ecological differences between fragment edges and interiors indicate that our forest fragments do demonstrate edge and interior transitions; however, these edge effects simply do not translate to alterations in forest C storage.

Although forest fragments of all types throughout our study region demonstrated constancy in AGC stocks along the edge–interior gradient, the mechanisms driving this trend seem to differ for different fragments. In the majority of fragments, we observed a shift in the distribution of AGC stocks towards smaller tree size classes with increasing proximity to the forest edge. Similar to what is observed in tropical studies (Laurance et al. 2000; Nascimento and Laurance 2004), we noticed a decline in large trees towards the forest edge in these fragments, particularly within 30 m of the forest edge (e.g., Fig. 4b). However, unlike tropical results (e.g., Dantas de Paula et al. 2011), increased productivity at the forest edge (i.e., higher stem density) in smaller size classes of trees compensates for this loss of large trees, with a greater percentage of AGC stocks held in saplings and small trees towards the forest edge. Thus, we found that two opposite mechanisms occur which appear to drive C stocks at the forest edge. The dearth of large trees
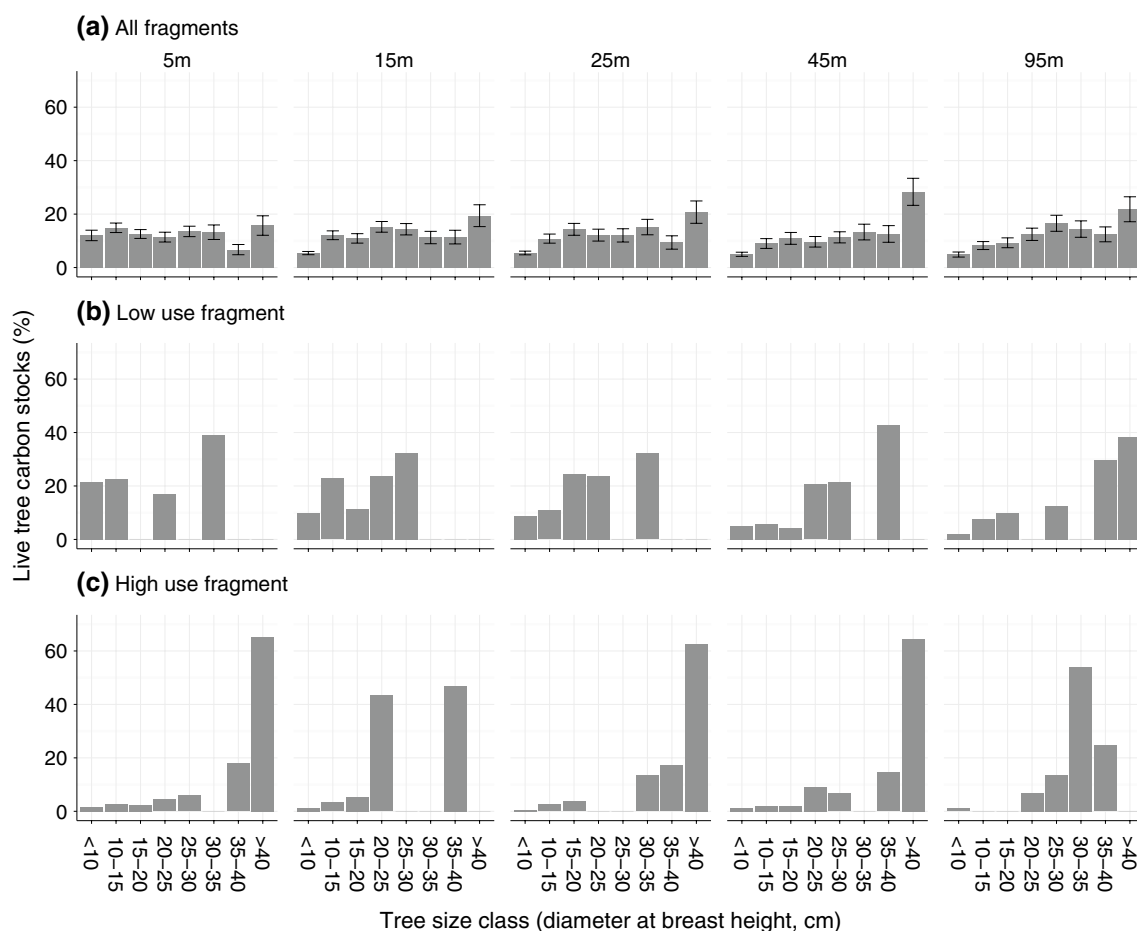
Fig. 4 Allocation of live tree carbon stocks across an edge-to-interior gradient in forest fragments with different size structures in Montérégie QC in relation to tree size class. **a** Allocation across all study fragments (mean ± SE), **b** a typical low-use forest fragment, and **c** a typical high-use fragment by human management, likely for maple syrup production

observed at the forest edge supports H1, while our finding of increased productivity of a diverse community of small trees at the forest edge supports H2. The combined effect of these two mechanisms results in no net change in the magnitude of AGC stocks with increasing proximity to the edge, but rather a shift in the physical allocation of C within forest fragments.

In a subset of study fragments, however, the constancy of AGC across the edge–interior gradient appears to arise for a different reason. In approximately one-quarter of the studied fragments, we did not observe a decline in large trees at the fragment edge but rather their persistence across the entire gradient (e.g., Fig. 4c). We suspect that this pattern may be due to forest management in this human-dominated region. While some level of anthropogenic influence is pervasive in all of the studied forest fragments, throughout our fieldwork we noted that certain forest stands are subject to notably more intensive use—predominantly for maple syrup production. In these managed forests, colloquially referred to as "sugar bushes," we observed that

landowners are changing the natural structure of the forest edge (e.g., through practices such as thinning and selecting over time for large maple trees). Thinning practices would also explain the lower stem densities found in small fragments, as small stands in the Montérégie are often forest remnants retained by farmers as sugar bushes.

While the retention of large trees may seem counterintuitive in the context of human use and management of the forest, the fact that forest use in this region is most commonly aimed at maple syrup production leads to a preference for larger trees, and consequently different effects on C storage than we might expect in a more traditionally managed forest (Ziter et al. 2013). These large trees are likely particularly important for maintaining AGC at the forest edge, as we observed little change in the amount of C held in smaller trees at forest edges in these fragments. These results stand in stark contrast to the results of tropical forest studies, where the loss of large emergent trees at the forest edge is a major contributor to the loss of AGC stocks (Dantas de Paula et al. 2011). Future studies

of forest C storage in agricultural landscapes would benefit from incorporating human management into the study framework, as it potentially exerts a large influence on forest carbon stocks.

The maintenance of high AGC stocks at fragment edges in our study is surprising, and has conservation implications in this highly fragmented region. While temperate forest fragmentation impacts biodiversity (Honnay et al. 2005), dispersal of organisms (Tewksbury et al. 2002; Damschen et al. 2014), and species interactions (Simonetti et al. 2007), our study indicates that there may be less of an effect on AGC than anticipated in the Montérégie, at least due to edge effects. This constancy in AGC stocks across the edge–interior gradient in forest fragments presents evidence that, in regions already subject to fragmentation, even small and irregularly shaped fragments remain valuable contributors to AGC storage, and, from a C perspective, are as worthy of conservation attention— on a per hectare basis—as larger, lower edge-to-area ratio fragments.

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