

Functional diversity and management mediate aboveground carbon stocks in small forest fragments

CARLY ZITER,^{1,†} ELENA M. BENNETT,² AND ANDREW GONZALEZ¹

¹*Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, Quebec H3A 1B1 Canada*

²*Department of Natural Resource Sciences and McGill School of Environment, McGill University, 21, 111 Lakeshore Road, Sainte-Anne-de-Bellevue, Montreal, Quebec H9X 3V9 Canada*

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Abstract. Improved landscape connectivity is increasingly considered a viable management strategy to maintain biodiversity, ecosystem functions, and services. How landscape structure affects biodiversity, ecosystem services, and their relationship, however, is still unclear in many cases, including the service of climate regulation. The effects of forest fragmentation on carbon storage remain largely unknown, compounded by uncertainty in both the direction and magnitude of the relationship between carbon storage and biodiversity. We investigated the effects of forest fragmentation and management on carbon stocks and biodiversity in the Montérégie, QC. We quantified total aboveground carbon stocks in 24 small forest fragments of two sizes (~10 ha, ~100 ha), and two levels of connectivity, using a combination of satellite data, field-based methods, and allometry. We correlated this data with both woody plant species richness and functional dispersion to determine the relationship between biodiversity and carbon stocks in these forest fragments. We found functional dispersion was a significant predictor of aboveground carbon stocks, interacting with forest management and connectivity in this fragmented forest system. Both synergies and tradeoffs between biodiversity and carbon stocks were observed. Unmanaged forest stands stored less carbon on average than managed, but demonstrated a significant positive relationship between functional dispersion and aboveground carbon stocks, corroborating the results of biodiversity-ecosystem function experiments. The slope of the relationship was significantly greater in connected fragments than isolated, suggesting improved forest connectivity may strengthen the relationship between biodiversity and aboveground carbon stocks in this region. Managed stands exhibited a significant negative relationship, demonstrating that anthropogenic influence can alter the link between biodiversity and carbon stocks in natural systems. Our results suggest that considering management, connectivity, and functional diversity may increase accuracy in estimating landscape level carbon stocks. Additionally, the significant contributions of small forest fragments to regional diversity and service provision emphasizes the important role these fragments can play in conservation efforts.

Key words: biodiversity and ecosystem function; carbon storage; connectivity; ecosystem services; forest management; fragmentation; functional diversity; Quebec; temperate forests.

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† **E-mail:** carly.ziter@mail.mcgill.ca

INTRODUCTION

The relationship between biodiversity and

ecosystem functions and services is of considerable interest to ecologists (Reiss et al. 2009), spawning numerous theoretical and experimen-

tal studies over the past two decades. Findings from many biodiversity-ecosystem function (BEF) experiments suggest a positive, but saturating, relationship between species richness and ecosystem function (Balvanera et al. 2006, Cardinale et al. 2007, 2011), with biodiversity increasing in importance when multiple functions and services are considered (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010, Isbell et al. 2011). However, while knowledge in the BEF field has progressed tremendously in the past 20 years (Cardinale et al. 2012), it remains unclear the extent to which similar results would be observed beyond the controlled context of an experiment. Criticisms of whether experimental results transfer to natural systems often come down to issues of scale, and realism. BEF studies are often criticized because they are performed at scales that are too small, and too short to be relevant to real world management (Kremen and Ostfeld 2005, Balvanera et al. 2006). Studies outside of experimental systems have been less common; and, unlike their experimental counterparts, often produce conflicting results (Jiang et al. 2009). To integrate biodiversity and ecosystem services into management for multifunctional landscapes (Chan et al. 2006), we need to complement our existing experimental knowledge of BEF with well-designed field studies, moving towards a better understanding of the role of biodiversity in providing ecosystem functions and services in coupled human-natural systems (e.g., see Gamfeldt et al. 2013).

Forests are recognized as hotspots for biodiversity and ecosystem service provision, and so are often managed for multiple functions (Paquette and Messier 2010, Messier et al. 2013). Given projected trends in climate, managing for carbon (C) sequestration and storage—an ecosystem function by which we quantify the ecosystem service of climate regulation—is currently of particular interest in forest ecosystems (Canadell and Raupach 2008, Rhemtulla et al. 2009, Carlson et al. 2010, McKinley et al. 2011). This raises the question of whether or not strategies can be found to conserve both C and biodiversity, a “win-win” scenario (Huston and Marland 2003, Chan et al. 2006, Nelson et al. 2008, Díaz et al. 2009, Strassburg et al. 2010, Wendland et al. 2010).

BEF studies conducted in forests comprise a

surprisingly small, although growing, component of the BEF literature (Scherer-Lorenzen et al. 2005). Of studies that have been done, most find a positive relationship between diversity and function (Vilà et al. 2007, Lei et al. 2009, Paquette and Messier 2011, but see Vilà et al. 2003), although few extend this relationship explicitly to services (e.g., Schwenk et al. 2012, Gamfeldt et al. 2013). Among studies that explicitly address C stocks, or storage, there is disagreement as to the nature of the correlation between C and forest biodiversity, with studies reaching different conclusions with respect to both the direction and magnitude of the relationship. While some studies find a positive correlation between species diversity and C (Caspersen and Pacala 2001, Ruiz-Jaen and Potvin 2011), most note that forest composition, or particular structural or functional traits, are more important than simple measures of richness for determining C stocks (Balvanera et al. 2005, Bunker 2005, Kirby and Potvin 2007, Wang et al. 2011, Conti and Diaz 2013). This is in line with a recent shift away from a species-centric view of biodiversity in BEF studies, towards more multifaceted metrics such as functional and phylogenetic diversity (Díaz et al. 2007, Mokany et al. 2008, Cadotte et al. 2009, 2011, Lavorel 2013).

One possible reason for conflicting results is that, thus far, studies investigating forest biodiversity and ecosystem function have largely ignored the issue of *landscape structure* (the composition, configuration, and proportion of different habitat types across a landscape), despite the ubiquity of fragmentation in temperate forests (Wade et al. 2003) and the potential for habitat fragmentation to impact landscape structure and thereby alter ecosystem function. Fragmentation can impact function through turnover in species composition from patch to patch, and spatial variation in diversity (e.g., species richness) among patches (Gonzalez et al. 2009). These changes may in turn, albeit indirectly, affect ecosystem functions and processes such as primary productivity, nutrient cycles, and food web dynamics that arise as consequences of fragmentation (Ives and Cardinale 2004, Gonzalez and Loreau 2009, Staddon et al. 2010). Habitat connectivity can positively affect plant species richness, for example by increasing seed dispersal, facilitating pollen movement, and

altering foraging (Tewksbury et al. 2002), even in areas with seemingly small distances of isolation between patches. Damschen et al. (2006) found a net positive effect on native plant species richness in patches connected by corridors, compared to patches isolated by 150 m. Additionally, surrounding forests may have the potential to buffer existing forest fragments from microclimatic edge effects; in tropical forests, landscape level influences such as increasing forest cover and structural connectivity influenced microclimatic differences between forest fragments and the surrounding matrix, with air temperature and moisture in larger and more connected fragments deviating less from the surrounding matrix (Pinto et al. 2010). However, the majority of forest fragmentation studies focus primarily on summary metrics such as species richness and composition (Estades and Temple 1999, Honnay et al. 1999, Petit et al. 2004, Uezu et al. 2005, Damschen et al. 2006, Echeverría et al. 2007), and dispersal of organisms (Tewksbury et al. 2002, McEuen and Curran 2004, Kolb and Diekmann 2005, Pardini et al. 2005), and rarely make the link to ecosystem functions or services (but see Billings and Gaydoss 2008).

Consequently, the effects of forest heterogeneity on landscape level C dynamics are poorly understood. Biomass is typically averaged across the landscape (Houghton 2005) or considered additive—whereby a number of forest patches is considered to act the same as an equal area of continuous forest (Smithwick et al. 2003)—rather than accounting for the spatial variability in biodiversity and ecosystem function that accompanies fragmentation. This is surprising given the evidence from tropical systems that fragmentation can considerably alter forest biomass and carbon cycles, among other biological processes (Laurance et al. 2002, 2011). By failing to take into account forest heterogeneity and fragmentation patterns, we risk substantial over or underestimation of C stocks (Houghton 2005). The few studies that have looked at landscape structure with respect to C in temperate systems have found that the spatial arrangement of fragments is important, with C stocks sensitive to changes in fragmentation patterns (Smithwick et al. 2003, Robinson et al. 2009). However, neither study took into account fragment connectivity or management. In fact, changes to

landscape structure, such as differences in patch size and connectivity, may drive variability in biodiversity and ecosystem function (Staddon et al. 2010), potentially altering forest C stocks. Another potential driver is the increased anthropogenic influence that often accompanies fragmentation, as forests become more accessible to human use and management with fragmentation, and remnant fragments are often retained as managed stands. Given the prevalence of highly fragmented landscapes and the desire to implement forest connectivity as a conservation strategy, we need to know whether, and how, fragmentation is likely to affect forest C, as well as the relationship between C and biodiversity.

Here, we address the effects of forest fragmentation on biodiversity, carbon stocks, and their relationship in a region with high levels of forest fragmentation in southern Quebec. We investigated the effect of forest fragment size and level of isolation, as well as the intensity of forest management on diversity (species richness and functional diversity of woody plants) and total aboveground C stocks in small forest fragments. We also investigated whether synergies or trade-offs occur between diversity and C stocks, and the factors that may be driving these relationships.

MATERIALS AND METHODS

Study area and site selection

The Montérégie is an administrative region of Quebec, southeast of the island of Montreal. The region spans the area between the St. Lawrence River and the US–Canada border, containing densely populated cities, rural towns, and agricultural lands; thus, the region is a mix of protected areas, private and public green space, and urban development, representative of many such peri-urban regions across the country. Much of the region is characterized by fragmented forest within a soy-corn agricultural matrix. The current study is restricted to the Vallée du Richelieu regional county municipality (RCM), and the 6 bordering RCMs, an area of approximately 4700 km² (Fig. 1).

Site selection was based primarily upon three factors: fragment size, level of connectivity, and site ecoforestry attributes. Sites were limited to forest fragments representative of the greater

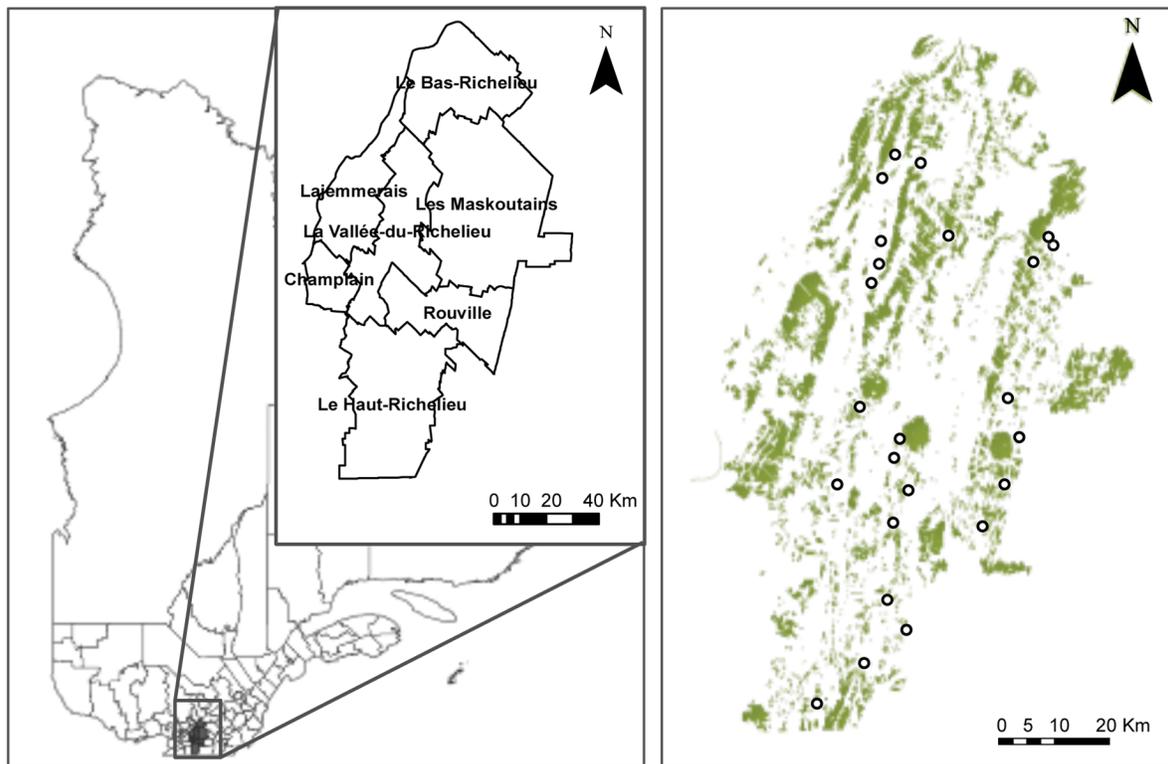


Fig. 1. Administrative boundaries of the study area within Montérégie, QC, left, and forest fragments ($n = 1702$) within the study area, right. Circles indicate site locations.

region in terms of forest type, drainage, and age. Information about these factors for each fragment was obtained by averaging the available Système d'information écoforestière (SIEF) data for all polygons within a single fragment. Sites considered for selection demonstrated the following attributes: $>70\%$ deciduous forest cover; $>70\%$ satisfactory/moderate drainage class; and a minimum age class of 41–60 yrs. Forest cover type and drainage class were chosen to represent the most prevalent within the region, while a minimum age cutoff was established to ensure presence of mature trees within all sites.

Potential sites were then restricted to those falling within two different size categories, small fragments of ~ 10 ha, and large fragments of ~ 100 ha. The two size classes were chosen to reflect the pattern of forest fragmentation in the region: over 90% of fragments in the study region are <100 ha, with 53% of fragments <10 ha. Such fragment sizes are common in fragmentation studies, such as the Biological Dynamics of Forest

Fragments Project, which used small fragments of 1–10 ha, and large fragments of 100 ha (Laurance et al. 2002).

Connectivity was the third factor that helped determine sites selected for the study. Connectivity measures were based primarily on FRAGSTATS patch proximity metrics (PROX, which takes into account the number, size, and distance of forest fragments within a given distance of the fragment in question) within a buffer of 150m, as well as (secondarily) the Euclidean Nearest Neighbor (ENN) distance (e.g., in the event that two connected/isolated patches had similar PROX measures, the patch with the lower/higher ENN was prioritized). Patch Proximity was chosen as the primary metric by which to measure connectivity under the hypothesis that the total amount of nearby forest cover is likely to provide buffering effects beyond those explained by the simple distance to nearest forest edge. For each size class, possible sites were arranged from the highest to lowest connectivity, based on these

FRAGSTATS metrics. The sites with the highest connectivity levels, relative to the rest of the region, were chosen as “connected” sites, and the sites with the lowest relative connectivity levels were chosen as “isolated” sites. Sites intersected by major highways were eliminated.

Twenty-four fragments were chosen in total, 6 each of small isolated, small connected, large isolated, and large connected. Final sites had areas of 10.3 ± 0.65 ha (mean \pm SE) for small and 107.8 ± 8.78 ha for large fragments. Isolated sites have a PROX measure of 0, and an ENN of 514 ± 98 m. Connected sites have a PROX measure of 2504 ± 947.9 , and an ENN of 84 ± 4.9 m. All forest fragments used in the study are privately owned, and permission was obtained from all landowners prior to data collection.

Field methods

Within each site, two 100 m long transects were established, from the southwest (SW) and northwest (NW) facing edges towards the interior, at a distance of at least 50 m from plot corners. The two transect directions were chosen to account for any major differences with respect to aspect, as edge effects are predicted to be greater on the southern edge of a fragment and less on the northern edge. Due to typical field, and thus forest, orientation in the Montérégie, these directions were modified to SW and NW (compass bearings) such that transects were oriented perpendicular to the forest edge in the majority of cases. Five 10×10 m plots were established along each transect at distances of 0 m, 10 m, 20 m, 40 m, and 90 m from the forest edge to account for the presence of any edge to interior gradients in forest fragments. Due to irregularity in the shape of some small fragments that caused total fragment diameter to be less than 200 m, the 5th plot was omitted in 5 of the 48 transects (i.e., transects were prevented from crossing the midpoint of a fragment).

Within each plot, all live woody plants (trees and large shrubs, hereafter “trees”), and standing dead wood (snags) ≥ 1 cm diameter at breast height (DBH, measured at 1.3 m) and ≥ 1.5 m tall were surveyed, as well as all fine and coarse downed woody debris (DWD) ≥ 1 cm in diameter. All live trees were identified to species. DBH was recorded for all adult trees (≥ 9 cm DBH), as well as the DBH class of all saplings (trees < 9 cm

DBH, following Quebec MRNF size classes of 1–3, 3–5, 5–7, 7–9 cm DBH; Boudreau and Philibert 2011). Species ID, where possible, and DBH was also recorded for all snags following the same protocol as live trees. DWD was surveyed following Hooper et al. (2001), using a modified version of the Van Wagner (1968) method (Bruederle and Stearns 1985). A 10-m sample line was established in a random compass direction within each plot, and the diameter at the point of intersection and decay class (modified from USDA recommendations; Harmon et al. 2008; Appendix A: *Downed woody debris (DWD)*) of each piece of DWD ≥ 1 cm diameter was recorded.

All transects were assigned a management status of either “managed” or “unmanaged” based on field observations. While a baseline level of management is ubiquitous in this region composed predominantly of secondary forest, some sites were notably more intensively managed than others, most often for maple syrup production. Sites were considered “managed” where there was considerable evidence of the following: substantial removal of woody debris and/or saplings and/or undergrowth (i.e., piles of cleared branches, several small stumps, stacked firewood), and/or; maple tapping activity (i.e., tap-lines or spigots in trees, an active sugar shack).

Biodiversity indices

Two indices of woody plant biodiversity were calculated for each transect: Species Richness, and Functional Diversity. Species Richness (SR) is the total number of species present within a transect. Functional diversity was calculated at the transect level, following the methods of Paquette and Messier (2011). Functional traits for each tree species were assembled from the literature where available, including: maximum height, growth rate, leaf size, leaf longevity, leaf mass per area, leaf nitrogen content, wood density and decay resistance, vegetative reproduction, seed mass, pollination vector, shade, drought and water-logging tolerance and mycorrhizal infection type (see Supplement). Functional diversity was calculated using functional dispersion (FDis, Laliberté and Legendre 2010), using R’s “FD” package (Laliberté and Shipley 2011). Functional dispersion is a distance based

metric, calculating the average distance of each species to the centroid of all species in the functional trait space, weighted by relative abundances. It is independent of species richness. We calculated FDis indices based on all (weighted) available traits, as well as a set of FDis indices built on reduced groups of traits based on a priori knowledge, adapted from the methods of Paquette and Messier (2011). These indices were constructed from combinations of seed mass, wood density, maximum height, vegetative reproduction, and growth rate, as well as leaf mass per area (LMA) and leaf nitrogen content—traits known to be important for biomass production. We then used 10-fold cross validation, using R (R Development Core Team, version 2.15) to choose the most appropriate FDis index to use in our general linear models (see *Analysis* below), based on the model with the lowest average mean square error.

Aboveground carbon stocks

Aboveground carbon (AGC) stocks (Mg/ha), including AGC stored in live trees, snags, and DWD, were calculated for all transects by summing the values for the plots along each transect, and dividing by the total sampled area, in ha.

Allometric equations (Jenkins et al. 2003) were used to convert all DBH measurements and species identification data to aboveground biomass (Appendix A: *Live Trees*). Jenkins et al. (2003, 2004) have developed a set of generalized allometric regression equations for aboveground biomass prediction for 10 species groups, based on a compilation of 2640 equations from the literature. All species in the study region were sorted into the appropriate species group (Table 1, Appendix A), and the corresponding equation applied to determine aboveground, dry weight biomass. Carbon stocks were estimated at 50% of dry-weight biomass, as per the common practice in the literature.

All identifiable snags were treated as above. For each 10 × 10 m plot containing unidentifiable snags, it was assumed that community composition of live trees within the same 10 × 10 m plot was representative of snag community composition. Species-group allometric equations were used to calculate an average biomass for each snag based on the distribution of species groups

present in the live tree community. A biomass reduction factor of 0.8874 (modified from UNFCCC recommendations, UNFCCC 2010) was applied to all snags to adjust for biomass loss due to the loss of leaves and branches from snags over time (Appendix A: *Standing dead wood (snags)*). Carbon stocks were then estimated at 50% of this final, adjusted biomass.

Volume of DWD was calculated following Hooper et al. (2001). Biomass was calculated from volume using density values for fine woody debris (FWD, <10 cm diameter) and coarse woody debris (CWD, ≥10 cm diameter) within each decay class (modified from USDA recommendations, Harmon et al. 2008) to account for changes in wood density with decomposition of DWD (Appendix A: *Downed woody debris (DWD)*). Carbon stocks were then estimated at 50% of this final, adjusted biomass.

Analysis

As both managed and unmanaged transects can occur within a single forest fragment, and management was a factor of interest, all comparisons were performed at the transect level. This raises a potential issue of non-independence between sample points, due to nesting of transects within fragments. To account for this, we first used linear mixed effects modeling (using R's "lmer", in the lme4 package, with sites as a random effect; Bates et al. 2011). As the random effect of the model (Sites) was found to explain very little of the variance (variance < 0.001), and did not change the outcome of the analysis, general linear models were considered appropriate for this analysis, and used throughout to facilitate interpretation and communication of results. One transect was removed from the analysis due to an observed lack of mature trees in the field.

The normality of distribution for all AGC stocks and diversity indices was tested prior to analysis using diagnostic plots and the Shapiro-Wilks test. Log or square root transformations were performed as necessary in order to improve data normality. We used general linear models (R Development Core Team 2012) to test the relationships between AGC stocks, biodiversity (SR and FDis), and the size, connectivity, and management of forest fragments. We used ANOVA (using R's "car" package, Fox and

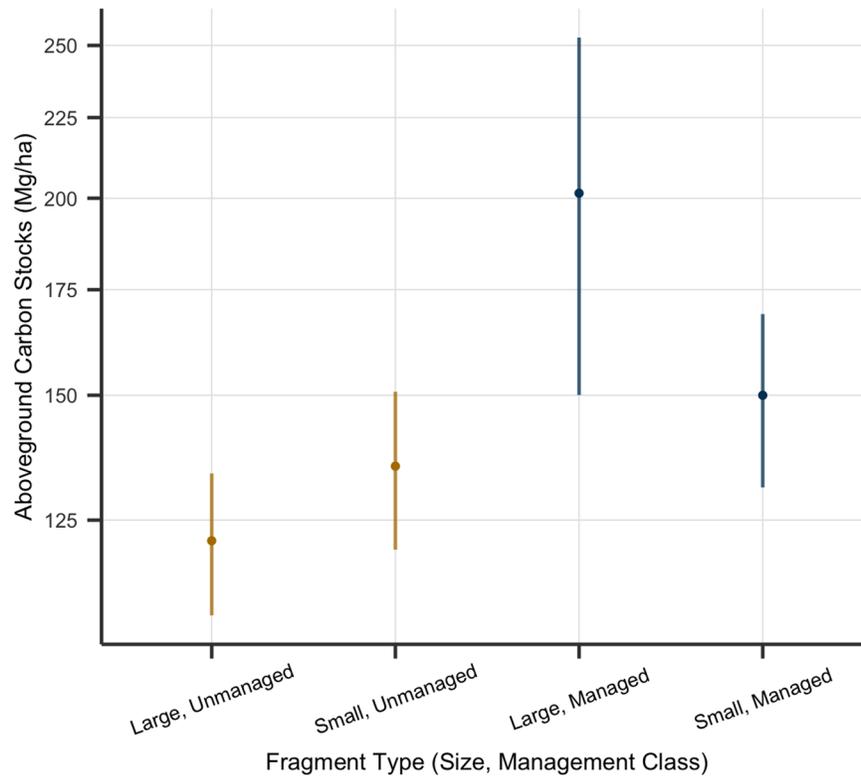


Fig. 2. Mean total aboveground carbon stocks for forest stands of two fragment sizes and management classes in Montérégie, QC. Unmanaged stands are represented in orange, and managed in blue. Bars represent 95% confidence intervals.

Weisberg 2011) to test the effects of forest fragment size, connectivity, and management on live, dead, and total AGC stocks, as well as on both SR and FDis. Post-hoc comparisons were conducted for significant interactions using Tukey HSD test. For each biodiversity index, we then used ANCOVA to test the effects of size, connectivity, and forest management on the relationship between AGC stocks and biodiversity.

RESULTS

Aboveground carbon stocks

Total AGC stocks of the forest transects ranged from 82.07 to 269.81 Mg/ha (average 140 Mg/ha). There was a significant effect of management ($F_{1,39} = 15.2$, $p < 0.001$) on $\log(\text{total AGC})$, as well as a significant management \times fragment size interaction ($F_{1,39} = 5.2$, $p < 0.05$), with the highest AGC stocks occurring in large, managed fragments (Fig. 2). AGC stocks in live wood closely

mirrored these overall patterns. Carbon held in all dead wood pools also followed a similar pattern to overall AGC stocks, with a significant effect of fragment size, i.e., greater C in large fragments, on $\log(\text{DWD Carbon})$ ($F_{1,39} = 10.7$, $p < 0.01$), $\sqrt{\text{Snag Carbon}}$ ($F_{1,39} = 4.6$, $p < 0.05$), and $\sqrt{\text{Total Dead Wood Carbon}}$ ($F_{1,39} = 9.5$, $p < 0.01$). While the total amount of carbon held in dead wood was not significantly different in managed vs. unmanaged forest fragments, the percentage of the overall AGC pool composed of dead wood was significantly higher in unmanaged fragments ($16.2\% \pm 1.6\%$ [mean \pm SE] vs $8.8\% \pm 1.3\%$, $F_{1,39} = 6.4$, $p < 0.05$).

Biodiversity

A total of 52 species of trees/large shrubs were identified across the forest fragments we sampled (Table 1, Appendix A). The number of species present within a single transect ranged from 7 to 19 (14 ± 0.47). While connectivity alone

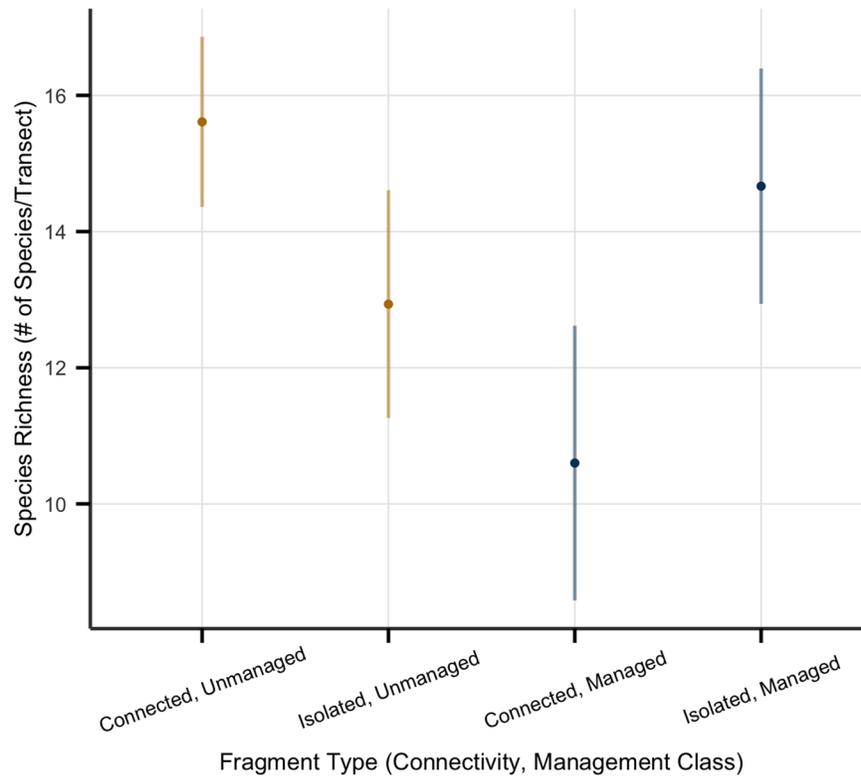


Fig. 3. Mean species richness for forest stands of two fragment connectivity levels and management classes in Montérégie, QC. Unmanaged stands are represented in orange, and managed in blue. Bars represent 95% confidence intervals.

did not significantly alter species richness, there was a significant management \times connectivity interaction ($F_{1,39} = 10.4$, $p < 0.01$), with unmanaged connected fragments exhibiting on average 2.7 species more than unmanaged isolated fragments ($p < 0.05$, Tukey's hsd), and 5 species more than managed connected fragments ($p < 0.01$, Tukey's hsd) (Fig. 3). There was no significant effect of fragment size on species richness.

The best functional diversity index tested included maximum height, growth rate, and vegetative reproduction ability—traits which relate to stand structural diversity and dominance, growth rate, and reproductive strategy, common in the BEF literature (Ackerly and Cornwell 2007, Chave et al. 2009, Lei et al. 2009, Paquette and Messier 2011)—as well as LMA, and leaf nitrogen content, which are both traits with notable effects on ecosystem processes (Diaz et al. 2004). There was no significant effect

of connectivity on functional diversity, but a significant effect of fragment size ($F_{1,39} = 5.9$, $p < 0.05$), driven by large, managed fragments: large fragments had lower levels of FDis overall than small fragments, with large, managed fragments exhibiting the lowest FDis (FDis = 0.111 ± 0.012 , 23% lower than the average FDis of 0.143 ± 0.0042) (Fig. 4).

Compositionally, the FDis gradient is driven not by any major differences in the presence or absence of specific species, but rather by which species occur together in high abundances. In sites with low FDis, the majority of the individuals are comprised of a few species, and these abundant species are quite functionally similar to one another. In sites with high FDis the majority of the individuals are divided among a greater number of species, with the fraction of individuals divided more evenly among values of the key functional traits (i.e., abundant species tend to be functionally different from one another)

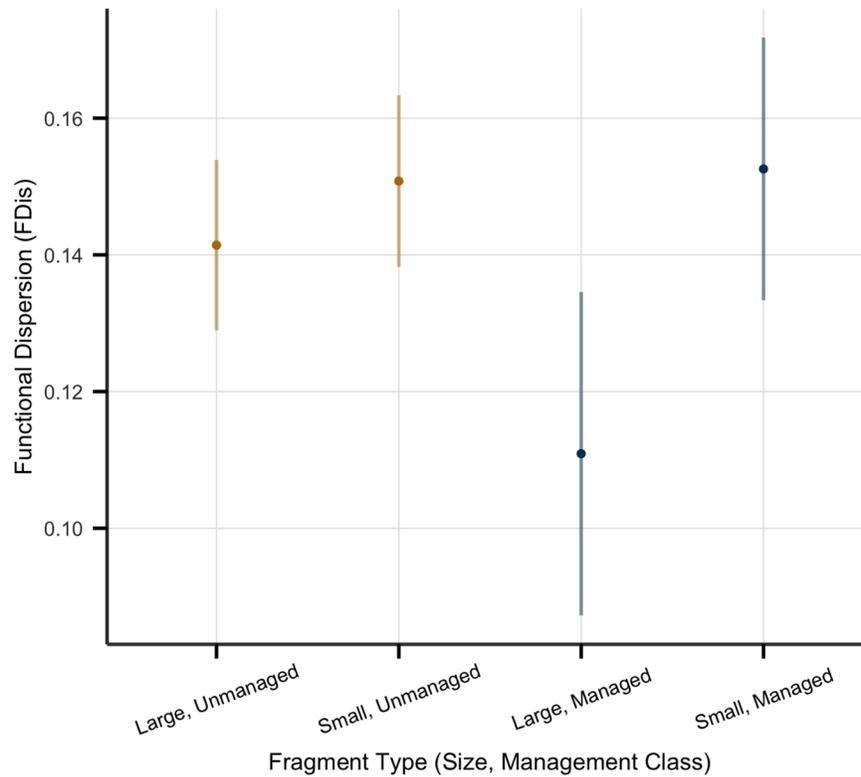


Fig. 4. Mean functional dispersion for forest stands of two size and management classes in Montérégie, QC. Unmanaged stands are represented in orange, managed stands are represented in blue. Bars represent 95% confidence intervals.

(Appendix: Fig. A2). Compositional differences between sites are most extreme at low values of FDis, where managed sites are comprised primarily of very tall, slow growing species (Appendix: Fig. A2C, D), and unmanaged sites with similarly low FDis are comprised primarily of shorter, rapidly growing species (Appendix: Fig. A2A, B).

Relationship between diversity and aboveground carbon stocks

Functional diversity was a significant predictor of AGC stocks, interacting significantly with management (FDis \times management interaction, $F_{1,39} = 43.64$, $p < 0.001$), and with connectivity (FDis \times connectivity interaction, $F_{1,39} = 4.72$, $p < 0.05$). The significant FDis \times connectivity interaction is driven by unmanaged fragments; the slope of the FDis-C relationship is significantly greater in unmanaged connected fragments compared to unmanaged isolated fragments

($F_{1,39} = 5.48$, $p < 0.05$). There is a significant positive relationship between FDis and $\log(\text{Total AGC})$ in unmanaged fragments, with an $\sim 8.9\%$ increase in C for each 0.01 unit increase in FDis (equivalent to $\sim 7\%$ of the total range of FDis across the study system) in unmanaged, connected fragments, and an $\sim 3.4\%$ increase in C for each 0.01 unit increase in FDis in isolated fragments. Managed fragments exhibited a significant negative relationship of similar magnitude, with an $\sim 5.0\%$ decrease in C for each 0.01 unit increase in FDis, with no significant difference between connected and isolated fragments (Figs. 5, 6). Fragment size did not significantly influence the relationship between functional diversity and carbon stocks. The relationship between species richness and $\log(\text{Total AGC})$ was not significant, nor were there any significant interactions between SR and other variables (connectivity, size, or management).

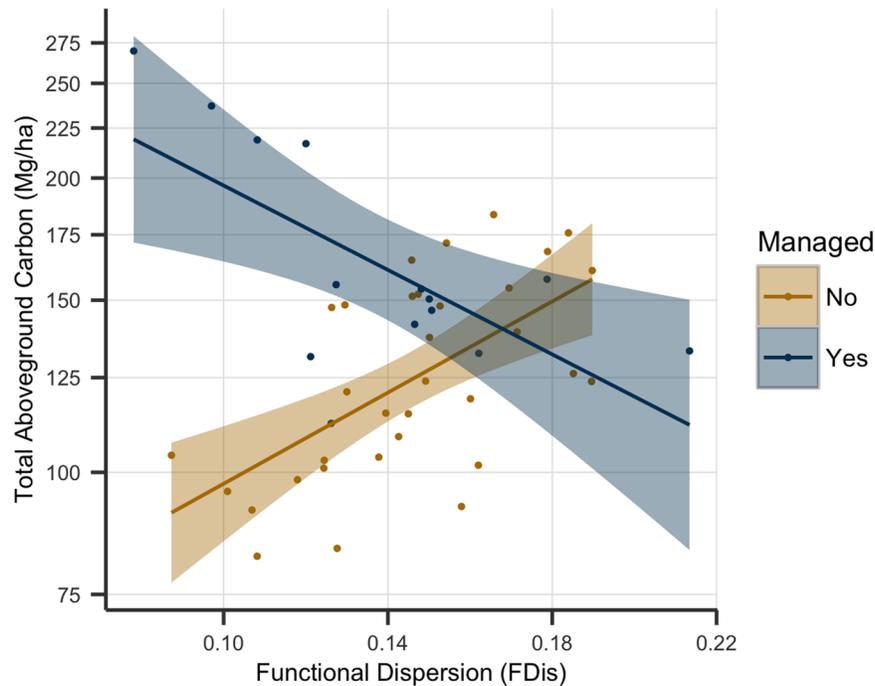


Fig. 5. Total aboveground carbon stocks as a function of functional diversity in managed and unmanaged forest stands in Montérégie, QC. Error bands represent 95% confidence intervals. In unmanaged forest stands, there is a significant positive relationship, whereas in managed forest stands, the relationship is significantly negative.

DISCUSSION

We found that connectivity and management can mediate the strength and sign of the relationship between functional diversity and aboveground carbon stocks in small forest fragments. Our results in unmanaged forest stands support the results of two decades of BEF research. The positive relationship we find between diversity and aboveground carbon stocks supports the positive relationship commonly found between diversity and biomass in experimental work (Balvanera et al. 2006, Cardinale et al. 2007, 2011), as well as in recent in situ forestry studies (Vilà et al. 2007, Lei et al. 2009, Paquette and Messier 2011, Gamfeldt et al. 2013). This synergistic relationship suggests that biodiversity conservation can lead to increased quantities of C stored at the landscape scale.

Additionally, the stronger relationship between FDis and C in unmanaged connected versus isolated fragments suggests that increasing the structural connectivity of forests across a

landscape may strengthen the synergy between biodiversity and C. We know that increased connectivity can have positive effects on regulating services such as pollination and pest control (Mitchell et al. 2013); our results suggest that connectivity can also be important for aboveground C stocks. Thus, conservation efforts focused on restoring ecological connectivity with ecosystem networks (Gonzalez et al. 2011), may benefit both functional biodiversity and ecosystem services linked to carbon storage, like climate change mitigation.

However, contrary to many BEF experiments, we find that species richness is not a strong predictor of function. Rather, functional dispersion, a metric of functional diversity, showed a strong relationship with C, albeit one for which the sign is dependent on the management context. Land use change has been shown to reduce functional diversity, and consequently ecosystem functions and services, beyond simple changes in species richness (Flynn et al. 2009), and recent work in forested systems supports

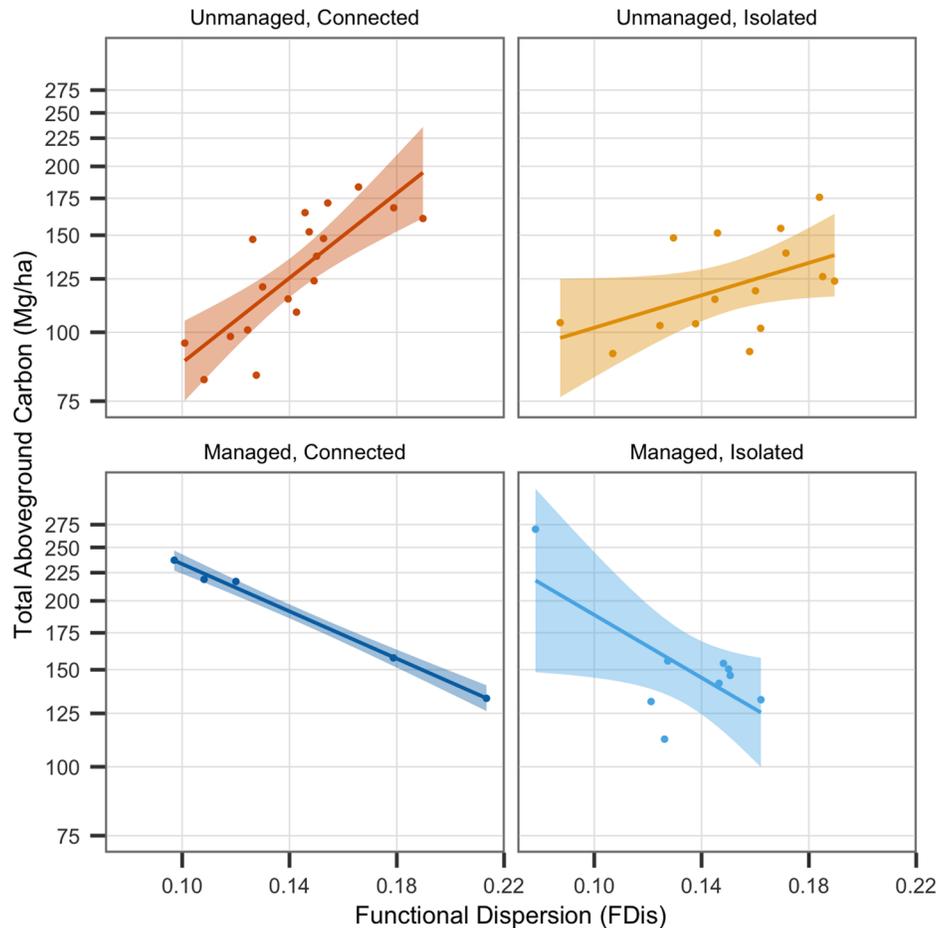


Fig. 6. Total aboveground carbon (AGC) stocks as a function of functional diversity in managed and unmanaged forest stands of two fragment connectivity levels in Montérégie, QC. Error bands represent 95% confidence intervals. In unmanaged forest fragments, there is a significantly greater positive relationship between AGC and functional diversity for connected than isolated fragments. In managed forest fragments, there is no significant difference between connected and isolated fragments.

this conclusion, with differences in tree functional traits often found to be more important for ecosystem function and provision of services than species richness alone (Balvanera et al. 2005, Bunker 2005, Kirby and Potvin 2007, Paquette and Messier 2011).

The relationship with FDis was qualitatively similar across a range of trait sets, however, our best model included an FDis based on maximum height, growth rate, and vegetative reproduction ability—traits that relate to stand structural diversity and dominance, growth rate, and reproductive strategy—as well as leaf mass per area, and leaf nitrogen content. While similar

species are present across the FDis gradient, sites at the higher end of the gradient tend to contain more even abundances of species that are functionally different, leading to a more even distribution of trait values within each trait. For example, the majority of individuals in a low diversity site may all be tall, fast growing trees (e.g., a mixture of *Fraxinus pennsylvanica* and *Acer rubrum*), or all tall, slow growing trees (e.g., a mixture of *Acer saccharum* and *Fagus grandifolia*), whereas the most abundant individuals in a high diversity site might be comprised of relatively equally abundant tall, fast growing trees, and small, slow to moderate growing trees (e.g., a

mixture of *Acer rubrum*, *Carpinus caroliniana*, and *Corylus cornuta*).

The context dependent nature of the FDis-C relationship in our system means that at low FDis levels, we see substantially different functional results at the same absolute level of FDis. That is, we see both synergies, and tradeoffs between diversity and carbon stocks in the same system. In comparing stand types with the greatest discrepancy in C stocks—unmanaged, connected stands and managed, connected stands at the lower end of the FDis gradient—we find that managed, connected stands are comprised predominantly of slow growing, very tall trees (maximum height of 30–35 m; Appendix: Fig. A2D), compared to much faster growing, shorter trees (maximum height 20–25 m) in unmanaged, connected stands (Appendix: Fig. A2B).

This mix of managed and unmanaged forest stands within the study area is one of the unique dimensions of our study. This mix exists because of the high degree of fragmentation in the landscape and very high fraction of forest fragments that are privately owned. While our unmanaged forests generated a positive relationship between C and FDis, this result was reversed in the presence of substantial human intervention. Our findings diverge from previous work showing temperate forest management to be detrimental to C stocks (Nunery and Keeton 2010, Powers et al. 2011), with managed stands storing more C on average than unmanaged in our system, and the greatest C stocks in the system occurring in managed stands of low functional diversity. This discrepancy may be due to a difference in the definition of management: typical forestry studies call periodic harvesting of considerable portions of biomass “management”, whereas here, management consists not of commercial harvesting, but of small-scale maple syrup production or low intensity wood removal (i.e., for firewood/personal use). Accordingly, in our system large, high wood density trees (and the C they store) are often purposely maintained within the stand, rather than removed. A comparable study is that of Kirby and Potvin (2007), where low intensity management in Panamanian forests was found to yield comparable C stocks to protected forests in the same region.

The negative carbon-biodiversity relationship we find in managed stands seems to be driven by forest stands in larger fragments (Appendix: Fig. A1), which are composed primarily of slow growing, very tall tree species—often manifest as high density, sugar maple dominated stands. Known colloquially as “sugar bushes,” such stands are common throughout the Montérégie and are managed for maple syrup production. Whether these stands are a result of years of managing for productivity, for example thinning of non-maple species, or whether historically, high productivity stands were retained during initial landscape fragmentation is unclear. Likely, some combination of both retention of productive stands and forest management through time has resulted in the patterns that we see today. Regardless of the historical context, management introduces a tradeoff in our present-day system. C stocks in managed stands are greater on average than those in unmanaged stands, but this often comes at the expense of functional biodiversity.

Interestingly, at the highest FDis levels found in our system, aboveground C stocks are approximately equal between forest stands, regardless of management class (Fig. 5). Thus, the tradeoff we see between C and biodiversity in managed stands only occurs at low levels of FDis; it is only when managed stands are reduced to relatively low levels of FDis that we achieve C stocks above the levels that we see in high diversity unmanaged stands. We hypothesize that this is related to differences in management goals. Our characterization of management as a binary variable is a simplification of reality. While the sites at the high end of the management gradient (low FDis, high C) are likely a result of fairly intensive management for sugar bushes, sites at the opposite end of the gradient (high FDis-low C) may be managed primarily for timber, and/or smaller-scale maple-tapping. The removal of a few valuable, often high wood density (i.e., high C) trees would explain the reduced C stocks in these stands, while a reduction of non-maple thinning explains the maintenance of high FDis even in the presence of management.

While connectivity strengthens the synergies we see in unmanaged forest stands, no such relationship was observed in managed stands.

However, due to the small sample size of this class of fragments in our study, it is difficult to say with certainty the role that connectivity plays in managed fragments; whether tradeoffs are altered due to connectivity is an interesting avenue for further research. Further research would also benefit from a more comprehensive scope with respect to the role of management and fragmentation in shaping forest C dynamics. While here we address total aboveground C stocks, this is only one piece of the puzzle in regards to climate regulation. Inclusion of belowground pools such as C stored in roots and soil could reveal additional relationships, as might an investigation of the rates of C emissions and sequestration, a temporal approach that is beyond the scope of the present work.

Despite its limitation to the aboveground carbon pool, the substantial differences in C stocks between forest fragments of different types within our study corroborates the view that forest C accounting based on spatial averaging or additive methods is likely to lead to inaccuracies in landscape-level C accounting (Houghton 2005). Despite largely similar ecoforestry traits, forest fragments in our study are not equal with respect to aboveground C stocks, with the differences mediated by functional diversity, forest management, and structural connectivity. These findings demonstrate that it is important to take forest heterogeneity into account when developing C budgets or creating management plans. Not all forest fragments are created equal with respect to the amount of C they store, and loss (or protection) of one fragment is not necessarily equivalent to loss of another. By failing to take into account forest functional diversity and fragmentation patterns, we risk substantial over or under-estimation of C stocks. With respect to conservation, the types of fragments that are prioritized should depend on the goal of the management strategy. If managing for high C stocks is the highest priority, protecting larger, managed stands of sugar maple may be an important goal. However, managing primarily for high C stands can result in tradeoffs with biodiversity. In our region, managing for connectivity may lead to a “win-win” scenario, whereby although the very highest levels of C are compromised, landscapes still achieve relatively high levels of carbon

sequestration, while also maintaining high functional diversity.

The landscape of the Montérégie is typical of many peri-urban, agricultural areas in North America, containing a high number of small forest fragments that is likely to increase as fragmentation becomes more prevalent with development. The ecological importance of small fragments is often questioned. Yet, here we find that small fragments perform on par with their larger counterparts in terms of C stored per unit area, with unmanaged fragments of only 10ha typically exhibiting equal or higher C/ha than 100ha fragments. In managed systems, the C-biodiversity tradeoff is driven by higher amounts of stored C in larger fragments. However, the smaller fragments are more likely to cluster at the “win-win” section of the graph, where high C meets high biodiversity (Appendix: Fig. A1). Indeed, since these fragments are being managed for a product other than C (i.e., maple syrup, firewood, recreation), these small fragments can be considered conservation “triple-wins”; and this is without considering any positive effects on wildlife, surrounding cropland, etc. If we consider the number of small fragments across the landscape, combined with the significant contributions that these fragments make to regional biodiversity and service provision, it is clear that they have an important role to play in conservation efforts.

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SUPPLEMENTAL MATERIAL

APPENDIX A

CARBON CALCULATION METHODS

Live trees

Each of the 52 species found in the study area was assigned to one of eight species groups from

Jenkins et al. (2003; see Table A1). Species in this study not present in the Jenkins et al. (2003) database were sorted first by genus, and then family. Six shrub species unrepresented at the family classification (*Corylus cornuta*, *Hamamelis*

Table A1. Each of the 52 species found in the study area as assigned to one of eight species groups from Jenkins et al. (2003), for which a generalized allometric regression equation has been developed.

Aspen/alder/ cottonwood/ willow	Soft maple/ birch	Mixed hardwood	Hard maple/ oak/ hickory/beech	Cedar/ larch	True fir/ hemlock	Pine	Spruce
<i>Populus balsamifera</i>	<i>Acer negundo</i>	<i>Fraxinus americana</i>	<i>Acer saccharum</i>	<i>Thuja occidentalis</i>	<i>Abies balsamea</i>	<i>Pinus banksiana</i>	<i>Picea glauca</i>
<i>Populus deltoids</i>	<i>Acer rubrum</i>	<i>Fraxinus nigra</i>	<i>Carya cordiformis</i>		<i>Tsuga canadensis</i>	<i>Pinus resinosa</i>	
<i>Populus grandidentata</i>	<i>Acer saccharinum</i>	<i>Fraxinus pennsylvanica</i>	<i>Carya ovata</i>			<i>Pinus strobus</i>	
<i>Populus tremuloides</i>	<i>Acer spicatum</i>	<i>Juglans cinerea</i>	<i>Fagus grandifolia</i>				
<i>Salix spp</i>	<i>Betula alleghaniensis</i>	<i>Malus domestica</i>	<i>Ostrya virginiana</i>				
<i>Alnus incana</i>	<i>Betula papyrifera</i>	<i>Prunus pennsylvanica</i>	<i>Prunus serotina</i>				
	<i>Betula populifolia</i>	<i>Prunus virginiana</i>	<i>Quercus macrocarpa</i>				
		<i>Tilia americana</i>	<i>Quercus rubra</i>				
		<i>Ulmus americana</i>					
		<i>Rhus typhina</i> ‡					
		<i>Cornus alternifolia</i> †					
		<i>Cornus sericea</i> †					
		<i>Ilex verticillata</i> †					
		<i>Sorbus decora</i> †					
		<i>Corylus cornuta</i> §					
		<i>Hamamelis virginiana</i> §					
		<i>Rhamnus cathartica</i> §					
		<i>Rhamnus frangula</i> §					
		<i>Viburnum lantanoides</i> §					
		<i>Viburnum lentago</i> §					

Note: Species in this study not present in the Jenkins et al. (2003) database were sorted first by genus, and then family. Six species not present at the family level were classified as mixed hardwoods.

† Genus used.

‡ Family used.

§ Family not in Jenkins et al. (2003) database.

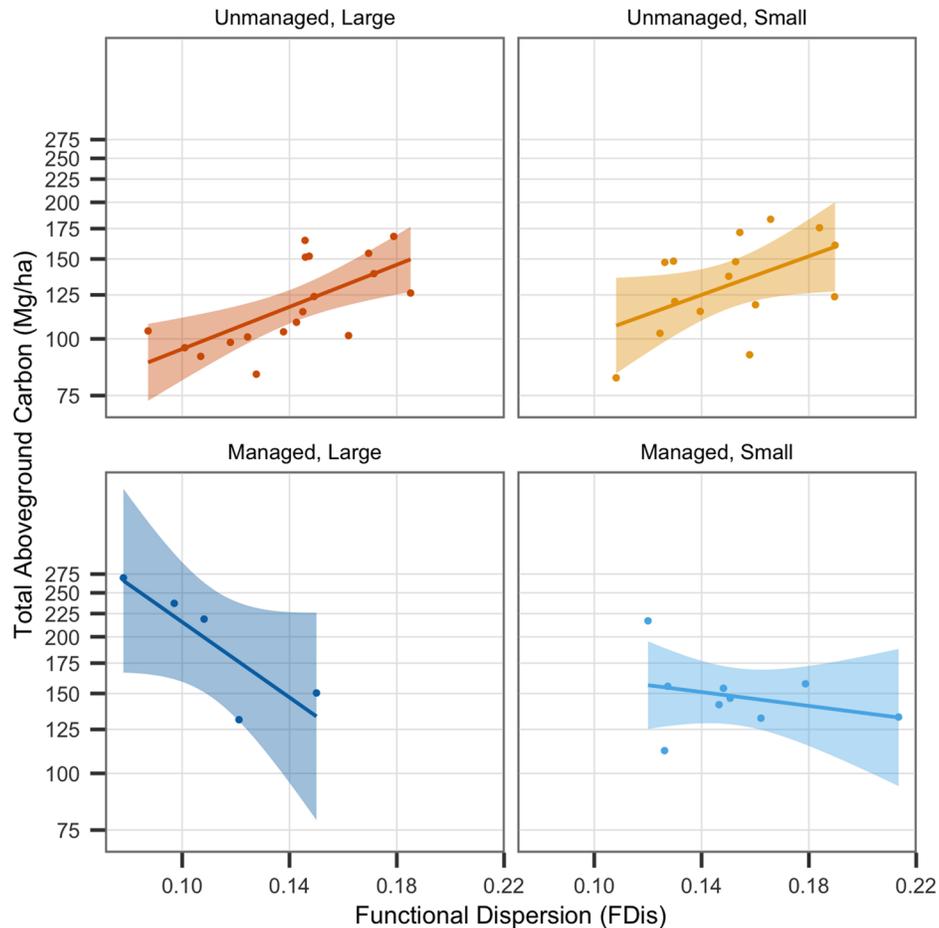


Fig. A1. Total aboveground carbon (AGC) stocks as a function of functional diversity in managed and unmanaged forest stands of two fragment sizes in Montérégie, QC. Error bands represent 95% confidence intervals. While size does not significantly change the relationship between FDis and carbon stocks, the negative relationship in unmanaged fragments seems to be driven primarily by large forest fragments, rather than small.

virginiana, *Rhamnus cathartica*, *Rhamnus frangula*, *Viburnum lantanoides* and *Viburnum lentago*) were classified as mixed hardwoods.

Generalized allometric equations (created from a database of 2640 equations compiled from the literature for tree species found in North America [Jenkins et al. 2003, 2004]) specific to each species group were then used to calculate the aboveground, dry-weight, biomass (kg) of all sampled trees using DBH measurements. For saplings, the median value of the DBH class was used (i.e., 2, 4, 6, or 8 cm DBH). Carbon was calculated as 50% dry weight biomass, as per the standard methodology in the literature.

Six of the 9254 live trees had DBHs greater

than the maximum DBH range for which the allometric equations were built, leading to possible over, or under-estimations of biomass in these cases, however more appropriate equations for the species and size of these trees could not be found in the literature.

Woody debris

Standing dead wood (snags).—All snags identifiable to species were treated by the same protocol as live trees, above. Not all snags were identified to species, due to loss of identifiable features such as leaves/bark as a result of decomposition. For each 10 × 10 m plot containing unidentified snags, it was assumed

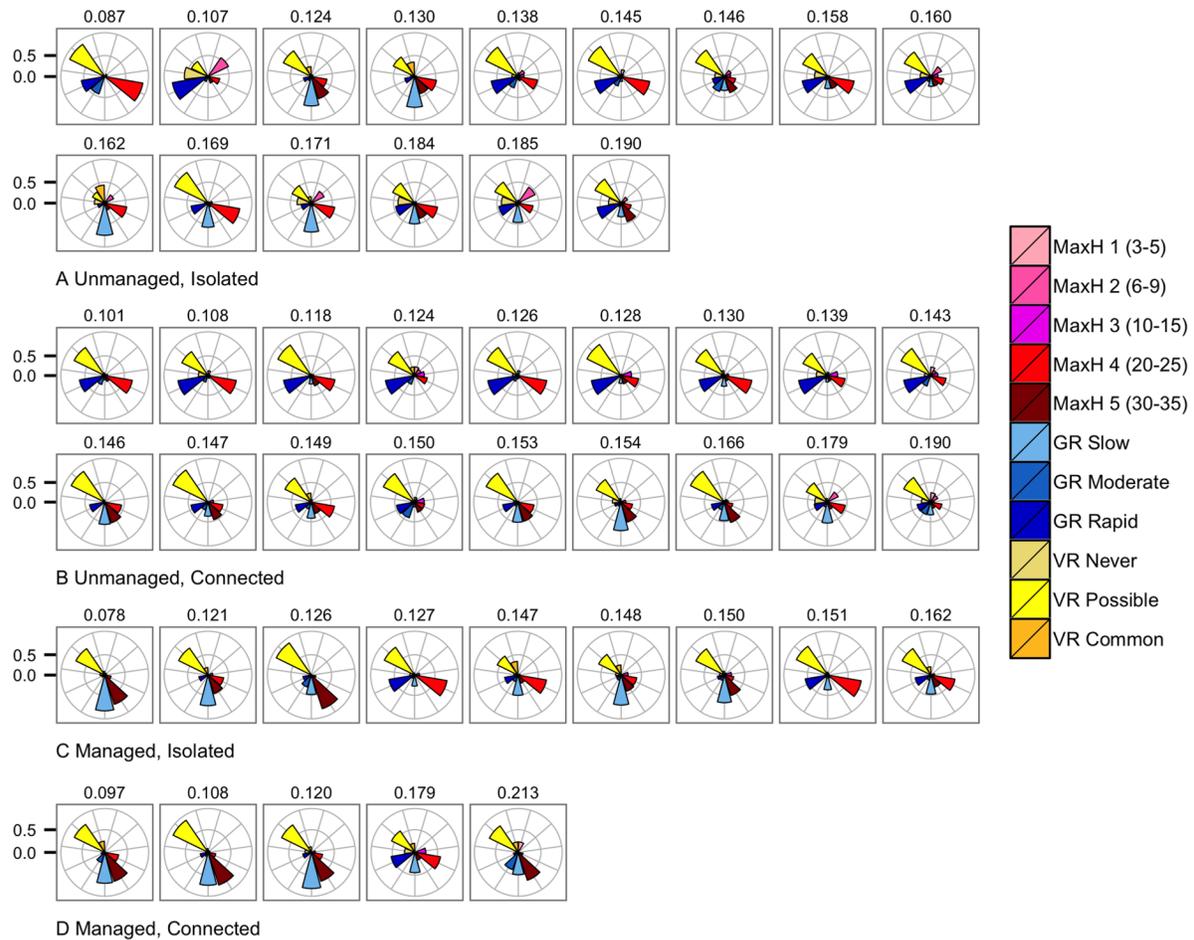


Fig. A2. Relative abundance (percentage of individuals) of trees displaying each trait value for three key functional traits. Each flower represents one forest stand (i.e., one transect). Each petal represents the relative abundance (percentage of individuals) displaying a given trait value. Pink/Red petals represent maximum height class (MaxH, in m), yellow petals represent frequency of vegetative reproduction (VR), and blue petals represent growth rate (GR). Sites are arranged from lowest functional dispersion (FDis) to highest within each site type (A–D), from left to right. The number above each flower is the FDis value for that site.

that community composition of dead trees was representative of the live tree community composition for the same 10×10 m plot. Biomass was calculated as follows for each snag: The snag was “replicated” once for each tree of each species group present in the same 10×10 m plot, and biomass calculated for each replicate-tree, using the snag’s DBH, and the appropriate species-group allometric equation. The average biomass was then taken from these replicate-trees, and served as the biomass of that particular snag.

As snags lose leaves and branches over time,

biomass reduction factors are used to adjust the biomass of snags for these lost components. The UNFCCC (2010) suggests a biomass reduction factor of either 0.975 or 0.8, depending on the magnitude of leaf and branch loss. As this was not quantified in the present study, an average of the two values (0.8875) was applied to all snags to adjust for lost biomass. Carbon stocks were then estimated at 50% of this final, adjusted biomass, as standard in the literature.

Downed woody debris (DWD)

Volume of downed woody debris was calcu-

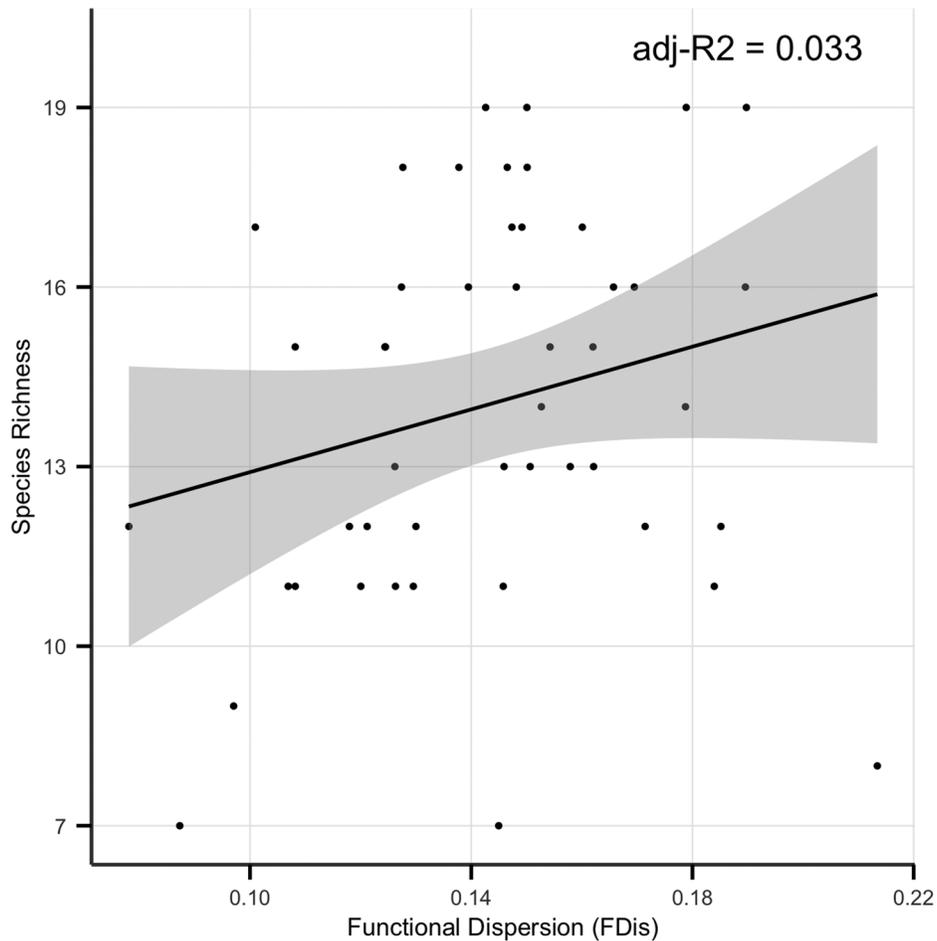


Fig. A3. Correlation between species richness and functional dispersion.

lated following Hooper et al. (2001), using the following formula,

$$V = (\pi \sum d/8L)(10000 \text{ m/ha})$$

where V is the volume of macro-litter in cubic meters per hectare, d is the diameter of litter at the point of intersection in meters, and L is the length of the sample line in meters (in our case, 10 m).

For the purposes of biomass estimation, DWD was split into two categories, fine woody debris (FWD, <10 cm diameter) and coarse woody debris (CWD, ≥ 10 cm diameter). Decay classes were assigned to aid in accounting for biomass loss due to decomposition, and were modified from USDA recommendations (Harmon et al.

2008).

Coarse woody debris (CWD).—Each piece of CWD was assigned to one of 2 decay classes. Decay class 1 combines the USDA decay classes 1 and 2, and decay class 2 combines USDA classes 3, 4 and 5. Qualitatively, CWD in decay class 1 show little evidence of decomposition, ranging from pieces retaining the majority of their leaves, to those exhibiting loss of leaves and small twigs/branches, with loosening bark. Logs in decay class 1 can always support their own weight. CWD in decay class 2 is what we would consider “rotten” in appearance, ranging from decomposition of the sapwood, but with heartwood intact, to highly decomposed pieces of CWD. Logs in decay class 2 are unable to support their own

weight along their length, and are often partially incorporated into the forest floor.

To convert the volume of CWD to mass, conversion factors were calculated from the USDA database of species-specific wood densities in each of their 5 decay classes. As it was not feasible to identify the vast majority of CWD to species, a single conversion factor was calculated for each of our two decay classes. To do this, an average wood density was calculated for each of the 5 USDA decay classes from the densities of all species present in the USDA database that were also present in our study system. We then used the average of the first two USDA decay classes for our decay class 1, and the average of USDA decay classes 3–5 for our decay class 2. The final wood density conversion factors for class 1 and 2 were 0.431 and 0.208 (g/cm³). Biomass for each decay class was calculated by multiplying CWD volume

by the appropriate conversion factor. Carbon stocks were then estimated at 50% biomass.

Fine woody debris (FWD).—Fine woody debris was treated similarly to coarse woody debris (see previous section). FWD was split into two size categories, 1–5 cm, and 5–10 cm, following USDA protocol. Two decay classes were used, “undecayed” and “decayed”, as recommended by the USDA. Conversion factors for each size and decay class were calculated as above (with the exception that there are only 2 USDA decay classes for FWD, rather than 5, and thus a second averaging step is unnecessary). The final wood density conversion factors for undecayed FWD were 0.56 (1–5 cm DBH) and 0.51 (5–10 cm DBH), and for decayed FWD 0.49 (1–5 cm DBH) and 0.48 (5–10 cm DBH) (all g/cm³). Biomass and carbon stocks were calculated as above.

SUPPLEMENT

Data and R code needed to conduct the analysis described in the main text, as well as detailed description of the functional trait data used for calculating functional diversity indices ([Ecological Archives C004-010-S1](#)).