

Title

A simple-to-use management approach to boost adaptive capacity of forests to global uncertainty

Authors

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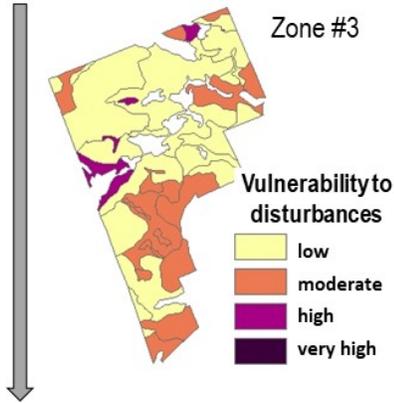
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Highlights

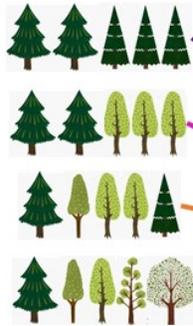
- High tree species richness does not always translate into functionally rich forests
- Assessing forest stand vulnerability to disturbances is a useful management guide
- Functionally enriching via natural regeneration or planting new species is proposed
- Foster regeneration of functionally rare species to enhance forest adaptive capacity
- Low-level planting of new species contributes to functional connectivity

Graphical abstract

Forest landscape:



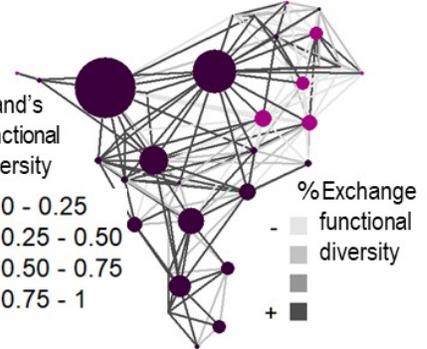
Tree species functional traits



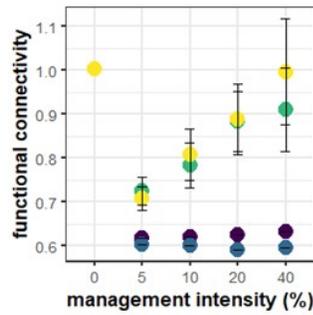
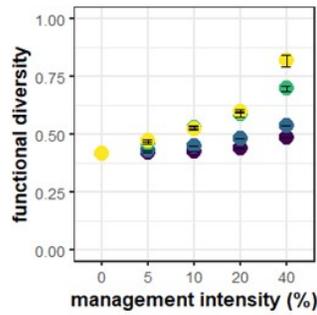
Stand's functional diversity

- 0 - 0.25
- 0.25 - 0.50
- 0.50 - 0.75
- 0.75 - 1

Functional network: forest stands are nodes



Indicators of forest adaptive capacity at the zone-level:



Management scenarios:

- harvest low
- harvest high
- harvest + plant low
- harvest + plant high

Abstract

Given the uncertainty of global environmental changes, forest managers need reliable and science-based tools to support planning decisions. To evaluate the state of forests as well as the outcomes of new management practices aimed at fostering the adaptive capacity of forest ecosystems, methods and metrics for practitioners should be self-explanatory, based on easily-available data, and straightforward to use. Here, we present and apply the functional network approach, a trait-based approach that scales-up from species functional traits to community-level functional diversity and from stands to landscape-level functional connectivity, to guide sustainable forest management when faced with global change. In the functional network approach, (1) tree and shrub species are clustered into functional groups based on selected functional traits, (2) forest stands become the nodes of the network, and (3) functional traits can be exchanged between nodes according to species dispersal capacity via functional connectivity. We complemented the functional network approach with an assessment of stand-level vulnerability to natural disturbances. This new approach was applied to a mixed temperate forest landscape in south-eastern Canada to test four management scenarios varying in intensity (5 - 40% of the landscape area) and silvicultural strategy, including planting tree species from rare functional groups or harvesting tree species from predominant functional groups. Managed stands were ranked according to functional diversity and vulnerability to disturbances, and species were considered for planting based on their contribution to functional diversity and level of vulnerability. We found that a species-rich forest may be a functionally poor ecosystem so its adaptive capacity and resilience may be strongly compromised in the face of high global uncertainty. In addition, both functional diversity and connectivity increased with more intense management, and when functionally rare species were planted. By adopting the functional network approach, forest practitioners have a new simple-to-use tool to evaluate landscape-level functional diversity, vulnerability, and functional connectivity. This tool can be used to inform both

plans for mitigating natural disturbances and strategies for enhancing overall ecosystem adaptive capacity to future environmental conditions and societal demands.

Key words

functional diversity, functional connectivity, vulnerability, forest management, network analysis, adaptive capacity

1. Introduction

Forest ecosystems and the associated biodiversity and services they provide are threatened by global environmental change (Gauthier et al., 2015; Miles et al., 2004; Parr et al., 2012). Novel combinations of environmental stressors never experienced before can undermine forest resilience, inducing undesired transitions to functionally poor states that offer fewer goods and services (Reyer et al., 2015; Trumbore et al., 2015). A warmer climate along with the intensification of natural disturbances like wildfires and insect outbreaks are leading to unprecedented biodiversity loss and the collapse of forest ecosystems worldwide (Boer et al., 2020; Cullingham et al., 2011; Martin et al., 2015; Seidl et al., 2017). New invasive exotic pests and diseases promoted by novel climate regimes and global trade are becoming increasingly problematic, directly threatening local plant biodiversity and ecosystem functioning (Gross et al., 2014; Lovett et al., 2016; Pureswaran et al., 2018). In addition, future societal demands on forests will not resemble the status quo. Interest in other forest products and services beyond timber are already changing markets and policies (Scarlat et al., 2015). The new global environmental and socio-economic conditions are, therefore, challenging the way we do forestry (Allen et al., 2011; Lawler et al., 2010),

and calling into question past and current silvicultural practices (Messier et al., 2019; Puettmann et al., 2009).

In view of an uncertain and changing climatic, environmental, and socio-economic future, managing forests as if they are deterministic and homogeneous ecosystems uninfluenced by social demands and natural stressors will likely fail in assuring long-term provisioning of goods and services (Messier et al., 2015). To counteract the challenges posed by global change, sustainable forest management should maximize resistance and adaptive capacity to guarantee ecosystem resilience to environmental disturbances (Allen et al., 2011; Millar et al., 2007; Oliver et al., 2015). Functional trait-based approaches have already been proposed to guide forest management practices focused on ecosystem services and functions (Cadotte, 2011), especially when considering abiotic and biotic disturbances (Tomimatsu et al., 2013), and to foster the adaptive capacity of forest ecosystems (Bussotti et al., 2015).

Functional effect traits predict ecosystem processes and functioning (e.g. stability, productivity, and nutrient balancing) while functional response traits explain how communities respond to and recover from disturbances and environmental change (Petchey and Gaston, 2006; Thomson et al., 2011; Violle et al., 2007). Functional trait-based approaches scale-up species effect and response traits to predict community- and ecosystem-level dynamics as well as responses to environmental change (Suding et al., 2008). Functional diversity measures trait diversity within a community or ecosystem, and when explicitly considering response traits, it accounts for a variety of community-level responses to environmental changes (Hillebrand and Matthiessen, 2009). A forest ecosystem with a high diversity of functional responses is considered more resilient, as it has a higher capacity to recover following disturbances and can better adapt to novel environmental conditions (Mori et al., 2013). Another important feature contributing to the maintenance of ecological functions in forest landscapes faced with

global uncertainty is functional connectivity (Noss, 2001). In the context of forest management, functional connectivity is defined as the potential for seed dispersal of species and traits among forest stands and/or patches that accounts for the exchange of organic and genetic material, contributing to the distribution of functional traits across the landscape (Craven et al., 2016). Higher functional connectivity should translate into greater forest adaptive capacity. Higher dispersal rates of genetic material among and between adjacent stands will likely increase functional response diversity of communities, thereby improving the ability of the ecosystem to self-organize, recover from disturbances, and adapt to new environmental conditions (Millar et al., 2007; Mori et al., 2013).

Although functional trait-based approaches can guide sustainable forest management, to operationalize interventions that enhance such functional features, forest managers need quantitative tools, metrics, and benchmarks to functionally characterize tree communities. Indeed, they require methods for selecting silvicultural practices that promote certain functional outcomes, such as identifying which tree species to plant and in what proportion (Laughlin, 2014). In this context, the *functional network approach* has recently been proposed to guide forest management in view of uncertain future environmental and socio-economic changes as well as novel disturbance regimes (Aquilué et al., 2020). The functional network approach is based on (1) tree species functional traits as a way of characterizing forest functional diversity at multiple spatial scales (i.e. at the stand-, patch-, and landscape-level), and (2) network theory to account for the spatial distribution of functional diversity and the dispersal of traits across the landscape.

In the functional network approach, a forest landscape is represented as a network of heterogeneous but adjacent elements, where forest stands are treated as nodes in the network. Species dispersal capacity is used to designate links between nodes. A source node is connected to a sink node only if at least one species at the source node is within the dispersal range of the sink node. Relative

dispersal capacity within forest stands and between adjacent stands will influence the dispersal of species and, therefore, functional traits. After having characterized tree community functional diversity, metrics of network theory are applied to evaluate landscape-level functional connectivity (Saura et al., 2011). Through an analysis of these indicators, one can evaluate the landscape-scale impacts of common silvicultural practices (e.g. tree-planting, shelterwood cutting, thinning) and natural disturbances (Aquilué et al., 2020). We illustrate how to apply the functional network approach using the Haliburton Forest, a private forest in south-eastern Ontario, Canada, as a case study. We first cluster common tree and shrub species into functional groups based on both response and effect traits. Second, we characterize stand- and landscape-scale functional diversity, compute stand-level vulnerability to multiple natural disturbances, and evaluate various forest management scenarios differing in intensity (i.e. amount of area targeted) and strategy followed. Finally, we propose practical recommendations for adapting current forest management strategies to challenges associated with global drivers of environmental change in our study landscape, provide guidelines for applying the functional network approach in other forested regions, and discuss the application of such methods by forest managers.

2. Methods

2.1. Study area

The Haliburton Forest is a privately-owned forest in south-eastern Ontario that covers more than 34,000 hectares of temperate mixed woodlands and encompasses eight disconnected forest zones (Fig. 1). Forest management and ownership is divided into these eight zones, ranging from 62 to 27,600 ha and consisting of different levels of species richness (Table S1). The forest comprises a total of 36 tree species (11 coniferous and 25 deciduous), dominated by *Acer saccharum* (35% of canopy cover occupancy), *Tsuga canadensis* (14%), *Betula alleghaniensis* (11%), *Acer rubrum* (9%), *Fagus*

grandifolia (5%), *Picea* species (5%), *Abies balsamea* (4%), and *Populus* species (3.5%). The eight forest zones are divided into 4,538 forest stands greater than one hectare in size, with 94% of them smaller than 20 hectares. Species composition is primarily mixed, and nearly all forest stands (93%) contain between three and seven species.

The Haliburton Forest & Wildlife Reserve is a multi-use private stewardship company with the dual objectives of providing sustainably sourced forestry products as well as recreational services. Although sustainable forestry is carried out throughout the area, Zone 1 is the core area of the Haliburton Forest where most of the recreational activities (summer and winter hiking trails, fishing, dog sled tours) are concentrated and where the two sawmills they operate are located. The forestry division designs and implements silvicultural strategies, logging operations, and infrastructure development for the Haliburton Forest and neighbouring woodlots. Management strategies to influence tree species composition include shelterwood (~30% of the area) and clearcutting with seed trees (~5% of the area). Experimental or supplemental plantings are uncommon (<1% of the area) and, in a few situations, single tree selection harvesting is used to decrease the presence of shade-intolerant species (such as poplars).

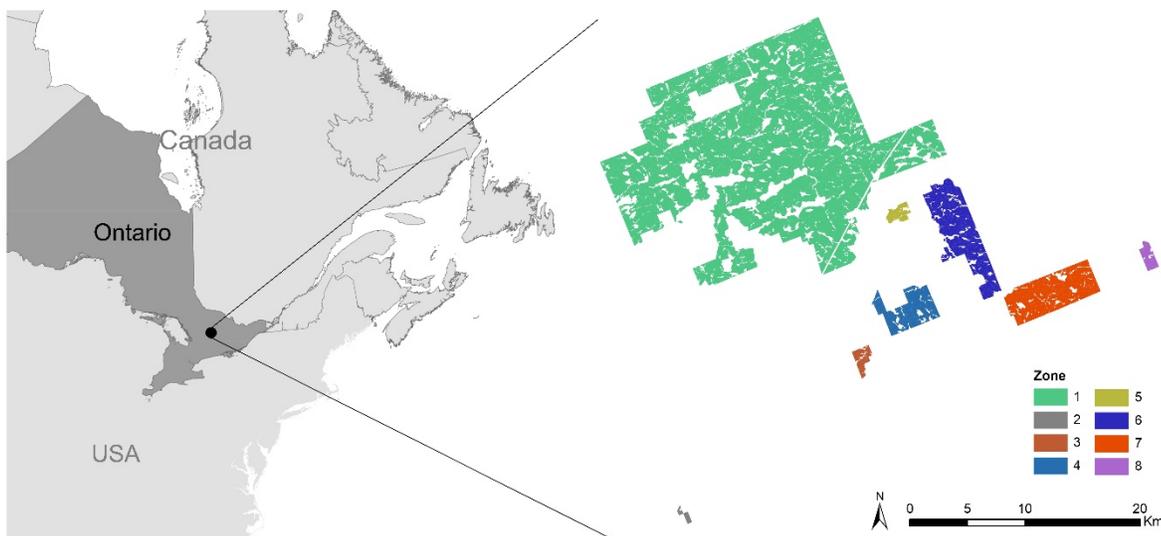


Figure 1: Geographic location of the Haliburton Forest in Ontario, Canada (left panel) and the eight forest zones in the Haliburton Forest (right panel).

2.2. Functional groups

In addition to the 36 tree species currently present in the Haliburton Forest, we included 44 other tree and shrub species found in biogeographical regions surrounding the study area (e.g. the Mixedwood Plains ecozone in Canada and Northern Lakes and Forests ecoregion in the United States). We did so to cover a larger array of traits and functions from species that could potentially grow in the study area, thus obtaining a larger representation of each functional group. Eight functional traits were selected to characterize each species: drought tolerance, shade tolerance, waterlogging tolerance, main seed dispersal vector, seed mass, wood density, leaf mass area, and taxonomic division (Table S2). Of these eight traits, drought, shade and waterlogging tolerance account for species susceptibility to environmental conditions (Niinemets and Valladares, 2006) while the other five relate to the capacity and mechanisms of species to respond to natural disturbances. To classify the species into functional groups, we first used a generalization of the Gower's distance metric to calculate a functional dissimilarity matrix (*ade4* R-package; Pavoine et al., 2009), and then we conducted an agglomerative clustering on this matrix to aggregate functionally similar tree species into functional groups (*cluster* R-package). The optimal number of clusters was determined by analyzing different measures of cluster validation (see details in Fig. S1 and Fig. S2).

The 80 tree and shrub species were divided into seven functional groups. All the groups were represented by some of the 36 species currently present in the landscape (Table 1). The two most abundant functional groups (groups 1 and 2) were shade-tolerant, drought- and flood-intolerant

deciduous species, mainly represented by *Acer saccharum* and *Acer rubrum*, and shade-tolerant, drought-intolerant conifer species, mainly represented by *Tsuga canadensis*, *Abies balsamea* and *Picea* species (Fig. S3). Drought-tolerant, shade-intolerant conifer species, such as *Pinus* and *Larix* species, are not well represented in the Haliburton Forest (group 6), nor are drought-tolerant to mid-drought-tolerant deciduous species (groups 3 and 5). Short-lived, pioneer, shade-intolerant tree species are poorly represented (group 4). The functional group least represented includes species commonly found in urban areas such as parks, streets and avenues, and rarely found in natural environments (group 7). As such, this functional group was not considered in our analyses.

2.3. Functional diversity

As an indicator of functional diversity, we chose the exponent of the Shannon diversity index applied to the relative abundance of tree functional groups in each stand (Jost, 2006). It was calculated as follows: $fdiv_k = \exp(-\sum_{i=1}^n p_i \cdot \log(p_i))$ where n is the total number of functional groups present in stand k and p_i the relative abundance of functional group i within stand k . $fdiv_k$ ranged from 1 to n (the least and the most functionally diverse tree communities, respectively), but to facilitate its interpretation, we linearly rescaled it from $[1, n]$ to $[0, 1]$ (i.e. minimum to maximum functional diversity, respectively). To compute this indicator at zone- and landscape-levels, relative functional group abundance was weighted by stand size.

Table 1: Functional group classification for the 36 species present in the Haliburton Forest.

Functional group	Main common characteristics	Species	Relative abundance
1	Deciduous, shade tolerant, drought and flood intolerant, wind dispersed	<i>Acer freemanii</i> , <i>Acer nigrum</i> , <i>Acer platanoides</i> , <i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Betula alleghaniensis</i> , <i>Fraxinus americana</i> , <i>Fraxinus nigra</i> , <i>Ostrya virginiana</i> , <i>Tilia americana</i> , <i>Ulmus americana</i>	57.6%
2	Conifers, shade tolerant, drought and flood intolerant, wind dispersed	<i>Abies balsamea</i> , <i>Picea glauca</i> , <i>Picea mariana</i> , <i>Picea rubens</i> , <i>Pinus strobus</i> , <i>Thuja occidentalis</i> , <i>Tsuga canadensis</i>	29.3%
3	Deciduous, shade tolerant, mid-drought tolerant, flood intolerant, animal dispersed	<i>Fagus grandifolia</i> , <i>Prunus cerasus</i> , <i>Prunus serotina</i>	5.4%
4	Deciduous, shade intolerant, drought intolerant, wind dispersed	<i>Betula papyrifera</i> , <i>Populus balsamifera</i> , <i>Populus grandidentata</i> , <i>Populus tremuloides</i>	4.3%
5	Deciduous, mid-shade tolerant, drought tolerant, animal dispersed	<i>Carya ovata</i> , <i>Crataegus canadensis</i> , <i>Morus rubra</i> , <i>Quercus palustris</i> , <i>Quercus rubra</i>	2.9%
6	Conifers, shade intolerant to mid-shade tolerant, drought tolerant, wind dispersed	<i>Larix laricina</i> , <i>Larix leptolepis</i> , <i>Pinus banksiana</i> , <i>Pinus resinosa</i>	0.4%
7	Cultivated deciduous in urban areas	<i>Aesculus hippocastanum</i> , <i>Gymnocladus dioicus</i>	0.01%

2.4. Functional connectivity

We built a functional network of forest stands for each forest zone following Aquilué et al. (2020) (Fig. 2). In this network, nodes represent forest stands that are only connected if at least one species of the tree community in stand *A* can disperse to stand *B* according to species seed dispersal capacity (Table S2). The distance between pairs of stands was explicitly calculated as the minimum Euclidean distance between the margins of the stands (as opposed to using the distance between stands' centroids, which is

the usual estimation of the distance between two spatial entities). Node quantitative attributes include $fdiv_A$, while link strength was calculated as the percentage of functional diversity in A that can disperse to B : $p_{A \rightarrow B} = \log(m) \cdot \exp(-\sum_{i=1}^m q_i \cdot \log(q_i)) / (\log(n) \cdot fdiv_A)$, where n is the number of functional groups in A , m the number of functional groups in A that are able to disperse to B , and q_i the relative abundance of functional group i in stand k that can travel to B .

Functional connectivity at the landscape scale was quantified using the equivalent connectivity index weighted by the number of patches $ECn = \sqrt{PC_{num}} / num.patches$, where $PC_{num} = \sum_{i=1}^s \sum_{j=1}^s fdiv_i \cdot fdiv_j \cdot p_{i \rightarrow j}^*$, s is the number of nodes, $fdiv_i$ and $fdiv_j$ the functional diversity of node i and j , respectively, and $p_{i \rightarrow j}^*$ is the maximum product probability of dispersal between i and j (where a product probability of a path between node i and j is the product of the weights $p_{A \rightarrow B}$ of all links in that path) (Saura et al., 2011). The equivalent connectivity index measures the capacity of maintaining functional diversity at the landscape scale.

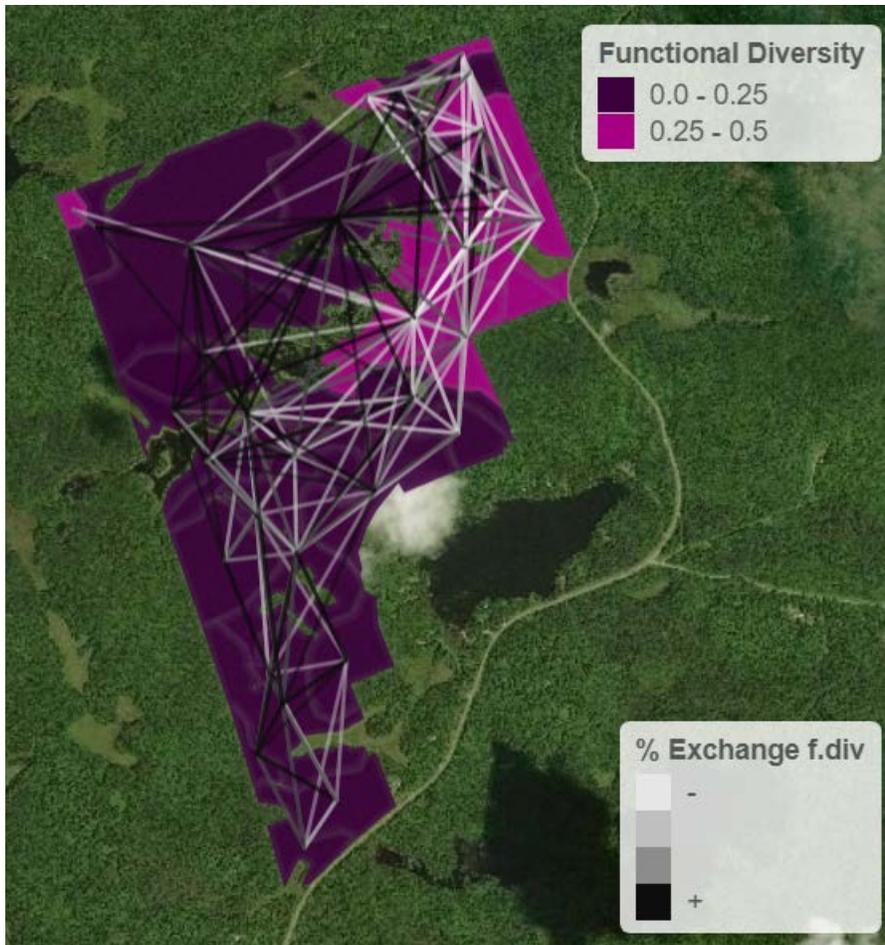


Figure 2: Forest stands of Zone 3 in the Haliburton Forest. Stands become the nodes of the functional network. Stand-level functional diversity is computed as the richness and evenness of functional groups present within each tree community. Lines linking nodes become darker with an increase in the proportion of functional diversity that can move from node to node.

2.5. Species vulnerability index

To list and order tree species according to their vulnerability to abiotic and biotic disturbances, we followed the scoring system described in Matthews et al. (2011) for the Climate Change Tree Atlas (Prasad et al., 2007), a large USDA project assessing tree species habitat suitability given climate

change projections. Scores account for the potential influence, ranging from -3 (strongly negative) to 3 (strongly positive), of each source of disturbance on species, including pathogens, insect pests, browsing, invasive plants, drought, flood, ice, wind, crown fires, temperature gradient, and air pollution (Table S3). Scores were not available for five species currently present in the study area, namely *Acer freemanii* (0.14% relative abundance over total relative abundance), *Acer platanoides* (0.02%), *Crataegus canadensis* (0.18%), *Larix leptolepis* (0.01%), and *Prunus cerasus* (0.01%). To these five species, we assigned the raw scores of taxonomically or functionally similar species (*Acer saccharinum*, *Acer saccharum*, *Prunus virginiana*, *Larix laricina*, and *Prunus americana*, respectively). Following Matthews et al., (2011), literature scores were modified using two multipliers accounting for uncertainty (i.e. the adequacy and consistency of information on each tree species) and future relevance of each disturbance type in the Haliburton Forest (Table S4). Future relevance multipliers were revised using local expert knowledge and environmental predictions (Thomas McCay, pers. Comm.). For each species, a vulnerability index was then calculated as the mean of the weighted scores, and rescaled from 0 (least vulnerable) to 10 (most vulnerable). Vulnerability classes were built on the 0.25 quantiles of the vulnerability index distribution (that is, species were classified as having low ($\leq 25\%$), moderate ($>25\% - \leq 50\%$), high ($>50\% - \leq 75\%$), or very high ($>75\%$) vulnerability to disturbances according to their position in the vulnerability index distribution). Vulnerability index at the stand-level resulted from weighting species vulnerability index by their relative abundance within the stand.

2.6. Forest management in the face of global change

We assumed that management plans aimed at increasing functional diversity would promote forest adaptive capacity to natural disturbances (Díaz and Cabido, 2001; Mori et al., 2013). Such management strategies involve reducing the abundance of species from well represented functional groups to promote

the regeneration of species from less represented groups, or to enrich forest stands with new species from less represented groups. We designed four simple management scenarios for the Haliburton Forest, combining harvesting and planting in digital maps, to modify the relative abundance of coexisting species and eventually add native species found in its bioregion (following Laughlin et al., (2017)). In this experiment, harvesting and planting instantly modified species abundance (i.e. temporal forest dynamics was not explicitly considered; see section 4.3 in the Discussion), and harvesting did not differentiate tree size or age. Table 2 details the management scenarios and their silvicultural strategies used to reach these objectives. Management scenarios HRV.LOW and HRV.HIGH implied only harvesting at low and high levels, respectively, while management scenarios PL.LOW and PL.HIGH implied low vs. high level harvesting and planting, respectively. For each of the four scenarios, we compared the effects of intervening on 5%, 10%, 20% and 40% of the area in each of the eight zones (from now on referred to as management intensity), representing an increasing intervention gradient at the landscape scale, from low to very high. In all scenarios, harvesting always targeted species from the two most abundant functional groups (e.g. groups 1 and 2). For the two scenarios that included planting, only one species with low or moderate vulnerability from less represented functional groups (e.g. groups 3 to 6) was randomly selected to be planted. The different scenarios compared were meant to represent approximately 30 years of forest management.

We ranked forest stands to prioritize management interventions. Such rankings were similar in all four scenarios. Rankings were based on the stand-level vulnerability index and the total number of functional groups present in the stand and in adjacent stands. Forest stands in need of intervention were those with the lowest number of functional groups and the greatest vulnerability index. We assumed that a functional group was sufficiently represented when its total relative abundance was $\geq 5\%$, below which its contribution to stand dynamic was assumed to be minimal. Thus, increasing their

representation within tree communities ensures long-term viability of as many functional groups as possible. Once a stand was selected for management in PL.LOW and PL.HIGH scenarios, we randomly removed half of the adjacent stands from those potentially requiring management. We did so to account for the fact that neighbouring stands are positively affected by new plantations in the targeted stand given the functional connectivity of the landscape, and to avoid concentrating all management efforts in the same area. This would promote local long-term functional diversity by the dispersion of species traits from rare functional groups to adjacent stands.

We replicated each management scenario 20 times and tested significant differences between scenarios ($p\text{-value} < 0.05$) with an analysis of covariance ANCOVA (*car* R-package; Fox and Weisberg, 2019), setting the management intensity as the continuous variable and the management strategy as the categorical variable. We also tested the significance of the interaction between management intensity and management strategy. Analyses were conducted with the programming software R v.3.6.2 (R Core Team, 2020).

Table 2: Management scenarios proposed for the Haliburton Forest.

Code	Silvicultural strategy	Description stand-level silvicultural strategy	Management intensity
HRV.LOW	Low-level harvesting of dominant functional groups	Harvest 25% basal area of the two most abundant functional groups to favour natural regeneration and growth of species from the least represented functional groups. Executed only in stands with current presence of the least represented functional groups. No planting.	5, 10, 20, 40
HRV.HIGH	High-level harvesting of dominant functional groups	Harvest same as for HRV.LOW but at 75% rate. No planting.	5, 10, 20, 40
PL.LOW	Low-level harvesting of dominant functional groups and planting less represented functional groups	Harvest the two most abundant functional groups to randomly retain 60% - 70% of their basal area. Patches to be managed are prioritized by functional diversity in increasing order (from low to high) and vulnerability in decreasing order (from very high to low). Trees are planted as much as harvested. For each least represented functional group, one low to moderate vulnerable species is planted in a random abundance of 5% - 20%, in such a way to increase the relative abundance of the two least represented functional groups. Not all least represented functional groups may be planted under this strategy.	5, 10, 20, 40
PL.HIGH	High-level harvesting of dominant functional groups and planting less represented functional groups	Harvesting and planting same as for PL.LOW but retaining 20% - 30% of the canopy cover of the two most abundant functional groups and tree species from the least represented functional groups are planted in a random abundance of 5% - 40%.	5, 10, 20, 40

3. Results

3.1. Functional diversity and connectivity

Mean functional diversity for the whole Haliburton Forest was 0.4 (1 being the maximum value for this indicator). The highest functional diversity was 0.41 and 0.42 in Zones 1 and 3, respectively, while it ranged between 0.30 and 0.35 in Zones 4, 5, and 6, and was lower than 0.30 in Zones 2, 7, and 8 (Fig. 3). Although functional diversity in Zone 3 was higher than in Zone 1, the most functionally diverse stands were found in Zone 1 (Fig. 3). Stands hosting species of a single functional group (i.e. functional diversity of 0), represented 50% of all stands in the Haliburton Forest. The percentage of stands with a

functional diversity score of 0 was lower than 50% in Zones 2 (29%), 3 (21%), 4 (41%) and 5 (47%). Zone 6 included the largest percentage (58%) of communities with species from only one functional group. The distribution of functional groups across the eight zones in the Haliburton Forest was fairly even (Fig. S3). Functional groups 1 to 4 were represented in the eight Zones, even if shade tolerant, mid-drought-tolerant deciduous species (functional group 3) were rarely represented in Zones 2, 7, and 8; and pioneer, shade-intolerant deciduous species (group 4) were rarely represented in Zones 5 and 6. Drought tolerant deciduous species dispersed by animals (species in group 5) were missing in Zones 2, 7, and 8 while drought tolerant conifers (species in group 6) were missing in Zones 3 and 5.

The most functionally connected zones in the Haliburton Forest were Zones 2, 3, and 8 ($ECn = 1.0$; Fig. 4). Moderate levels of functional connectivity were found also in Zones 7 ($ECn = 0.8$), 5 ($ECn = 0.7$; Fig. 4), and 4 ($ECn = 0.5$). Zone 6 was poorly connected ($ECn = 0.2$), as was Zone 1 ($ECn = 0.1$) which was the least functionally connected zone. We found that zone-level functional diversity did not explain functional connectivity (p -value: 0.249), but when excluding Zone 3 (it is both highly functionally connected and highly functionally diverse), functional connectivity was negatively correlated to zone-level functional diversity (p -value: 0.005).

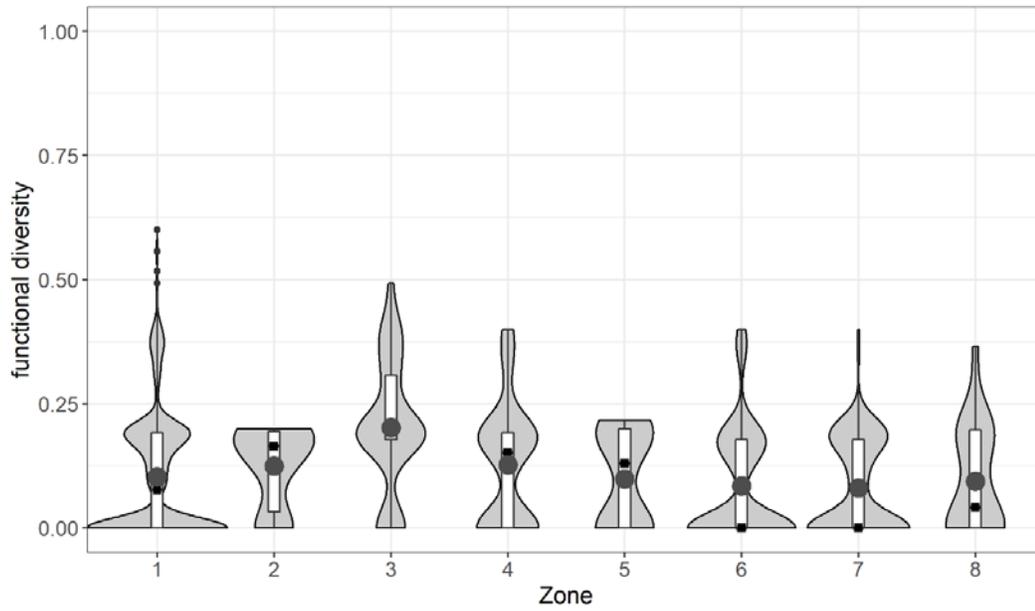


Figure 3: Distribution of stand-level functional diversity per forest Zone in the Haliburton Forest. The violin shows the kernel probability density of the distribution, the box the interquartile range, thick black line the median value, and large dark grey point the mean value.

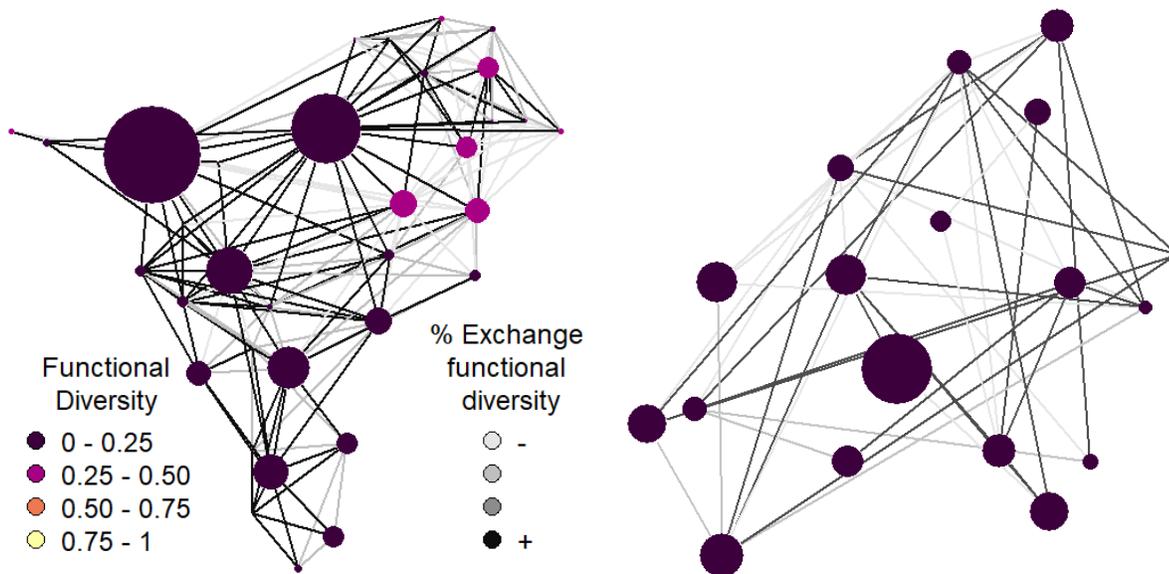


Figure 4: Functional network of Zones 3 (224 ha, 34 stands; left) and 5 (215 ha, 19 stands; right). Each node corresponds to a forest stand. Node size is proportional to stand area. Lines linking nodes become darker with an increase in the proportion of functional diversity that can move from node to node.

3.2. Vulnerability to disturbances

All shade-tolerant, drought-intolerant conifers in functional group 2 (e.g. *Abies balsamea*, *Picea glauca*, *Picea mariana*, *Picea rubens*, *Pinus strobus*, *Thuja occidentalis*, and *Tsuga canadensis*) were classified as either highly or very highly vulnerable (Table S5), as were the shade-tolerant, intermediately drought-tolerant deciduous species in group 3 (e.g. *Fagus grandifolia*, *Prunus cerasus*, and *Prunus serotina*). Yet, eight out of 11 species in the most abundant functional group (represented by late successional, drought-intolerant deciduous species) exhibit low to moderate vulnerability to disturbances (Table S5). In terms of relative abundance, these species accounted for 51.3% of the total canopy, whereas species exhibiting high to very highly vulnerability for accounted for 48.7%.

At the stand-level, 42.3% of stands were highly or very highly vulnerable to biotic and abiotic disturbances that will likely impact the region. In Zone 1 (representing 81% of the entire landscape) 12%, 44%, 23% and 21% of the stands exhibited low, moderate, high or very high vulnerability to natural disturbances, respectively (Fig. 5). In the remaining Zones, the percentage of stands classified as low or moderate vulnerability was between 64% and 85%, except in Zone 6, where up to 50% of the stands were highly or very highly vulnerable (Table S6).

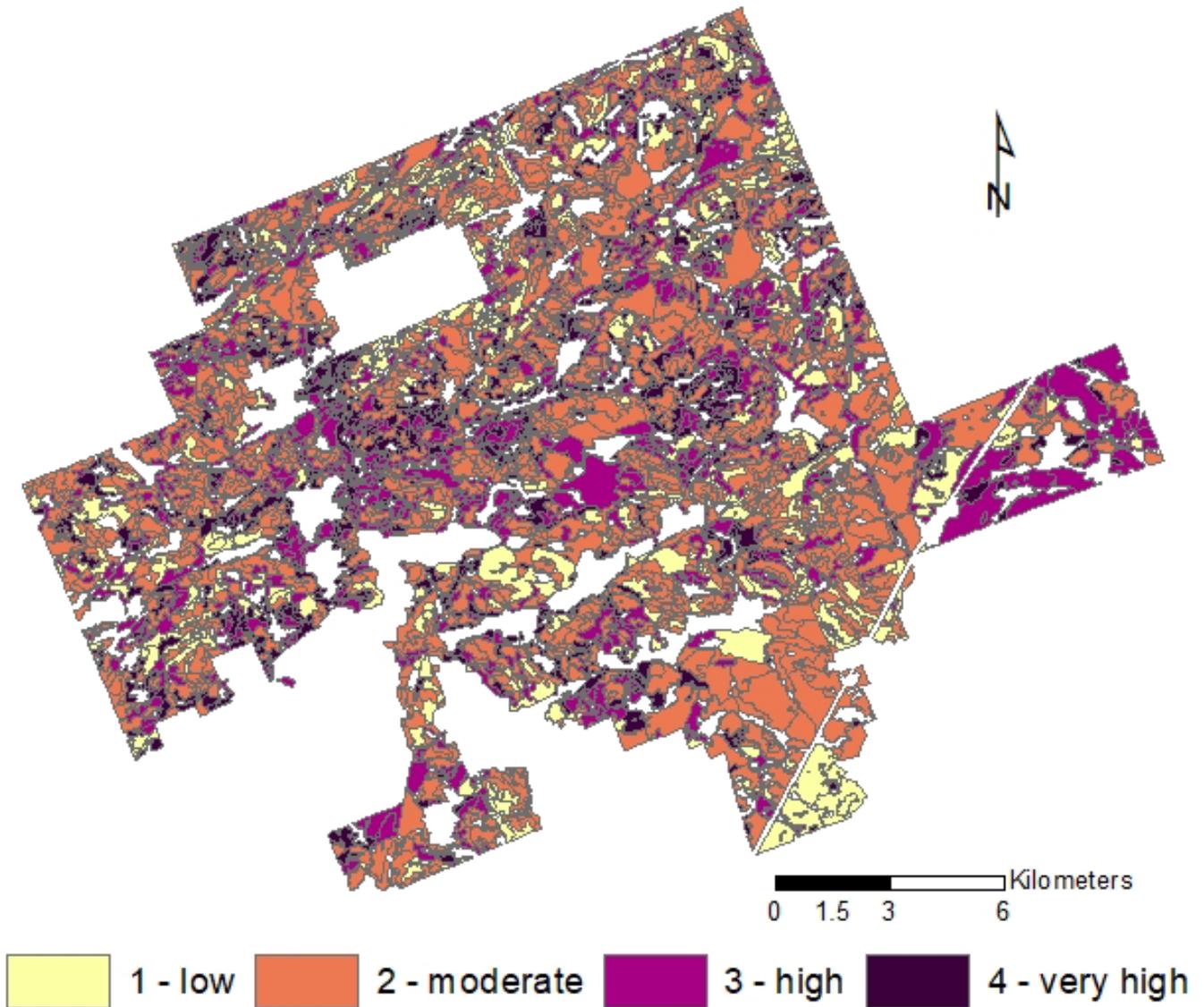


Figure 5: Stand-level vulnerability in the Haliburton Forest Zone 1 (27 699 ha, 3 628 forest stands).

3.3. Management strategies for forest resilience

In all Zones of the Haliburton Forest, both management intensity and the strategy of silvicultural practice significantly contributed to increasing functional diversity and functional connectivity, as did the interaction between the two variables (Table S6). Functional diversity increased proportionally with management intensity, with greater increases observed for harvesting-planting scenarios than for

harvesting-only scenarios (Fig. 6). In Zones 1 and 5 however, increases in zone-level functional diversity under high-level harvesting (HRV.HIGH) were comparable to those obtained under the low-level or high-level harvesting-planting scenarios (PL.LOW and PL.HIGH), depending on the management intensity (Fig. 6). In all Zones and at any management intensity, highly reducing species abundance of the two most abundant functional groups (HRV.HIGH) always induced greater increases in zone-level functional diversity than low-level harvesting strategies. Although PL.HIGH implied higher levels of harvesting and planting than PL.LOW, in Zones 1, 5, and 6 PL.LOW showed greater increases in functional diversity than PL.HIGH at any management intensity (Fig. 6).

Functional connectivity presented a more complex behaviour following management (Fig. 7). Overall, low-level harvesting and planting was the most beneficial silvicultural strategy to increase functional connectivity in most Zones for any management intensity. Yet, in Zones 7 and 8, PL.HIGH produced equal or greater connectivity than PL.LOW. Functional connectivity of all Zones, except Zones 5 and 6, was reduced when the dominant species were harvested and any new species were planted (Fig. 7). Indeed, in Zones 4 and 8, planting new species at a management intensity of 20% and in Zones 3 and 7 at a management intensity of 40% could rarely compensate for the loss of connectivity induced by harvesting.

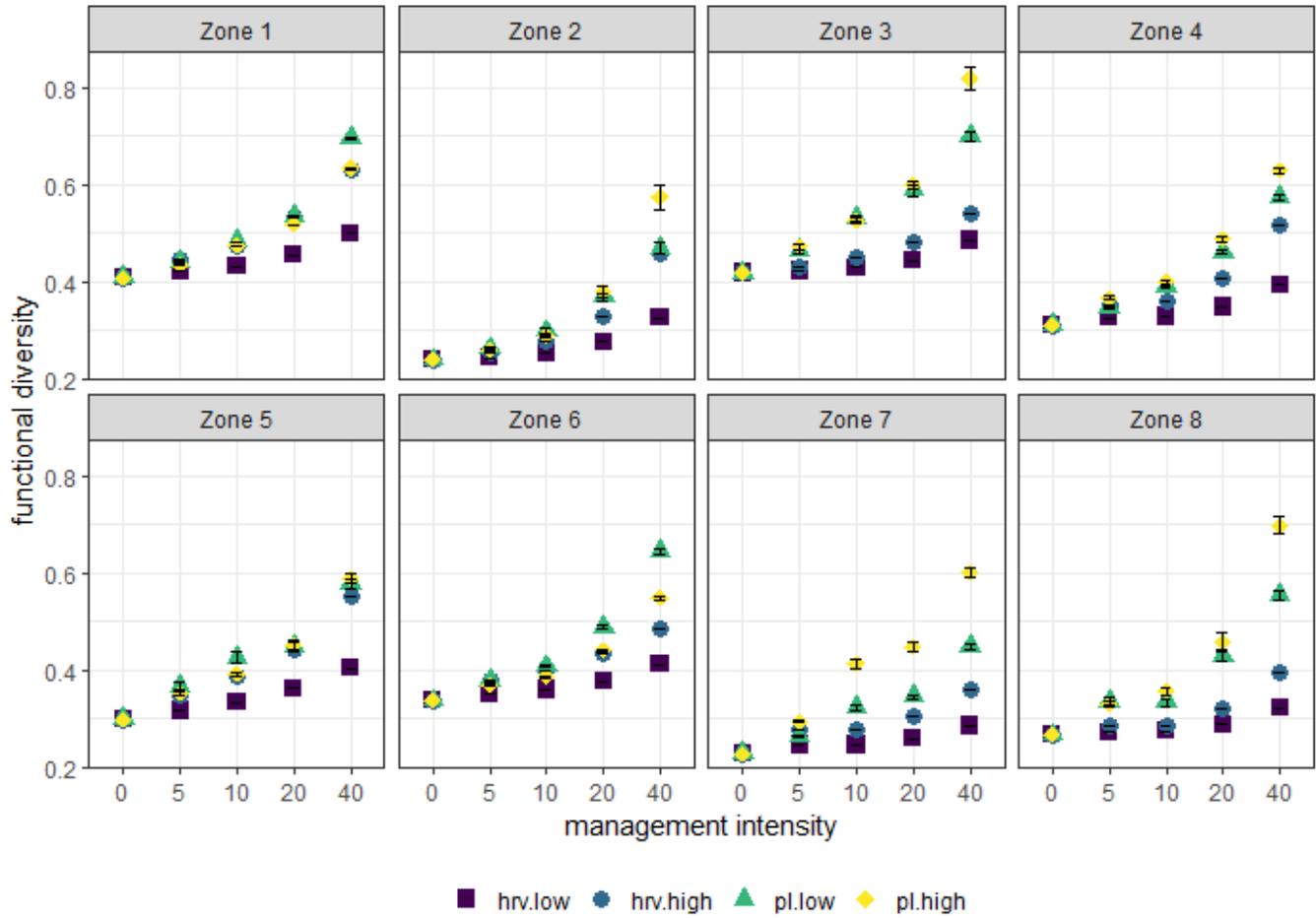


Figure 6: Changes in functional diversity from current (0%) to highest (40%) management intensity among the four management scenarios (Table 2) for each Zone. Black segments indicate the 95% CI.

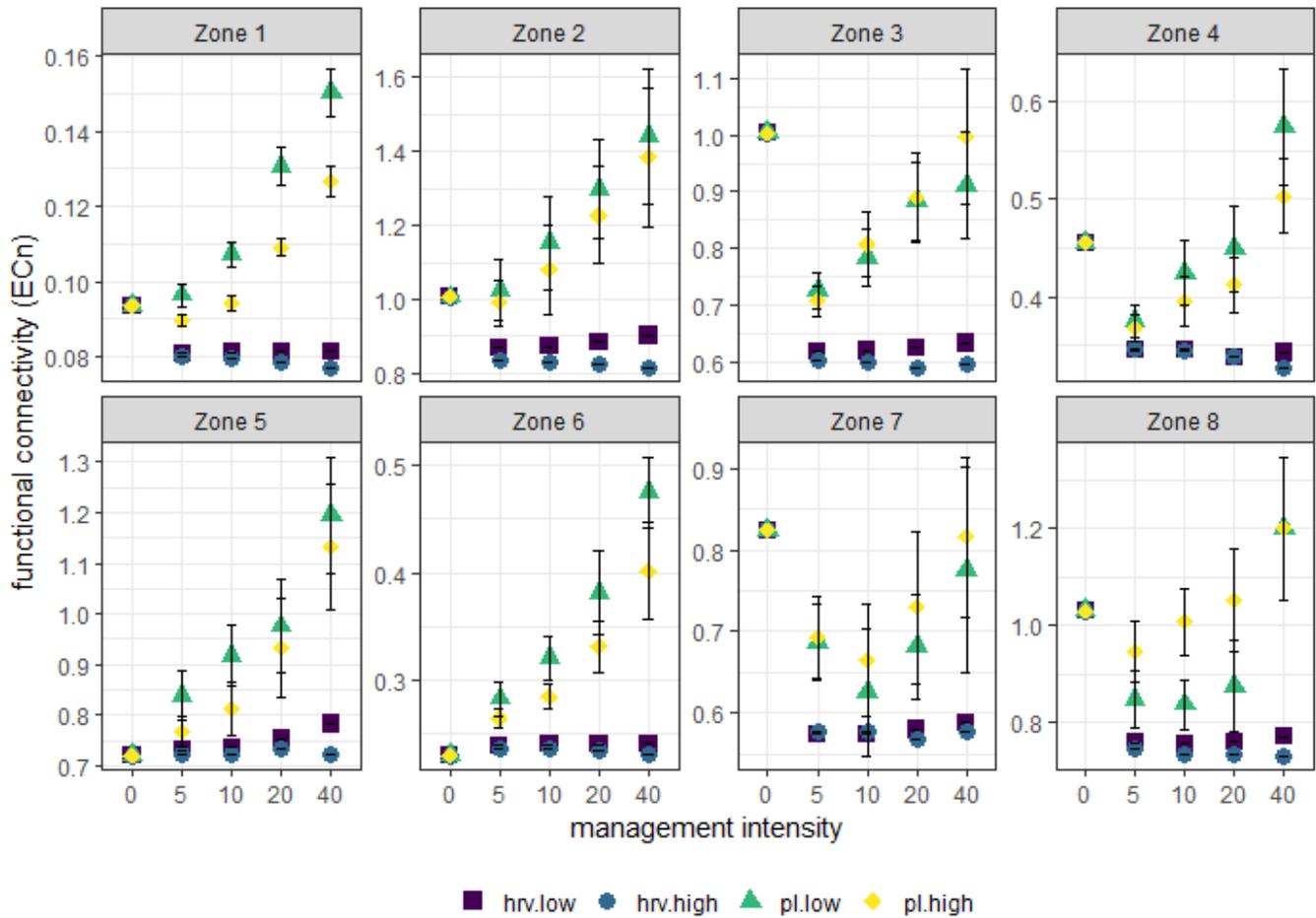


Figure 7: Changes in functional connectivity from current (0%) to highest (40%) management intensity among the four management scenarios (Table 2) for each Zone. Black segments indicate the 95% CI. Y-axis scale is customized for each Zone.

Overall, under the combination of harvesting and planting, stand-level vulnerability generally did not change and even decreased except for a small number of patches (Table 3). On average, under the PL.LOW strategy, vulnerability decreased in 5.2%, 7.5%, 18.1% and 23.7% of the patches under management intensity 5%, 10%, 20% and 40%, respectively, and increased in 0.6% and 8.5% of the patches under management intensity 5% and 40%, respectively. On average, under the PL.HIGH

strategy, vulnerability decreased between 3.9% and 19.0% of patches while it increased between 0.3% and 2.7% under 5% and 40% management intensity, respectively (Table 3). Stand-level vulnerability never changed in harvesting-only scenarios as only species' relative abundance varied within the stands, not species composition.

Table 3: Mean number of patches \pm standard deviation where vulnerability class changed following harvesting-planting management scenarios. The two harvesting-only scenarios are not displayed since they implied no changes in composition. Vulnerability classes are coded as 1 – low, 2 – moderate, 3 – high, and 4 – very high, with absolute differences among vulnerability levels reported here. A negative difference means that stand-level vulnerability decreased following management while a positive difference means that vulnerability increased.

Management scenario	Management intensity	Vulnerability class change					
		-3	-2	-1	0	1	2
PL.LOW	5%	20 \pm 3	120 \pm 4	88 \pm 5	4100 \pm 3	27 \pm 1	-
	10%	23 \pm 4	148 \pm 5	156 \pm 5	3932 \pm 6	96 \pm 4	1 \pm 0
	20%	48 \pm 6	408 \pm 6	334 \pm 6	3432 \pm 6	134 \pm 5	2 \pm 1
	40%	48 \pm 6	447 \pm 6	537 \pm 12	2955 \pm 7	360 \pm 3	8 \pm 2
PL.HIGH	5%	1 \pm 1	18 \pm 2	153 \pm 7	4172 \pm 6	12 \pm 2	1 \pm 0
	10%	1 \pm 0	19 \pm 2	246 \pm 5	4042 \pm 7	48 \pm 5	1 \pm 0
	20%	5 \pm 1	62 \pm 4	558 \pm 7	3677 \pm 10	53 \pm 4	1 \pm 0
	40%	4 \pm 1	60 \pm 3	764 \pm 7	3410 \pm 7	115 \pm 5	2 \pm 0

4. Discussion

4.1. Functional diversity, functional connectivity, and vulnerability to disturbances in the Haliburton Forest

In this paper, we show how a simple-to-use approach based on functional traits and species' vulnerability to natural disturbances can be adopted by forest managers (see below in section 4.2) to decide where and how to intervene to positively affect functional connectivity and diversity, both being good indicators of the overall adaptive capacity of forest landscapes to global uncertainty. Our results show that forested landscapes with stands composed of many tree species are not always functionally diverse (acknowledging that functional diversity strictly depends on the set of functional traits analyzed (Laughlin, 2014)). This aligns with findings from past studies showing that species richness does not always positively correlate with functional diversity (Cadotte et al., 2011). For example, Haliburton Forest is a considerably species-rich landscape for a northern temperate forest, comprised of 36 tree species overall, with most of the stands containing between three to seven species. However, only shade-tolerant, drought- and flood-intolerant conifer and deciduous species are well represented, making this landscape particularly sensitive to natural disturbances that are likely to impact the region in the near future (Bonsal et al., 2011; Lovett et al., 2016). Indeed, drought-tolerant conifers and deciduous species are mostly absent, as are early-successional species usually facilitated by stand-replacing disturbances (Table 1).

Our results reveal that well-targeted active forest management has the potential to positively influence both functional diversity and connectivity at the landscape-scale while reducing community vulnerability to disturbances. In the Haliburton Forest, functional diversity increased by managing species abundances and tree community composition, and as expected, the increase was proportional to the level of harvesting and planting (Fig. 6). Other studies have shown that planting less vulnerable tree

species in key locations while diversifying forest ecosystem functionality is a promising strategy to help forest ecosystems adapt to future climates and thus increase their overall resilience (Duveneck and Scheller, 2015; Hof et al., 2017; Laughlin et al., 2017). We further investigated how functional connectivity was affected by management. In most zones, it was negatively influenced by both low- and high-level harvesting although the low-level harvesting and planting strategy had a positive effect in five of the eight zones (Fig. 7).

In the study area, representative of temperate mixed forests in north-eastern North America and south-eastern Canada, more than 40% of the tree communities were categorized as highly or very highly vulnerable to a wide range of natural disturbances. This was mostly due to the elevated presence of drought-intolerant conifer species in group 2 and early-successional deciduous species (*Populus* spp. and *Betula papyrifera*) in group 4. All these species are strongly negatively affected by insect pests, invasive plants and drought (Table S3). Our vulnerability mapping is consistent with similar analyses developed for other regions in North America. For example, Coops and Waring (2011) found that 30% of the fifteen conifer species present in the Pacific northwest study region were vulnerable to future climate (i.e. the contraction in the potential distribution range). Across Canada, a recent assessment based on functional traits showed that 22 of the most abundant species were highly vulnerable to drought and likely inclined to migration failure, and that 49% of the current distribution of six eastern tree species was projected to fall outside their climatic hydric niche (Aubin et al., 2018). Tree species will likely be exposed to more frequent drought episodes in this century, which will lead to increased establishment failures caused by drought (Aubin et al., 2018; DeSoto et al., 2020).

Vulnerability to biotic and abiotic disturbances could be reduced by planting native species of neighbouring regions not currently present in the study area (e.g. assisted population migration or assisted range expansion *sensu* Pedlar et al., 2012). This strategy could minimize the risk of forest cover

loss, particularly from present or future insect outbreaks. In North America, there are, on average, 2.5 new non-native insects becoming established every year (Lovett et al., 2016). This means that tree species currently unaffected by insect outbreaks may be severely attacked in the future. Successful forest management strategies need to focus not only on current vulnerability of tree species to known disturbances (i.e. native insects) but on diversifying forest ecosystems to cope with unknown stressors and disturbances (Dymond et al., 2014) .

4.2. Functional trait-based management

Although forest planning has so far been mostly based on timber yield and has favored the most productive species based on a taxonomic basis, there is evidence that management based on functional diversity might be more effective to build forests better adapted to cope with an uncertain future (Cadotte, 2011). That is, managing to foster forest resistance to disturbances and adaptive capacity to global uncertainty cannot be simply designed on a taxonomic basis (Lavorel et al., 2011; Mori et al., 2013). Functionally based approaches describe species by their effect and response traits as a way to mechanistically predict ecosystem processes and responses to disturbances and environmental changes (Suding et al., 2008). Such approaches have been extensively applied to tropical forest ecosystems, mainly to assess the impacts of land-use changes (Flynn et al., 2009; Mayfield et al., 2010), logging operations (Baraloto et al., 2012; Maeshiro et al., 2013), and natural disturbances (Carreño-Rocabado et al., 2012) on community functional (response) diversity. Although the functional trait framework has been proposed to guide forest management and ecological restoration (Laughlin, 2014), it has rarely been applied for such purposes. Ostertag et al., (2015) adopted the framework for a restoration project in Hawaiian lowland wet forests, and Laughlin et al., (2017) used a trait-based approach to set restoration

objectives for fire-prone, mixed conifer forests in the United States to cope with warmer and drier climatic conditions.

In the Haliburton Forest, a temperate mixed woodland, we first clustered tree and large shrub species into seven functional groups and calculated functional diversity as the richness and evenness of functional groups present within each community. This helped identify stands that did not require any specific silvicultural intervention to become functionally diverse, or that could be effectively diversified by harvesting-only strategies, for example, in Zones 1, 2, and 5 of the study area. Although many stands were functionally poor, a few functionally diverse stands were already present. In such cases, reducing the abundance of functionally redundant species and ensuring the natural regeneration of species with less represented functional traits would be enough to maximize functional diversity, without requiring interventions that include planting species currently absent in the landscape. This is highly relevant since ensuring successful establishment, growth and self-regeneration of novel tree species may require additional effort in vast landscape settings (Seastedt et al., 2008). We also identified stands that could be effectively diversified with a combination of low-level harvesting and planting (i.e. high-level harvesting-planting were not needed). In Zones 1 and 6, high-level harvesting-planting not only removed functionally redundant species but also species with functional traits less represented and which could not be easily compensated by high rates of planting. Harvesting levels must therefore be limited to avoid having counteractive effects on functional diversity and connectivity. Because a positive contribution to functional connectivity is strictly dependent on species seed dispersal capacity, favoring functional diversity with tree species having high dispersal rates should be promoted as much as possible. Such species would contribute to enhancing both stand-level and landscape-level functional diversity.

We believe that the method presented in this study could be easily applied by local managers to evaluate forestry interventions based on principles of the functional network approach. Foresters should first agree on the list of tree and large shrub species of interest in their forest region and the list of key functional traits. Most functional trait values can be obtained from local field measures (Maeshiro et al., 2013) or from freely available databases (Aubin et al., 2012; Kattge et al., 2020; Tavşanoğlu and Pausas, 2018). Once functional traits by species have been gathered, the next steps are to compile communities' composition and relative species abundance information, as well as forest stand maps. Updated forest inventories and stand maps are often available and already in use by local managers. Vulnerability scores can be retrieved from the literature accounting for disturbances (negative and positive) influence on species (Matthews et al., 2011). It is also important to remember that the functional diversity indicator will be influenced by the final list of functional traits used. We suggest including traits, both response and effect, that represent varied functions and processes, are sensitive to the disturbances likely to impact the region of study, and are meaningful for the management objectives (Laughlin et al., 2017; Ostertag et al., 2015). Example data and R-scripts to (1) cluster tree species into functional groups, (2) compute stand-level functional diversity, and (3) compute stand-level vulnerability are available on Github: https://github.com/nuaquilue/Simple-to-use_Functional_Network.

4.3. Methodological aspects and future research

The approach used in this study to quantify both stand- and landscape-scale vulnerability relies on expert knowledge to rank the future relevance and likely impact of disturbances on the region of interest (Table S4) (Matthews et al., 2011). However, unexpected feedback and non-linear interactions between disturbances, climate change, and forest dynamics may force changes in the ranking system (Buma, 2015; Chmura et al., 2011; Turner, 2010). If the vulnerability of tree species is to be included in

sustainable forest management decisions, we argue that a more local and accurate prediction of risk and exposure to most types of natural disturbances will certainly better frame vulnerability assessments. If these are not available for all or some of the disturbance types, a panel of experts, including foresters, climatologists, entomologists, and economists, among others, is advisable to assess the potential impact of disturbances on the region (Drescher et al., 2013).

In this study we did not explicitly consider the temporal and spatial dynamics of ecological processes on forest landscapes such as growth, mortality, regeneration and natural disturbances. We assessed changes in species composition and relative abundance within forest stands in a static environment assuming that trees planted within the harvesting-planting scenarios were instantaneously ready to disperse seeds. We acknowledge that dynamic tools such as forest landscape dynamic models offer more reliable predictions of the spatio-temporal dynamics of forest ecosystems (Shifley et al., 2017). Such models typically account for interacting global change drivers with sometimes non-additive effects to study forest responses to both management and natural disturbances (Duveneck and Thompson, 2019; Keane et al., 2015). Coupling simulation modelling with network analysis, as shown by Mina et al., (2020) can help in evaluating the dynamic interactions of climate change, management and disturbances, and their effects on forest succession, key ecosystem services, and adaptive capacity to a variety of disturbances. However, such modelling frameworks are usually very high data-demanding environments that require considerable expertise that could be beyond the capabilities of forest managers. Indeed, we are aware that most forest companies and agencies rarely have access to process-based models specifically calibrated to the properties they manage, to actually derive fine-scale predictions resulting from the interactions between climate change effects on vegetation dynamics, natural disturbances, and targeted management prescriptions. Instead, we deliberately focused then on presenting and explaining how a simple-to-use tool based on the functional network approach could

provide a means for forest managers to implement and evaluate different forest management scenarios to increase the adaptive capacity of forest stands and landscapes to uncertain climatic and biotic stressors.

Finally, although beyond the scope of this paper, further development of this approach should identify how key ecosystem services such as timber products, carbon, biodiversity and water are affected by forest management. Such studies should account for the supply, flow, and demand of regional-scale ecosystem goods and services, potential trade-offs amongst them, and impacts on biodiversity (Schirpke et al., 2019; Varela et al., 2018). Furthermore, studies incorporating both economic and operational evaluations to quantify the feasibility of such management scenarios, particularly when planting, would be highly recommended.

5. Conclusions

To guide forest management in an uncertain environmental and socio-economic future, local studies that apply scientific- and data-based methods, incorporate expert knowledge, and include a global perspective may provide useful insights on how to shape current forestry practices to cope with emerging global environmental changes. Management interventions to increase functional diversity and the ability of a forest ecosystem to self-organize and adapt to future environmental conditions can be optimized when viewing and analyzing forest landscapes as networks. Moreover, grouping shrub and tree species into a few functional groups greatly simplifies the ability to select the most appropriate mixture of tree species that maximize functional diversity. Evaluating species local vulnerability to current and likely future natural disturbances also offers valuable information to guide harvesting and planting operations. Because taxonomically rich forest ecosystems do not necessarily translate into functionally rich ecosystems, their adaptability and resilience to certain natural disturbances and future environmental conditions may be strongly compromised. Practitioners may benefit from applying the

functional network approach on their woodlands to explicitly identify functionally poor tree communities, highly or very-highly vulnerable areas, and tree species to be planted or encouraged through natural regeneration that will strongly contribute to forest adaptability. A new generation of management plans may then arise, acknowledging the increasingly uncertain future environmental conditions by promoting practices that increase forest adaptability.

Authors' contributions

NA and CM conceived the research; KM prepared geospatial and species relative abundance data at the stand-level; VL and MM gathered raw scores to compute the species vulnerability index; NA and KM clustered tree species into functional groups; NA built the functional network, modelled the management scenarios and analyzed the data; NA led the writing of the paper, CM, KM, VL, and MM provided feedback and comments on the text.

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Supplementary Material

A simple-to-use management approach to boost forests adaptive capacity to global uncertainty

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Table S1: Area, number of stands, stand size and number of species per stand in the eight zones of the Haliburton Forest.

Zone	Area (ha)	Area (%)	Number of stands ^a	Stand size (ha) ^b	Number of species per stand ^b
1	27.669	81	3.638	7.57 ± 10.9 [1; 184]	4.76 ± 1.42 [1; 8]
2	62	0.2	14	4.36 ± 4.65 [1; 17]	5.71 ± 1.07 [3; 7]
3	224	0.7	34	6.56 ± 7.78 [1; 36]	6.03 ± 1.14 [4; 8]
4	1.170	3.4	164	7.15 ± 10.9 [1; 104]	5.54 ± 1.36 [2; 8]
5	215	0.6	19	11.4 ± 5.88 [2; 27]	5.32 ± 1.42 [3; 7]
6	2.392	7	321	7.45 ± 9.36 [1; 75]	5.29 ± 1.23 [2; 8]
7	2.199	6.4	145	15.2 ± 17.0 [1; 132]	5.03 ± 1.20 [3; 8]
8	221	0.6	20	11.0 ± 9.78 [2; 32]	4.85 ± 1.39 [3; 7]

^a Stands of size > 1 ha

^b Mean value ± standard deviation [minimum; maximum]

Table S2: Values of eight functional traits and seed dispersal distance of the 80 tree species of the Haliburton Forest biogeographical region. Functional trait values were obtained from Niinemets and Valladares, (2006) and Aubin et al., (2012). Seed dispersal distance was only used to set links between nodes in the functional network and calculate link's weights. It was derived from the effective seeding distance, i.e. the farthest distance that 95% of the seed rain can reach in any direction away from the parent tree (He and Mladenoff, 1999), used in the forest landscape model LANDIS-II (Duveneck et al., 2014; Lucash et al., 2017). When dispersal distance was not available from LANDIS-II, we used values available from the literature (Vittoz and Engler, 2007) or from species belonging to the same *Genus*. Seed dispersal distance was set at half of cell size (50 m) in cases of unavailable data (13 species only).

Species	Drought tolerance	Shade tolerance	Waterlogging tolerance	Dispersal vector	Seed mass (g/1000 seeds)	Wood density (g/cm ³)	Leaf mass area (g/m ²)	Phylogenetic division	Seed dispersal distance (m)
Abies balsamea	1.00	5.01	2.00	Wind	0.9345	0.33	143.00	Gymnosperm	60
Acer freemanii	2.36	3.52	2.24	Wind	2.0554	0.47	71.09	Angiosperm	100
Acer negundo	3.03	3.47	2.75	Wind	1.5682	0.42	37.04	Angiosperm	100
Acer nigrum	3.35	3.00	1.52	Wind	1.7497	0.52	70.63	Angiosperm	100
Acer platanoides	2.73	4.20	1.46	Wind	2.1183	0.52	47.32	Angiosperm	100
Acer rubrum	1.84	3.44	3.08	Wind	1.3927	0.49	71.09	Angiosperm	100
Acer saccharinum	2.88	3.60	3.37	Wind	2.3064	0.44	69.60	Angiosperm	100
Acer saccharum	2.25	4.76	1.09	Wind	1.7497	0.56	70.63	Angiosperm	50
Aesculus hippocastanum	2.82	3.43	1.39	Unassisted	4.1132	0.50	72.99	Angiosperm	50
Betula alba	1.27	1.85	2.98	Wind	0.0682	0.53	65.97	Angiosperm	40
Betula alleghaniensis	3.00	3.17	2.00	Wind	0.3010	0.55	46.08	Angiosperm	45
Betula glandulosa	1.10	1.56	4.27	Wind	0.0719	0.52	63.00	Angiosperm	40
Betula lenta	3.00	2.58	1.00	Wind	0.2304	0.60	68.50	Angiosperm	100
Betula nigra	1.53	1.45	2.85	Wind	0.3502	0.49	84.75	Angiosperm	40
Betula papyrifera	2.02	1.54	1.25	Wind	0.1139	0.48	85.51	Angiosperm	60
Betula populifolia	2.34	1.50	1.00	Wind	0.0414	0.45	58.44	Angiosperm	100
Carpinus caroliniana	2.02	4.58	2.30	Wind	1.4314	0.58	54.05	Angiosperm	130
Carya cordiformis	4.00	2.07	2.50	Animal	3.4469	0.60	44.05	Angiosperm	30
Carya ovata	3.00	3.40	1.38	Animal	3.6256	0.64	70.68	Angiosperm	30
Celtis occidentalis	3.85	3.17	2.65	Animal	2.1052	0.49	82.64	Angiosperm	30
Corylus americana	2.88	3.50	1.27	Animal	2.8955	0.52	105.26	Angiosperm	50
Crataegus canadensis	3.70	2.06	1.45	Animal	2.0386	0.62	99.00	Angiosperm	50
Crataegus crus-galli	4.98	1.67	1.27	Animal	2.2170	0.62	99.00	Angiosperm	50

Fagus grandifolia	1.50	4.75	1.50	Animal	2.4265	0.56	60.83	Angiosperm	30
Fraxinus americana	2.38	2.46	2.59	Wind	1.5832	0.55	69.13	Angiosperm	70
Fraxinus nigra	2.00	2.96	3.50	Wind	1.7505	0.45	71.94	Angiosperm	100
Fraxinus pennsylvanica	3.85	3.11	2.98	Wind	1.5224	0.53	87.72	Angiosperm	5
Gleditsia triacanthos	4.98	1.61	2.69	Animal	2.2294	0.60	76.12	Angiosperm	50
Gymnocladus dioicus	3.69	2.50	1.14	Water	3.2658	0.53	76.12	Angiosperm	50
Juglans cinerea	2.38	1.88	1.27	Animal	4.1470	0.36	60.98	Angiosperm	38
Juglans nigra	2.38	1.93	1.83	Animal	4.0532	0.51	32.79	Angiosperm	38
Larix laricina	2.00	0.98	3.00	Wind	0.4771	0.49	120.00	Gymnosperm	46
Larix leptolepis	2.43	1.23	2.03	Wind	0.6911	0.45	106.95	Gymnosperm	46
Liriodendron tulipifera	2.60	2.07	1.30	Wind	1.7412	0.40	70.62	Angiosperm	50
Magnolia acuminata	1.27	3.03	1.52	Animal	1.9519	0.44	94.87	Angiosperm	50
Malus domestica	3.04	1.93	1.04	Animal	1.4431	0.65	38.70	Angiosperm	50
Morus rubra	2.88	2.34	1.57	Animal	0.3979	0.64	67.30	Angiosperm	50
Nyssa sylvatica	2.00	3.52	1.87	Animal	2.1644	0.46	54.64	Angiosperm	50
Ostrya virginiana	3.25	4.58	1.07	Wind	1.2151	0.63	37.04	Angiosperm	50
Picea abies	1.75	4.45	1.22	Wind	0.9031	0.37	235.18	Gymnosperm	60
Picea glauca	2.88	4.15	1.02	Wind	0.5315	0.33	302.86	Gymnosperm	27
Picea mariana	2.00	4.08	2.00	Wind	0.3263	0.38	294.12	Gymnosperm	79
Picea rubens	2.50	4.39	2.00	Wind	0.6335	0.37	263.00	Gymnosperm	80
Pinus banksiana	4.00	1.36	1.00	Wind	0.6532	0.42	243.90	Gymnosperm	16
Pinus nigra	4.38	2.10	1.39	Wind	1.2788	0.42	324.90	Gymnosperm	40
Pinus resinosa	3.00	1.89	1.00	Wind	1.0000	0.41	294.12	Gymnosperm	100
Pinus rigida	4.00	1.99	2.00	Wind	0.9542	0.47	204.50	Gymnosperm	90
Pinus strobus	2.29	3.21	1.03	Wind	1.2553	0.34	121.92	Gymnosperm	60
Pinus sylvestris	4.34	1.67	2.63	Wind	0.8451	0.42	292.76	Gymnosperm	40
Populus balsamifera	1.77	1.27	2.63	Wind	0.0934	0.31	83.46	Angiosperm	200
Populus canadensis	1.89	2.11	3.37	Wind	0.2967	0.35	80.92	Angiosperm	500
Populus deltoides	1.57	1.76	3.03	Wind	0.3324	0.37	80.92	Angiosperm	500
Populus grandidentata	2.50	1.21	2.00	Wind	0.0607	0.36	70.45	Angiosperm	500
Populus tremuloides	1.77	1.21	1.77	Wind	0.0414	0.35	79.66	Angiosperm	500
Prunus americana	2.45	2.17	1.52	Animal	2.8871	0.41	86.09	Angiosperm	30
Prunus cerasus	3.11	2.66	1.04	Animal	2.2185	0.41	66.54	Angiosperm	30
Prunus nigra	2.65	2.10	1.23	Animal	2.6381	0.41	66.54	Angiosperm	30
Prunus pensylvanica	2.65	2.10	1.23	Animal	1.6484	0.36	50.00	Angiosperm	30
Prunus serotina	3.02	2.46	1.06	Animal	1.9289	0.47	57.94	Angiosperm	5
Prunus virginiana	2.88	2.59	1.11	Animal	1.9143	0.36	84.03	Angiosperm	30
Quercus alba	3.56	2.85	1.43	Animal	3.4768	0.63	92.26	Angiosperm	3

Quercus bicolor	3.35	2.98	2.58	Animal	3.5391	0.64	82.75	Angiosperm	34
Quercus coccinea	4.00	2.07	1.00	Animal	3.2860	0.60	95.00	Angiosperm	50
Quercus ellipsoidalis	3.62	2.25	1.26	Animal	3.1928	0.61	105.26	Angiosperm	30
Quercus imbricaria	3.85	2.09	2.43	Animal	3.0394	0.61	95.82	Angiosperm	34
Quercus macrocarpa	3.85	2.71	1.82	Animal	3.7886	0.58	92.74	Angiosperm	18
Quercus muehlenbergii	4.97	2.22	1.26	Animal	3.0767	0.61	95.82	Angiosperm	34
Quercus palustris	2.38	2.49	3.49	Animal	3.0366	0.58	82.75	Angiosperm	1100
Quercus rubra	2.88	2.75	1.12	Animal	3.4975	0.56	88.03	Angiosperm	3
Rhamnus cathartica	3.46	1.93	2.25	Animal	1.3560	0.61	75.48	Angiosperm	1
Rhus typhina	4.00	1.56	1.00	Animal	1.0864	0.45	65.79	Angiosperm	50
Robinia pseudoacacia	4.11	1.72	1.07	Unassisted	1.3054	0.66	56.82	Angiosperm	50
Salix bebbiana	1.00	1.00	3.00	Wind	0.0719	0.36	88.23	Angiosperm	50
Salix nigra	1.77	1.34	4.68	Wind	0.0253	0.36	55.87	Angiosperm	50
Thuja occidentalis	2.71	3.45	1.46	Wind	0.3979	0.29	223.00	Gymnosperm	45
Tilia americana	2.88	3.98	1.26	Wind	2.0410	0.32	60.81	Angiosperm	20
Tsuga canadensis	1.00	4.83	1.25	Wind	0.6021	0.38	122.55	Gymnosperm	30
Ulmus americana	2.92	3.14	2.46	Wind	0.7782	0.46	66.27	Angiosperm	91
Ulmus rubra	3.00	3.31	1.73	Wind	1.0406	0.48	59.88	Angiosperm	91
Ulmus thomasii	2.00	3.22	1.00	Wind	1.7889	0.57	64.10	Angiosperm	91

Table S3: Raw scores expressing the potential influence (-3 strongly negative to 3 strongly positive) of natural disturbances on species obtained from Matthews et al., (2011).

Species	Browsing	Disease	Drought	Flood	Ice	Insect pest	Invasive plants	Temp. gradient	Wind	Vuln. Index	Vuln. Class
<i>Abies balsamea</i>	-1	-2	-2	1	-1	-3	-2	-2	-2	5.71	Very high
<i>Acer freemanii</i> *	-1	-1	-2	3	-3	-1	-1	2	-2	4.98	Moderate
<i>Acer negundo</i>	-1	-1	3	2	-2	-1	-1	3	-2	4.33	Low
<i>Acer nigrum</i>	-1	-1	-1	-1	-1	-1	-1	2	-1	4.92	Low
<i>Acer platanoides</i> *	-1	-1	-1	-2	-1	-1	-1	1	1	4.92	Low
<i>Acer rubrum</i>	-1	-1	1	2	1	0	-1	2	1	4.11	Low
<i>Acer saccharinum</i>	-1	-1	-2	3	-3	-1	-1	2	-2	4.98	Moderate
<i>Acer saccharum</i>	-1	-1	-1	-2	-1	-1	-1	1	1	4.92	Low
<i>Betula alleghaniensis</i>	-2	-3	-1	-1	-1	-2	-2	1	-1	5.50	Very high
<i>Betula lenta</i>	-1	-3	-1	-1	-1	-2	-2	1	-1	5.38	High
<i>Betula nigra</i>	-1	-1	-2	1	-1	-1	-2	2	-1	5.04	Moderate
<i>Betula papyrifera</i>	-1	-2	-2	-1	-1	-2	-2	0	-1	5.50	Very high
<i>Betula populifolia</i>	-1	-3	-1	-1	-1	-2	-2	1	-1	5.38	High
<i>Carpinus caroliniana</i>	-1	0	-2	0	1	0	-2	1	1	4.70	Low
<i>Carya cordiformis</i>	1	-1	2	-1	-1	-2	-2	1	2	4.48	Low
<i>Carya ovata</i>	-1	-2	-1	-1	-1	-2	-2	2	1	5.14	Moderate
<i>Celtis occidentalis</i>	-1	-1	2	-1	-1	-1	-2	2	-1	4.68	Low
<i>Crataegus canadensis</i> *	-2	-1	-1	-2	-1	-2	-2	1	-1	5.44	Very high
<i>Fagus grandifolia</i>	1	-2	-1	-3	-1	-2	-2	1	-1	5.20	High
<i>Fraxinus americana</i>	-2	-2	-1	0	-1	-3	-2	0	-1	5.60	Very high
<i>Fraxinus nigra</i>	2	-2	-2	2	-1	-3	-2	0	1	5.00	Moderate
<i>Fraxinus pennsylvanica</i>	-2	-2	1	3	-1	-3	-2	0	1	5.06	Moderate
<i>Gleditsia triacanthos</i>	-1	-1	2	1	1	-2	-2	2	1	4.48	Low
<i>Gymnocladus dioicus</i>	-1	-1	-1	-1	-1	-2	-2	1	-1	5.26	High
<i>Juglans cinerea</i>	-1	-3	-2	-1	-1	-2	-2	1	-1	5.50	Very high

<i>Juglans nigra</i>	-1	-2	-2	0	-1	-2	-2	1	-1	5.38	High
<i>Larix laricina</i>	-1	-1	1	-1	0	-2	-2	1	-2	5.02	Moderate
<i>Larix leptolepis</i> *	-1	-1	1	-1	0	-2	-2	1	-2	5.02	Moderate
<i>Magnolia acuminata</i>	2	2	-2	-1	-1	-2	-2	1	-2	4.90	Low
<i>Morus rubra</i>	-1	-2	-1	1	-1	-1	-2	2	-1	4.98	Moderate
<i>Nyssa sylvatica</i>	-2	-1	-1	0	-1	-1	-2	1	-1	5.16	Moderate
<i>Ostrya virginiana</i>	-1	-1	1	-2	1	-1	-2	3	1	4.56	Low
<i>Picea glauca</i>	-1	-1	-1	-1	-1	-2	-2	2	-1	5.20	High
<i>Picea mariana</i>	-1	-2	-2	-1	-2	-2	-2	1	-2	5.56	Very high
<i>Picea rubens</i>	-1	-2	-2	-1	-1	-1	-2	1	-2	5.34	High
<i>Pinus banksiana</i>	-1	-2	2	-1	-1	-2	-2	2	-1	4.90	Low
<i>Pinus resinosa</i>	-1	-2	-2	-1	-2	-3	-2	1	1	5.54	Very high
<i>Pinus rigida</i>	-1	-2	-1	-2	-1	-2	-1	2	-1	5.20	High
<i>Pinus strobus</i>	-1	-2	-3	1	-1	-2	-2	-1	1	5.44	Very high
<i>Populus balsamifera</i>	-1	-1	-2	3	-1	-2	-2	-2	-1	5.32	High
<i>Populus deltoides</i>	-1	-3	1	1	-1	-3	-2	3	-1	5.06	Moderate
<i>Populus grandidentata</i>	1	-1	-2	-1	1	-1	-1	1	1	4.62	Low
<i>Populus tremuloides</i>	-1	-2	-2	-1	0	-2	-1	3	-2	5.20	High
<i>Prunus americana</i>	-1	-1	-1	-1	-1	-2	-2	1	-1	5.26	High
<i>Prunus cerasus</i> *	-1	-1	-1	-1	-1	-2	-2	1	-1	5.26	High
<i>Prunus pensylvanica</i>	-1	-2	-2	-1	-1	-2	-2	-1	-1	5.56	Very high
<i>Prunus serotina</i>	-2	-2	2	-3	-1	-3	-1	2	-2	5.24	High
<i>Prunus virginiana</i>	-2	-1	-1	-2	-1	-2	-2	1	-1	5.44	Very high
<i>Quercus alba</i>	-1	-3	1	-2	0	-3	-2	3	-1	5.18	High
<i>Quercus bicolor</i>	-1	-1	-1	1	-1	-2	-2	2	-2	5.14	Moderate
<i>Quercus coccinea</i>	-1	-3	1	-1	-1	-3	-2	2	-1	5.24	High
<i>Quercus ellipsoidalis</i>	-1	-1	3	-1	-1	-2	-2	-2	-1	4.96	Low
<i>Quercus imbricaria</i>	-2	-2	2	1	-1	-1	-2	1	-1	4.80	Low
<i>Quercus macrocarpa</i>	-1	-2	3	-2	-1	-2	-2	-1	0	4.96	Low
<i>Quercus muehlenbergii</i>	-1	-2	1	-1	-1	-2	-2	3	-1	4.96	Low

<i>Quercus palustris</i>	-1	-3	-1	2	-1	-3	-2	2	-1	5.30	High
<i>Quercus rubra</i>	-1	-2	1	-1	-1	-3	-2	2	1	5.06	Moderate
<i>Robinia pseudoacacia</i>	-1	-2	-2	-2	-1	-2	-2	2	-1	5.44	Very high
<i>Salix nigra</i>	1	-1	-2	2	-1	-2	-2	2	-1	4.90	Low
<i>Thuja occidentalis</i>	-1	-1	-2	-1	-2	-2	-2	-1	-1	5.56	Very high
<i>Tilia americana</i>	-1	-1	-1	2	1	-2	-2	2	-1	4.90	Low
<i>Tsuga canadensis</i>	-2	-2	-2	-1	-1	-3	-2	-1	-2	5.89	Very high
<i>Ulmus americana</i>	-1	-3	-2	-2	-3	-2	-2	2	1	5.50	Very high
<i>Ulmus rubra</i>	-1	-3	1	-1	-1	-2	-2	2	-1	5.08	Moderate
<i>Ulmus thomasi</i>	0	-3	-1	-1	-1	-2	-2	-1	-1	5.38	High

* Species in the study area without scores informed in the literature. We assigned scores of functionally and taxonomically similar species to be able to compute the vulnerability index.

Table S4: Multiplier accounting for the likely future relevance of each natural disturbance in the study region under climate change conditions, ranging from 1 – not highly relevant to 4 – extremely relevant, and 0 – inexistent; and multiplier accounting for uncertainty (0.5 – low to 1 – high).

Natural disturbance	Future relevance	Uncertainty
Browsing	2	0.75
Disease	1	0.75
Drought	2	0.75
Flood	1	0.75
Ice	1	0.75
Insect pest	4	0.5
Invasive plants	3	0.5
Temperature gradient	1	0.75
Wind	1	0.75

Table S5: Current and potential forest tree species in Haliburton Forest classified according to the vulnerability index and grouped by functional group. Species in bold are those not currently present in the Haliburton Forest. Potential tree species missing scores needed to compute the vulnerability index were *Liriodendron tulipifera* (group 1), *Picea abies* (group 2), *Prunus nigra*, *Rhus typhina* (group 3), *Betula alba*, *Betula glandulosa*, *Populus canadensis*, *Salix bebbiana* (group 4), *Corylus americana*, *Crataegus crus-galli*, *Malus domestica*, *Rhamnus cathartica* (group 5), and *Pinus nigra*, *Pinus sylvestris* (group 6). Species in functional group 7 that are commonly found in urban settings are not presented here as they will not be considered for planting in natural areas.

Functional group	Low vulnerable	Moderate vulnerable	High vulnerable	Very high vulnerable
1	<i>Acer negundo</i> , <i>Acer nigrum</i> , <i>Acer rubrum</i> , <i>Acer platanoides</i> , <i>Acer saccharum</i> , <i>Carpinus caroliniana</i> , <i>Ostrya virginiana</i> , <i>Tilia americana</i>	<i>Acer freemanii</i> , <i>Acer saccharinum</i> , <i>Fraxinus nigra</i> , <i>Fraxinus pennsylvanica</i> , <i>Ulmus rubra</i>	<i>Betula lenta</i> , <i>Ulmus thomasii</i>	<i>Betula alleghaniensis</i> , <i>Fraxinus americana</i> , <i>Ulmus americana</i>
2			<i>Picea glauca</i> , <i>Picea rubens</i>	<i>Abies balsamea</i> , <i>Picea mariana</i> , <i>Pinus strobus</i> , <i>Thuja occidentalis</i> , <i>Tsuga canadensis</i>
3	<i>Magnolia acuminata</i>	<i>Nyssa sylvatica</i>	<i>Fagus grandifolia</i> , <i>Juglans nigra</i> , <i>Prunus americana</i> , <i>Prunus cerasus</i> , <i>Prunus serotina</i>	<i>Juglans cinerea</i> , <i>Prunus pennsylvanica</i> , <i>Prunus virginiana</i>
4	<i>Populus grandidentata</i> , <i>Salix nigra</i>	<i>Betula nigra</i> , <i>Populus deltoides</i>	<i>Betula populifolia</i> , <i>Populus balsamifera</i> , <i>Populus tremuloides</i>	<i>Betula papyrifera</i>
5	<i>Carya cordiformis</i> , <i>Celtis occidentalis</i> , <i>Gleditsia triacanthos</i> , <i>Quercus ellipsoidalis</i> , <i>Quercus imbricaria</i> , <i>Quercus macrocarpa</i> , <i>Quercus muehlenbergii</i>	<i>Carya ovata</i> , <i>Morus rubra</i> , <i>Quercus bicolor</i> , <i>Quercus rubra</i>	<i>Quercus alba</i> , <i>Quercus coccinea</i> , <i>Quercus palustris</i>	<i>Crataegus canadensis</i>
6	<i>Pinus banksiana</i>	<i>Larix laricina</i> , <i>Larix leptolepis</i>	<i>Pinus rigida</i>	<i>Pinus resinosa</i>

Table S6: Percentage of stands with low, moderate, high or very high vulnerability to natural disturbances per zone in the Haliburton Forest.

Zone	Low vulnerability	Moderate vulnerability	High vulnerability	Very high vulnerability
1	11.6	44.4	23.3	20.7
2	42.9	21.4	35.7	
3	47.1	38.2	14.7	
4	32.3	45.1	16.5	6.1
5	15.8	52.6	26.3	5.3
6	5	45.2	31.1	18.7
7	71.7	10.3	9.7	8.3
8	55	25	10	10

Table S7: Analysis of variance (type II tests) of the interaction between management intensity (percentage of area managed) and the silvicultural strategy on functional diversity and functional connectivity on the eight zones of the Haliburton Forest.

Zone	Variable	Functional diversity				Functional connectivity			
		Sum sq	Df	F value	Pr (>F)	Sum sq	Df	F value	Pr (>F)
1	Intensity	1.50829	1	65453.2	< 2e-16	0.02267	1	2499.9	< 2e-16
	Strategy	0.34107	3	4933.6	< 2e-16	0.09610	3	3532	< 2e-16
	Intensity:Strategy	0.1836	3	2655.8	< 2e-16	0.02803	3	1030	< 2e-16
	Residuals	0.00728	316			0.00287	316		
2	Intensity	1.97473	1	18983	< 2e-16	1.7957	1	586.6	< 2e-16
	Strategy	0.43701	3	1400.3	< 2e-16	9.6331	3	1048.91	< 2e-16
	Intensity:Strategy	0.33743	3	1081.2	< 2e-16	1.8051	3	196.55	< 2e-16
	Residuals	0.03287	316			0.9674	316		
3	Intensity	1.64694	1	11426.4	< 2e-16	0.4633	1	180.089	< 2e-16
	Strategy	1.36228	3	3150.5	< 2e-16	4.1447	3	537.003	< 2e-16
	Intensity:Strategy	0.56536	3	1307.5	< 2e-16	0.6497	3	84.177	< 2e-16
	Residuals	0.04555	316			0.813	316		
4	Intensity	1.62645	1	36010.7	< 2e-16	0.23401	1	689.97	< 2e-16
	Strategy	0.64965	3	4794.6	< 2e-16	0.78467	3	771.2	< 2e-16
	Intensity:Strategy	0.25307	3	1867.7	< 2e-16	0.37581	3	369.36	< 2e-16
	Residuals	0.01427	316			0.10717	316		
5	Intensity	1.56755	1	15229.92	< 2e-16	1.7553	1	1803.53	< 2e-16
	Strategy	0.50907	3	1648.67	< 2e-16	3.6429	3	1247.66	< 2e-16
	Intensity:Strategy	0.15203	3	492.36	9.60e-14	1.3263	3	454.25	< 2e-16
	Residuals	0.03252	316			0.3076	316		
6	Intensity	1.16367	1	66619	< 2e-16	0.31549	1	2735.76	< 2e-16
	Strategy	0.44091	3	8413.9	< 2e-16	0.94673	3	2736.49	< 2e-16
	Intensity:Strategy	0.3124	3	5961.6	< 2e-16	0.34503	3	997.31	< 2e-16
	Residuals	0.00552	316			0.03644	316		
7	Intensity	1.01961	1	3549.05	< 2e-16	0.16596	1	95.352	< 2e-16
	Strategy	1.39452	3	1618	< 2e-16	1.43137	3	274.137	< 2e-16
	Intensity:Strategy	0.39385	3	456.97	< 2e-16	0.19646	3	37.626	< 2e-16
	Residuals	0.09078	316			0.54998	316		
8	Intensity	1.81445	1	10945.9	< 2e-16	0.9893	1	370.94	< 2e-16
	Strategy	1.499	3	3014.3	< 2e-16	5.2964	3	661.93	< 2e-16
	Intensity:Strategy	0.74404	3	1496.2	< 2e-16	1.2325	3	154.03	< 2e-16
	Residuals	0.05238	316			0.8428	316		

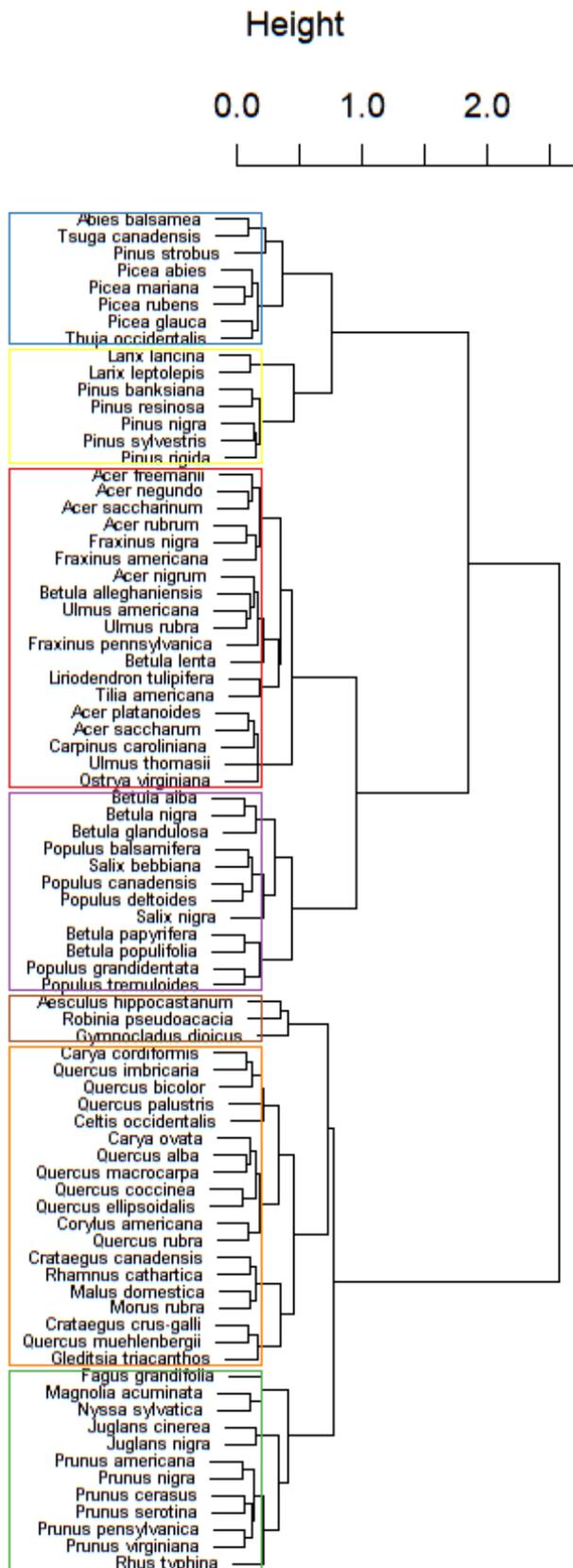


Figure S1: Functional dendrogram of the 80 tree species analyzed in this study. Species are classified into seven functional groups according to the similarities between the functional traits considered (Table S2).

Functional groups listed in Table 1 are coded by colour as follows: 1 – red, 2 – blue, 3 – green, 4 – violet, 5 – orange, 6 – yellow, and 7 – brown.

To determine the optimal number of clusters, we analyzed three measures of cluster validation (implemented in the *clValid* R-package (Handl et al., 2005)): (1) connectivity, as the extent of nearest neighbours in the data space are clustered together (minimised); (2) the Dunn index, the ratio between the inter-cluster separation and the intra-cluster distance defining cluster compactness and how well-separated the clusters are (maximised); and (3) the average silhouette width, defining how well an observation is clustered and the average distance between clusters (maximised, see Fig.S2).

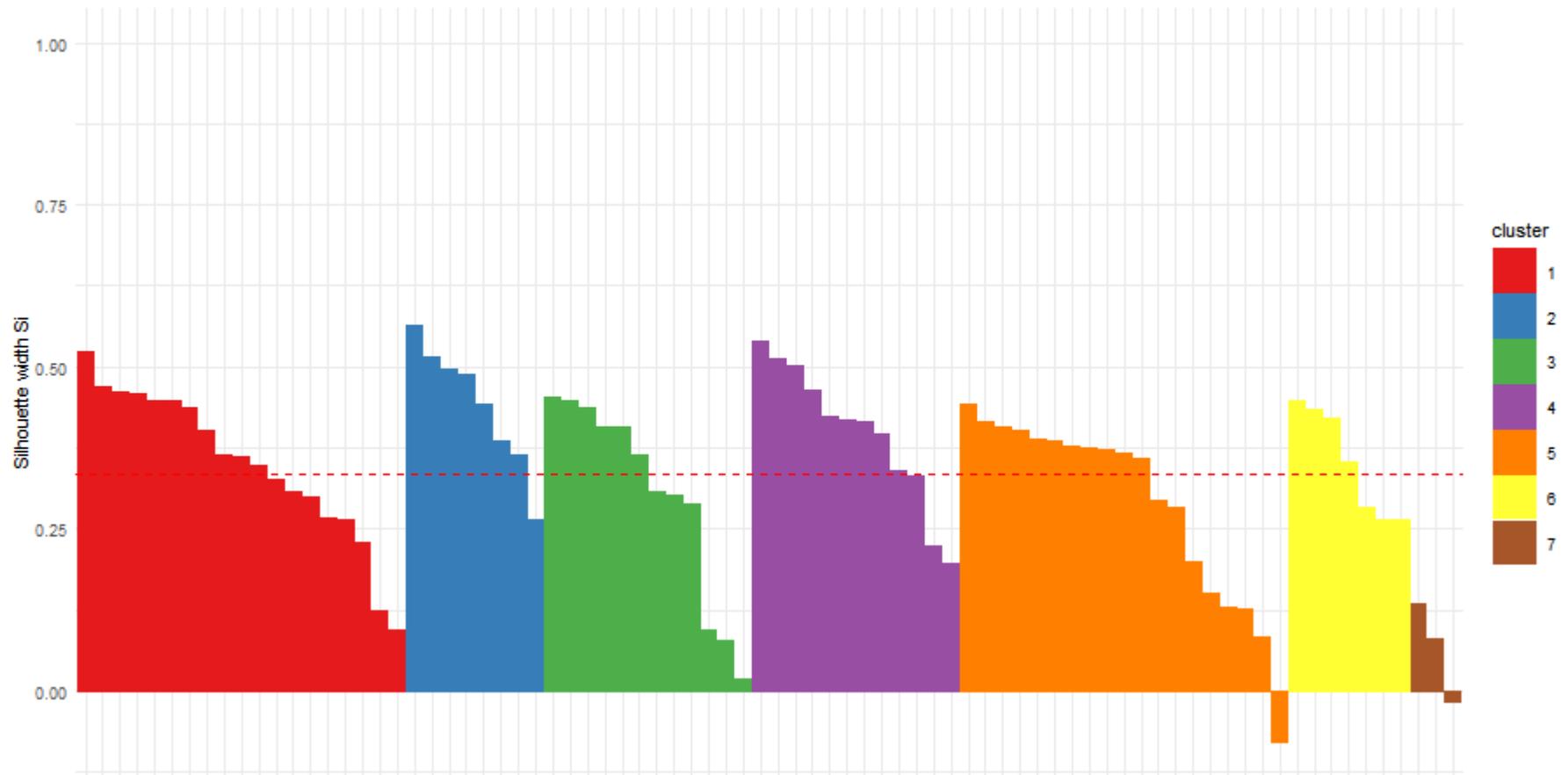


Figure S2: Silhouette plot of the 80 tree species analyzed in this study. Average silhouette width is 0.33.

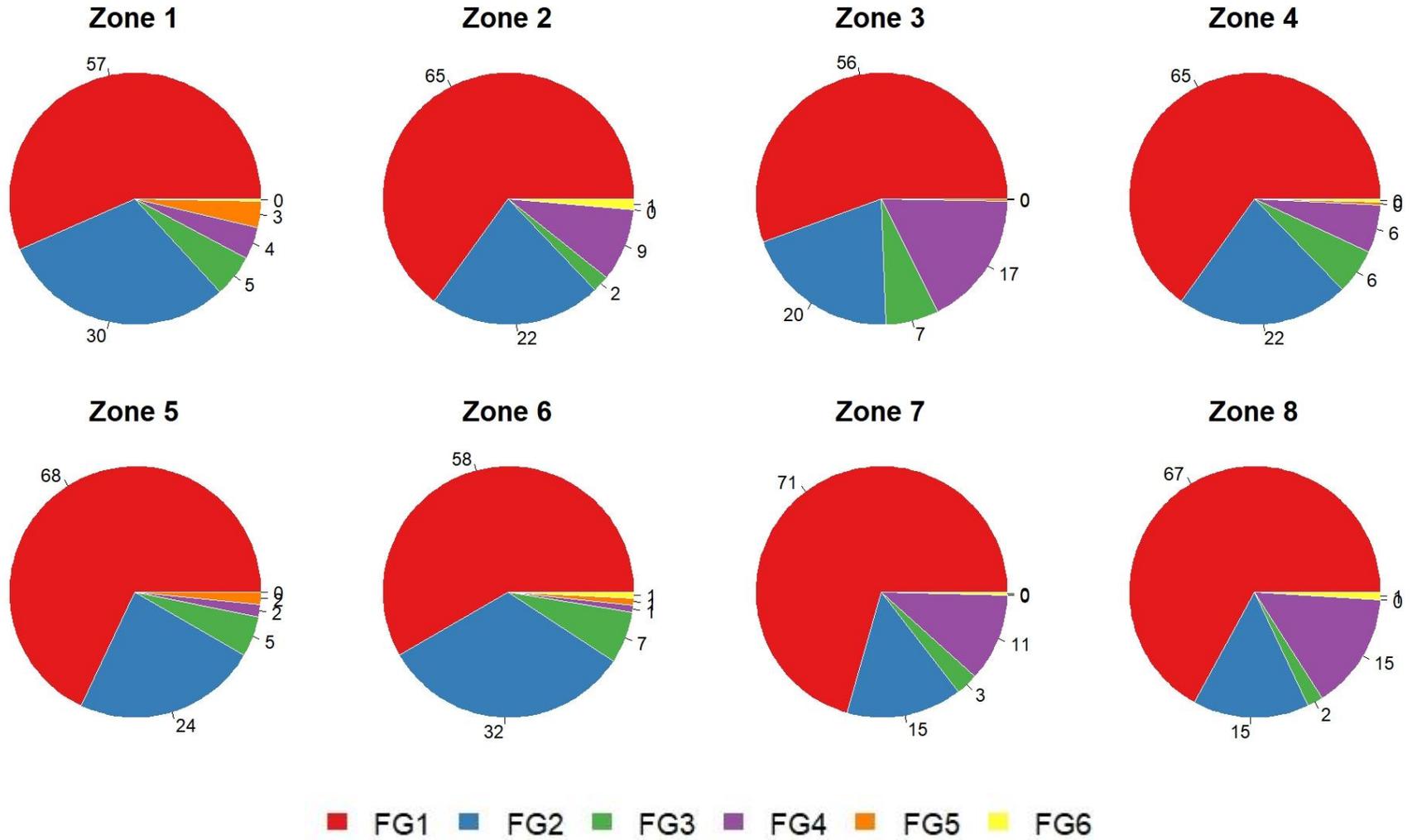


Figure S3: Once tree species were classified into functional groups (Table 1), per each zone in the Haliburton Forest, the abundance of all species belonging to the same functional group was summed up to then compute the relative abundance of the six main functional groups within zone. Numbers around each pie chart indicate the percentage of relative abundance of each functional group within each zone.

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