

Response diversity, functional redundancy, and post-logging productivity in northern temperate and boreal forests

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Abstract. The development of efficient ecosystem resilience indicators was identified as one of the key research priorities in the improvement of existing sustainable forest management frameworks. Two indicators of tree diversity associated with ecosystem functioning have recently received particular attention in the literature: functional redundancy (FR) and response diversity (RD). We examined how these indicators could be used to predict post-logging productivity in forests of Québec, Canada. We analysed the relationships between pre-logging FR and RD, as measured with sample plots, and post-logging productivity, measured as seasonal variation in enhanced vegetation index obtained from MODIS satellite imagery. The effects of the deciduous and coniferous tree components in our pre-disturbance diversity assessments were isolated in order to examine the hypothesis that they have different impacts on post-disturbance productivity. We also examined the role of tree species richness and species identity effects. Our analysis revealed the complementary nature of traditional biodiversity indicators and trait-based approaches in the study of biodiversity–ecosystem-functioning relationships in dynamic ecosystems. We report a significant and positive relationship between pre-disturbance deciduous RD and post-disturbance productivity, as well as an unexpected significant negative effect of coniferous RD on productivity. This negative relationship with post-logging productivity likely results from slower coniferous regeneration speeds and from the relatively short temporal scale examined. Negative black-spruce-mediated identity effects were likely associated with increased stand vulnerability to paludification and invasion by ericaceous shrubs that slow down forest regeneration. Response diversity outperformed functional redundancy as a measure of post-disturbance productivity most likely due to the stand-replacing nature of the disturbance considered. To the best of our knowledge, this is among the first studies to report a negative significant relationship between a component of RD and ecosystem functioning, namely coniferous RD and forest ecosystem productivity after a stand-replacing disturbance.

Key words: coniferous trees; deciduous trees; disturbances; ecosystem functioning; functional diversity; functional effect groups; functional redundancy; resilience; sustainable forest management.

INTRODUCTION

Natural and anthropogenic transformations of forest ecosystems threaten their capacity to sustain the provision of numerous ecological services (MacDicken et al. 2015, Thom and Seidl 2016). In the face of such uncertainty, the development of efficient resilience indicators capable of predicting ecosystems response to disturbances has been identified as one of the key research priorities in the improvement of existing sustainable forest management frameworks (Mori et al. 2017). Specifically, developing indicators capable of predicting primary productivity following natural and anthropogenic disturbances could be a very useful step toward that goal. While primary productivity is not the only ecosystem service provided by forests, it is considered to be a main concern of forest management (Mori et al. 2017), since it is one of the key supporting ecosystem processes other services depend on (Millennium Ecosystem Assessment 2005). For instance, primary productivity regulates the strength of cascading effects of large herbivores on

community function and structure (Pringle et al. 2007), and directly influences carbon dynamics (Hulvey et al. 2013). Preventing the decline of forest productivity following harvesting is therefore of particular interest to forest managers (Bose et al. 2014).

Tree diversity has been shown to play a fundamental role in temperate and boreal forest productivity (Liang et al. 2016). In these types of forest, species richness positively influences biomass production across all vegetation layers (Zhang et al. 2017). This relationship is stronger for overstory tree species richness, which is also positively associated with ecosystem multifunctionality and understory plant species richness (Gamfeldt et al. 2013). Primary productivity is also significantly affected by the traits of the dominant species due to species identity effects (Grossman et al. 2017). While compositional and functional tree diversity have been shown to contribute to forest productivity (Zhang et al. 2012), these two components of biodiversity can be independent of one another and have distinct impacts on ecosystem functioning. For instance, in an experimental study where functional diversity was allowed to vary independently from tree species richness, Tobner et al. (2016) showed that stands with identical species richness and greater functional diversity can be significantly more productive. Such discrepancies

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can be further magnified when the impact of disturbances is considered: following the flooding of a grassland experimental study, species richness reduced plant community resistance to flood while functional traits drove post-disturbance increase in biomass (Fischer et al. 2016).

Functional diversity indicators help define mechanistic links between biodiversity and function, including responses to disturbances (Cadotte et al. 2011). However, due to the large number of indicators available (Laliberté and Legendre 2010), indicator selection is highly dependent on the objective of the study. Two particularly promising functional diversity-based indicators of ecosystem resilience to disturbances have been highlighted by recent reviews on this subject: functional redundancy (FR) and response diversity (RD; Mori et al. 2013, 2017). The concept of FR is based on the insurance hypothesis put forward by Yachi and Loreau (1999): ecosystem functioning should be less affected by the absence or extinction of a species that can be replaced by another one that contributes similarly to ecosystem functioning, than by one for which no analogue is readily available. RD represents the different capacity that species within a given functional effect group (i.e., species that perform similar functions) respond to disturbances (Mori et al. 2013). In theory, greater inter-specific variation in responses to environmental fluctuations within each functional effect group should prevent disturbances from eliminating the majority of a given functional group, thus ensuring the preservation of the corresponding ecosystem functions (Elmqvist et al. 2003).

To date, empirical evidence demonstrating the ability of RD and, to a lesser degree, FR, to be adequate indicators of resilience to disturbances is still scarce, especially for forest ecosystems (Mori et al. 2017). The few real-world studies that do exist tend to be limited in scope and scale (Mori et al. 2013), or tend to indirectly test the linkages between functional traits and ecosystem functioning (Laliberté et al. 2010). Additionally, studies of the importance of RD in other taxa are not always conclusive (Cariveau et al. 2013). Although experimental studies on the relationships between FR, RD, and ecological resilience are more common, they usually focus on grassland ecosystems (Pillar et al. 2013) and their ability to infer real-world biodiversity–ecosystem-functioning relationships is restricted. Among other issues, such studies typically exclude disturbances that substantially influence biodiversity–ecosystem-functioning relationships (Brose and Hillebrand 2016).

We present a large-scale empirical study of northern temperate and boreal forest plots in Québec (eastern Canada) aiming to improve our understanding of the real-world relationships between pre-disturbance functional diversity indicators (functional redundancy, response diversity) and post-disturbance productivity trajectories within a management-relevant context. We treat deciduous and coniferous species as two functional effect groups because they contribute differently to ecosystem productivity, they are easily identified by forest managers, and changes in their composition should greatly influence ecosystem processes and services (see *Methodology: Functional effect groups*). We examined forest plots recovering from logging to test the hypothesis that pre-disturbance coniferous and deciduous functional redundancy and response diversity are good

indicators of post-disturbance productivity. We also controlled for tree species richness and species identity effects in order to assess whether trait-based approaches improve our understanding of biodiversity–ecosystem functioning when these traditional approaches are considered. In order to test this hypothesis, we built 10-yr time series of EVI (enhanced vegetation index), a remotely sensed primary productivity indicator (Huete et al. 2002), for forest plots of Québec (eastern Canada) that were clear cut immediately before the beginning of the time series. We further discussed underlying mechanisms driving these relationships and explored the management implications of our results.

METHODOLOGY

Study area

We quantified pre-disturbance tree functional diversity metrics from temporary sampling plots selected from the Quebec provincial forest inventory programs conducted between 1992 and 2009 (MFFP 2016). Among these plots, a subset was selected according to four criteria. First, plots had to have been measured and then clear cut between 2000 and 2006, so that an uninterrupted 10-yr post-disturbance time series of MODIS data was available. Hence, the 10-yr time series started between 2000 and 2006 and ended between 2011 and 2015. Second, in order to test the hypothesis that functional effect groups were important for determining post-disturbance productivity, plots needed to include at least one species from each group (deciduous and coniferous species). Both groups had to be present because Rao quadratic diversity, the measure used to calculate response diversity, can only be calculated when all functional groups are present. Otherwise, missing values are generated (Laliberté and Legendre 2010). Third, we discarded plots sampled more than 10 yr before they were clear cut. For all other plots, we considered unlikely that forest communities underwent major changes within 10 yr if no stand-replacing disturbances occurred. Finally, only temporary plots located in MODIS (moderate-resolution imaging spectroradiometer) 250-m pixels where over 80% of the area had undergone the same disturbance were kept. If the majority of a neighboring MODIS pixel had been clear cut but the pixel in which the temporary plot was positioned had not, the plot was associated with the neighboring MODIS pixel instead.

A total of 796 plots were selected according to these criteria (Fig. 1). These plots were spread across a latitudinal gradient that encompasses multiple bioclimatic domains: sugar maple–bitternut hickory (*Carya cordiformis*), sugar maple–yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*)–yellow birch, balsam fir–white birch (*Betula papyrifera*), and black spruce (*Picea mariana*)–feathermoss (Robitaille and Saucier 1998). Each plot consisted of a circular area of 400 m². Within this area, all trees whose diameter at breast height (DBH) was greater than 9 cm were recorded and their DBH was measured (MFFP 2016). A smaller 40-m² circular plot in which all saplings (DBH ≤ 9 cm) were identified and counted by DBH class was located at the center of each 400-m² plot. Sampling effort varied between main vegetation zones

(deciduous, coniferous, and mixed) and followed a random stratified design (MFFP 2016).

Functional effect groups

We adopted a hierarchical effect–response functional trait framework to analyze the relationships between tree functional redundancy, response diversity, and ecosystem productivity (Laliberté et al. 2010). We first employed an unsupervised hierarchical clustering algorithm to identify functional effect groups using six effect traits: (1) average maximum height; (2) leaf phenology (whether species lose all foliage seasonally or not); (3) nutrient uptake strategy (presence of arbuscular mycorrhiza, ectomycorrhizal, or both); (4) nitrogen content per leaf mass unit; (5) wood density; and (6) leaf mass per area (R's base package hclust algorithm; R Core Team 2017). These traits are publicly available (Paquette et al. 2015) and have been suggested as effect traits associated with tree growth, photosynthetic rate, and productivity (Cornelissen et al. 2003). The clustering algorithm followed Ward's minimum variance method and was applied to a Gower dissimilarity matrix (caret R package, version 6.0-62; Kuhn et al. 2015). A visual inspection of the resulting dendrogram (Appendix S1) revealed two main functional effect groups: coniferous and deciduous species.

Considering deciduous and coniferous species as having distinct effects on forest productivity and, more generally, on function, makes sense for a number of reasons. First, in the study area, species within these two groups support distinct animals (Drapeau et al. 2000) and can be conceived of as “umbrella” species that reflect functional diversity in the understory layers (Fourrier et al. 2015). Second, coniferous species have greater leaf mass per area, which is associated with longer leaf lifespan, increased leaf defenses and reduced decomposition, growth, and maximum photosynthetic rates (Data S1; Cornelissen et al. 2003). Third, wood density,

which is associated with carbon storage capacity, relative growth rate, and stem defenses (Cornelissen et al. 2003), tends to be greater in deciduous species (Data S1). Finally, coniferous species have a narrower range of average maximum height (Data S1), a functional trait that has been linked to competitive vigor, stress response strategies, and aboveground biomass (Cornelissen et al. 2003). Overall, separating the effects associated with these two groups also allows us to identify potentially opposing effects on post-logging productivity, if they are present.

Functional redundancy and response diversity

We measured deciduous and coniferous pre-disturbance functional redundancy (FR) and response diversity (RD) on each identified plot following the framework and code provided by Ricotta et al. (2016). FR was estimated with the six previously mentioned effect traits used to establish the functional effect groups: average maximum height, leaf phenology, nutrient uptake strategy, nitrogen content per leaf mass unit, wood density, and leaf mass per area. The following seven functional response traits were used to estimate RD: average maximum height, growth rate, wood density, vegetative reproduction capacity, seed mass, shade tolerance, and capacity to establish seed banks. These response traits are directly associated with tree regeneration speed and strategies: these influence tree species ability to colonize sites after disturbance and are key aspects of post-disturbance recovery (Cornelissen et al. 2003). Deciduous and coniferous response diversity were calculated as the Rao quadratic diversity. This functional-dispersion-based indicator estimates the average distance between two randomly selected individuals within the functional trait space (Zoltan 2005). Functional redundancy was calculated as 1 minus the ratio of Rao quadratic diversity and the Simpson index. Thus, this indicator compares the observed functional diversity

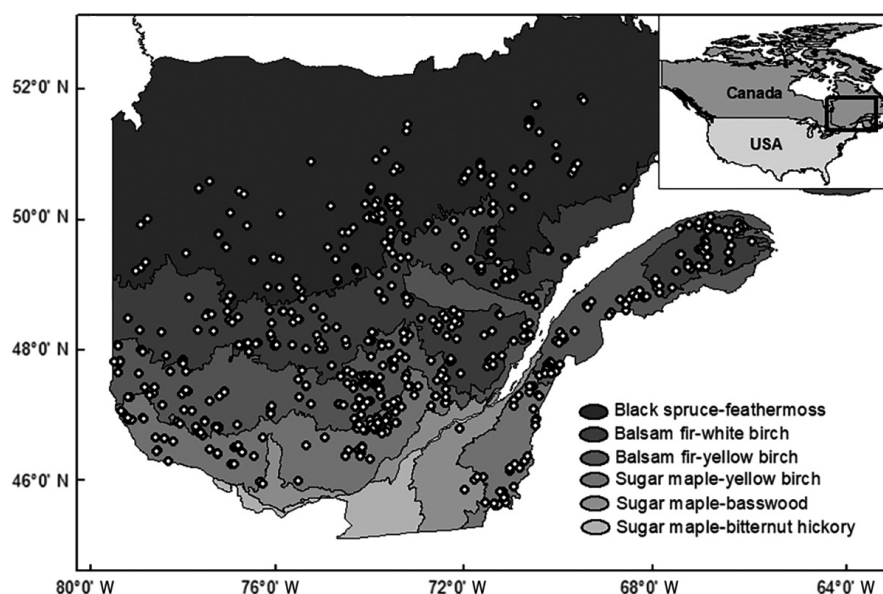


FIG. 1. Map of the study area: Québec, Canada. White points represent study plots. Background shading represents bioclimatic domains.

with that of the most functionally distinct community possible that shares an identical abundance distribution (Ricotta et al. 2016). Gower dissimilarity matrices were chosen because they can handle both missing values and mixed variable types (continuous, ordinal and categorical). These two metrics were not remeasured after clear-cutting took place (post-disturbance period). Species response trait values were weighted by basal area relative abundance. Most trait values were collected by a previous study (Paquette et al. 2015). Missing values and additional variables were collated from other online data sources (Data S1).

Ecosystem productivity metric

Post-disturbance 10-yr productivity time series were built using 16-d MODIS EVI (enhanced vegetation index) data. EVI is a productivity indicator based on the surface reflectance of solar radiation that has clear links to primary productivity (Pettorelli et al. 2005). The MODISTools R package (Tuck et al. 2014) was used to download each temporary plot's 250-m pixel EVI and pixel reliability data from the MOD13Q1 MODIS product (Didan et al. 2015). The original 16-d time series data were smoothed using TIMESAT (Jönsson and Eklundh 2004). EVI data contribution to the smoothing functions was weighted using the complementary reliability layer and outliers were removed by multiplying the weights from a seasonal trend decomposition with the original weights. Asymmetric Gaussian functions were then fit to the data. This type of function was chosen because it has been found to be among the top two performing smoother functions for this kind of data set (Hird and McDermid 2009) and appeared to perform slightly better than the double logistic function for our data set. The seasonal variation of EVI (maximum EVI minus minimum EVI; svEVI), a productivity measure that has been shown to be significantly correlated with gross primary productivity in North America (Sims et al. 2006), was then calculated. In order to remove any badly smoothed data from the data set, svEVI points above the 0.999 and below the 0.001 percentiles of the distribution were removed.

Statistical analysis

Autoregressive linear regression models of svEVI (nlme R package; Table 1; Pinheiro et al. 2015) were built with the following explanatory variables: (1) yearly climate variables; (2) pre-disturbance stand characteristics; (3) year of logging; (4) site post-disturbance land cover class at the year 2013 (deciduous, coniferous or shrubland); (5) pre-disturbance tree species richness; (6) pre-disturbance relative abundance of the most abundant tree species of each functional group (black spruce and white birch); (7) pre-disturbance coniferous and deciduous FR and RD; (8) number of years since disturbance; and (9) a binary categorical variable (set at 1 for 2–5 yr after disturbance) that was introduced to allow the models to more realistically consider the relationships between FR, RD, and time since disturbance observed in the data. The first year after disturbance was not included in this categorical variable because the noise introduced by the time lag between the time since disturbance and the first growing season (from a few weeks up to several months)

had a greater impact on the first measurement of productivity.

Plot-level yearly climate variables (average annual temperature, annual precipitation, growing degree days over 5°C, potential evapotranspiration, water balance, and growing season length) were calculated using BioSIM (version 10; Régnière et al. 2014), a software tool that uses geographical coordinates, elevation, slope, and aspect to interpolate climate data. Pre-disturbance stand characteristics (age class, height class, density class, and cover type) were directly measured in the sampling plots (MFFP 2016). The top three principal components of climate and pre-disturbance stand characteristics were then extracted through two Principal Component Analysis (PCA). For the PCAs, a categorical variable (cover type) was transformed in three binary variables, ordinal variables were first transformed in numeric variables according to the middle point of each class, numeric variables were log-transformed, and data was centered by subtracting the mean and scaled by dividing the predictor values by the standard deviation (caret R package, version 6.0-62; Kuhn et al. 2015).

Considering that site productivity is greatly influenced by different post-logging regeneration trajectories, post-disturbance land cover class was estimated using the land cover type 3 of the MODIS MCD12Q1 product (Friedl et al. 2010). This MODIS product provides an estimate of the land cover class at a spatial resolution of 500 m, which is larger than the one svEVI was estimated at, but is still likely to reflect the type of regeneration of the disturbed area. Although this MODIS product was not available for the whole time series (it ended in the year 2013 and was not available for the whole time series up to that year), its value by the year 2013 was included in the regression models as an indicator of the type of vegetation the disturbed area was likely regenerating into.

Since the identity of the tree species present can have considerable impacts on ecosystem processes (Hooper and Vitousek 1997) and it has been suggested that primary productivity can be substantially influenced by the traits of the dominant species (Grime 1998), the possible influence of species identity effects on post-disturbance productivity was also assessed. In order to do this, within-group pre-disturbance basal area relative abundance of the most abundant species within each functional group (deciduous, white birch; coniferous, black spruce) was added to the candidate model set.

A total of 10 autoregressive linear regression models with svEVI as the response variable were built. Models shared all previously mentioned variables except FR, RD, and species relative abundances. These variables were added to distinct models as combinations of two groups of variables: (1) functional diversity metrics (FR and RD, FR only, and RD only) and (2) species relative abundance (none, black spruce, and white birch). A null model with tree species richness but without FR, RD, or species relative abundance was also included in the candidate model set. All input variables were standardized to a mean of 0 and a standard deviation of 0.5 in order to set all effect sizes on comparable scales and facilitate their interpretation (Grueber et al. 2011). The temporal correlation structure of our data set was accounted for by specifying unique plot ID as a random effect with an

TABLE 1. Candidate model sets built to test the influence of functional redundancy (FR), response diversity (RD), and species identity effects on the RD–post-disturbance-productivity relationship.

Model parameters	Model									
	1	2	3	4	5	6	7	8	9	10
Time after disturbance	X	X	X	X	X	X	X	X	X	X
Early years	X	X	X	X	X	X	X	X	X	X
Year of logging	X	X	X	X	X	X	X	X	X	X
Climate	X	X	X	X	X	X	X	X	X	X
Stand chars	X	X	X	X	X	X	X	X	X	X
Tree species richness	X	X	X	X	X	X	X	X	X	X
Land cover	X	X	X	X	X	X	X	X	X	X
Coniferous FR		X	X		X	X		X	X	
Deciduous FR		X	X		X	X		X	X	
Coniferous RD	X	X		X	X		X		X	
Deciduous RD	X	X		X	X		X		X	
Black spruce	X	X	X							
White birch							X	X	X	
Marginal R^2	0.48	0.49	0.48	0.47	0.47	0.46	0.47	0.46	0.47	0.45
Conditional R^2	0.71	0.71	0.71	0.7	0.71	0.7	0.7	0.7	0.71	0.7
ΔAIC_c	0	7.98	9.11	22.3	28.54	29.13	32.48	37.63	38.23	51.19

Notes: Models are sorted by increasing values of AIC_c (second-order Akaike information criterion) and the top model is located on the left. “X” indicates that the parameter is used in the model. Time after disturbance is the number of growing seasons after clear cut; early years is a binary categorical variable with value 1 for years 2 to 5; year of logging is the calendar year when the stand was clear-cut; climate represents the top three principal components of the previously described PCA of climate variables; stand chars represents the top three principal components of the previously described PCA of stand characteristics variables; tree species richness is the pre-disturbance number of tree species; land cover is the MODIS post-disturbance land cover at year 2013; FR is functional redundancy; RD is response diversity; black spruce and white birch are the basal area relative abundance among the corresponding functional effect group.

autocorrelation structure of order 1. The best models were selected according to the AIC_c (second-order Akaike Information Criterion; Burnham and Anderson 2003).

RESULTS

Functional redundancy and response diversity

The model including coniferous and deciduous pre-disturbance response diversity and black spruce relative abundance was the top model within the main candidate model set (Table 1). Our analysis also shows that functional diversity can complement species richness and species identity effects in explaining post-disturbance productivity: the top model was more parsimonious than models that did not include either functional diversity or species richness, and models that considered the tree community as a whole, instead of splitting it into two functional effect groups (Data S1). The fixed component of the top model explained approximately 48% of the observed variation and the whole model explained approximately 71% (Table 1). All models were substantially more parsimonious than the null model that did not consider FR, RD, or any species identity effects (Table 1).

Our analyses revealed a significant negative relationship between coniferous RD and post-disturbance productivity (Table 2). Two dominant species mixtures likely mediate this relationship. First, black-spruce–balsam-fir-dominated stands are common throughout our study area (Fig 2h). These plots tend to have relatively low levels of pre-disturbance coniferous RD and high levels of post-disturbance productivity (top parabola in Fig. 3a, b). Second, balsam fir–white spruce stands are also relatively common and have high levels of

pre-disturbance coniferous RD and low levels of post-disturbance productivity (bottom parabola in Fig. 3a).

We found a significant positive relationship between pre-disturbance deciduous RD and post-disturbance productivity (Table 2). This result supports the initial hypothesis that increased RD should lead to increased post-disturbance

TABLE 2. Generalized linear mixed effect model coefficients from the top model.

Parameter	Estimate	SE	P
Intercept	0.264	0.0040	<0.00001
Time after disturbance	0.075	0.0018	<0.00001
Early years	0.041	0.0014	<0.00000
Year of logging	0.000	0.0041	0.97810
Climate PC1	0.005	0.0022	0.01690
Climate PC2	0.008	0.0015	<0.00001
Climate PC3	−0.003	0.0011	0.00770
Stand chars PC1	0.046	0.0052	<0.00001
Stand chars PC2	0.013	0.0041	0.00120
Stand chars PC3	0.020	0.0043	<0.00001
Tree species richness	0.040	0.0074	<0.00001
Land cover: deciduous	0.045	0.0052	<0.00001
Land cover: shrub	0.031	0.0066	<0.00001
Coniferous RD	−0.029	0.0047	<0.00001
Deciduous RD	0.013	0.0062	0.03510
Black spruce	−0.027	0.0047	<0.00001

Notes: Variable estimate effect sizes have been centered and standardized (Grueber et al. 2011), so they are directly comparable. PC denotes principal components. SE denotes standard error. Variable nomenclature follows the same code as Table 1. The reference level for the land cover variable is coniferous regeneration. $P \leq 0.05$ indicates significant parameters.

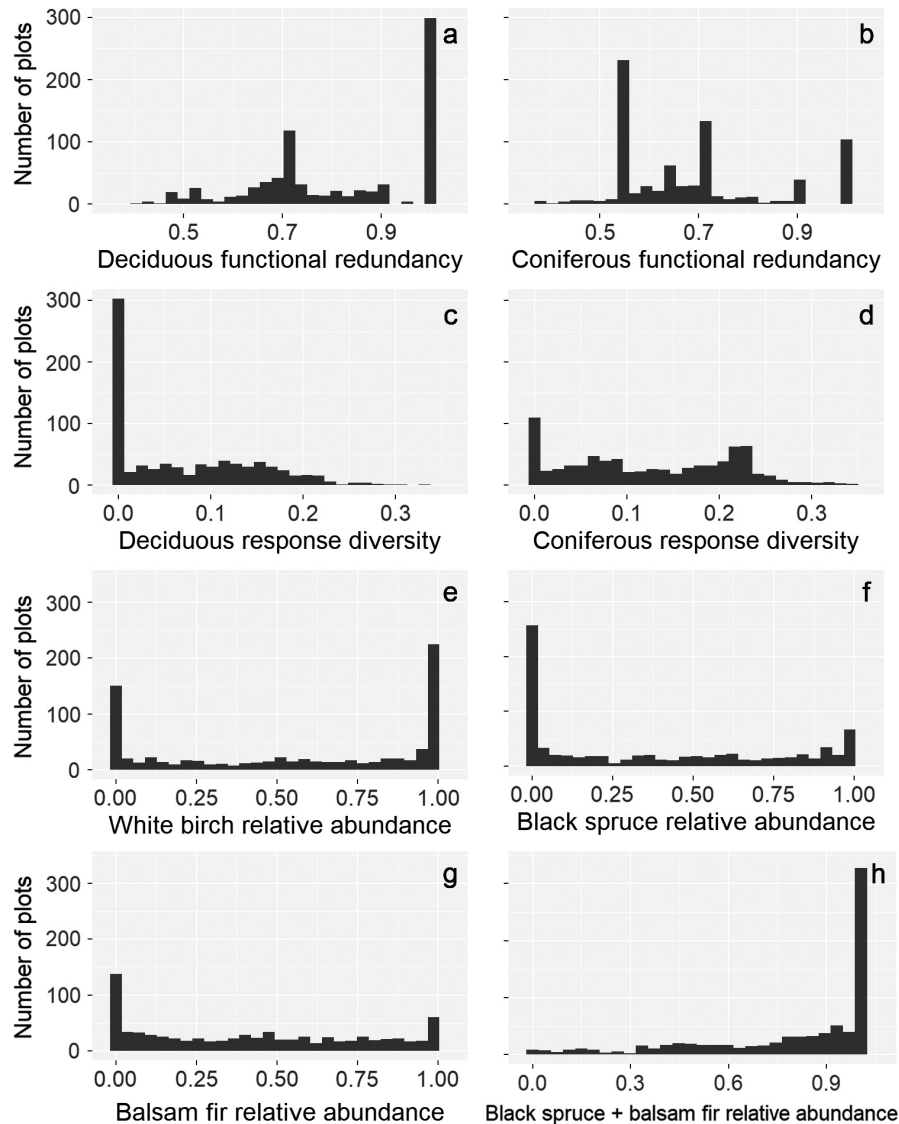


FIG. 2. Histograms of (a) deciduous functional redundancy, (b) coniferous functional redundancy, (c) deciduous response diversity, (d) coniferous response diversity, (e) white birch relative abundance, (f) black spruce relative abundance, (g) balsam fir relative abundance, and (h) sum of black spruce and balsam fir relative abundance. Species relative abundance is the basal area relative abundance within the corresponding functional effect group.

productivity. While significant, the P value of this relationship is relatively close to the commonly accepted significance threshold of 0.05. The P value is only marginally significant probably because of the large number of plots whose deciduous component is dominated by a single deciduous species, namely white birch (Fig. 2a, e): these plots have low values of deciduous RD and post-disturbance productivity (Fig. 3c). Deciduous and coniferous functional redundancy were not present in the top model of our candidate model set (Table 1).

Species identity effects

Since functional effect groups were often dominated by a few species, species identity effects were widespread in our study area. The pre-disturbance deciduous effect group of ~38% of all plots ($n = 299$) was dominated by white birch. This resulted in a large number of plots with maximal

pre-disturbance deciduous functional redundancy (FR; Fig. 2a) and minimal pre-disturbance deciduous response diversity (RD; Fig. 2c). White birch is a species of particular interest, since it dominated the deciduous component in 25.6% of the plots in our data set ($n = 204$; Fig. 2e).

The coniferous functional effect group was less dominated by any single species, but significant species identity effects were still present. Hence, fewer plots had maximal levels of pre-disturbance coniferous FR (Fig. 2b) and minimal levels of pre-disturbance coniferous RD (Fig. 2d). Nevertheless, black spruce and balsam fir were particularly dominant within the coniferous functional effect group: over three-quarters of the coniferous basal area was occupied by black spruce and balsam fir in 69.6% of our plots ($n = 554$; Fig. 2h).

Black spruce identity effects appear to play an important role in post-disturbance productivity: black spruce relative abundance was a significant variable negatively correlated

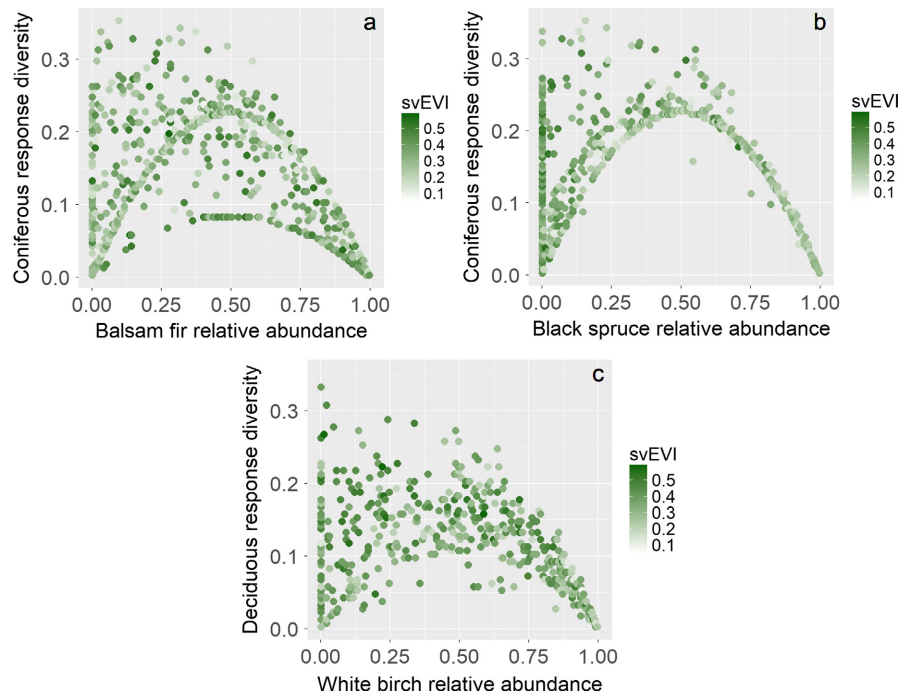


FIG. 3. (a) Balsam fir and (b) black spruce relative abundance plotted against coniferous response diversity and (c) white birch relative abundance plotted against deciduous response diversity. Species relative abundance is the basal area relative abundance within the corresponding functional effect group. Points are colored according to the seasonal variation of the enhanced vegetation index (svEVI) measured 3 yr after disturbance.

with post-disturbance productivity (Table 2). Black spruce relative abundance also appears to be negatively associated with coniferous RD, as plots where black spruce was less dominant tended to have greater levels of pre-disturbance coniferous RD (Fig. 3b). Direct white birch identity effects on post-disturbance productivity do not appear to be significant: models containing this variable were considerably less parsimonious than the top model (Table 1).

DISCUSSION

The complementarity between traditional species-oriented biodiversity indicators, such as species richness, and functional diversity indicators reported in this study highlights the contribution of trait-based approaches to the study of biodiversity–ecosystem–functioning relationships. While the complementary nature of the effect of these facets of biodiversity and tree productivity has been reported elsewhere (Paquette and Messier 2011), few studies have explicitly addressed these relationships with respect to disturbances. For example, a simulation study of a temperate central European forest found that the positive effects of tree species richness on net primary productivity resilience to simulated natural disturbances was likely mediated by changes in functional diversity (Silva Pedro et al. 2015). However, direct effects of changes in functional diversity were not assessed. As functional diversity indicators can be independent of species richness (Ricotta et al. 2016), it is important to take into account both contributions when studying biodiversity–ecosystem relationships.

The absence of pre-disturbance functional redundancy (FR) from the top model is possibly due to the severity of the analysed disturbance. According to Yachi and Loreau (1999), FR should be an efficient indicator of ecosystem resilience to disturbances because the impact of the loss of a given species on ecosystem functioning should be reduced when there are multiple species performing similar functions. Indeed, this hypothesis appears to hold when partial disturbances are considered (Pillar et al. 2013). However, as our results suggest, this is unlikely to be the case when severe stand-replacing disturbances occur: as these types of disturbances tend to extirpate all mature trees from a given area, a larger pool of species performing similar functions is unlikely to improve post-disturbance performance of those ecosystem functions.

In the face of such severe disturbances, response diversity (RD) is more likely to influence post-disturbance ecosystem functioning. Instead of measuring how similarly species perform a given ecosystem function, this indicator quantifies how species within the same functional group respond to various types of disturbances (Elmqvist et al. 2003). As disturbance response is trait dependent (Mori et al. 2013), an appropriate trait selection can allow researchers to successfully quantify species responses to stand-replacing disturbances. The relevance of this variable is supported by the significant negative and positive relationships reported between coniferous and deciduous RD and post-disturbance productivity, respectively. The observed differences in effect direction likely result from the different regeneration speeds of these two functional groups and the relatively short temporal scale examined (up to 10 yr after clear cutting took

place). Considering that, following severe disturbances, deciduous species tend to occupy the upper canopy cover faster than the main shade-tolerant coniferous species within our study area (Pothier and Auger 2009), we are more likely to detect the effect of multiple deciduous regeneration strategies on post-disturbance productivity within such a relatively short period of time. As their coniferous counterparts are slower to recover, we were probably only able to detect the effect of a limited number of regeneration strategies on post-disturbance productivity. A bias in the relationships between the seasonal variation of EVI and gross primary productivity across vegetation composition types could have also potentially influenced the observed results: while the EVI–gross-primary-productivity relationship is strong in coniferous forests, it is generally stronger in deciduous forests (Huet et al. 2010). These results might also have been affected by the response traits used: even though all chosen response traits are associated with tree regeneration speeds and strategies (Cornelissen et al. 2003), their importance might vary according to forest type.

Black-spruce-mediated identity effects influenced the magnitude of the effect of coniferous RD and FR on post-disturbance productivity. The observed negative black-spruce–productivity relationship is supported by the mass-ratio hypothesis, which proposes that some ecosystem functions are mainly dictated by the dominant species (Grime 1998). This hypothesis has previously been proposed as an alternative mechanism to explain productivity in grassland ecosystems (Sasaki and Lauenroth 2011) and has been promoted as an important underlying process driving productivity in forests (Grossman et al. 2017, Mori et al. 2017). Moreover, identifying significant identity effects of well-studied tree species facilitates the interpretation of functional diversity indexes, as it allows us to interpret the results in light of ecological processes that are not necessarily directly related to the ecophysiological traits examined in this study. For instance, black-spruce-dominated stands are known to be at a considerably greater risk of decreased productivity due to paludification and invasion by ericaceous shrubs (Thiffault et al. 2013). Therefore, these negative effects on productivity associated with black spruce likely mediate the observed negative relationship between coniferous response diversity and post-logging productivity.

While our results suggest that common species play a more critical role in ecosystem functioning, the number and nature of the services in question needs to be taken into account before strong conclusions are drawn. In the literature, it is unclear whether common or rare species are more important in dictating biodiversity–ecosystem-functioning relationships. Common species appear to be more influential when productivity is the ecosystem function under consideration (Vile et al. 2006), but some regulating and recreational services appear to be more dependent on rare species (Zavala et al. 2004). These relationships are further complicated when multifunctionality, one of the main objectives of sustainable forest management (Gustafsson et al. 2012), is directly acknowledged. Even though primary productivity directly influences other ecosystem functions (e.g., carbon storage; Hulvey et al. 2013), multifunctionality was not directly considered in our analyses. Further studies are needed to disentangle these complex relationships, as the few published

scientific articles on this issue have found evidence of the importance of both rare (Soliveres et al. 2016) and dominant species (Lohbeck et al. 2016) in driving ecosystem multifunctionality.

Ideally, further real-world studies should also focus on larger spatial and temporal scales and should take cross-scale interactions into account, as extrapolating from small-scale, short-term experiments might lead to erroneous conclusions (Brose and Hillebrand 2016). In fact, cross-scale interactions are known to influence local and regional ecosystem functioning stability (Loreau et al. 2003). For instance, Higgins and Scheiter (2012) showed that the impacts of abrupt, small-scale regime shifts in vegetation cover are decreased at a landscape-level due to their asynchrony and Craven et al. (2016) demonstrated how interactions between local response diversity and habitat connectivity affect landscape-level resilience of a temperate forest. Furthermore, a multi-trophic, large-scale study recently showed that ecosystem functioning drivers at small scales likely differ from those at larger scales: while identity and niche complementarity effects drove small-scale ecosystem productivity, ecosystem functioning at larger scales was only directly associated with total biomass and species richness (Barnes et al. 2016). The influence of temporal scales should also be considered: mechanisms driving ecosystem function may vary across time (Loreau and de Mazancourt 2013) and short-term post-disturbance productivity does not necessarily equate to long-term productivity. The use of novel methodologies, such as structural equation modelling (Barnes et al. 2016) and probability density-based functional diversity indexes (Carmona et al. 2016), should allow future research to improve our understanding of complex cross-scale biodiversity–ecosystem-functioning relationships and help inform policy and ecosystem management.

CONCLUSIONS

Our study is one of the first to use real-world data of sampled forest plots spread across a large spatial area to analyze the direct relationships between post-disturbance productivity and two functional diversity indicators associated with ecosystem resilience: functional redundancy and response diversity. We found significant response diversity–ecosystem-productivity relationships after logging in forested ecosystems, including opposing effects of coniferous and deciduous response diversity: deciduous response diversity was positively associated with post-logging productivity, while the effect of coniferous response diversity on the response variable was negative. We also report negative black-spruce-mediated identity effects that likely resulted from increased stand vulnerability to paludification and post-disturbance invasion by ericaceous shrubs.

Our results reveal the complementary nature of traditional biodiversity indicators and trait-based approaches in the study of biodiversity–ecosystem-functioning relationships in dynamic forest ecosystems. Regarding the functional diversity indicators studied, these results suggest that response diversity is a more appropriate indicator of ecosystem productivity recovery after logging within northern temperate and boreal forests than functional redundancy. This is likely due to the capacity of response diversity to quantify

the effect of species' disturbance response strategies. The relatively short time scale considered and the use of a single ecosystem function, primary productivity, must be taken into account when interpreting these results. Future work should focus on disentangling the complex relationships between biodiversity and multiple ecosystem functions and on assessing these relationships at multiple spatial and temporal scales, as these are essential aspects to take into account in sustainable ecosystem management frameworks.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1727/full>

DATA AVAILABILITY

Data available from the Québécois Ministry of Forest, Fauna, and Parks: <https://www.donneesquebec.ca/recherche/fr/dataset/placettes-ec-hantillons-permanentes-1970-a-aujourd-hui/resource/72828f8a-d008-4119-b246-89e6103120cb>