



## Harvesting influences functional identity and diversity over time in forests of the northeastern U.S.A.



M.T. Curzon<sup>a,\*</sup>, A.W. D'Amato<sup>b</sup>, S. Fraver<sup>c</sup>, B.J. Palik<sup>d</sup>, A. Bottero<sup>e</sup>, J.R. Foster<sup>a,b</sup>, K.E. Gleason<sup>f</sup>

<sup>a</sup> Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue North, Saint Paul, MN 55108, USA

<sup>b</sup> Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, USA

<sup>c</sup> School of Forest Resources, University of Maine, Orono, ME 04469, USA

<sup>d</sup> USDA Forest Service, Northern Research Station, 1831 Hwy 169 E., Grand Rapids, MN 55744, USA

<sup>e</sup> Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

<sup>f</sup> Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512, USA

### ARTICLE INFO

#### Article history:

Received 28 December 2016

Received in revised form 24 May 2017

Accepted 31 May 2017

#### Keywords:

Functional diversity  
Silviculture  
Temperate forest  
Disturbance  
Functional identity  
Plant traits  
Productivity  
Forest management

### ABSTRACT

Concern over global environmental change and associated uncertainty has given rise to greater emphasis on fostering resilience through forest management. We examined the impact of standard silvicultural systems (including clearcutting, shelterwood, and selection) compared with unharvested controls on tree functional identity and functional diversity in three forest types distributed across the northeastern United States. Sites included the Argonne, Bartlett, and Penobscot Experimental Forests located in Wisconsin, New Hampshire, and Maine, respectively. We quantified functional trait means for leaf mass per area, specific gravity, maximum height, height achieved at 20 years, seed mass, drought tolerance, shade tolerance, and flood tolerance as well as standard functional diversity measures from standing biomass reconstructed at the beginning and end of a 20-year study period using increment cores and historic inventory data. As expected, functional identity differed between harvest methods with means for plant traits associated with later stages of succession (e.g. shade tolerance) increasing in stands managed with selection systems. Opposite trends occurred with greater canopy disturbance, and functional diversity indices remained stable over time in the absence of disturbance. Estimates of functional diversity and functional identity hold promise as important approaches for evaluating outcomes of forest management, particularly as the connections among functional diversity, delivery of ecosystem services, and ecosystem resilience are further developed.

© 2017 Published by Elsevier B.V.

### 1. Introduction

Interest in managing forests for climate adaptation and mitigation has added to the spectrum of objectives that policymakers, landowners, and managers must strive to balance (Park et al., 2014). Managing forests for different suites of species may factor into adaptation approaches as the value of different forest species increasingly lies not only in their ability to meet demands for forest products and ecosystem services, but also in varying abilities to endure environmental change such that provision of those products and services continues in a predictable way (Aubin et al., 2016). Outcomes of management approaches have traditionally been viewed through their impacts on the relative abundance of various tree species and life forms (Toumey, 1925). However, consideration of species traits may factor into the development of

adaptation approaches leading to a shift in emphasis to managing for an array of functional attributes within a given community (Aubin et al., 2016; Gavinet et al., 2016), assuming that a diversity of functional traits translates to greater resilience (Elmqvist et al., 2003; Brang et al., 2014; Gazol and Camarero, 2016). In order to develop adaptive management approaches for temperate forests that address global change, we must evaluate the extent to which forest management practices influence the distribution and abundance of functional traits in a community. Our ability to do so previously has been hampered by a dearth of long-term empirical data.

A broad suite of factors is projected to profoundly influence the structure and function of forest ecosystems over the next century (Millar et al., 2007). For example, future successional processes and stand development may differ from expectations as changing disturbance regimes and climatic conditions differentially affect the regeneration success of certain tree species and elevate levels of tree mortality (Carnicer et al., 2011; Martinez-Vilalta and

\* Corresponding author.

E-mail address: [mcurzon@umn.edu](mailto:mcurzon@umn.edu) (M.T. Curzon).

Lloret, 2016). Non-native, invasive species have altered the composition and function of many communities (Paillet, 2002) and are expected to become an increasingly important component of forested regions around the globe (Lovett et al., 2016). Even native species with altered population dynamics can alter fundamental ecosystem processes (Horsley et al., 2003; McKee and Aukema, 2015). Thus, it has become more important to understand how management actions influence forest communities in terms of the traits that determine species' response to environmental change ("response traits"; Lavorel and Garnier, 2002; Suding et al., 2008) in order to improve prediction of management outcomes in light of new threats (Keddy and Shipley, 1989; Prach and Walker, 2011).

Functional diversity also contributes directly to the provision of ecosystem services (Isbell et al., 2011; Lavorel, 2013), largely through "effect traits", those traits that drive species' influence on ecosystem processes (Suding et al., 2008). Trade-offs exist in traits within species that may be summarized by a fast-slow economic spectrum in which faster-growing, less competition-tolerant species dominate early successional stages and are gradually replaced by slower-growing species that tolerate shade and competition to greater degrees (Reich, 2014; Woodall et al., 2015; Kunstler et al., 2016). The implications of this trade-off include balancing maximum short-term productivity with long-term provision of ecosystem services such as carbon storage and nitrogen retention (Grigulis et al., 2013). Evidence also suggests trade-offs may exist between stress tolerances, with negative correlations commonly observed between drought and shade tolerance and drought and flood tolerance across continents and most woody taxa (Niinemets and Valladares, 2006).

Silviculture has long been used to intervene in succession and manage forest composition and structure based on knowledge of the autecology or silvics of tree species (Baker, 1934; Puettmann, 2011), but the impact of harvest decisions on functional identity (mean value of functional traits in a community) and functional diversity is rarely quantified (but see Baraloto et al., 2012; Neill and Puettmann, 2013) despite the value of this knowledge for understanding forest responses to future disturbance and stress (Chmura et al., 2011). We used long-term data from three U.S. Forest Service Experimental Forests in the northeastern U.S. to assess the impacts of commonly used silvicultural methods (clearcutting, shelterwood, selection, crop tree release) relative to controls on functional identity and functional diversity in northern hardwood and mixed conifer forests. Based on previous studies in tropical and subtropical forest ecosystems (e.g. Böhnke et al., 2014; Bu et al., 2014; Vicente-Silva et al., 2016) we expected functional dispersion (a measure of functional diversity that describes the distribution and spread of species in trait space; Laliberte and Legendre, 2010) to remain stable over time in mature, undisturbed forest. Theory predicts that disturbance filters species by their traits and, resultingly, can reduce functional dispersion (Diaz et al., 1998). While even-aged (e.g. shelterwood and clearcutting) and uneven-aged (e.g. selection) silvicultural systems differ in the amount of canopy removed at a given point of time, harvests for both constitute a disturbance in which resources are removed from the system (White and Pickett, 1985). Thus, we expected treated stands to have lower functional dispersion compared to undisturbed controls and greater functional divergence (greater expression of more extreme trait values), depending on treatment. Additionally, we hypothesized stands managed with shelterwood and clearcutting systems would exhibit functional identity representative of early- to mid-successional communities (i.e., lower shade tolerance, higher drought tolerance, lower leaf mass per area; Connell and Slatyer, 1977; Bazzaz, 1979; Horn, 1981) relative to controls and stands managed with selection to assume

functional identities indicative of later-successional stages, more similar to unharvested controls.

## 2. Methods

### 2.1. Study sites

The three study sites consist of U.S. Forest Service Experimental Forests distributed across the northern forest region of the north-eastern United States. The Argonne Experimental Forest (AEF), located in north-central Wisconsin, is dominated by *Acer saccharum* Marshall (sugar maple), *Tilia americana* L. (American basswood), *Fraxinus americana* L. (white ash), and *Betula alleghaniensis* Britton (yellow birch). Mean annual temperature is 5 °C, and mean annual precipitation is 81.3 cm (Adams et al., 2008). The Bartlett Experimental Forest (BEF) in north-central New Hampshire is dominated by *A. saccharum*, *Tsuga canadensis* L. (eastern hemlock), *Fagus grandifolia* Ehrh. (American beech), *B. alleghaniensis*, *F. americana*, and *A. rubrum* L. (red maple). Annual temperature averages 6.2 °C (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, accessed 6 Dec 2016), and mean annual precipitation is 127 cm (Adams et al., 2008). The Penobscot Experimental Forest (PEF) in Maine is dominated by *T. canadensis*, *Abies balsamea* L. (balsam fir), *Picea rubens* Sarg. (red spruce), *Pinus strobus* L. (Eastern white pine), *A. rubrum*, and *Populus tremuloides* Michx. (trembling aspen). The site has an average annual temperature of 6.6 °C, and receives an average of 106 cm of precipitation annually (Adams et al., 2008). Structural characteristics such as density of trees with DBH > 50 cm and basal area in unharvested control stands (Appendix A) fell within the range reported for old-growth forests of the same types in each respective region (Tyrrell et al., 1988).

### 2.2. Dataset

Sampling plots for this study were superimposed on or placed adjacent to existing permanent plots associated with ongoing silvicultural studies that varied the type of harvest treatment in each experimental forest (Appendix A). Each treatment was replicated at least three times, but the study design differed slightly at each site and is described in greater detail in Appendix A. The control stands at each site are uneven-aged with some trees having recruited to breast height by the mid-1800s (or as early as the 1700s in the case of the BEF, Appendix A). In 2010, structural characteristics, including diameter at breast height (DBH, 1.4 m), were recorded on each plot for all trees with DBH greater than 10 cm. A single increment core was collected at breast height for each tree resulting in 326–547 cored trees per site. Cores were cross-dated visually (Yamaguchi, 1991). Ring-widths were then measured using a Velmex measuring stage to a precision of 0.01 mm, and dating was confirmed with the statistical program COFECHA (Holmes, 1983). The beginning of each silvicultural study varied with treatment implementation and initial sampling occurring in the 1950s or earlier in most cases (Appendix A). We limited our analyses to the 20-year period 1989–2009, a time frame that includes harvests in stands managed with selection systems (dates provided in Appendix A). By examining responses during this period only, we ensured that canopy closure had occurred across all stands included in the study, limited the influence of naturally occurring mortality on analysis, and kept a consistent time frame across sites.

### 2.3. Forest structure reconstruction

In order to quantify forest structure in each plot as it existed in 1989, tree diameters were reconstructed based on annual growth

rings moving backwards in time, starting with diameter measurements from 2010. Annual growth rings record growth changes inside the bark, so this process required using species-specific bark ratios to estimate the diameter outside bark for each year (Dixon and Keyser, 2015). Above-ground woody biomass was then estimated using species-specific allometric equations (Appendix B) for each tree in each year. We calculated biomass increment as the difference between estimates in tree biomass for consecutive years.

Because only those trees surviving to the sampling dates in 2010 were cored, reconstructing historic stand composition and structure required inventory data collected prior to and immediately following harvest treatments occurring 1989–2009. Such inventories were available for plots located at the Argonne and Penobscot EF. At the Bartlet EF, only control plots are presented for analyses of change over time as limited historical inventory data precluded harvest reconstructions. With observations from cored trees, we built site-specific multilevel models that predicted observed growth for each species in each year in order to impute missing annual growth increments for the trees harvested between 1989 and 2009 (Appendix C). We then predicted diameter growth increments for harvested trees (identified from historic inventories) from the fixed effect of tree size (DBH), allowing the slope for DBH to vary as a random effect by year. We also allowed the intercept to vary as a random effect by year and species. An auto-regressive error structure was included to account for temporal autocorrelation. Once the DBH for each harvested tree had been reconstructed for each year, biomass increment was estimated as described above. Natural mortality was not included in analyses given the difficulty in assigning specific years to dead trees recorded in the periodic inventories.

#### 2.4. Plant traits

Our estimates of functional identity included eight plant traits divided into two groups, effect and response traits, based on whether they related more closely to effects on ecosystem processes or response to environmental factors (Lavorel and Garnier, 2002; Cornelissen et al., 2003; Lavorel et al., 2007; Suding et al., 2008). Effect traits included wood specific gravity, height at maturity, maximum height at 20 years (a proxy for growth rate), leaf mass per area, and seed mass. Drought tolerance, shade tolerance, and flood tolerance were included as response traits. While many aspects of forest ecosystem function are important to understand and maintain, our selection of traits was informed by current knowledge of influences on tree growth (e.g., Violle et al., 2007), as growth closely relates to provision of forest products and carbon sequestration, two concerns dominating many forest management decisions. Species-wide trait means were collected from the literature (Appendix D). Trait values were standardized to the standard deviate (z-score) across all species within each site to equalize trait weighting and to meet statistical assumptions for analyses (Villéger et al., 2008). The functional identity for each site consists of the individual community-weighted means (CWM) for each of the effect and response traits defined as

$$CWM_{aj} = \sum (s_{ij} * t_i) \quad (1)$$

where  $CWM_{aj}$  = mean for trait  $a$  in plot  $j$ ,  $s_{ij}$  = relative abundance of species  $i$  in plot  $j$ , and  $t_i$  = trait value for species  $i$  (Lavorel et al., 2008). Relative abundance was defined based on above-ground, standing biomass for trees recruited into the forest canopy (DBH > 10 cm) at time of sampling. We tested correlations between each trait pair for each individual site using Kendall's  $\tau$ . A Bonferroni-adjustment was applied to protect against inflated Type 1 error with multiple testing, but actual p-values are also reported.

We further assessed the influence of community functional diversity on growth by calculating two standard functional diversity indices, functional divergence (FDiv) and functional dispersion (FDis), separately for effect traits and response traits. FDiv quantifies the representation of extreme versus moderate trait values in a community. Higher FDiv indicates greater abundance-weighted expression of extreme (high or low) trait values (Mason et al., 2005; Villéger et al., 2008). FDis simultaneously describes the volume of trait space occupied by a community and the spread of species within that space (Laliberte and Legendre, 2010; Mouillot et al., 2013). Indices were calculated using the FD package (Laliberte and Shipley, 2011) in R (R Core Team, 2013, v 3.0.2).

#### 2.5. Hypothesis testing

We tested the effect of silvicultural treatment on two measures of diversity and eight individual traits by analyzing means observed at the end of the study in 2009 as well as the rate of change ( $\Delta$ ) observed for each variable 1989–2009. Each response variable was assessed with multilevel (mixed-effect) ANOVA using the SAS MIXED procedure (SAS Institute, Cary, NC, US). At the AEF, each treatment was replicated nine times across the site with blocking. Here, a random effect was included that allowed the intercept to vary by block. At the other sites, treatments were replicated three times, but blocking was not included in the original study design. Sites were analyzed individually given the unique ecological and silvicultural context of each location. Residuals were examined visually to ensure homogeneity of variance, and some response variables required an ln-transformation to meet ANOVA assumptions.

### 3. Results

#### 3.1. Site characteristics and relationships between traits

Across treatments at a site, raw functional identity, quantified without standardizing trait values, was more similar between the AEF and BEF than to the PEF as expected given the dominance of hardwood species in the former two sites. This similarity is particularly evident with leaf mass per area, seed mass, and specific gravity (Appendix E).

Even though sites shared many species in common (Appendix B), correlations between community-weighted trait means and multi-trait functional diversity indices differed (Tables F.1 and F.2). At the AEF, most traits and functional diversity indices correlated with each other with only three pairs, flood tolerance with maximum height, flood tolerance with LMA, and FDiv (response) with FDis (effect) showing no evidence of significant relationships at this site. The negative correlations (e.g. between shade tolerance and FDis (effect), FDis (response), drought tolerance, and flood tolerance) suggest the existence of trade-offs at the stand scale (Tables F.1 and F.2). At the BEF, maximum height and shade tolerance (positively correlated with each other) both correlated negatively with growth rate (Table F.1). At the PEF the only significant relationship was a negative correlation between growth rate and shade tolerance, a trend observed consistently across all three sites (Table F.1).

#### 3.2. Change in functional diversity and functional identity over time

None of the functional diversity indices observed in unharvested control stands showed significant change over the course of the study at any site (Fig. 1, panels A, C, and E). At the AEF, mean shade tolerance and specific gravity decreased while mean maximum growth rate increased, and at the BEF, shade tolerance

increased over time in control stands (Fig. 1). Similar to diversity measures, individual response and effect traits remained stable over this period at the PEF.

Within sites, the most severe treatments (e.g., heavy selection at AEF and shelterwood at PEF), led to changes in functional diversity that exceeded changes observed for less severe treatments (Fig. 1). At the AEF, heavy selection resulted in lower  $\Delta$ FDIs for effect traits and greater  $\Delta$ seed mass and  $\Delta$ specific gravity than the other treatments. While significant change over 20 years ( $\Delta \neq 0$ ) was observed for flood tolerance, growth rate, leaf mass, and shade tolerance in response to some harvest treatments at this site, means did not differ significantly among treatments (Fig. 1). At BEF, shade tolerance in the control stand increased over the course of the study, and at the PEF, FDis and FDiv significantly increased for both effect and response traits in the shelterwood treatments. Change in drought tolerance was greater, and changes in flood and shade tolerance were significantly lower, for the shelterwood treatment relative to controls and selection at PEF.

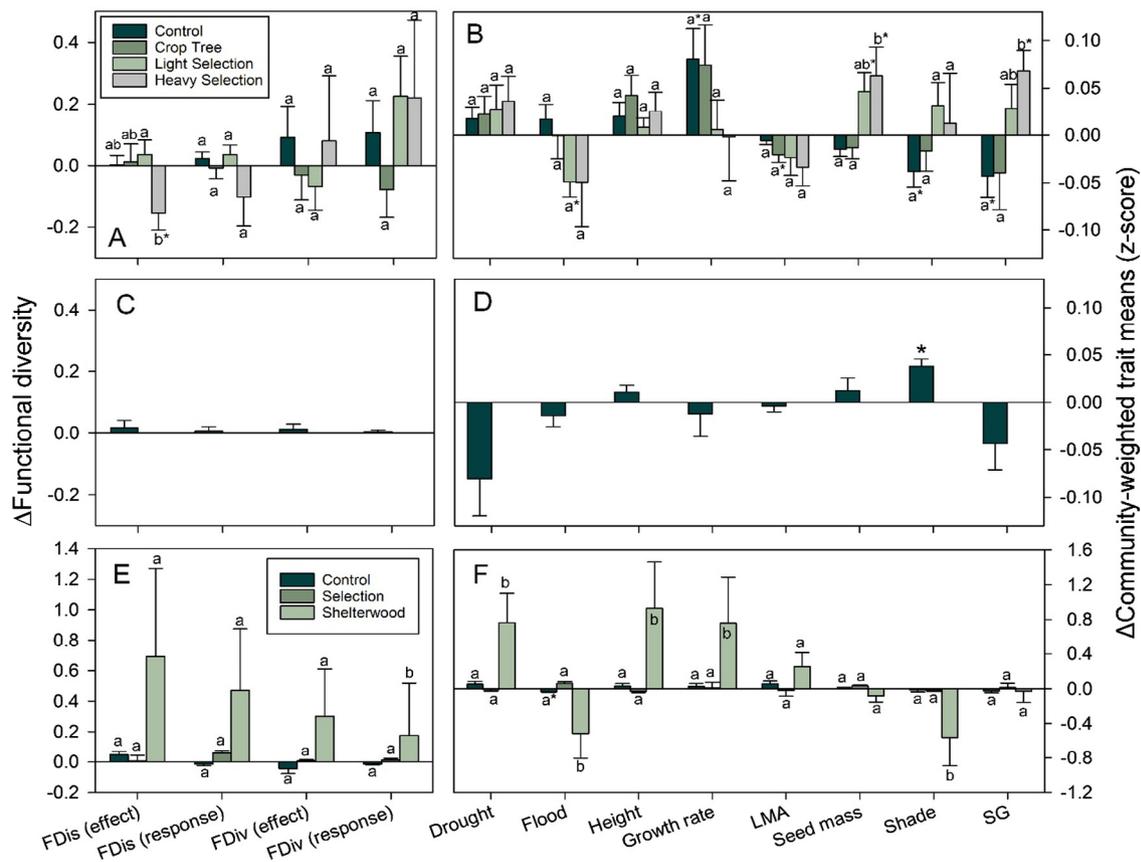
### 3.3. Management effects on functional identity and functional diversity after 20 years

Although differences in the rate of change for multiple traits and indices were observed at the AEF as reported above, no differences between treatments persisted by the conclusion of the study period in 2009 (Fig. 2). However, differences among treatments were apparent at both the BEF and PEF. At both sites, stands managed with selection systems had lower drought tolerance than

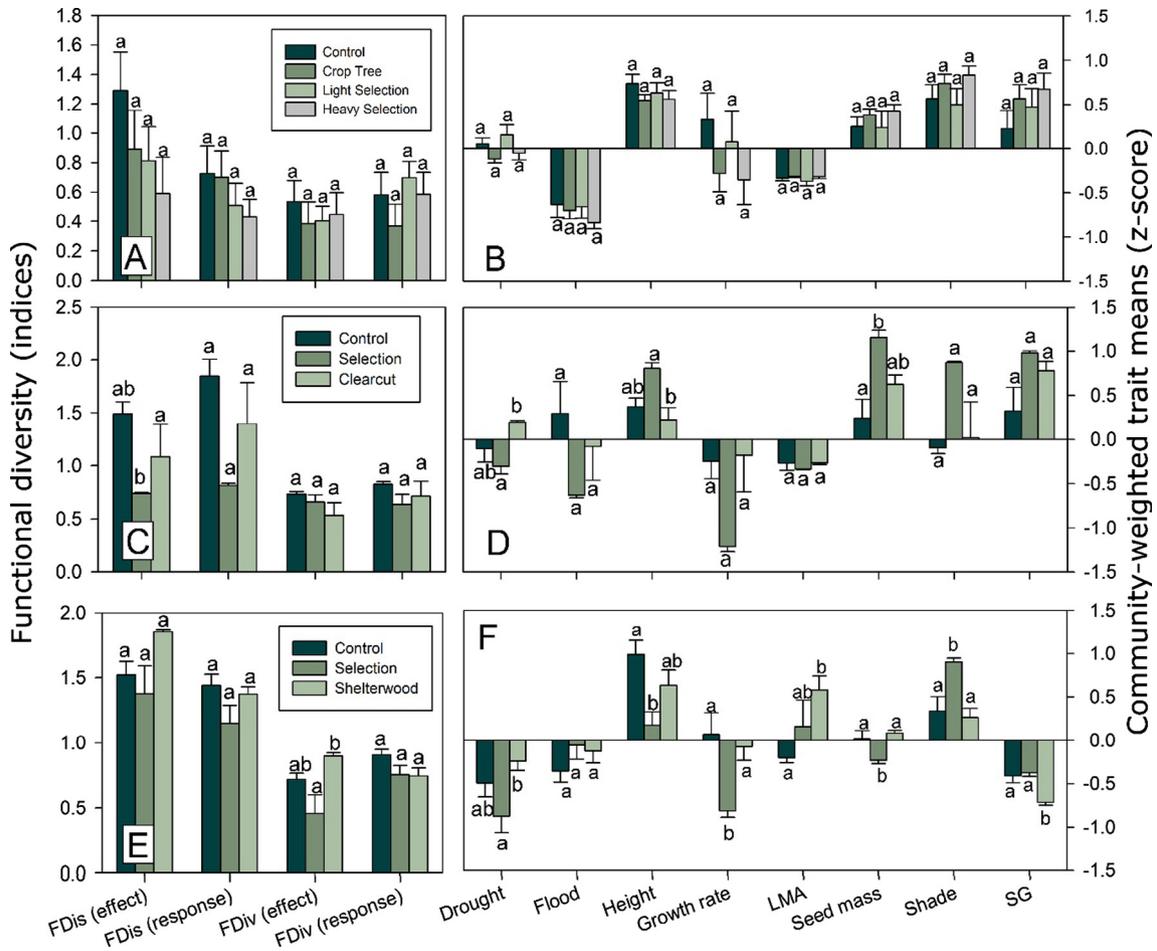
stands managed with systems involving greater canopy removal at a single point in time (clearcut and shelterwood, Fig. 2). At the BEF selection increased maximum height relative to clearcutting as expected, and at the PEF selection reduced maximum height relative to the control. Selection also increased shade tolerance and reduced early growth rate relative to other treatments at the PEF with similar, but insignificant trends suggested by means at the BEF (Fig. 2).

## 4. Discussion

Knowledge of tree functional traits has been used to guide the development of silvicultural systems for centuries, particularly with regard to the use of response traits, such as shade tolerance, to anticipate regeneration and growth responses to various harvest severities (Dean, 2012). The challenges and uncertainties associated with managing within the context of changing environmental conditions and disturbance regimes has increased the relevance of viewing forest management outcomes from a functional trait-based perspective, particularly as trade-offs among different objectives need to be assessed. Despite relatively low power of the experiments examined, this work demonstrated the ability of silvicultural treatments to affect the expression of traits in a community with resultant impacts on functional identity and diversity over time. This predictability in response suggests that measures of functional identity and diversity may be readily integrated into management outcomes evaluated in north temperate forests and potentially influence components of resilience.



**Fig. 1.** Change ( $\Delta$ ) 1989–2009 in functional diversity indices (left) and in community-weighted trait means (right) over 20 years at the Argonne Experimental Forest (panels A–B), Bartlett Experimental Forest (panels C–D) and Penobscot Experimental Forest (panels E–F). Abbreviations are as follows: functional dispersion, FDis; functional divergence, FDiv; leaf mass per area, LMA; specific gravity, SG. Lowercase letters indicate significant differences between treatments determined using *post hoc* Tukey-adjusted pairwise comparisons ( $p \leq 0.05$ ), and error bars give standard error. Asterisks indicate a change in index value different from zero (*t*-tests or Wilcoxon signed-rank tests, as appropriate;  $p \leq 0.05$ ).



**Fig. 2.** Functional diversity (left) and functional identity (right) as they varied among treatments at the end of the study period in 2009 at the Argonne Experimental Forest (A–B), Bartlett Experimental Forest (C–D), and Penobscot Experimental Forest (E–F). Error bars indicate standard error and lower-case letters indicate differences between treatments within each site as determined with *post hoc* Tukey-adjusted pairwise comparisons ( $p \leq 0.05$ ).

Patterns in functional identity and diversity largely reflected the influence of overstory disturbance on the stress tolerance, growth strategies, and leaf morphology of regenerating species. There was a lack of change over time in functional diversity measures in unharvested control stands, which corroborates studies from tropical and subtropical forests reporting stability in functional diversity in later stages of succession (Böhnke et al., 2014; Bu et al., 2014; Vicente-Silva et al., 2016) and extends their applicability to temperate forests. In contrast, selection diminished the FDis of effect traits at the BEF. Reductions in FDis (and other responses) may have occurred with selection treatments at the AEF and PEF, as suggested by trends in means based on 2009 standing biomass (Fig. 2); however, we were unable to detect them given the low power of our experiments. The significant negative trajectory of functional dispersion in response to heavy selection at the AEF (Fig. 1) suggests that clearer differences in management approaches may emerge in the future with both selection treatments reducing functional dispersion. These changes will likely continue to reflect strong *Acer saccharum* dominance of the regeneration layer despite the presence of a diversity of other tree species in the overstory at the AEF (cf. Kern et al., 2012). These trends also may have been stronger at the BEF if the thinning applied to clearcut stands in 2003 had not focused on removal of early-successional species (Appendix A). Future work building off this framework with greater replication may be able to further

elucidate the long-term functional outcomes of different silvicultural treatments in these and other systems.

Selection systems involve less severe canopy disturbance than other silviculture systems such as clearcutting and shelterwood, and they are often considered favorably in terms of minimizing harvest impacts, relative to even-aged approaches. Given the lower level of disturbance, it might be expected that functional diversity would be greater in forests managed with selection than with other methods. Our results suggest otherwise and affirm other studies that have demonstrated that single-tree selection can decrease other measures of biodiversity such as species richness (Neuendorff et al., 2007) and simplify forest structure (Angers et al., 2005; Kenefic and Nyland, 2007). For example, single-tree selection has led to greater *Acer saccharum* dominance in northern hardwood forests of the Lake States region (Neuendorff et al., 2007; Bolton and D'Amato, 2011) and has interacted with impacts from the introduced beech bark disease (*Cryptococcus fagisuga* Lind. and *Nectria* spp.) in northeastern North America to encourage increased regeneration of *Fagus grandifolia* (Leak, 2005; Nyland et al., 2006). Harvest methods that encourage regeneration of highly shade tolerant species may lead to a stand-scale trade-off in functional dispersion of both effect and response traits as well as in growth rate (approximated with height at 20 years), drought tolerance, and flood tolerance (Appendix E), at least in northern hardwood stands located in the Lake States region. While growth rate

and shade tolerance correlated negatively with each other at the BEF and PEF as well, other relationships are not consistent across sites.

Observations at the BEF and PEF supported hypotheses that individual traits generally believed to influence successional status (Bazzaz, 1979) would respond accordingly to harvest treatments. Mean growth rate was lower and shade tolerance higher in stands managed with selection relative to other treatments. Also, drought tolerance was higher in stands managed with silvicultural systems that promote early to mid-successional stages (clearcutting and shelterwood; Bazzaz, 1979). Although specific gravity positively correlates with some aspects of drought tolerance within species (Hacke et al., 2001; Chave et al., 2009), and has been shown to correlate positively with stand development in tropical forests (Whitfeld et al., 2014; Vicente-Silva et al., 2016), the same trends did not occur here at the stand scale. The relationship between this particular trait and function varies (Chave et al., 2009; Hoffmann et al., 2011), for example between angiosperms and gymnosperms in relation to freeze/thaw and drought-induced cavitation (Hacke et al., 2001; Hacke and Sperry, 2001), and illustrates the need for continued research that refines understanding of the relationships between management and traits with particular attention to underlying mechanisms (Aubin et al., 2016). Nonetheless, this research yielded predictable responses for some commonly measured traits and indices and demonstrates that functional identity and functional diversity may inform management aimed at increasing adaptive capacity in these forests.

## 5. Conclusions

Our results support other findings that suggest functional diversity remains stable over time in the absence of major disturbance, extending the applicability of those studies to northern forests of the northeastern United States. We also demonstrate that silvicultural prescriptions can be used to manage the functional identity of forest ecosystems, and that outcomes are largely consistent with expectations based on our understanding of disturbance impacts to forest community composition. Lastly, our results suggest managing with selection systems may reduce functional dispersion and involve trade-offs between stress tolerances and diversity.

As natural resource managers seek tools for addressing the effects of global environmental change, assessments of functional diversity and functional identity provide another lens through which to view management outcomes. This study confirms the utility of a trait-based approach and, by quantifying responses that have occurred across forest types given conditions in the recent past, provides a baseline for future comparisons. Ongoing research will expand on how functional identity and diversity directly influence adaptive capacity in these forests.

## Acknowledgements

The authors thank J. Brissette, D. Kastendick, L. Kenefic, C. Kern, W. Leak, M. Yamasaki, and other USDA Forest Service scientists and technicians for their work collecting and maintaining the long-term silvicultural studies that supported this research. We also thank A. Bale, P. Klockow, K. Gill, J. Pzswaro, and M. Reinikainen, for their time and effort in the field and lab. Funding was provided by the U.S. Department of Interior Northeast Climate Science Center and the U.S. Department of Agriculture Forest Service Northern Research Station.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.05.056>.

## References

- Adams, M.B., Loughry, L.H., Plaughter, L.L., 2008. Experimental Forests and Ranges of the USDA Forest Service Revised General Technical Report NE-321. USDA Forest Service, Northeastern Research Station, Newton Square, PA. 183 p.
- Angers, V.A., Messier, C., Beaudet, M., Leduc, A., 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *For. Ecol. Manage.* 217, 275–293.
- Aubin, I., Munson, A.D., Cardou, F., Burton, P.J., Isabel, N., Pedlar, J.H., Paquette, A., Taylor, A.R., Delagrangé, S., Kebli, H., Messier, C., Shipley, B., Valladares, F., Kattge, J., Boisvert-Marsh, L., McKenney, D., 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environ. Rev.* 24, 164–186.
- Baker, F.S., 1934. *Theory and Practice of Silviculture*. McGraw-Hill, New York, NY, USA.
- Baraloto, C., Herault, B., Paine, C.E.T., Massot, H., Blanc, L., Bonal, D., Molino, J., Nicolini, E.A., Sabatier, D., 2012. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. *J. Appl. Ecol.* 49, 861–870.
- Bazzaz, F.A., 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* 10, 351–371.
- Böhne, M., Kröber, E., Wirth, C., Brhelheide, H., 2014. Maintenance of constant functional diversity during secondary succession of a subtropical forest in China. *J. Veg. Sci.* 25, 897–911.
- Bolton, N.W., D'Amato, A.W., 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. *For. Ecol. Manage.* 262, 1215–1222.
- Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Bončina, Chauvin, C., Drössler, L., García-Güemes, C., Heir, C., Kerr, G., Lexer, M.J., Mason, B., Mohren, F., Mühlthaler, U., Nocentini, S., Svoboda, M., 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* 87, 492–503.
- Bu, W., Zang, R., Ding, Y., 2014. Functional diversity increases with species diversity along successional gradient in a secondary tropical lowland rainforest. *Trop. Ecol.* 55, 393–401.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Peñuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl. Acad. Sci. USA* 108, 1474–1478.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12, 351–366.
- Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D. L., Shaw, D.C., St. Clair, J.B., 2011. Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. *For. Ecol. Manage.* 261, 1121–1142.
- Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111, 1119–1144.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Porter, K., 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Aus. J. Bot.* 5, 335–380.
- Dean, T.J., 2012. A simple case for the term “tolerance”. *J. Forest.* 110, 463–464.
- Diaz, S., Cabido, M., Casnoves, F., 1998. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* 9, 112–122.
- Dixon, G.E., Keyser, C.E., 2015. Northeast (NE) Variant Overview – Forest Vegetation Simulator Internal Report. USDA Forest Service, Forest Management Service Center, Fort Collins, CO, USA, p. 54.
- Elmqvist, T., Folk, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., Norbert, J., 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* 9, 488–494.
- Gavin, J., Pervost, B., Fernandez, C., 2016. Introducing resprouters to enhance Mediterranean forest resilience: importance of functional traits to select species according to a gradient of pine density. *J. Appl. Ecol.* <http://dx.doi.org/10.1111/1365-2664.12716>.
- Gazol, A., Camarero, J.J., 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. *J. Ecol.* 104, 1063–1075.
- Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M., Kastle, E., Arnoldi, C., Bardgett, R.D., Poly, F., Pommier, T., Schloter, M., Tappener, U., Bahn, M., Clement, J., 2013. Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *J. Ecol.* 101, 47–57.
- Hacke, U.G., Sperry, J.S., 2001. Functional and ecological xylem anatomy. *Perspect. Plant Ecol. Evol. Syst.* 4, 97–115.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126, 457–461.
- Hoffmann, W.A., Marchin, R.M., Abit, P., Lau, O.L., 2011. Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Glob. Change Biol.* 17, 2731–2742.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- Horn, H., 1981. Some causes of variety in patterns of secondary succession. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), *Forest Succession: Concepts and Application*. Springer-Verlag, New York, pp. 24–35 (Chapter 4).
- Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13, 98–118.

- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477, 199–202.
- Keddy, P.A., Shipley, B., 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 49, 234–241.
- Kenefic, L.S., Nyland, R.D., 2007. Cavity trees, snags, and selection cutting: a northern hardwood case study. *N. J. Appl. For.* 24, 192–196.
- Kern, C.C., Reich, P.B., Montgomery, R.A., Strong, T.F., 2012. Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? *For. Ecol. Manage.* 267, 134–143.
- Kunstler, G., Falster, D., Coomes, D., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fluery, S., Hanewinkel, M., Hérault, B., Kattge, J., Kurokawa, H., Onoda, Y., Penuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.-Fang, G., Stal, G., Swenson, N.G., Thompson, J., Westerland, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529, 204–207.
- Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305.
- Laliberte, E., Shipley, B., 2011. FD: Measuring Functional Diversity from Multiple Traits and Other Tools for Functional Ecology: R Package 'FD' Version 1.0-11. Available at: <<http://CRAN.R-project.org/package=FD>>.
- Lavorel, S., 2013. Plant functional effects on ecosystem services. *J. Ecol.* 101, 4–8.
- Lavorel, S., Diaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., McIntyre, S., Pausas, J.G., Perez-Harguindeguy, N., Roumet, C., Urcelay, C., 2007. Plant functional types: are we getting any closer to the Holy Grail? In: Canadell, J.G., Pataki, D.E., Pitelka, L.F. (Eds.), *Terrestrial Ecosystems in a Changing World*. Springer Berlin Heidelberg, pp. 149–164.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
- Leak, W.B., 2005. Effects of small patch cutting on sugar maple regeneration in New Hampshire northern hardwoods. *N. J. Appl. For.* 22, 68–70.
- Lovett, G.M., Weiss, M., Liebhold, A.M., Holmes, T.P., Leung, B., Lambert, K.F., Orwig, D.A., Campbell, F.T., Rosenthal, J., McCullough, D.G., Wildova, R., Ayres, M.P., Canham, C.D., Foster, D.R., LaDeau, S.L., Weldy, T., 2016. Nonnative forest insects and pathogens in the United States: impacts and policy options. *Ecol. Appl.* 26, 1437–1455.
- Martinez-Vilalta, J., Lloret, F., 2016. Drought-induced vegetation shifts in terrestrial ecosystems: the key role of regeneration dynamics. *Global Planet. Change* 144, 94–108.
- Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118.
- McKee, F.R., Aukema, B.H., 2015. Influence of temperature on the reproductive success, brood development and brood fitness of the eastern larch beetle *Dendroctonus simplex* LeConte. *Agri. For. Entomol.* 17, 102–112.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.
- Mouillot, D., Graham, N.A.J., Villegger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177.
- Neill, A.R., Puettmann, K.J., 2013. Managing for adaptive capacity: thinning improves food availability for wildlife and insect pollinators under climate change conditions. *Can. J. For. Res.* 43, 428–440.
- Neuendorff, J.K., Nagel, L., Webster, C.R., Janowiak, M.K., 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. *N. J. Appl. For.* 24 (3), 196–202.
- Niinemets, U., Valladares, E., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
- Nyland, R., Bashant, A.L., Bohn, K.K., Verostek, J.M., 2006. Interference to hardwood regeneration in northeastern North America: ecological characteristics of American beech, striped maple, and hobble-bush. *N. J. Appl. For.* 23, 122–132.
- Paillet, F.L., 2002. Chestnut: history and ecology of a transformed species. *J. Biogeogr.* 29, 1517–1530.
- Park, A., Puettmann, K., Wilson, E., Messier, C., Kames, S., Dhar, A., Amalesh, 2014. Can boreal and temperate forest management be adapted to the uncertainties of 21st century climate change? *Crit. Rev. Plant Sci.* 33, 251–285.
- Prach, K., Walker, L.R., 2011. Four opportunities for studies of ecological succession. *Trends Ecol. Evol.* 26, 119–123.
- Puettmann, K.J., 2011. Silvicultural challenges and options in the context of global change: “simple” fixes and opportunities for new management approaches. *J. Forest.* 6, 321–331.
- Reich, P.B., 2014. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D.H., Hooper, D.U., Jackson, S.T., Navas, M., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.* 14, 1125–1140.
- Toumey, J.W., 1925. *Foundations of Silviculture upon an Ecological Basis*. Edward Bros, Ann Arbor, MI.
- Tyrrell, L.E., Nowacki, G.J., Crow, T.R., Buckley, D.S., Nauertz, E.A., Niese, J.N., Rollinger, J.L., Zasada, J.C., 1988. Information about Old Growth for Selected Forest Type Groups in the Eastern United States General Technical Report NC-197. North Central Forest Experiment Stations, Saint Paul, MN. 507 p.
- Vicente-Silva, J., Bergamin, R.S., Zanini, K.J., Pillar, V.D., Müller, S.C., 2016. Assembly patterns and functional diversity of tree species in a successional gradient of Araucaria forest in Southern Brazil. *Nat. Conserv.* 14, 67–73.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
- Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Humel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892.
- White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego, pp. 3–13 (Chapter 1).
- Whitfield, T.J.S., Lasky, J.R., Damas, K., Sosanika, G., Molem, K., Montgomery, R.A., 2014. Species richness, forest structure, and functional diversity during succession in the New Guinea lowlands. *Biotropica* 46, 538–548.
- Woodall, C.W., Russell, M.B., Walters, B.F., D’Amato, A.W., Zhu, K., Saatchi, S.S., 2015. Forest production dynamics along a wood density spectrum in eastern US forests. *Trees* 29, 299–310.
- Yamaguchi, D.K., 1990. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* 21, 414–416.