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Bioenergy harvest impacts to biodiversity and resilience vary across aspen-dominated forest ecosystems in the Lake States region, USA

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Keywords

Aspen; Biodiversity; Bioenergy harvest; Community composition; Disturbance; Functional diversity; *Populus tremuloides*; Recovery; Resilience

Abbreviations

LTSP = Long Term Soil Productivity;
SOH = stem-only harvest; WTH = whole-tree harvest; FFR = whole-tree harvest plus forest floor removal; FRic = functional richness;
FDiv = functional divergence; FDis = functional dispersion; FEve = functional evenness;
SR = species richness; SE = species evenness.

Nomenclature

Gleason & Cronquist (1991)

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Abstract

Questions: Does the increase in disturbance associated with removing harvest residues negatively impact biodiversity and resilience in aspen-dominated forest ecosystems? How do responses of functional diversity measures relate to community recovery and standing biomass?

Location: Aspen (*Populus tremuloides,* Michx.) mixedwood forests in Minnesota and Michigan, USA.

Methods: Three levels for two factors, organic matter removal and compaction, were fully crossed, resulting in nine experimental treatments that spanned a range of disturbance severity. Each treatment was replicated three times at each of three sites dominated by the same tree species but having different soil textures (clay, silty loam, sandy). Community composition and taxonomic diversity (species richness, species evenness, Shannon diversity index) were quantified based on woody species abundance sampled 5, 10 and 15 yr after disturbance. Community composition response was assessed using non-metric multidimensional scaling. Functional diversity (functional richness, evenness, dispersion and divergence) was also estimated using eight species effect and response traits. Finally, we examined community recovery as well as responses of species and functional diversity to disturbance severity over time using repeated measures ANOVA.

Results: Two responses indicated a potentially negative impact of whole-tree harvest relative to conventional, stem-only harvest: functional richness on silty loam soils and species evenness on clayey soils. Otherwise, negative impacts were restricted to forest floor removal or increased compaction. Recovery in community composition was reduced by the most severe treatments, particularly forest floor removal, across the study, but the responses of functional and taxonomic diversity varied among sites, with some measures increasing as a result of severe disturbance.

Conclusions: Maximization of standing biomass may mean a short-term sacrifice in species and functional diversity. Also, examinations of forest management impacts on species and functional diversity and composition should apply multiple metrics and indices to ensure potential impacts are not obscured by the reliance on a single approach.

Introduction

Unprecedented global change and associated uncertainty about future conditions have increased the need for informed, sustainable forest management practices that maintain forest ecosystem health while also meeting demands for forest products. Removal of harvest residues for use as bioenergy feedstock has been proposed around the globe as a potential mitigation strategy for off-setting greenhouse gas emissions from fossil fuels (Perlack et al. 2005; Millar et al. 2007; Buford & Neary 2010). If demand for forest-derived bioenergy feedstock increases, the

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corresponding increase in anthropogenic disturbance frequency and severity will shape the composition, structure and function of resulting forest communities (Turner et al. 1998; Bernhardt-Romermann et al. 2008), as well as their resilience to future disturbances (Folke et al. 2004; Costa et al. 2012). Accordingly, understanding these effects and how they vary with disturbance severity and abiotic site conditions is imperative for informing future forest policy and management decisions designed to maintain critical forest functions in the face of change.

An ecosystem that maintains function despite drastic change has demonstrated resilience (Holling 1973). Less broadly, resilience can be defined as the level of disturbance necessary to prompt a state shift in ecosystem identity and function (*ecological resilience;* Holling 1996; Folke et al. 2004) or the length of time required for an ecosystem to recover pre-disturbance characteristics (*engineering resilience*; Holling 1996; Larson et al. 2008). Heterogeneity in composition and structure may contribute to greater resilience in forest ecosystems (Perry & Amaranthus 1997; Bergeron et al. 1999; Fischer et al. 2006). Along those lines, taxonomic diversity has long been associated with resilience and provision of ecosystem services (Tilman 1996; Folke et al. 2004; Lavorel 2013), although those relationships vary with scale, species interactions, and species traits (Hooper & Vitousek 1997; Tilman et al. 1997; Loreau et al. 2001). Despite much research and recent progress, quantifying resilience and incorporating related principles in forest management remains challenging.

Functional diversity has potential to improve assessments of ecosystem health and restoration success relative to traditional taxonomic approaches (Folke et al. 2004; Suding et al. 2008; Mayfield et al. 2010; Laughlin 2014; Levine 2016). By incorporating traits related to nutrient cycling and other processes, associated indices may enable a more direct assessment of disturbance impacts to ecosystem function (Diaz & Cabido 2001; Mason et al. 2005; Mouillot et al. 2013). As disturbance severity increases and resulting conditions filter species by their traits, functional richness (the total volume in functional trait space occupied by a community given its composition) and associated functional diversity measures are expected to decrease (Cornwell et al. 2006; Flynn et al. 2009; Mouillot et al. 2013). Anthropogenic disturbance may cause such declines in functional diversity, which can reduce resilience (Laliberte et al. 2010).

Many studies have examined biodiversity–ecosystem function relationships along disturbance severity or stress gradients, but those gradients are usually linear and based on a single variable (i.e. Wilson & Tilman 2002; Chillo et al. 2011), whereas the effects of disturbance may be more complex (Townsend et al. 1997; Roberts 2007). In forests, disturbance severity is often quantified in terms of overstorey tree mortality (i.e. Oliver & Larson 1990; Peterson & Leach 2008); however, disturbance events may also impact understorey vegetation and soil conditions. Accounting for the multidimensional nature of these impacts enables comparisons across both natural and anthropogenic disturbance types and increases the likelihood that more subtle changes to composition and diversity will be observed (Roberts 2007). For example, comparisons among plant functional group responses to thinning treatments vs comparable canopy cover in unharvested forest have demonstrated that ancillary disturbance caused by harvest operations might drive functional change (Neill & Puettmann 2013). Nevertheless, the utility of quantifying functional diversity to assess disturbance impacts that accompany resource procurement, restoration or achievement of other objectives remains largely untested at operational scales.

With this study, we primarily set out to determine whether harvest residue removal, an emerging issue in sustainable forest management, negatively impacts biodiversity and resilience. Secondarily, we compared established methods for quantifying biodiversity and functional responses to determine whether responses were congruent among methods and how trends in biodiversity measures compared to observed standing biomass.

Methods

Study sites

This study utilizes data from three USDA Forest Service installations of the Long Term Soil Productivity (LTSP) study distributed across the Laurentian Mixed Forest Province in the northern US (Table 1; Powers et al. 2005). Aspen (*Populus tremuloides,* Michx.) dominated all forest stands prior to treatment (Curtis Importance Value ≥ 50%), but sites differed in soil texture, ranging from clayey to sandy. Keeping with the original intent of the LTSP study, we compared responses across site types that vary in quality for the dominant species, aspen (Stone 2001; Powers 2006).

Experimental design

We quantified disturbance severity using two fully crossed factors related to removing residues following conventional harvest. Organic matter removal levels included stem-only harvest (SOH), in which shrubs and merchantable tree stems were removed, leaving behind harvest residues, whole tree harvest (WTH) in which all above-ground portions of trees and shrubs were removed, and whole tree harvest plus forest floor removal (FFR). Harvest operations occurred in winter and are described in detail by Stone (2001). Soil compaction was applied in

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Table 1. Site locations and descriptions.

Study Site	Harvest Year	Location	Aspen (% Pre-Harvest Biomass)	Site Index[a] (m)	Precipitation ($cm \cdot yr^{-1}$)	Soils	Soil Texture
Chippewa NF	1993	47°18′ N, 94°31′ W	58	23	64	Frigid Haplic Glossudalfs	Silty loam
Ottawa NF	1992	46°37′ N, 89°12′ W	50	17–18	77	Frigid Vertic Glossudalfs	Clayey
Huron NF	1994	44°38′ N, 83°31′ W	57	19	75	Frigid Entic Haplorthods, Frigid Typic Udipsamments	Sandy

[a] Average height (m) for aspen, age 50.

spring using tractors or front-loaders with varying loads (see Stone 2001 for more details) and included three levels: no additional compaction above normal levels associated with conventional harvesting (C0), moderate compaction (C1) and heavy compaction (C2). Moderate and heavy compaction treatments were intended to increase soil bulk density by 15% and 30%, respectively, over C0 (Stone 2001), but results varied with soil texture (Voldseth et al. 2011). Bulk density was calculated based on 100 g subsamples of 12 soil cores collected in each plot. Each sample was oven-dried at 105 °C and weighed, so that calculations could be corrected for the difference between air-dry and oven-dry weight. Woody debris was removed from SOH-treated stands prior to the compaction treatment, measured and replaced. Stands regenerated naturally and primarily vegetatively through root suckers or stump sprouts.

Treatments were applied to 40 × 40 m (0.16 ha) plots and replicated three times at the Chippewa and Huron sites. Due to operational difficulties, treatment implementation at Ottawa differed, with five replicates of the WTH/C0 treatment, two replicates of SOH/C1 and one application of SOH/C2. All other treatments at Ottawa were replicated three times as at other sites.

Field sampling

Prior to harvest, all trees > 10 cm DBH (1.4 m) in each 0.16-ha plot were inventoried with DBH and species recorded. Additionally, diameter at 15 cm height and species for woody plants < 10 cm DBH were recorded in four 1.13-m radius (4 m^2) subplots per plot.

During the first post-harvest sampling period (5 yr), tree and shrub regeneration was measured in four systematically located 1.26-m radius (5 m^2) circular subplots per 0.16-ha plot at Chippewa and Ottawa. For the first post-harvest sampling period at Huron and in all remaining periods at all sites, nine systematically located 1.78-m radius (10 m^2) subplots were sampled. Diameter (at 15-cm height) and species name were recorded for each woody stem at least 15-cm tall. Species abundance was quantified with above-ground biomass ($Mg \cdot ha^{-1}$) estimated using species-specific allometric equations (Perala & Alban 1994; Jenkins et al. 2004; Appendix S1). The change in subplot size over time was necessary to accommodate changing vegetation structure and could have led to an increase in species richness between years 5 and 10 at Chippewa and Ottawa. However, we did not detect any significant interactions between time and the two treatment factors for species richness, species evenness and functional richness, suggesting the impact of increasing plot size was minimal.

Community composition

Treatment effects on compositional structure of the tree and shrub community 15 yr post-harvest were examined using non-metric multidimensional scaling (NMS; Kruskal 1964; Mather 1976; MjM Software Design, Gleneden Beach, OR, US). One ordination for each site included all periods in order to estimate engineering resilience (recovery), defined as the Euclidean distance between pre- and post-treatment plots in multi-dimensional species space. Additionally, we assessed recovery by quantifying the distance between pre- and post-treatment plots along each of three NMS axes, as three-dimensional solutions had the least stress and were determined as optimal for each site. This second approach allowed us to relate specific conditions (described below) to differences in community structure resulting from treatments such that the mechanisms driving composition could be interpreted. Ordinations were rigidly rotated to align the first axis with change in time such that differences among treatments were most apparent along other axes. Smaller distances between plots and smaller differences between pre- and post-treatment scores were interpreted as indicating faster recovery and greater resilience. For each ordination, species abundance, based on above-ground biomass, was relativized across plots such that analysis revealed which conditions most affected individual species (MjM Software Design). Species occurring in fewer than three plots at each site were removed to reduce noise and prevent potential bias in community analysis (MjM Software Design). These species were not excluded from analyses described below that focused on diversity rather than community structure. Dissimilarity matrices for all ordinations were calculated using Sørensen distances.

In order to improve interpretation of treatment impacts to community composition, four measures of disturbance

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severity were quantified and related to NMS axes using Kendall's tau. This included the change in soil bulk density (difference in bulk density observed prior to and immediately after compaction treatments), live biomass removed at harvest (estimated using species-specific allometric equations; Appendix S1), the volume of pre-existing coarse woody debris retained following treatment and the change in forest floor thickness between pre- and immediately post-treatment.

Species traits

We focused on eight quantitative plant traits related to effects on ecosystem processes and disturbance response (Cornelissen et al. 2003; Lavorel et al. 2007; Suding et al. 2008). Traits included seed mass, maximum height at maturity, leaf lifespan, specific gravity, leaf mass per area, drought tolerance, flood tolerance and shade tolerance ($r < 0.7$ for all pairs). Species-wide trait value means were collected from the literature (Appendix S2). Values were standardized to the standard deviate (z-score) across all species observed within the study to equalize the weighting of traits and to meet statistical assumptions (Villeger et al. 2008).

Functional diversity

To date, there is no single, all-encompassing index for quantifying the complexity of functional diversity (Mason et al. 2005; Mouillot et al. 2013). Instead, similar to taxonomic diversity, multiple indices that describe different aspects of function complement one another when interpreted together (Mouillot et al. 2013). We quantified functional evenness (FEve), functional richness (FRic), functional divergence (FDiv) and functional dispersion (FDis) to collectively assess the effect of biomass harvest disturbance. Briefly, FEve parallels species evenness in that increased evenness corresponds to increased equity in the abundance of species across multi-dimensional functional trait space (Mason et al. 2005; Villeger et al. 2008). FRic describes the relative volume of functional trait space that is occupied, given the species composition of a community (Mason et al. 2005; Villeger et al. 2008). FDiv quantifies the representation of extreme vs moderate trait values in a community; higher FDiv indicates greater abundance-weighted expression of extreme (high or low) trait values (Mason et al. 2005; Villeger et al. 2008). Lastly, FDis simultaneously describes the volume of trait space occupied by a community and the spread of species within that space (Laliberte & Legendre 2010; Mouillot et al. 2013). Each index was estimated for the woody community in each plot prior to treatment as well as 5, 10 and 15 yr post-harvest using the plant traits listed above with the FD package in R (v 3.0.2; R Foundation for Statistical Computing, Vienna, AT). Change (Δ) between pre-treatment and each post-harvest sampling year was used as the unit for analysis.

Treatment effects

The effect of harvesting treatments on community species richness (change since pre-treatment in the number of tree and shrub species present; ΔSR), species evenness (change in the relative abundance of those species; ΔSE), diversity (change in the Shannon diversity index; ΔH'), ΔFEve, ΔFRic, ΔFDiv and ΔFDis was assessed with mixed-model repeated measures ANOVA using the SAS MIXED procedure (SAS Institute, Cary, NC, US). Each site was analysed separately because soil texture, the main characteristic distinguishing them, was not replicated. The statistical model was as follows:

$$\begin{aligned} Y_{ijkl} = {} & \mathrm{OMR} + \mathrm{CPT} + \mathrm{TIME} + \mathrm{PLOT} + (\mathrm{OMR} * \mathrm{CPT}) \\ & + (\mathrm{OMR} * \mathrm{TIME}) + (\mathrm{CPT} * \mathrm{TIME}) + (\mathrm{OMR} * \mathrm{CPT} \\ & * \mathrm{TIME}) + e_{ijkl} \end{aligned}$$

where OMR is organic matter removal, CPT is compaction, TIME is years since harvest and Y_{ijkl} is one of the response variables listed above at the ith level of OMR, the jth level of CPT, the kth level of time and the lth level of plot. Random intercepts were included for PLOT. Type III sums of squares were used to account for the unbalanced design at Ottawa, and factor levels were distinguished with *post-hoc* Tukey-adjusted pair-wise comparisons where significant effects of main factors were detected (indicated in Tables 2–4).

Results

We predicted that increasing disturbance severity would reduce resilience and decrease diversity across the study. Whole-tree harvest caused reductions in two response variables compared to stem-only harvest, but negative impacts were largely restricted to forest floor removal or increased compaction. Most diversity measures decreased monotonically with increasing disturbance severity on clayey soils, as predicted, but on silty loam and sandy soils responses varied and interactions between organic matter removal and compaction complicated trends.

Community composition

The optimal NMS solution for each site included three dimensions and explained 66.7% of variability in community composition on silty loam (stress = 16.5%), 66% of variability on clay (stress = 14.25%) and 55.5% of

Table 2. Treatment effects on recovery of woody species composition over 15 yr after harvest based on distances between pre- and post-treatment plots along three NMS axes as detected using repeated measures ANOVA.

Site	Source	*df*	Axis 1		Axis 2		Axis 3	
			F	*P*-value	*F*	*P*-value	*F*	*P*-value
Chippewa (Silty Loam)	OMR	2	**8.37**	**0.0007**	**3.94**	**0.0252**	0.02	0.985
	CPT	2	0.2	0.8168	**13.86**	**<0.0001**	2.22	0.1181
	TIME	2	1.08	0.3481	0.75	0.4752	**9.65**	**0.0003**
	OMR*CPT	4	2.1	0.0928	**10.83**	**<0.0001**	0.69	0.5996
	OMR*TIME	4	1.11	0.3599	0.55	0.6974	0.9	0.4692
	CPT*TIME	4	0.04	0.9976	2.1	0.0932	1.73	0.1563
	OMR*CPT*TIME	8	0.31	0.9589	1.04	0.4192	0.47	0.8709
Ottawa (Clay)	OMR	2	1.28	0.287	**7.67**	**0.0012**	0.65	0.5271
	CPT	2	**5.25**	**0.0084**	0.11	0.9004	0.47	0.6277
	TIME	2	**6.69**	**0.0026**	**8.91**	**0.0005**	0.45	0.6382
	OMR*CPT	4	**4.09**	**0.0059**	0.45	0.7713	0.39	0.8153
	OMR*TIME	4	0.54	0.6339	0.33	0.8553	1.33	0.7252
	CPT*TIME	4	1	0.4188	0.9	0.4683	0.34	0.944
	OMR*CPT*TIME	8	1.11	0.3693	2.03	0.0615		
Huron (Sandy)	OMR	2	1.4	0.2552	**3.56**	**0.0353**	1.11	0.3362
	CPT	2	1.16	0.3225	2.74	0.0736	2.61	0.0827
	TIME	2	**18.52**	**<0.0001**	0.16	0.8495	1.7	0.1915
	OMR*CPT	4	0.75	0.5648	**6.66**	**0.0002**	0.38	0.822
	OMR*TIME	4	1.27	0.294	0.58	0.6779	1.31	0.2773
	CPT*TIME	4	0.29	0.8817	0.59	0.6694	0.07	0.9909
	OMR*CPT*TIME	8	0.29	0.9651	0.31	0.9596	0.33	0.9489

CH, Chippewa; HM, Huron; OT, Ottawa; OMR, organic matter removal; CPT, compaction.

Bold type indicates significant effects ($P < 0.05$). Correlations of individual species and environmental characteristics with each NMS axis are provided in Appendix S3, Tables 4.2 and 4.3.

Table 3. Repeated measures ANOVA results for measures of taxonomic diversity.

Site	Source	*df*	ΔSR		ΔSE		ΔH’	
			F	*P*-value	*F*	*P*-value	*F*	*P*-value
Chippewa (Silty Loam)	OMR	2	**3.78**	**0.0293**	1.32	0.2752	2.20	0.1204
	CPT	2	**11.70**	**<0.0001**	**13.12**	**<0.0001**	**10.05**	**0.0002**
	TIME	2	**13.60**	**<0.0001**	0.43	0.6506	0.04	0.9654
	OMR*CPT	4	2.41	0.0604	**2.96**	**0.0280**	**3.00**	**0.0263**
	OMR*TIME	4	2.00	0.1081	0.37	0.8259	0.41	0.8010
	CPT*TIME	4	2.33	0.0674	0.82	0.5174	0.29	0.8852
	OMR*CPT*TIME	8	0.49	0.8584	0.32	0.9552	0.36	0.9349
Ottawa (Clay)	OMR	2	**6.39**	**0.0034**	**4.51**	**0.0159**	**7.07**	**0.0020**
	CPT	2	0.86	0.4278	**6.97**	**0.0021**	**5.07**	**0.0099**
	TIME	2	**28.00**	**<0.0001**	0.79	0.4573	0.18	0.8354
	OMR*CPT	4	2.03	0.1045	2.01	0.1073	2.37	0.0653
	OMR*TIME	4	0.76	0.5595	0.46	0.7646	0.76	0.5562
	CPT*TIME	4	0.29	0.8830	0.21	0.9316	0.25	0.9109
	OMR*CPT*TIME	8	1.22	0.3063	0.54	0.8207	0.53	0.8283
Huron (Sandy)	OMR	2	0.28	0.7542	**4.50**	**0.0157**	**3.52**	**0.0367**
	CPT	2	0.76	0.4739	**6.44**	**0.0031**	**6.47**	**0.0031**
	TIME	2	1.60	0.2116	0.43	0.6512	0.13	0.8814
	OMR*CPT	4	2.49	0.0545	**3.28**	**0.0177**	**2.96**	**0.0281**
	OMR*TIME	4	0.26	0.9012	0.14	0.9645	0.09	0.9860
	CPT*TIME	4	0.37	0.8311	0.31	0.8702	0.16	0.9577
	OMR*CPT*TIME	8	0.33	0.9527	0.17	0.9939	0.16	0.9954

OMR, organic matter removal; CPT, compaction; SR, species richness; SE, species evenness; H’, Shannon’s diversity index.

Bold text indicates $P < 0.05$.

Table 4. Repeated measures ANOVA results indicating functional diversity responses to treatment.

Site	Source	*df*	ΔFR		ΔFDv		ΔFDs		ΔFE	
			F	*P*-value	*F*	*P*-value	*F*	*P*-value	*F*	*P*-value
CH (Silty Loam)	OMR	2	**5.60**	**0.0100**	**8.36**	**7E-04**	3.17	0.0502	1.07	0.3497
	CPT	2	1.10	0.3510	**5.50**	**0.0070**	**7.30**	**0.0020**	**5.26**	**0.0080**
	TIME	2	1.60	0.2130	2.78	0.0709	0.07	0.9348	**3.89**	**0.0270**
	OMR*CPT	4	1.20	0.3050	1.57	0.1962	**2.63**	**0.0440**	1.70	0.1629
	OMR*TIME	4	1.70	0.1750	0.13	0.9722	1.56	0.1991	1.50	0.2164
	CPT*TIME	4	0.70	0.5880	0.75	0.5640	0.70	0.5983	0.80	0.5313
	OMR*CPT*TIME	8	0.50	0.8810	0.92	0.5114	0.11	0.9985	0.60	0.7707
OT (Clay)	OMR	2	2.70	0.0790	0.28	0.7568	2.28	0.1133	**8.41**	**7E-04**
	CPT	2	0.90	0.4110	**6.49**	**0.0030**	**8.65**	**6E-04**	1.07	0.3499
	TIME	2	1.20	0.3010	2.30	0.1105	0.06	0.9404	0.27	0.7618
	OMR*CPT	4	2.30	0.0770	1.24	0.3054	**2.77**	**0.0370**	1.63	0.1812
	OMR*TIME	4	0.70	0.5860	0.51	0.7255	0.93	0.4518	1.58	0.1941
	CPT*TIME	4	0.60	0.6890	**10.4**	**<0.0001**	0.40	0.8061	0.42	0.7901
	OMR*CPT*TIME	8	0.50	0.8230	0.28	0.9686	0.56	0.8067	1.07	0.3965
HM (Sandy)	OMR	2	**3.20**	**0.0500**	1.80	0.1745	2.29	0.1111	**4.49**	**0.0160**
	CPT	2	**6.00**	**0.0000**	0.54	0.5832	**5.18**	**0.0090**	0.04	0.9631
	TIME	2	**11.00**	**0.0000**	0.32	0.7292	0.25	0.7794	0.18	0.8358
	OMR*CPT	4	0.70	0.6040	0.08	0.9881	0.55	0.7028	**4.99**	**0.0020**
	OMR*TIME	4	0.10	0.9690	0.45	0.7727	0.02	0.9989	0.28	0.9184
	CPT*TIME	4	0.60	0.6980	0.15	0.9633	0.24	0.9169	0.23	0.9184
	OMR*CPT*TIME	8	0.10	0.9990	0.14	0.9966	0.08	0.9996	0.54	0.8220

OMR, organic matter removal; CPT, compaction; ΔFEve, change in functional evenness; ΔFDiv, change in functional divergence; ΔFDis, change in functional dispersion; ΔFRic, change in functional richness.
Bold text indicates $P < 0.05$.

variability on sandy soils (stress = 18.2%). No differences in recovery as defined by the Euclidean distance between plots were detected (Appendix S3). However, treatments impacted recovery in terms of distance between pre- and post-treatment plots along Axes 1 and 2 (Fig. 1, Table 2).

Time affected Axis 1 scores on all but silty loam soils, with community composition at 5 and 10 yr post-harvest more dissimilar from pre-harvest values than 15 yr post-harvest (Table 2). On silty loam and sandy soils the OMR treatment also affected orientation along Axis 1 (Table 2).

Effects of treatments on community composition were more evident along Axis 2 across the study, and FFR generally decreased recovery (Table 2, Fig. 1). On sandy and silty loam soils, the combination of C2 and FFR reduced recovery relative to SOH at the same compaction level, and FFR decreased recovery compared to WTH on clayey soils (Table 2). The greatest recovery on clay occurred early (5 and 10 yr following treatment), with no differences between years 10 and 15, whereas temporal trends were not observed at other sites.

No environmental variables correlated with Axis 1, but, in accordance with the relationships reported above, change in forest floor thickness correlated with Axis 2 across sites. This association with was not observed until the 10- and 15-yr periods on silty loam and sandy soils, respectively, whereas a correlation on clayey soils diminished after the 5-yr period (Appendix S3). On silty loam and clayey soils, Δbulk density was correlated with Axis 2, whereas no relationship occurred on sandy soils (Appendix S3). Species associations are presented in Appendices S3 and S4.

Tree and shrub taxonomic diversity

Species richness (SR) and composition varied across the study, with only 23.5% of all 34 species observed occurring at all sites. Both factors affected ΔSR, ΔSE and ΔH′, but few consistent treatment effects emerged (Fig. 2, Table 3). WTH reduced ΔSE relative to SOH, but otherwise no negative effects were strictly associated with the removal of harvest residues. On silty loam soils FFR resulted in higher ΔSR than WTH (Fig. 2), but on clayey soils the opposite trend emerged, and no effect of treatment was observed on sandy soils. Compaction affected ΔSR only on silty loam, where species richness increased relative to pre-treatment values following C0, resulting in higher ΔSR than with C1 and C2 (Fig. 2). Time only affected ΔSR and only at two sites where it increased with years since treatment; otherwise, effects on ΔSR, ΔSE and ΔH′ remained relatively unchanged after 15 yr.

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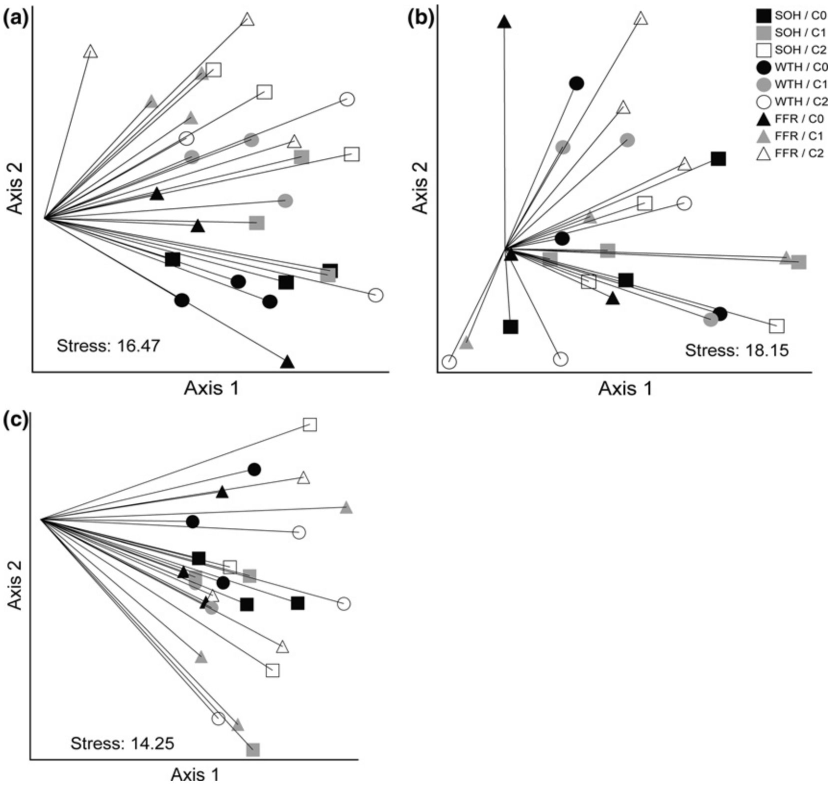

Fig. 1. Successional vectors from NMS ordination of treated plots in woody species space from pre-treatment to 15 yr after harvest. Vectors have been translated to origin such that the length and direction of vectors pictured in 2-D space are relative to one another. Sites appear separately with Chippewa in panel (**a**), Huron in panel (**b**) and Ottawa in panel (**c**). The legend in panel (**b**) applies to all. Treatment abbreviations: SOH, stem only harvest; WTH, whole tree harvest; FFR, forest floor removal; C0, no additional compaction; C1, moderate compaction; C2, heavy compaction. Correlations for all species and proxy treatment variables are listed in supplementary materials (Appendix S4, Table 4.1).

Functional diversity measures

As with taxonomic diversity, functional diversity responses varied across sites (Fig. 3). The only negative impact of WTH relative to SOH was reduced ΔFRic on silty loam soils. Heavy compaction (C2) had negative effects on sandy soils but positive effects were observed on silty loam, and contrary to expectations, the FFR treatment increased ΔFRic relative to WTH on both silty loam and sandy soils. Most changes to functional diversity persisted over the course of the study. Further details are provided in Appendix S4.

Standing biomass and diversity

Prior to treatment, *P. tremuloides* dominated all 81 stands included in this study. Fifteen years post-treatment, ten of the 81 plots exhibited a change in dominance that might be interpreted as a state shift in which trees constituted <50% of standing biomass. Of those plots, seven occurred on silty loam soils. ΔFDis was higher in plots dominated by shrubs rather than trees ($n = 7$, 20; z = 2.5982, $P = 0.0112$). ΔFEve was also higher for shrub-dominated plots (z = 2.7991, $P = 0.0026$) while ΔFRic did not differ between groups. Including all treatments across the site, there was a negative correlation between the proportion of biomass constituted by trees and functional dispersion 15 yr post-treatment on silty loam soils ($r = -0.45$, $P = 0.0196$). A similar trend occurred on clayey soils ($\tau = -0.47$, $P = 0.0007$), but not on sandy soils ($\tau = -0.054$, $P = 0.692$).

Discussion

Changes in demand for existing and emerging forest-derived goods, combined with a growing need to manage for adaptive capacity and resilience increase the importance of understanding the impacts of forest management practices on community composition, taxonomic diversity and functional diversity. Overall, the additional removal of residues (whole-tree harvest) decreased ΔFRic on silty loam and ΔSE on clayey soils, but had less effect on sandy soils (Figs. 2 and 3). Based solely on these results, one might conclude that the utilization of harvest residues for

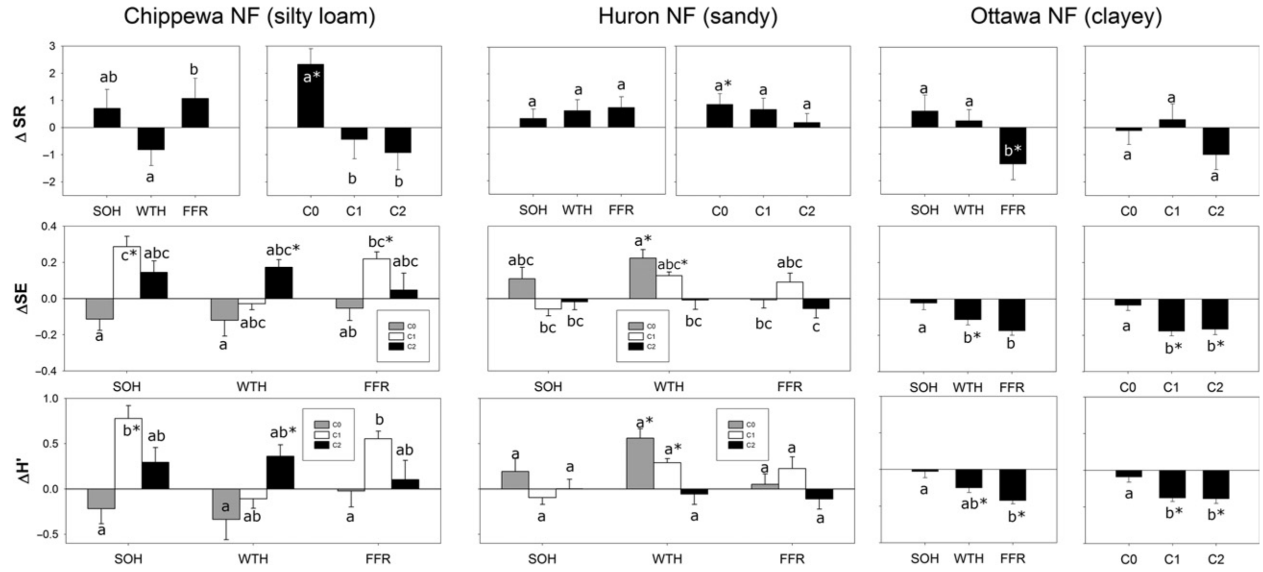

Fig. 2. Change in taxonomic diversity from pre-harvest to 15 yr post-harvest by treatment. Lowercase letters indicate significant differences ($P < 0.05$) where they occur. Four panels show means for each of the nine factorial combinations because of a significant OMR × CPT interaction. Otherwise, mean change is presented by factor. Panels are organized by site (indicated across the top) and by taxonomic diversity index (indicated along the left). Abbreviations for indices: SE, species evenness; SR, species richness; H', Shannon's diversity index; SOH, stem-only harvest; WTH, whole-tree harvest; FFR, forest floor removal; C0, no additional compaction; C1, moderate compaction; C2, heavy compaction.

bioenergy is a sustainable practice on sandy soils and that there is only a need for greater caution in implementation on finer-textured soils due to the risk of negative impacts to diversity. However, the delayed emergence of an association between forest floor removal and community composition as well as observed reductions in productivity (Curzon et al. 2014) and nutrients (Ca; Voldseth et al. 2011) underscore the importance of long-term studies and the use of multiple aspects of community structure and function to inform management recommendations and avoid unintended consequences to ecosystem sustainability.

Based on our results, the effect of removing harvest residues for bioenergy production on functional diversity likely varies depending on site conditions, as did the effect of removing the forest floor, which, while not typical of management in the US, occurs on landings and skid trails and was historically practiced in Europe (Sayer 2007). Forest floor removal and heavy compaction both reduced functional richness compared to pre-treatment and also resulted in lower ΔFRic than other treatments on clayey soils (Fig. 3). On silty loam soils, the increase in severity between stem-only harvest and whole-tree harvest corresponded with lower ΔFRic as well (and lower K at 10 yr; Voldseth et al. 2011), but functional richness associated with whole-tree harvest was more similar to pre-treatment (Fig. 3), and the increase in disturbance with the additional removal of the forest floor led to greater ΔFRic and no change in 10-yr observations of soil cations from WTH (Voldseth et al. 2011). The most holistic of the functional diversity measures we tested, ΔFDis (Laliberte & Legendre 2010), also increased with the removal of the forest floor on silty loam soils but only in combination with compaction. These patterns are all opposite to previous work examining above-ground standing tree biomass, dominated by *P. tremuloides* (Curzon et al. 2014), and are further supported by the negative correlation between functional dispersion and tree biomass reported in this study. ΔFDis and ΔFEve may have responded to changes in the abundance of *P. tremuloides* at this site rather than directly to the filtering effect of higher disturbance severity. Those conditions (i.e. severe compaction on silty loam soils) that impair or slow the regeneration of *P. tremuloides* (i.e. Bates et al. 1993) may indirectly increase different aspects of diversity by reducing site occupancy by this species and, correspondingly, competition for light and other resources. Functional dispersion was generally higher with increased shrub abundance, but this increase in functional diversity corresponded with a decrease in standing biomass (representative of productivity). Our results support those reported in other studies that show negative relationships between biomass production or C storage and species richness (Reich et al. 2012) and functional dispersion in boreal forests (Ziter et al. 2013).

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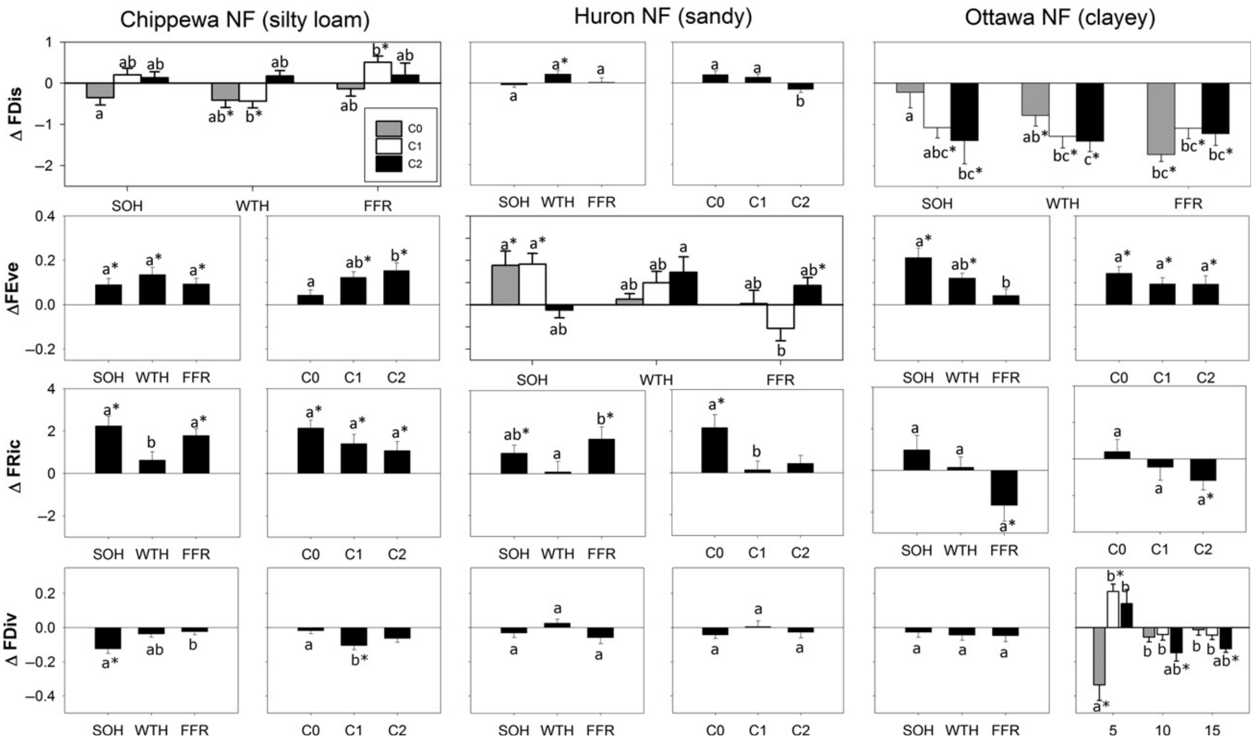

Fig. 3. Change in functional diversity from pre-harvest to 15 yr post-harvest by treatment. Lowercase letters indicate significant differences among treatments ($P < 0.05$) where they occur. Asterisks indicate a change in index value more than zero (*t*-tests or Wilcoxon signed-rank tests, as appropriate; $P < 0.05$). Two panels show means for each of the nine factorial combinations because of a significant OMR*CPT interaction. Otherwise, mean change is presented by factor. Panels are organized by site (indicated across the top) and by functional diversity index (indicated along the left). Abbreviations for indices: FDiv, functional divergence; FRic, functional richness; FEve, functional evenness; and FDis, functional dispersion; C0, no additional compaction; C1, moderate compaction; C2, heavy compaction.

The shift in dominance from tree to shrub species and lack of recovery evident in community composition on silty loam soils following the combination of forest floor removal and compaction suggests the severity of this disturbance exceeded the ecological resilience of this ecosystem. Such a change in community composition and structure will undoubtedly affect the provision of ecosystem services, particularly if current conditions persist. Both functional and taxonomic diversity are generally viewed as desirable because of the potential they have for increasing community and ecosystem resilience (Walker et al. 1999; Elmqvist et al. 2003; Folke et al. 2004). However, interpreting these measures should be done with caution as an increase may not be qualitatively greater, but instead indicative of a shift in community composition and structure to a less desirable state, as observed here, and may have different long-term consequences. Thus, we argue for the use of a suite of indicators to assess the impacts of a given management practice on ecosystem structure and function vs focusing on single metrics that, although designed to describe common relationships, may not fully capture potential impacts.

Conclusions

Whole-tree harvest resulted in lower functional richness and species evenness than conventional, stem-only harvest in two cases, but recovery in community composition was only negatively impacted by more severe treatments. While biodiversity was not negatively impacted on sandy soils, observations of reduced standing biomass reported elsewhere for the same site suggest whole-tree harvest may not be advisable. The response of species and functional diversity along the disturbance gradient tested in this study suggests maximization of standing biomass may mean a short-term sacrifice in species and functional diversity in a system dominated by species regenerating vegetatively (i.e. coppice systems). Guidelines aimed at mitigating impacts from management related to the procurement of bioenergy feedstock from forests should take site differences into account and strive to minimize soil disturbance during harvest entries.

Several measures of species and functional diversity increased as a shift in dominance from tree to shrub species occurred following the most severe disturbance treatment on silty loam soils. This finding highlights the need for a baseline of comparison, as an increase in functional diversity measures may coincide with substantial negative impacts from anthropogenic disturbance. It also reinforces previous suggestions that no single index or measure fully captures the complexity of functional change, but that multiple approaches used in combination may be most effective and worthwhile.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. References and study details for equations used to estimate biomass.
Appendix S2. Species traits.
Appendix S3. Species composition supplementary material.
Appendix S4. Supplementary results.