

Assessing the ecological impacts of biomass harvesting along a disturbance severity gradient

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Abstract. Disturbance is a central driver of forest development and ecosystem processes with variable effects within and across ecosystems. Despite the high levels of variation in disturbance severity often observed in forests following natural and anthropogenic disturbance, studies quantifying disturbance impacts often rely on categorical classifications, thus limiting opportunities to examine potential gradients in ecosystem response to a given disturbance or management regime. Given the potential increases in disturbance severity associated with global change, as well as shifts in management regimes related to procurement of biofuel feedstocks, there is an increasing need to quantitatively describe disturbance severity and associated responses of forest development, soil processes, and structural conditions. This study took advantage of two replicated large-scale studies of forest biomass harvesting in *Populus tremuloides* and *Pinus banksiana* forests, respectively, to develop and test the utility of a continuous, quantitative, disturbance severity index (DSI) for describing postharvest response of plant communities and nutrient pools to different levels of biomass removal and legacy retention (i.e., live trees and coarse woody material). There was a high degree of variability in DSI within categorical treatments associated with different levels of legacy retention and regression models using DSI as a predictor explained a portion of the variation (>50%) for many of the ecosystem- and community-level responses to biomass harvesting examined. Nutrient losses associated with biomass harvesting were positively related to disturbance severity, particularly in *P. tremuloides* forests, with postharvest nutrient availability generally declining along the gradient of impacts. Consistent with expectations from ecological theory, species richness and diversity of woody plant communities were greatest at intermediate disturbance severities and regeneration densities of dominant trees species were most abundant at highest levels of disturbance. Although categorical benchmarks will continue to be the primary way through which management guidelines are conveyed to practitioners, evaluation of their effectiveness at sustaining ecosystem functioning should be through continuous analyses, such as the DSI approach used in this study, to allow for the more precise identification of thresholds that ensure a range of desirable outcomes exist across managed landscapes.

Key words: biological legacy; downed woody material; *Pinus banksiana*; *Populus tremuloides*; soil nutrient stocks; variable retention harvest.

INTRODUCTION

Disturbances in ecological systems can occur across a gradient of severity, and the wide range of responses

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generated in ecosystem process and structure can be difficult to generalize (Frelich 2002, Keeley 2009, D'Amato et al. 2011). Quantification of this gradient is commonly approached categorically using disturbance-related vegetation mortality (Grime 1979, Frelich 2002), occasionally including forest floor disruption in forested ecosystems (e.g., Roberts 2004, 2007), but this categorical representation may oversimplify the range of disturbance effects on ecological processes. Ecosystem responses to both natural and management-related disturbances are complex and multi-dimensional, which may limit the scope of interpretation and confound

attempts to generalize resulting patterns (Puettmann et al. 2012). Management-related disturbances in forest ecosystems may be particularly difficult to interpret (Ellison and Gotelli 2004) because the inherent complexity of forests can lead to interactions that create nonlinear responses (Messier et al. 2013). Therefore, an integrated approach that explicitly recognizes severity gradients and incorporates disturbance legacies would fill a key knowledge gap and provide better information about the complex ecological outcomes of forest management decisions (Roberts et al. 2016).

Contemporary forest management is increasingly focused on balancing timber production with ecological objectives (Puettmann et al. 2012), and practices are intentionally structured to mimic natural disturbance regimes (Long 2009, Palik and D'Amato 2017). The resulting levels of disturbance severity may be closely related to deliberate management decisions, which are designed to sustain long-term ecological integrity, including the retention of live-tree legacies and transfer of biomass to detrital pools (Gustafsson et al. 2012, Schaedel et al. 2017). However, while many parallels exist between natural and anthropogenic disturbances, there are also significant disparities that complicate the development of useful generalizations across the two (Blair et al. 2016, Roberts et al. 2016). For example, wildfire and harvest disturbances differ in the size and amount of woody material remaining, as well as the relative amount of disturbance to the soil (Tinker and Knight 2000, D'Amato et al. 2011). Moreover, experiments in managed ecosystems have the luxury of obtaining predisturbance data, while natural disturbances are generally limited to using comparable undisturbed controls. However, as management guidelines move away from homogenous stand-wide harvests (i.e., clearcuts without retention of live-tree legacies) in favor of ecological silvicultural approaches that emulate the high degree of spatial complexity of natural disturbances (Roberts et al. 2016), it is increasingly relevant to understand the effects of within-stand variations in disturbance severity.

The greater within-stand variation in disturbance severity fostered by ecological forestry approaches poses a considerable challenge to both scientific evaluation and resource monitoring (Puettmann et al. 2012, O'Hara and Nagel 2013), and this challenge is further complicated by the renewed focus on procuring bioenergy feedstocks using biomass harvesting. Although biomass harvesting prescriptions often emphasize legacy retention to meet ecological objectives (i.e., retaining a specified number or percentage of live trees and/or deadwood on the site), they may actually increase disturbance severity by removing large amounts of biomass components that would have been retained in traditional harvests (Achat et al. 2015). As a result, changes in both overstory and forest floor must be used in assessing disturbance severity (Royo et al. 2016). Other research shows that analyzing biomass harvests using broad treatment severity categories fails to account for

within-treatment diversity in residual stand structure (Littlefield and Keeton 2012, Klockow et al. 2013). Therefore, an examination of the impacts of biomass harvesting using a continuous approach would address these categorical limitations and may permit the detection of thresholds, above which increases in disturbance severity may trigger dramatic, nonlinear changes in forest communities (Frelich and Reich 1999, Peterson and Leach 2008). It may also mitigate other challenges associated with predicting long-term forest responses, such as the site-specific responses and limited spatial or temporal scales that often confound experimental manipulations.

Few studies have applied a continuous approach to quantifying multi-dimensional forest disturbances (Roberts 2007, Peterson and Leach 2008, Brewer et al. 2012, Royo et al. 2016). Roberts (2007) developed a three-dimensional continuous model, with ecological response to harvesting varying as a function of both overstory and ground layer disturbance severity. Although the model only focused on the herbaceous understory community, it captured the range of disturbance severity when fitted to the data of three previous studies and provides a framework for comparing anthropogenic and natural disturbances. Non-categorical approaches have been used to assess the cumulative severity of a natural disturbance (wind throw) followed by salvage logging (Peterson and Leach 2008, Brewer et al. 2012, Royo et al. 2016) and have relied on post-disturbance measures of surviving trees, soil disturbance, and downed woody material to quantify disturbance impacts. No research to date that we know of has developed or tested a single quantitative index to assess the complex overstory and forest floor impacts of biomass harvesting on forest ecosystems managed with ecological forestry approaches.

Our objective was to expand on previous research by applying a continuous analytical approach representing multiple disturbance impacts to forest management regimes designed to procure bioenergy feedstocks and meet ecological objectives. We developed a single integrated index of disturbance severity using the total change in aboveground biomass, including logging slash necromass (deadwood, bark, branches, and foliage), in pre- and postharvest forests. We then evaluated the utility of this index using a variety of ecosystem- and community-level variables within two, operational-scale experiments. The first experiment took place in aspen (*Populus tremuloides* Michx.) and the second in jack pine (*Pinus banksiana* Lamb) forests, both of which are ecologically and economically important forest types across the upper Great Lakes region of North America and are currently being explored for use in the woody energy market (Domke et al. 2008). The two forest types have contrasting edaphic factors and postharvest regeneration strategies, but they shared the common management objective of bioenergy harvesting with legacy retention, which made them ideal study systems for

evaluating biomass harvest disturbance. We hypothesized that using a continuous, integrated approach to quantify complex, harvest-related disturbance would be more informative for describing postharvest vegetation and soil responses than a categorical analysis because it would capture more variability and reveal subtle differences in the complex experimental design. This would be supported by linear gradients or thresholds spanning treatment categories with models explaining a high degree of variation in postharvest conditions.

MATERIALS AND METHODS

Study area and experimental design

We collected data on ecosystem and community properties at two, fully replicated, operational-scale, biomass harvesting experiments in northern Minnesota, USA. The first experiment was located in trembling-aspen-dominated (*Populus tremuloides* Michx.) hardwood forests in northeastern Minnesota (aspen experiment). Soils ranged from silt loams to stony loams of glacial origin. Stand age ranged from 55 to 68 yr, and all had regenerated naturally after clearcut harvests. Other commonly occurring tree species included paper birch (*Betula papyrifera* Marshall), red maple (*Acer rubrum* L.), black ash (*Fraxinus nigra* Marshall), balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) Britton), and white spruce (*Picea glauca* (Moench) Voss.), as well as occasional northern white cedar (*Thuja occidentalis* L.) and eastern white pine (*Pinus strobus* L.).

The second experiment was located in jack pine (*Pinus banksiana* Lamb.) forests in northcentral Minnesota (jack pine experiment). Sites were located on glacial outwash plains with loamy sand to sandy loam soils. Stand age ranged from 49 to 65 yr with establishment occurring following a combination of clearcut harvesting and fire (Gill et al. 2016). Other commonly occurring canopy tree species included trembling aspen, bigtooth aspen (*P. grandidentata* Michx.), paper birch, red maple, balsam fir, black spruce, red pine (*Pinus resinosa* Ait.), bur oak (*Quercus macrocarpa* Michx.), and northern red oak (*Q. rubra* L.).

The aspen and jack pine experiments followed identical experimental designs intended to investigate variable levels of slash and green-tree retention within biomass harvests. Both experiments consisted of four replicate sites, each approximately 40.5 ha in size. The replicate sites contained harvested stands with levels of slash and green-tree retention nested in a 3 × 3 completely randomized block design with an untreated control. The stands were each 4.1 ha in size, which allowed for operational-scale implementation of the treatments. Slash retention treatments included retaining all slash on the site (stem-only harvest, SOH), retaining no slash on the site (whole-tree harvest, WTH), and retaining 20% of the slash onsite (20 SR), which is the current recommended site-level guideline for biomass harvest in

several regions, including Minnesota (MFRC 2007). The green-tree retention treatments included no trees retained (clearcut harvest, NONE), retention of intact aggregates (AGR), and retention of dispersed trees (DISP). At the aspen experiment, the AGR treatment consisted of retaining two round areas of intact forest, each approximately 0.1 ha, within the harvested stand. One intact aggregate, approximately 0.2 ha in size, was retained in the AGR treatment at the jack pine experiment. In the DISP treatment, individual green trees were retained across the entire stand at a prescription of 15–30 trees/ha at approximately 21 m spacing.

Field measurements and variables

Six 0.04-ha, circular plots were established in each stand prior to harvest at the aspen experiment. Following the harvest, the two AGR-treatment plots were adjusted such that the entire plot fell within the aggregate. The remaining four plots were left in the open, harvested condition. Plot establishment was similar at the jack pine experiment, with the exception that, since only one aggregate was retained for the AGR treatment, a total of four plots per stand were used (one inside aggregate and three in the open, harvested condition). A range of stand structural, ecosystem, and community characteristics were measured in the 0.04-ha plots (Table 1). Measurements were taken during the growing season prior to harvest (2009 for aspen and 2012 for jack pine) and in growing seasons in subsequent postharvest years (2010 for aspen and 2013 for jack pine). At the aspen experiment, forest structural and biomass pool components, including large woody stems (trees), smaller woody stems (saplings and shrubs/advance regeneration), litterfall, fine woody material (FWM; ≤7.5 cm diameter), coarse woody material (CWM > 7.5 cm diameter), herbaceous vegetation, organic horizon, mineral soil, fine roots, and coarse roots were measured as described in Klockow et al. (2013). This included collection of forest floor (15 cm diameter sample area) and mineral soil samples (6.35 cm diameter core to 20 cm depth) at three locations within each 0.04-ha plot. Biomass pools were estimated using the species-specific allometric biomass equations in Jenkins et al. (2003) and nutrient stocks in all woody components (trees, saplings, shrubs, FWM, and CWM) were estimated using destructive sampling to derive species-specific nutrient concentrations as described in Klockow et al. (2014). The nutrient concentrations of other ecosystem components (litterfall, herbaceous vegetation, soil organic horizon, coarse and fine roots, and mineral soil) were also analyzed. Nutrient analyses included total C and N by combustion on a LECO Truspec CHN Macro analyzer (LECO Corporation, St. Joseph, Michigan, USA), and Ca, K, Mg, and P by Inductively Coupled Plasma Atomic Emission Spectrometry (ICP-AES) analysis with a Perkin Elmer Optima 3000 ICP Spectrometer (Perkin Elmer, Waltham, Massachusetts, USA). The same

TABLE 1. Summary of variables measured for examining disturbance impacts on ecosystem structure and function.

Variable	Unit	Calculation
Disturbance severity index (DSI) ^{†,‡}		Change in total aboveground biomass, including live and dead trees, saplings, and woody material (coarse and fine), between pre- and postharvest forests.
Aboveground nutrient losses (N, Ca, K, Mg, P, and C) ^{†,‡}	kg/ha	Sum of aboveground nutrient stocks (trees, saplings, seedlings, shrubs, herbaceous vegetation, FWM, and CWM), live and dead, for each year. Postharvest values were subtracted from the preharvest total.
Nutrient availability [†]	$\mu\text{g}\cdot 10\text{ cm}^{-2}\cdot 24\text{ weeks}^{-1}$	Assessed using ion-exchange resins during first growing season following harvest at aspen experiment.
Organic horizon mass [†]	Mg/ha	Change in mass from pre- to postharvest.
Litterfall mass [†]	Mg/ha	Postharvest (aspen experiment only).
Seedling and advance regeneration densities ^{†,‡}	stems/m ²	Postharvest tallies for aspen and total stems at aspen experiment; total stems at jack pine experiment.
Woody stem diversity and composition ^{†,‡}		Postharvest community structure (species richness, <i>S</i> ; evenness, <i>E</i> ; Shannon diversity index, <i>H'</i> ; Simpson diversity index, <i>D</i>) and Bray-Curtis compositional dissimilarity (pre- to postharvest) were computed using tallies of all live woody stems (trees, saplings, and seedlings).

Note: Disturbance severity index (DSI) was used as a continuous explanatory variable and all others were response variables.

[†] Measured at aspen experiment.

[‡] Measured at jack pine experiment.

measurement protocols were followed at the jack pine experiment, with the exception of litterfall and nutrient availability, which were not measured. In addition, due to the short field season in 2013, measurements in AGR and control plots were incomplete at the jack pine experiment and were not included in the subsequent analysis, since they are not comparable to the preharvest values.

Postharvest plant-available nutrients (NO_3^- , NH_4^+ , Ca, Mg, K, P) were assessed at the aspen experiment using ion-exchange resins (Plant Root Simulators, PRS probes; Western Ag Innovations, Saskatoon, Saskatchewan, Canada). These resin probes are inserted vertically into the soil and continuously adsorb nutrients from the soil solution, which minimizes soil disturbance. Four anion and four cation probes were installed at two locations within each plot (11 m from plot center at 30° and 150° azimuths). The intensity of resin probe and soil sampling used may have been too limited to detect all of the heterogeneity created by the harvesting treatments; however, this level of sampling represents what was logistically feasible given the operational scale and level of replication for the experiments. Nutrient availability was assessed during the growing season from early May to late October 2010 (approximately 24 weeks), and probes were replaced about halfway through the growing season to prevent saturation. Probes were returned to the laboratory and rinsed with distilled water to remove residual soil before sending to Western Ag Innovations for analyses of NO_3^- , NH_4^+ , P, K, Ca, Mg. Values from the four probes at each plot location were pooled to account for soil heterogeneity, and extreme outlier values were identified as those greater than [upper quartile + (3) × (interquartile range)] or less than [lower quartile - (3) × (interquartile range)] and excluded (<6% of data set; Johnson et al. 2010). The two azimuth values were averaged to produce one value for each plot.

A disturbance severity index (DSI) was computed for each plot as the change in total aboveground biomass, including live and dead trees, saplings, and woody material (coarse and fine), between pre- and postharvest forests. The calculated biomass change was standardized by dividing by the preharvest biomass, and the resulting DSI was used as the continuous explanatory variable in statistical analyses. Disturbance severity is generally defined as vegetation killed by a disturbance; however, in the case of this formulation of the index, it is better interpreted as aboveground biomass removed by disturbance given the inclusion of slash necromass in our calculations. Because detrital legacies are often deliberately retained as part of ecological forestry treatments and to sustain ecosystem processes following biofuel feedstock harvests, we felt the inclusion of necromass was more appropriate for quantifying disturbance impacts. Calculated in this manner, negative values can correspond to undisturbed plots that have gained live aboveground biomass through growth, as well as disturbed plots in which detrital pools have increased due to increased necromass loading from harvesting activities or other disturbance. In contrast, positive values indicate areas experiencing a net reduction in aboveground biomass following disturbance.

Statistical analyses

We examined the impacts of biomass harvesting on forest biomass, nutrient stores, and vegetation communities using an integrated, non-categorical approach. We used DSI as a continuous explanatory variable on a per-plot basis within a mixed model regression framework, with all models incorporating the random effects of stand nested within site to avoid pseudoreplication. A preharvest covariate was included when the variable only

constituted a postharvest measurement (e.g., seedling density and Shannon's index), rather than a measurement of pre- to postharvest change (e.g., lost N and Bray-Curtis dissimilarity). Denominator degrees of freedom were estimated using the containment method. First- and second-order polynomial regressions were examined for variables where we expected potential curvilinear responses to disturbance (e.g., species diversity), whereas only first-order models were used for variables where linear responses were more plausible (e.g., aboveground nutrient loss). All models were compared using the Akaike information criterion corrected for sample size (AIC_c ; Sugiura 1978) to select the most appropriate fit. Quadratic terms resulting in a decrease in model AIC_c indicated a nonlinear fit. For clarity, we focused on interpreting each ecosystem response in terms of the best-approximating model, which balances model fit against the potential to broadly apply beyond the present data set (Burnham and Anderson 2002).

We verified regression model assumptions (linearity and homoscedasticity) through visual inspection of model residuals, and non-conforming data were transformed when necessary to meet these assumptions. A constant was added prior to the transformation to variables containing negative values, equal to the variable minimum plus 0.01, to ensure that all data were included. Continuous modeling with DSI was performed in the nlme package (Pinheiro et al. 2016) for R (R Core Team 2016), with model fit via maximum likelihood. For each response variable model set, relative model AIC_c support was assessed by calculating Akaike weights (w_i). In addition to w_i , we also evaluated the predictive power of models by calculating the marginal (fixed-effects only) R^2 (Bartoń 2017).

We performed two-way analyses of variance (ANOVA) and covariance (ANCOVA) using the MIXED procedure in SAS to interpret DSI in the context of categorical treatment levels. To compare disturbance severity among biomass harvesting regimes, we tested for differences among the various levels of slash (SOH, 20 SR, and WTH) and green-tree retention (AGR, DISP, and NONE), as well as their interaction (slash \times green-tree retention). Controls were excluded because the lack of slash treatments precluded analysis within the factorial design. A preharvest covariate was included when the variable only constituted a postharvest measurement (not when the variable was the pre/post difference). Plots were averaged within a stand, and stand values were used as the experimental unit (Klockow et al. 2013).

RESULTS

Disturbance severity index

DSI explained a significant proportion of the variation for many of the ecosystem- and community-level responses to biomass harvesting with variable legacy

retention (Tables 2 and 3). The best-fitting models in the aspen experiment included both linear and quadratic terms, whereas linear terms were the best-approximating forms for all variables analyzed in the jack pine experiment. DSI values ranged from -0.67 to 0.91 in the aspen experiment and 0.38 to 0.95 in the jack pine experiment, and differences in DSI values among the treatments were inconsistent.

In the aspen experiment, ANOVA analyses revealed that DSI values varied across the slash retention treatments ($P = 0.01$; SOH < 20 SR and WTH), but values did not differ among green-tree retention treatments ($P = 0.97$), nor was there a slash by green-tree retention interaction ($P = 0.25$). Undisturbed control stands tended to have the lowest DSI values (-0.28 to 0.17), whereas clearcut stands exhibited a wide range of DSI values (-0.67 to 0.91 across all levels of slash retention).

In the jack pine experiment, the range of DSI values was confined to higher values than those at the aspen experiment because undisturbed controls and green-tree aggregates, which occupied lower values at the aspen experiment, were not included in the analysis. DSI varied among the slash treatments ($P = 0.04$; SOH < WTH) and the green-tree retention treatments ($P < 0.01$; DISP < NONE), and there was not a significant slash \times green-tree retention interaction ($P = 0.46$).

Aboveground nutrient losses, postharvest nutrient availability, litterfall, and forest floor mass

The best-approximating models for estimating changes in aboveground nutrient stocks at the aspen experiment indicated a positive, linear relationship with DSI (w_i $AIC_c = 0.58$ to 1.00 ; $R^2 = 0.20$ – 0.86 ; Table 2; Fig. 1) for all nutrients. *Data SI: Model Comparisons* provides the full set of model comparisons for each response variable. Models were less consistent for postharvest nutrient availability ($w_i = 0.69$ to 0.81 ; $R^2 = 0.00$ – 0.22), change in forest floor mass ($w_i = 0.58$; $R^2 = 0.03$), and postharvest litterfall ($w_i = 0.70$; $R^2 = 0.47$) at the aspen experiment (Table 2). Plant-available ammonium, nitrate, and phosphorus all increased with increasing DSI, while calcium and potassium remained stable and magnesium decreased (Fig. 2).

At the jack pine experiment, the best-approximating models for estimating the change in aboveground nutrient stocks indicated a linear relationship with DSI, but the fits were less robust than those observed at the aspen experiment ($w_i = 0.39$ – 1.0 ; $R^2 = 0.00$ to $R^2 = 0.61$; Table 3; Fig. 3). Similarly, the intercept-only null model was the best-supported model of change in forest floor mass ($w_i = 0.39$; $R^2 = 0.00$; Table 3).

Postharvest community structure

DSI explained much of the variation in community structure post-biomass harvesting at the aspen experiment. Both total seedling density and aspen seedling

TABLE 2. Parameters for best-approximating regression models for predicting ecosystem and community responses to disturbance severity (DSI) at the aspen experiment.

Variable	Intercept	DSI	DSI ² †	Pretreatment value	AIC _c weights	Marginal R ²
Change in total aboveground nutrient stocks‡						
N¶	29895.4	122211.6			1.00	0.20
Ca	369.0	3577.5			1.00	0.78
K¶	13.5	55.0			1.00	0.86
P¶	1229.4	9559.69			1.00	0.53
Mg	35.4	345.5			1.00	0.78
C	34.9	348.19			1.00	0.82
Postharvest nutrient availability§						
NO ₃ ⁻	1.83	0.84			0.69	0.09
NH ₄ ⁺ ‡‡	2.63	1.46			0.99	0.22
Ca§§	3721.165				0.72	0.00
Mg¶¶	6.55	-0.27			0.86	0.07
K¶¶	2.80				0.77	0.00
P‡‡	2.58	2.27			1.00	0.19
Change in forest floor mass (Mg/ha)‡	0.45	-63.2			0.58	0.03
Postharvest litterfall (Mg/ha)¶¶	1.50	-5.19			0.70	0.47
Postharvest regeneration and woody stem community structure						
Total seedling densities¶¶	1.77	1.44		0.01	0.73	0.35
Aspen seedling densities††	1.68	6.21	0.96		0.55	0.42
Species richness	2.96	-13.49	-8.33	0.43	1.00	0.41
Evenness¶¶	0.46	-0.40	0.30		0.31	0.04
Shannon¶¶	0.28	-4.42	-2.44	0.98	0.98	0.32
Simpson§§	-0.01	-0.58	-0.31	0.30	0.94	0.23
Bray-Curtis (pre- to postharvest)‡‡	0.59	1.14	0.43		0.99	0.28

Note: AIC_c, Akaike information criterion corrected for sample size.

† Quadratic DSI terms evaluated for forest floor, litterfall, and community structure only.

‡ Total aboveground nutrient stock (pre- minus postharvest).

§ Assessed by Plant-Root Simulator probes during growing season following harvest.

¶-¶¶ Data were transformed prior to analysis as follows: ¶, second power; ||, square root; ††, cube root; ‡‡, natural log; §§, fourth power; ¶¶, fourth root. Variables containing negative values had a constant added prior to the transformation.

TABLE 3. Parameters for best-fitting regression models for predicting ecosystem and community responses to disturbance severity at the jack pine experiment.

Variable†	Intercept	DSI	Pretreatment value	AIC _c weights	Marginal R ²
Change in total aboveground nutrient stocks‡					
N§	32.38	30.47		0.99	0.09
Ca§	22.59	-7.63		0.57	0.03
K§	33.39	27.24		0.97	0.07
P§	16.46	13.57		0.98	0.07
Mg§	24.8	17.75		0.92	0.06
C¶	2.75	5.20		1.00	0.61
Change in forest floor mass (Mg/ha)	-1.82			0.39	0.00
Postharvest regeneration and woody stem community structure					
Total seed densities§	3.05		0.07	0.69	0.08
Species richness§	2.27	-0.89	0.03	0.29	0.22
Evenness	0.10		0.58	0.58	0.21
Shannon	-0.07	-1.95	1.32	0.66	0.28
Simpson	0.05	-0.32	0.53	0.51	0.21
Bray-Curtis (pre- to postharvest)	0.50			0.69	0.00

† Postharvest litterfall and nutrient availability (PRS probes) were not measured at the jack pine experiment.

‡ Total aboveground nutrient stock (pre- minus postharvest).

§-|| Data were transformed prior to analysis as follows: §, square root; ¶, cube root; ||, second power.

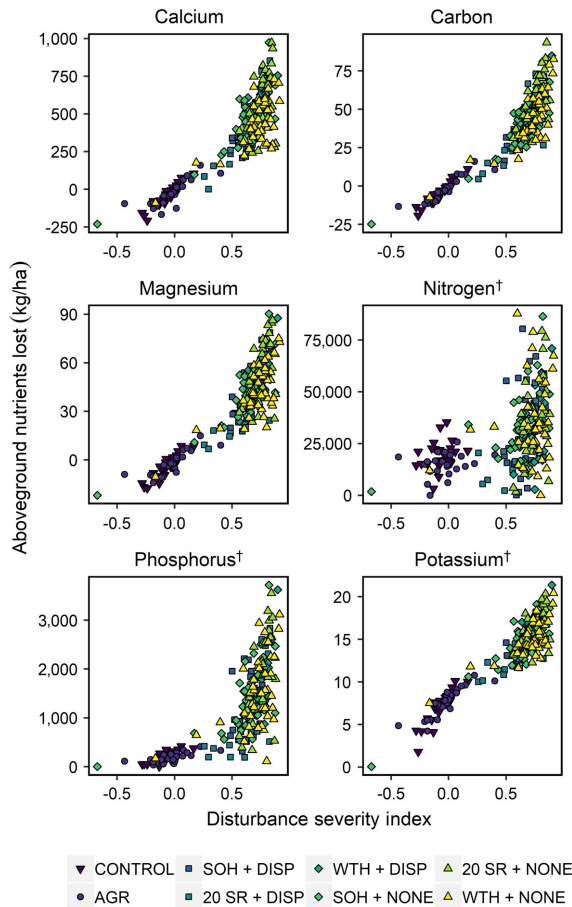


FIG. 1. Relationships between aboveground nutrient losses from biomass harvesting and disturbance severity index (DSI) in aspen-dominated forests of northern Minnesota. Nutrient losses represent the preharvest sum of all aboveground stocks (live and dead biomass) minus the 1-yr postharvest sum; each point represents one plot. DSI is calculated as the change in total live and dead aboveground biomass between pre- and postharvest forests and is standardized by dividing by the preharvest biomass. See Table 2 for best-approximating models for response each variable. Panels marked with † show transformed response variables with corresponding transformation listed in Table 2. AGR, aggregate green-tree retention; DISP, dispersed green-tree retention; NONE, no green trees retained; SOH, stem-only harvest; 20 SR, 20% slash retained; WTH, whole-tree harvest.

density increased linearly with DSI ($w_i = 0.73$, $R^2 = 0.35$ and $w_i = 0.55$, $R^2 = 0.42$, respectively; Table 2; Fig. 4). Species richness, Shannon’s index (H'), and Simpson diversity all tended to be higher at intermediate DSI values ($w_i = 1.00$, $R^2 = 0.41$; $w_i = 0.98$, $R^2 = 0.32$; $w_i = 0.94$, $R^2 = 0.23$, respectively; Table 2; Fig. 4). Species evenness varied minimally with DSI ($w_i = 0.31$, $R^2 = 0.04$), while the Bray-Curtis dissimilarity index showed a more substantial quadratic increase with DSI ($w_i = 0.99$, $R^2 = 0.28$; Fig. 4).

DSI was not a strong predictor of variation in community structure at the jack pine experiment. For

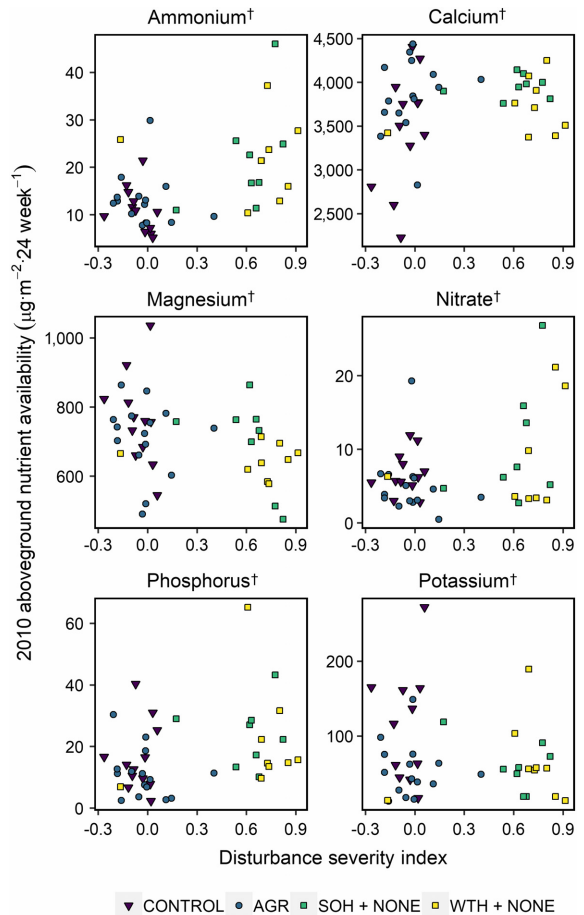


FIG. 2. Relationships between nutrient availability as assessed by Plant Root Simulator (PRS) probes 1 yr following biomass harvest and disturbance severity index in aspen-dominated forests of northern Minnesota. Points represent the mean of two probes per plot. See Table 2 for best-approximating models and Fig. 1 for treatment definitions. Panels marked with † show transformed response variable with corresponding transformation listed in Table 2.

seedling density and evenness, pretreatment covariate-only models had higher AIC support ($w_i = 0.69$, $R^2 = 0.08$; $w_i = 0.58$, $R^2 = 0.21$, respectively) than alternative models incorporating DSI. While linear models of species richness, Shannon’s index, and Simpson diversity as functions of DSI and pretreatment values had the greatest AIC_c support, model performance was weak to moderate ($w_i = 0.29$ – 0.66 , $R^2 = 0.21$ – 0.28 , Table 3; Fig. 5). For Bray-Curtis dissimilarity, the null intercept-only model had greater AIC_c support than either DSI model ($w_i = 0.69$, $R^2 = 0.00$).

DISCUSSION

In forest ecosystems, disturbance severity reflects the amount of biomass transferred from live to dead pools, as well as the amount of forest floor and soil removed or

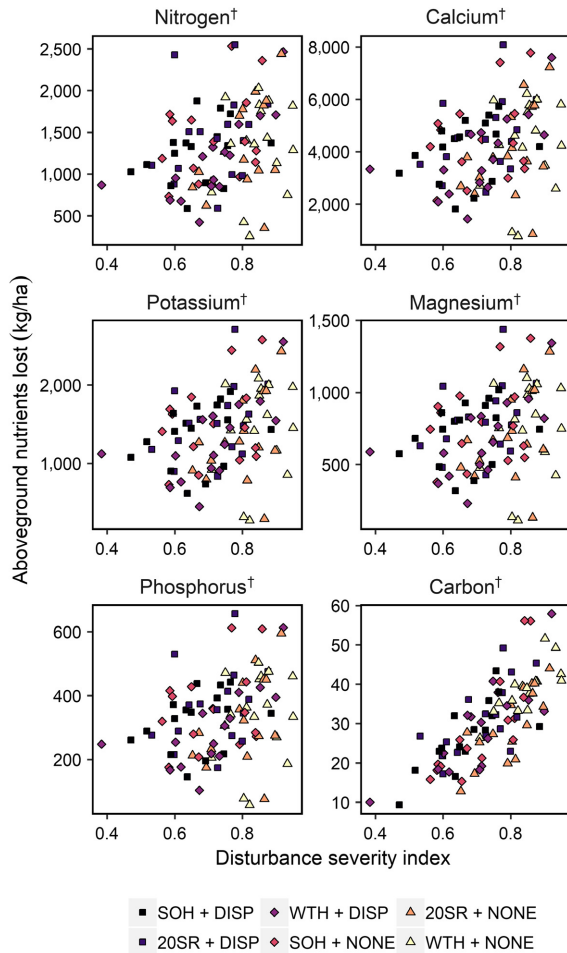


FIG. 3. Relationships between aboveground nutrient losses from biomass harvesting and disturbance severity index in jack pine forests of northern Minnesota. Nutrient losses represent the preharvest sum of all aboveground stocks (live and dead biomass) minus the 1-yr postharvest sum; each point represents one plot. See Table 3 for best-approximating models and Fig. 1 for treatment definitions. Panels marked with † show transformed response variable with corresponding transformation listed in Table 3.

destroyed (Roberts 2004). Comparisons of disturbance types, which presumably differ in severity, have long been approached using categorical analyses (Grime 1979, Frelich 2002, Roberts 2004, 2007), perhaps because forest disturbances are discrete events by definition (White and Pickett 1985). However, this approach ignores the likelihood that severity is variable within a disturbance type, and, in fact, there may be substantial overlap in severity among disturbances (i.e., a gradient of severity within and among disturbance types that only emerge when examined at a finer spatial scale; Roberts 2007, Peterson and Leach 2008, Flower and Gonzalez-Meler 2015, Stuart-Haëntjens et al. 2015, Peterson 2019). While often addressed in the context of natural disturbance, this issue may increasingly extend to

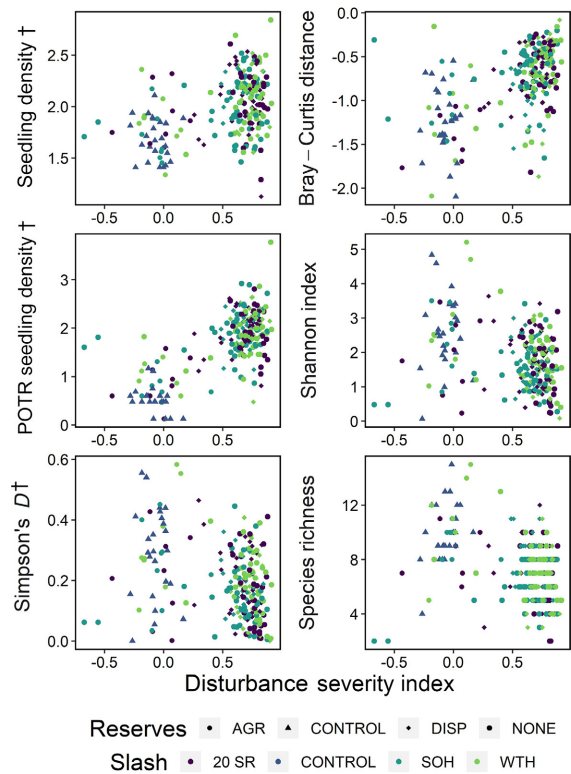


FIG. 4. Relationships between woody stem community characteristics and disturbance severity index in aspen-dominated forests of northern Minnesota; each point represents one plot. Community indices were assessed 1 yr postharvest. See Table 2 for best-approximating models and Fig. 1 for treatment definitions. Panels marked with † show transformed response variable with corresponding transformation listed in Table 2. POTR, *Populus tremuloides*.

managed forests, where deliberate retention of varying amounts of structural legacies, such as living and dead trees, are integrated into silvicultural prescriptions to better sustain ecological functions compared to timber-focused management regimes (Palik and D'Amato 2017). This practice, in effect, creates gradients of disturbance severity within and among stands. We explored the implications of using an integrated, continuous representation of disturbance severity in the form of a disturbance severity index (DSI) to capture the dynamic and heterogeneous responses of biomass harvesting with legacy retention in two contrasting, sub-boreal forest ecosystems. We found that models using this more continuously variable representation of severity explained differing amounts of variability in changes dependent on response variables; generally more for aboveground nutrient stocks and in aspen-dominated ecosystems compared to vegetation community variables and in jack pine-dominated ecosystems. Collectively, our results demonstrate that biomass harvesting operations generate a gradient of disturbance severity, particularly when deliberate retention of legacies is prescribed, and

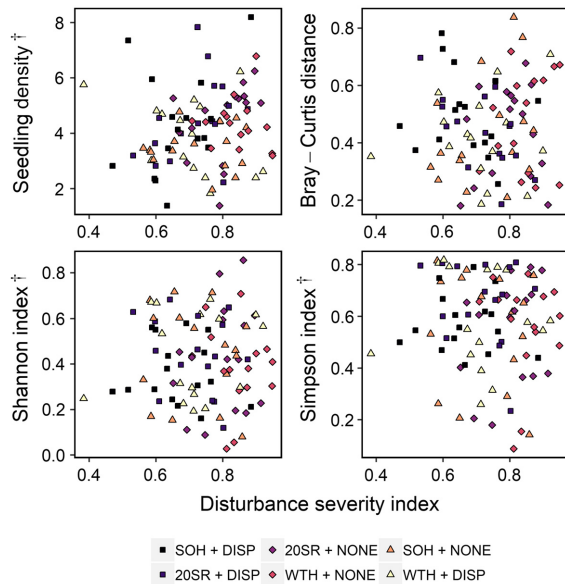


FIG. 5. Relationships between woody stem community characteristics and disturbance severity index in jack pine-dominated forests of northern Minnesota; each point represents one plot. Community indices were assessed 1-yr postharvest. See Table 3 for best-approximating models and Fig. 1 for treatment definitions. Panels marked with † show transformed response variable with corresponding transformation listed in Table 3.

support the conclusion that assessing these impacts warrants analyses that accommodate variable impacts without relying upon treatment categories (Attwill 1994).

Most of the variables we examined were responsive to differences in biomass harvesting disturbance severity. In both forest types, the magnitude of losses for nutrients was positively related to disturbance severity, consistent with previous studies documenting inconsistent impacts of harvest and/or disturbance on nutrient dynamics (Bormann et al. 1968, Vitousek and Melillo 1979). Nutrient stock responses were more pronounced in aspen compared to jack pine. The greater magnitude of response in the aspen stands may be a consequence of differences in the range of retention treatments examined (e.g., jack pine treatments did not include untreated stands), but it may also be related to the disproportionate effects of aspen dynamics on nutrient pools (e.g., calcium; Alban 1982, Ste-Marie et al. 2007) and the impact of vegetative sprouting in aspen on postharvest responses (Kurth et al. 2014). As such, any disturbance severity impacts on overstory aspen may elicit a greater response than a similar level of impact on overstory jack pine. Nutrient availability responses to disturbance, which we only examined in aspen, displayed more variability than nutrient stocks, but, consistent with previous work in aspen-dominated forests (Roberts and Gilliam 1995), nutrient availability generally increased with disturbance severity.

Vegetation responses to biomass harvesting disturbance revealed some differences between the aspen and jack pine ecosystems. Seedling stem density and community changes were positively related to disturbance severity only in the aspen experiment. The predominance of regeneration via root suckering in aspen permits rapid recovery of this species following severe disturbance (Doucet 1989). Compared to the aspen experiment, the analyses of jack pine ecosystem responses suggested a low overall influence of either disturbance severity on the woody seedling community. Instead, post-treatment seedling community responses in jack pine stands largely reflected pretreatment conditions. The short (1-yr) postharvest timespan in this study may have been insufficient to observe considerable postharvest woody regeneration (and thus variation in community metrics) in the jack pine forest type, where the major tree species regenerates from seed (Greene et al. 1999). Cones contained in logging slash may be important contributors to postharvest regeneration of jack pine (Chrosiewicz 1990), and any influences of slash removal on seedling responses may only become apparent over time. Mechanical harvesting, as opposed to fires, may also foster relatively less pronounced community responses in fire-adapted ecosystems such as jack pine (Blair et al. 2016).

Overall, our results for species richness and diversity of woody species appear to be consistent with the intermediate disturbance hypothesis (Horn et al. 1975, Connell 1978). Both richness and diversity were highest at intermediate disturbance severity in the aspen stands, and the negative relationships between disturbance severity and both variables in the jack pine stands may reflect the lack of low severity disturbances in that experiment, and, thus, still be consistent with the intermediate disturbance hypothesis.

Management implications and conclusions

The impacts of management on forest ecosystem response often vary in subtle ways across multiple spatial scales; however, general approaches for evaluating these impacts have relied almost exclusively on broad categorizations. Similarly, management guidelines for mitigating the ecological impacts of biomass harvest disturbance are often stated as broad benchmarks for legacy retention. Our results show that while such guidelines focus on achieving discrete targets over a management unit, they may often result in a range of overlapping ecological impacts. This range was exemplified by the gradient in disturbance severity associated with treatment categories in our operational experiments, and it underscores the importance of accounting for spatially variable disturbance impacts through a continuous approach, such as the DSI applied in this work. From a practical standpoint, categorical benchmarks will continue to be the primary way through which management guidelines are conveyed to practitioners;

however, the science evaluating their effectiveness at sustaining ecosystem process should increasingly employ continuous approaches to allow for the identification of quantifiable thresholds that will ensure a range of desirable outcomes exist across managed landscapes, including those producing biomass feedstocks.

Beyond examining the range of management impacts, the DSI approach outlined in this study may also have utility in capturing the gradient of disturbance impacts following natural disturbance. Future studies should confirm whether integrated, continuous DSI applies similarly between natural and managed disturbances, particularly in terms of indicator species or functional traits that may be more critically influenced by disturbance type than broad community structure (Brewer et al. 2012). Not all studies will have the luxury of the pre-disturbance data afforded by planned experiments, such as those used in this study, but the use of reconstructions of living biomass from damaged stems may provide alternative proxies for levels of disturbance severity in a given area where such collections do not exist (cf. Peterson and Leach 2008). In light of observed and predicted increases in disturbance severity at a global scale (Dale et al. 2001), moving beyond categorical classifications of disturbance will be critical for describing ecosystem impacts and monitoring how levels and patterns of severity may be evolving over time in response to changing forest, landscape, and climate conditions. Quantifying these impacts will allow researchers to refine predictions of ecosystem response and recovery, and it will also serve to gauge the potentially compounding influence of post-disturbance management interventions like salvage logging (Peterson and Leach 2008). Although the field data collections required to estimate disturbance severity may increase the levels of time and investment necessary for ecological studies to examine disturbance impacts, these modifications will be critical as we seek to further understand the influence of natural and anthropogenic disturbances on ecosystem structure and function under changing environmental and land use regimes.

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LITERATURE CITED

- Achat, D. L., C. Deleuze, G. Landmann, N. Pousse, J. Ranger, and L. Augusto. 2015. Quantifying consequences of removing harvesting residues on forest soils and tree growth—a meta-analysis. *Forest Ecology and Management* 348:124–141.
- Alban, D. H. 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. *Soil Science Society of America Journal* 46:853–861.
- Attiwil, P. M. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. *Forest Ecology and Management* 63:247–300.
- Bartoń, K. 2017. MuMIn: multi-model inference. <http://CRAN.R-project.org/package=MuMIn>
- Blair, D. P., L. M. McBurney, W. Blanchard, S. C. Banks, and D. B. Lindenmayer. 2016. Disturbance gradient shows logging affects plant functional groups more than fire. *Ecological Applications* 26:2280–2301.
- Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. *Science* 159:882.
- Brewer, J. S., C. A. Bertz, J. B. Cannon, J. D. Chesser, and E. E. Maynard. 2012. Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? *Ecological Applications* 22:442–458.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 512 pp. Springer, New York, New York, USA.
- Chrosiewicz, Z. 1990. Site conditions for jack pine seeding. *Forestry Chronicle* 66:579–584.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302.
- Dale, V. H., et al. 2001. Climate change and forest disturbances. *BioScience* 51:723–734.
- D'Amato, A. W., S. Fraver, B. J. Palik, J. B. Bradford, and L. Patty. 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecology and Management* 262:2070–2078.
- Doucet, R. 1989. Regeneration silviculture of aspen. *Forestry Chronicle* 65:23–27.
- Domke, G. M., A. R. Ek, M. Kilgore, and A. J. David. 2008. Aspen in the Lake States: A research review. *NCASI Technical Bulletin* 955:1–46.
- Ellison, G. N., and N. J. Gotelli. 2004. A primer of ecological statistics. Sinauer, Sunderland, Massachusetts, USA.
- Flower, C. E., and M. A. Gonzalez-Meler. 2015. Responses of temperate forest productivity to insect and pathogen disturbances. *Annual Review of Plant Biology* 66:547–569.
- Frelich, L. E. 2002. Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge, UK.
- Frelich, L. E., and P. B. Reich. 1999. Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems* 2:151–166.
- Gill, K. G., A. W. D'Amato, and S. Fraver. 2016. Multiple developmental pathways for range-margin *Pinus banksiana* forests. *Canadian Journal of Forest Research* 46:200–214.
- Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29:824–839.
- Grime, J. P. 1979. Competition and the struggle for existence. In R. M. Anderson, B. D. Turner, and L. R. Taylor, editors. *Population dynamics*. Blackwell Scientific, Oxford, UK.
- Gustafsson, L., et al. 2012. Retention forestry to maintain multifunctional forests: a world perspective. *BioScience* 62:633–645.
- Horn, H. S., M. L. Cody, and J. M. Diamond. 1975. Markovian properties of forest succession. Markovian properties of forest succession. Harvard University Press, Cambridge, Massachusetts, USA.
- Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49:12–35.

- Johnson, D. W., D. W. Glass, J. D. Murphy, C. M. Stein, and W. W. Miller. 2010. Nutrient hot spots in some Sierra Nevada soils. *Biogeochemistry* 101:93–103.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18:116–126.
- Klockow, P. A., A. W. D'Amato, and J. B. Bradford. 2013. Impacts of post-harvest slash and live-tree retention on biomass and nutrient stocks of *Populus tremuloides* Michx.-dominated forests, northern Minnesota, USA. *Forest Ecology and Management* 291:278–288.
- Klockow, P. A., A. W. D'Amato, J. B. Bradford, and S. Fraver. 2014. Nutrient concentrations in coarse and fine woody debris of *Populus tremuloides* Michx.-dominated forests, northern Minnesota, USA. *Silva Fennica* 48:1–24.
- Kurth, V. J., J. B. Bradford, R. A. Slesak, and A. W. D'Amato. 2014. Initial soil respiration response to biomass harvesting and green-tree retention in aspen-dominated forests of the Great Lakes region. *Forest Ecology and Management* 328:342–352.
- Littlefield, C. E., and W. S. Keeton. 2012. Bioenergy harvesting impacts on ecologically important stand structure and habitat characteristics. *Ecological Applications* 22:1892–1909.
- Long, J. N. 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. *Forest Ecology and Management* 257:1868–1873.
- Messier, C., K. J. Puettmann, and K. D. Coates. 2013. Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge, Abingdon, UK.
- Minnesota Forest Resources Council (MFRC). 2007. Biomass harvesting guidelines for forestlands, brushlands, and open lands. Minnesota Forest Resources Council, St. Paul, Minnesota, USA.
- O'Hara, K. L., and L. M. Nagel. 2013. The stand: revisiting a central concept in forestry. *Journal of Forestry* 111:335–340.
- Palik, B. J., and A. W. D'Amato. 2017. Ecological forestry: much more than retention harvesting. *Journal of Forestry* 115:51–53.
- Peterson, C. J. 2019. Damage diversity as a metric of structural complexity after forest wind disturbance. *Forests* 10:85.
- Peterson, C. J., and A. D. Leach. 2008. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. *Ecological Applications* 18:407–420.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2016. nlme: Linear and nonlinear mixed effects models. <https://CRAN.R-project.org/package=nlme>
- Puettmann, K. J., K. D. Coates, and C. C. Messier. 2012. A critique of silviculture: managing for complexity. Island Press, Washington, D.C., USA.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Roberts, M. R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82:1273–1283.
- Roberts, M. R. 2007. A conceptual model to characterize disturbance severity in forest harvests. *Forest Ecology and Management* 242:58–64.
- Roberts, M. R., and F. S. Gilliam. 1995. Disturbance effects on herbaceous layer vegetation and soil nutrients in *Populus* forests of northern lower Michigan. *Journal of Vegetation Science* 6:903–912.
- Roberts, M. W., A. W. D'Amato, C. C. Kern, and B. J. Palik. 2016. Long-term impacts of variable retention harvesting on ground-layer plant communities in *Pinus resinosa* forests. *Journal of Applied Ecology* 53:1106–1116.
- Royo, A. A., C. J. Peterson, J. S. Stanovick, and W. P. Carson. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? *Ecology* 97:1566–1582.
- Schaedel, M. S., A. J. Larson, D. L. R. Affleck, R. T. Belote, J. M. Goodburn, and D. S. Page-Dumroese. 2017. Early forest thinning changes aboveground carbon distribution among pools, but not total amount. *Forest Ecology and Management* 389:187–198.
- Ste-Marie, C., D. Paré, and D. Gagnon. 2007. The contrasting effects of aspen and jack pine on soil nutritional properties depend on parent material. *Ecosystems* 10:1299–1310.
- Stuart-Haëntjens, E. J., P. S. Curtis, R. T. Fahey, C. S. Vogel, and C. M. Gough. 2015. Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity. *Ecology* 96:2478–2487.
- Sugiura, N. 1978. Further analysts of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics—Theory and Methods* 7:13–26.
- Tinker, D. B., and D. H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems* 3:472–483.
- Vitousek, P. M., and J. M. Melillo. 1979. Nitrate losses from disturbed forests: Patterns and mechanisms. *Forest Science* 25:605–619.
- White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction. Pages 3–13 in S. T. A. Pickett and P. W. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.

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