forest ecology

Harvest-Created Canopy Gaps Increase Species and Functional Trait Diversity of the Forest Ground-Layer Community

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Biodiversity conservation within managed forests depends, in part, on management practices that restore or maintain plant community diversity and function. Because many plant communities are adapted to natural disturbances, gap-based management has potential to meet this need by using the historical range of variation in canopy disturbances to guide elements of harvest design. We tested this hypothesis with a well-replicated gap size experiment in a second-growth northern hardwood forest. We evaluated plant communities within and among experimental gaps of differing size, 13 years after an initial harvest. We used a resampling approach to estimate how conventional and gap-based management affect diversity partitioning and species and trait diversity of ground-layer plants. These diversity measures highlight relevant scales and function of ground-layer plants among harvest gap sizes and scenarios. Results from our field experiment showed that, at the gap-level, increasing gap size increased functional trait diversity of plants, while species diversity was higher in gaps than uncut references and maximized in medium-sized (20–30 m diameter) gaps. In harvest scenarios created by resampling our empirical data, we found that at the stand scale, increasing harvest intensity (larger gaps and greater proportion of forest in gaps) increased species richness and variability in initial bloom times, tolerance to shade, and number of life-forms in the plant community. Based on the measures of diversity and function used in our study, our results suggest that size of harvest-created gaps and proportion of forest in gaps can be manipulated to attain biodiversity goals but evaluating the regional species pool and seed sources (e.g., presence of invasives, rare species) will be important to maintain or restore conservation value.

Keywords: understory plants, species richness, gap size, forest scenario simulation, natural disturbance-based silviculture, additive partitioning of richness, resampling estimation

Losses of biodiversity can degrade some ecosystem functions and, consequently, threaten the sustainability of ecosystem goods and services (Isbell et al. 2011, Zhang et al. 2012). Managing for biodiversity may be especially challenging in forest ecosystems because forests are expected to provide a wide range of goods and services, such as commodities and recreation, in addition to biodiversity (Burger 2009). A recent report found that 27% of the total number of forest-associated species is at risk of extinction in the United States, coincident with considerable losses in regional-scale forest cover (USDA Forest Service 2011). Situations such as this have elevated pressure on managed forests to both extract goods while sustaining services such as biodiversity. For example, the National Report on Sustainable Forests–2010 recommended that "flexible, adaptive management techniques that work with natural processes" be continually developed to sustain the many goods and services of US forests (USDA Forest Service 2011, p. viii).

Emulating natural disturbance regimes is one approach to restore or maintain biodiversity in managed forests (e.g., Franklin et al. 1997, Seymour and Hunter 1999, Seymour et al. 2002). This approach assumes that the patterns and processes characteristic of unmanaged forests support native flora and fauna; therefore, when management practices mimic patterns of natural disturbances, native biodiversity is more likely to persist (Seymour and Hunter 1999, Mitchell et al. 2002). For example, in wind-disturbed forests, native biodiversity could be maintained with a gap-based approach (Coates and Burton 1997). Harvest patterns would emulate historic frequency of gap sizes and densities, while allowing some timber extraction. This approach is based on the idea that canopy gaps are key influences on species assemblages, allowing species with

contrasting life-history traits, such as shade tolerance, to coexist (Leak and Filip 1977, Ricklefs 1977, Denslow 1980).

The association between canopy gaps and ground-layer species diversity is dependent on individual gap size. Given the extreme microclimate and high resource conditions of large gaps, they may be dominated by a relatively small number of species. Similarly, the moderate microclimate and low resource conditions of small gaps may also be dominated by a few species, albeit functionally different than those found in large gaps. However, medium gaps create resource conditions intermediate to small and large gaps, potentially capable of supporting more species, including those also found in small and large gaps (Connell 1978). Some authors have argued that this concept is the most applicable ecological framework for forest management and ground-layer plant diversity (Roberts and Gilliam 1995). Hence, gap size is a measure with potentially predictable effects on plant diversity that can be emulated in managed forests (Coates and Burton 1997).

Ideally, canopy gaps would play a role not only in plant diversity but also in plant community function. For decades, species diversity has been used as an index of biodiversity. More recently, biodiversity has been assessed with functional trait diversity measures or the actual value and range of species traits, rather than measures of the identity of species, because species are not uniformly dissimilar in trait values (Cadotte et al. 2011). Both types of diversity measures can be used together to predict an ecosystem's capacity to respond to change. For either measure, high (species or trait) diversity may provide "insurance" by increasing the odds that at least some species will have traits that confer a capacity to respond to variable conditions (Diaz and Cabido 2001). For example, simultaneous loss of species and trait variation in some modified sites was indicative of declines in ecosystem functioning (Mayfield et al. 2010), and recent reports suggest that such effects may be more important than previously expected (Isbell et al. 2011, Reich et al. 2012). Although there is much debate on how to measure diversity, measures of trait diversity represent a mechanistic link between the plant community and ecosystem function and, as such, may be particularly useful in managed ecosystems (Cadotte et al. 2011).

The relationship between harvest-created gaps and plant diversity has had little examination at gap and stand scales simultaneously, especially in terms of functional trait diversity. Studies of forest management have shown that species that invade after harvest have average trait characteristics described as ruderal, early seral, or weedy (e.g., Crow et al. 2002, Fahey and Puettmann 2007, Shields and Webster 2007), but few have considered functional trait diversity among management alternatives (Cadotte 2011). Linking species, traits, and ecosystem processes is critical to evaluating current management approaches and managing for change.

Here, we test the applicability of gap-based management to restore or maintain diversity of ground-layer vascular plants in a second-growth northern hardwood forest. Our objective was to examine species and trait diversity at the scale of a harvest gap and a managed forest. We use a robust field design that included circular, harvest-created gaps that were cleared of trees and tall saplings, differed in area by two orders of magnitude, and were replicated randomly across a uniform site. In a previous study at this site (Kern et al. 2013), we learned that quadrat-scale (1 m^2) ground-layer plant composition shifted away from uncut conditions as gap size, proximity to edge, and time increased. Species' functional traits and microenvironmental conditions were related to changes in ground-layer composition. Therefore, here, we asked whether these compo-

sitional trends resulted in changes in species and trait diversity among gap sizes or among alternative management scenarios. To estimate gap-level plant diversity, we use the experimental gaps to estimate species and trait diversity 13 years after harvest, or a time frame focused on long-term responses and not short-term, transient responses. We expected gaps intermediate in size to be more diverse than small or large gaps. To estimate forest-level plant diversity, we use a resampling approach to extrapolate our gap-level data to harvest scenarios that emulate various forests management approaches. We expected species and trait diversity to increase more with harvests modeled after moderate-severity wind storms (a gap-based, multicohort approach) than those modeled after conventional management practices.

Methods
Study Site

The study ecosystem is a 136 ha second-growth, northern hardwood forest located in the Chequamegon–Nicolet National Forest in northern Wisconsin (T40°N R12°E). Similar to many forests in the region, the study ecosystem regenerated after exploitive timber harvesting during the early 20th century. Before study installation in 1994, the forest had had no recent management and was estimated to be 60 years old. Sugar maple (*Acer saccharum*) dominated the site. Average tree basal area among the blocks ranged from 25.3 to 30.6 m^2 ha^{-1} and tree density ranged from 59 to 92 trees ha^{-1}. The forest canopy was closed with an occasional small canopy gap created by recent single-tree blowdown. The topography is a hummocky kame-kettle complex with some cradles and knolls created from tip-up mounds (resulting from past canopy tree blowdowns). Soils are Stambaugh silt loam loess, overlying stratified sand and gravel. The habitat type is considered nutrient rich, mesic, and well suited for sugar maple growth and classified as *Acer-Tsuga/Dryopteris* (ATD) by Kotar et al. (2002). In 1994, approximately 70 species were identified in the ground-layer vascular plant community (including trees < 0.5 m tall). Of these, two species (*Juglans cinerea* and *Panax quinquefolius*) were of special concern and two (*Hieracium aurantiacum* and *Stellaria media*) were of introduced origin.

Regionally, the natural disturbance regimes of northern hardwood forests are primarily characterized by canopy gap disturbances. Low intensity disturbance events (10–19% canopy removed) that create small canopy gaps (mean gap areas of 12–121 m^2; mean upper limit < 250 m^2) tend to affect < 10% of typical stands per decade (Tyrrell and Crow 1994, Dahir and Lorimer 1996) and are pathways for canopy recruitment for > 60% of trees (Frelich and Lorimer 1991). More moderate disturbances (30–60% canopy removal) are estimated to occur once during the lifetime of a tree cohort (300–390 years) (Frelich and Lorimer 1991) and result in gap area distributions with maxima at ≈ 5,000 m^2 and distribution tails with ≈ 50% <40 m^2 and ≈ 9% >500 m^2 (Hanson and Lorimer 2007).

Field Experiment

Four of six relatively uniform areas were randomly selected within the study site as blocks (16–24 ha) for a randomized complete block experiment. Blocks were subdivided into 0.4-ha sections of which 18 were randomly assigned to one of six gap diameters (0 [reference area], 6, 10, 20, 30, and 46 m gaps) thrice (three replicates gap size^{-1} block^{-1}). Experimental gaps were created by dormant-season timber harvesting (trees ≥ 2.5 cm dbh) in 1994 (two blocks)

and 1995 (two blocks). The resulting design consisted of 12 reference areas (0.4 ha square, uncut patches) and 56 experimental gaps (four marked gaps were not cut). Gap openings were measured in 1997 and 2008 from gap center to dripline in cardinal and subcardinal directions (eight total radii). In 1997, gap area ranged from 9.9 m^2 to 1,986 m^2 (gap diameter to canopy height ratio [D:H] range from 0.1 to 2.2). By 2008, most small gaps were closed and similar to the forest matrix conditions, while large gaps remained open.

In addition to gap creation, the four blocks were also thinned (except for the reference areas) in 1994–1995 following first harvest entry guidelines in Erdmann (1986), a Lake States management publication for converting even-aged northern hardwood forests to uneven-aged stand conditions. To improve residual stand vigor, this first thinning entry (an "improvement cut") removed trees anticipated to die from self-thinning, disease, damage, or those that had minimal potential to gain economic value before the next harvest entry. The thinning reduced the forest matrix density by 26%. The mean basal area of forest matrix was 23 m^2 ha^{-1} ($\pm$1.8 SE), while reference areas remained uncut at 31.1 m^2 ha^{-1} ($\pm$0.3).

Deer exclosures were installed on a subset of the experimental units (one reference area, 20 m gap and 46 m gap per block; 12 total exclosures) in 1997 and were maintained for four years. The responses analyzed in this study showed no relationship with deer exclosures; consequently, the data were combined into the larger data set.

Field Sample Plots

Sample plots (1.0 m^2) were arrayed in four transects radiating in cardinal directions from gap centers into the adjacent forest matrix (5–10 m). In reference areas and 30 and 46 m gaps, sample plots were spaced 5.5 m apart along transects, and, in 6, 10, and 20 m gaps, they were spaced 3.7 m apart. In each sample plot, we assessed vascular plant species (including trees less than 0.5 m tall) for abundance by cover class: 0; one or two individuals and < 1% cover; 3–20 individuals and < 1% cover; >20 individuals and/or 1–5%; 5–25%; 26–50%; 51–75%; 76–100%. Individuals were identified to species except the following six genera: *Botrychium*, *Carex*, *Galium*, *Viola*, *Equisetum*, and *Fragaria*. Nomenclature follows the PLANTS Database (USDA Natural Resources Conservation Service (NRCS) 2009). Field data were collected during midsummer (late June–early August) over four survey periods: preharvest (1994 [two blocks]–1995 [two blocks]) and postharvest in 1997, 2000 (two blocks)–2001 (two blocks), and 2008. We were interested in longer term responses and not shorter term, transient responses. Thus, only the 2008 data or the ~13th year after harvest, were analyzed in this study.

Plant Traits

We compiled widely available traits by species. Traits included life-form, potential maximum height, leaf and seed length, an index of shade tolerance, and potential first month of bloom. We also compiled the origin (native or introduced to western Great Lakes region) and an index or coefficient of conservatism (Swink and Wilhelm 1994, Wisconsin State Herbarium 2011) for each species. The coefficients (0–10) describe species' affinity for disturbance. We categorized species with low coefficients (0–3) as those with strong affinity to highly disturbed habitats and species with high coefficients (7–10) as those with strong affinity to undisturbed conditions (*sensu* Wolf et al. 2008). Species were also cross-referenced
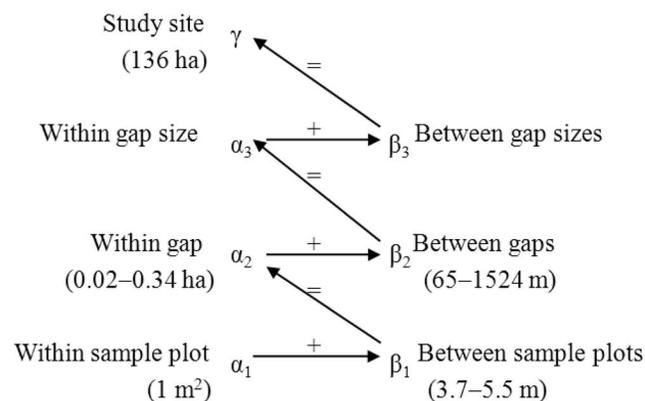

Figure 1. Diagram of ground-layer vascular plant α-, β-, and γ-diversity within a canopy gap size field experiment in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin. Estimates of species diversity were partitioned additively among levels of the study design, such that diversity at cumulative gap size (α_3) equaled the sum of diversity within sample plot (α_1), among sample plots (β_1), and among gap replicates (β_2). Spatial extent of each level is noted in parentheses. The spatial extent of diversity within gap size (α_3) was ~136 ha, which represented diversity of gap sizes in aggregate across the study site. Because the study's inference was gap level, we did not directly analyze diversity among gap sizes (β_3). However, the variation in species among gap sizes (β_3) plus the diversity within gap sizes (α_3) equaled the total observed species richness (γ) in our field experiment. (Adapted from Chandy et al. (2006).).

with regional endangered and noxious (Wisconsin State Herbarium 2011) species lists.

Gap Size Analysis

For analysis, we reclassified the gap-level diameter classes into four broader categories (closed, small, medium, and large gaps) to minimize differences in sampling effort and increase sample sizes. "Closed" gaps were the uncut reference areas (only 0 m sample plots). "Small" gaps represented edge (in forest but ≤ 5 m from gap dripline) and gap plots of 6 and 10 m gap diameters because ground-layer composition was similar among these locations and gap sizes (Kern et al. 2013). "Medium" gaps included gap plots from the 20 and 30 m gap diameters, while the gap plots of 46 m gap diameters were categorized as "large" gaps. The medium and large gap categories encompassed similar ranges in gap area and diameter to height ratios (unpubl. data, Kern). The closed, small, medium, and large gap size categories yielded 300, 246, 199, and 189 sample plots, respectively, from the field experiment.

Additive Diversity Partitioning

We evaluated the effect of gap size on species diversity using additive diversity partitioning. Additive diversity partitioning breaks total species richness into additive components comparable at multiples scales in the same units (e.g., number of species) as outlined by Lande (1996) and Veech et al. (2002). We partitioned diversity at three scales following the experimental design (Figure 1): sample plot (α_1), gap or closed patch replicate (α_2), and gap size (α_3) in aggregate across the site.

We partitioned three species diversity indices (equations in Lande 1996): richness (S_{obs}), Shannon diversity (H_{obs}), and Simpson diversity (λ_{obs}). Rare species influence these diversity measures

high to low, respectively. Thus, we interpreted these indices to represent the diversity of all, dominant, and very dominant species, respectively. We used PARTITION 3.0 software (Veech and Crist 2009) to partition the diversity measures, specifying our unequal sampling efforts and equal sample plot weight. Significance tests were computed with 1,000 replications of individual-based randomization on richness. For Shannon and Simpson diversities, we used sample-based randomization because our abundance data were based on cover, not individuals. To facilitate interpretation of Shannon and Simpson indices, we present results as "effective number of species" by $\exp(H_{obs})$ and $1/\lambda_{obs}$ transformations, respectively, which convert indices into units comparable to richness (Jost et al. 2010).

Validation of Gap Size Effects

To determine if sample size influenced our field experimental results, we compared results of analyses based on the complete, unequal sampling efforts (additive diversity partitioning) to analyses based on equal sampling efforts. To do this, we used a nonparametric approach, where we resampled the field experiment observations to generate multiple, random "subsets" of data for each gap size ($N=$ 1,000). Subsets were created through random selection without replacement. The random selection of plots was also stratified by replicate to capture the heterogeneity among replicates and maintain inference at the study site scale. One hundred and seventy-five plots were selected for each subset with the SURVEYSELECT procedure in SAS 9.2 (SAS Institute, Inc. 2008). Then, for each subset, we calculated species richness (α_3^* [* indicates estimation from resampling field observations]) of all species and of native species only with jackknife procedures using 1,000 permutations in BiodiversityR (Kindt and Coe 2005), an R software (R Development Core Team 2005) package built primarily on vegan (Oksanen et al. 2011) and Rcmdr (Fox et al. 2011) packages.

Trait Calculations

For each subset, we also used the standard deviation (SD) of abundance-weighted, log-transformed trait values for continuous (height, seed length, and leaf length) and ordinal (shade tolerance and first month of bloom) traits. The variation in the nominal trait, life-form, was expressed with a Shannon index. We used SD and Shannon diversity to represent trait variability to compare our results to other studies of diversity in managed ecosystems (e.g., Biswas and Mallik 2010, Mayfield et al. 2010). We also calculated the relative proportion of community cover among native or introduced origins and among coefficient of conservatism categories (0–3, 4–6, or 7–10). The distributions of richness, origin, coefficients, and trait estimates were compared with means plus one SD or seven-number summaries because confidence intervals were very narrow.

Harvest Scenario Analysis

To evaluate the effects of gap size on diversity at a forest scale, five management practices were depicted in harvest scenarios. Four of the harvest practices are common in northern hardwood forests and, thus, test the utility of conventional practices in maintaining native plant diversity. The fifth harvest practice is an alternative, ecological forestry approach to forest management.

These conventional alternatives were "no cutting," "thinning," or age-class conversion through "modified single-tree" or "group selection" cutting. In practice, the goal of thinning is to maintain an even-aged condition and accelerate the growth and development of dominant trees with the greatest potential to increase in value over time. Thinning removes dominant competitors in a spatially dispersed manner, while maintaining 80% canopy cover (Erdmann 1986, Wisconsin Department of Natural Resources 2008). We emulated the canopy patterns of thinning as forest canopies by selecting 20% of the sample plots from small gaps and 80% from closed forest. In age-class conversion though selection cutting, the goal is to develop new age classes over time with harvest-created gaps and to convert the even-aged forest structure to a relatively uneven-aged condition manageable within the selection system. The initial entry in the conversion process thins by removing lower quality trees and maintaining 80% canopy cover. In modified single-tree selection, 10% of the residual stand's canopy openness is allocated to dispersed, single-tree removals, while the other 10% of canopy openness is aggregated into larger openings created by harvesting groups of trees. In group selection, all of the residual stand's canopy openness is aggregated into larger openings (Erdmann 1986, Wisconsin Department of Natural Resources 2008). We emulated the canopy patterns of age-class conversion by selecting 80% of the plots from closed forest and then emulated gaps by selection method. We emulated modified single-tree selection with 10% of the sample plots from small gaps and 10% from medium gaps and group selection with 20% of the sample plots from medium gaps.

The fifth practice, "multicohort," emulated gap size distributions of moderate severity disturbances in northern hardwood forests (Hanson and Lorimer 2007, and see Methods/Study Site section), testing an alternative approach to maintaining native plant diversity (Coates and Burton 1997). We emulated the canopy openness patterns of multicohort with 20, 10, and 10% of the sample plots from small, medium, and large gaps, respectively. The five harvest scenarios, no cutting, thinning, modified (mod.) single-tree selection, group selection, and multicohort, represented an increasing range of canopy openness and harvesting intensity, respectively.

For each harvest scenario, we created mock ground-layer plant communities using a nonparametric resampling approach. Broadly, this approach was similar to the resampling approach used to validate gap size diversity and created replicates of plot data following specified gap size and proportion of forest in gaps for each scenario (Table 1). Specifically, we resampled the field experiment observations to generate multiple, random "subsets" of data ($N = 1,000$). Subsets had common sampling efforts of 175 plots that were selected with stratified (by replicate), random sampling without replacement. Each scenario was achieved by uniquely allocating the 175 plots among gap sizes and proportion of forest in gaps established for each scenario (Table 1). Because harvest-created gaps create edge conditions, we further allocated plots between gap openings and gap edges within each gap size (Table 1). Gap plots were located within the dripline of a gap and edge plots were located within the forest and ≤ 5.0 m from the dripline of a gap.

Species and trait diversity were again measured with SD and Shannon index. In addition, we calculated the species diversity of dominant and very dominant species expressed as "effective number of species" using $\exp(H_{obs})$ and $1/\lambda_{obs}$ transformations, respectively. In addition, we calculated mean compositional similarity among the harvest scenarios using the Bray–Curtis index and default settings in EstimateS 8.2 software (Colwell 2006).

Table 1. Harvest scenario description by overstory condition and compositional similarity of mock ground-layer plant communities 13 years after harvest based on resampling a canopy gap field experiment in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin.

		Scenario				
Variable	Description	No cutting	Thinning	Mod. single-tree	Group	Multicohort
Overstory condition	*Gap size (edge:gap plots)*	....Percent of forest canopy				
	Closed (n/a)	100	80	80	80	60
	Small (4:1)		20	10		20
	Medium (1:1)			10	20	10
	Large (3:7)					10
Ground-layer plant composition	*Scenario*	................................Relative similarity (0 = very dissimilar; 1 = very similar)..............................				
	Thinning	0.83				
	Mod. Single-tree	0.73	0.90			
	Group	0.79	0.82	0.94		
	Multicohort	0.70	0.86	0.96	0.90	

Gap plots were located within the dripline of a gap and edge plots were located within the forest and ≤ 5.0 m from the dripline of a gap.

Table 2. Gap size and characteristics of ground-layer plants 13 years after harvest within a canopy gap field experiment in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin.

		Gap size			
Variable	Description	Closed	Small	Medium	Large
Coefficient of conservatism	*Affinity for unaltered habitat*	....Relative proportion of community cover..			
	High (>6)	0.23 (0.02)	0.20 (0.01)	0.17 (<0.01)	0.08 (<0.01)
	Intermediate (4–6)	0.50 (0.03)	0.48 (<0.01)	0.29 (<0.01)	0.26 (<0.01)
	Low (<4)	0.27 (0.01)	0.32 (<0.01)	0.54 (<0.01)	0.65 (<0.01)
Origin	*Status in northern Wisconsin*	....Relative proportion of community cover..			
	Native	1.00 (<0.01)	0.99 (<0.01)	0.95 (<0.01)	0.97 (<0.01)
	Introduced	<0.01 (<0.01)	0.01 (<0.01)	0.05 (<0.01)	0.03 (<0.01)
Trait variation	*Life history*	....Standard deviation (*Shannon diversity)...			
	Height	0.44 (0.01)	0.41 (0.02)	0.37 (0.01)	0.35 (<0.01)
	Leaf size	0.27 (0.01)	0.27 (<0.01)	0.26 (<0.01)	0.31 (<0.31)
	Seed size	0.22 (<0.01)	0.24 (<0.01)	0.19 (<0.01)	0.20 (<0.01)
	Shade tolerance	0.56 (0.01)	0.64 (0.02)	0.65 (0.02)	0.65 (<0.01)
	First month of bloom	0.38 (0.02)	0.41 (0.02)	0.41 (<0.01)	0.43 (<0.01)
	Lifeform*	0.80 (0.01)	0.90 (0.01)	1.10 (<0.01)	0.99 (<0.01)

Values are means (standard deviation) of resampling ($N = 1,000$) the gap sizes randomly to a common sampling effort (175 plots).

* The variation in life-form is expressed as a Shannon index (H_{obs}).

Results

Species and Trait Diversity Among Gap Sizes

General Floristic Condition

At 13 years after harvest, the ground-layer plant communities of the experimental gaps were composed primarily of common and abundant native species (Table 2). One species of special concern observed prior to harvest remained on site (with only one observation, however). Ten introduced species were present after harvest but were minor in total abundance.

Species affinities for unaltered habitat varied among gap sizes. About half of the ground-layer plant communities in closed forest patches were characterized by species highly adapted to either disturbed or undisturbed conditions (Table 2). In harvest gaps, species adapted to disturbed conditions grew increasingly dominant as gap size increased, while the opposite was true for species adapted to undisturbed conditions.

Species Diversity

Medium-sized gaps had the highest aggregate species richness (α_3) (Figure 2A). Small and large gaps were slightly lower in species richness, with closed forest the lowest. These patterns among gap sizes were consistent regardless of whether species richness estimates were based on unequal (full data set) or equal (resampled) sampling efforts (Figures 2A and 3A). However, when comparing diversity of dominant and very dominant species, the effects of gap size on species richness were less distinct (Figure 2B and C).

Additive Partitioning of Species Diversity

Within gap size, partitions of species richness (α_3) were different ($P < 0.001$). Partitions of species richness within plots composed the smallest portion of the aggregate richness found in a given gap size, while the heterogeneity of species richness among gap replicates composed the largest portion (Figure 2A). Furthermore, partitions of Shannon and Simpson indices showed that within gap composition was largely composed of a similar suite of dominant species.

The overall drop in species richness (α_3) from all to dominant and very dominant species (Figure 2A–C, respectively) suggests that uncommon species comprise a large portion of the observed diversity within all gap sizes. Several of these uncommon species represented species of introduced origin. Although the estimated abundance of introduced species was quite low (Table 2), their influence on estimated species richness was notable (Figure 3). Excluding introduced species, estimates of native species richness were more similar between small and medium gap sizes, although large gaps and closed forest still lagged behind in native species numbers.
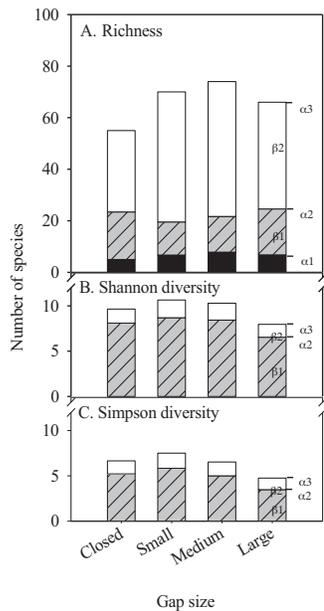
Figure 2. Ground-layer vascular plant diversity by canopy gap size in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin, 13 years after harvest. Stacked bars represent additive partitioning of (A) species richness, S_{obs}, (B) Shannon diversity, transformed to $\exp(H_{obs})$, and (C) Simpson diversity, transformed to $1/\lambda_{obs}$, where bars are shaded solid black, hatched gray, and solid white to represent diversity within sample plot (α_1), among plots (β_1), and among gap replicates (β_2), respectively, of aggregate gap sizes (α_3). Additive partitioning included complete sampling efforts of 300, 246, 199, and 189 sample plots in closed, small, medium, and large gap sizes, respectively.
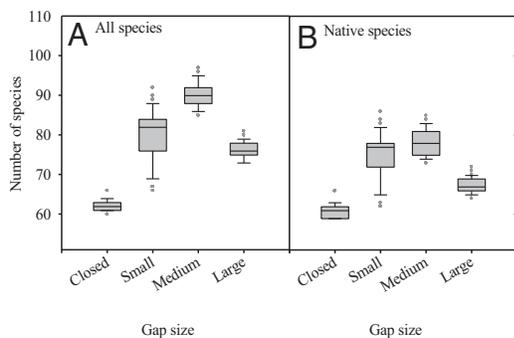

Figure 3. Estimated species richness of all (A) and native only (B) ground-layer plants 13 years after harvest based a canopy gap field experiment in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin. Values are jackknife estimates of gap size species richness ($\alpha_3{}^*$) at equal sampling effort (175 sample plots stratified by replicate and randomly-selected without replacement; $N = 1,000$). The richness distributions are denoted with box and whiskers indicating the 10th percentile, lower quartile, median, upper quartile, and 90th percentile and with individual points indicating the outliers.

Trait Diversity

Using a resampling approach, we found that harvest gap size affects trait diversity in unique ways at the gap level. Estimated trait diversity was usually greater in gap openings than closed forest patches (Table 1). For example, as gap size increased, variation in estimated first month of bloom, tolerance to shade, and life-form

also increased, suggesting that larger gaps accommodated a greater range of values in these traits. On the other hand, estimated height variation decreased with gap size.

Species and Trait Diversity Among Harvest Scenarios
General Floristic Condition

Composition among the harvest scenarios was more similar than dissimilar and was dominated by native species in all cases (Table 1). Single-tree selection, group selection, and multicohort were most similar to each other and thinning was most similar to no cutting. Further, mock ground-layer plant communities exhibited a greater diversity of dominant species and greater proportion of species with high affinity for disturbance as harvest scenario intensity increased (Table 3).

Species Diversity

Harvest scenarios increased estimated species richness relative to the no cutting scenario (Figure 4). In the thinning scenario, most estimates of species richness were greater than no cutting but less than scenarios with gap creation. In contrast, the two conversion practices of modified single-tree and group selection were similar in estimated richness distribution and largely did not overlap with the no cutting richness estimates. Further, the species richness estimates in the multicohort scenario were varied, differing as much as 40 species, but the overall distribution was higher in species richness compared to other scenarios.

Trait Diversity

Relationships between trait and species diversity varied among harvest scenarios (Figure 5). Some traits such as height, leaf, and seed traits had no relationship to species diversity, indicating that the additional species found in more intense harvest scenarios had similar height, leaf, and seed trait values to those in less intense scenarios. However, variation of bloom time, shade tolerance, and life-form had a positive association with species diversity as harvest scenario intensity increased (Figure 5). This relationship suggests that the additional species in more intense harvest scenarios possessed different traits than those in less intense harvest scenarios.

Discussion

Designing stand-level forestry practices that maintain or restore native plant communities is important to sustaining forest diversity. Here, we tested this idea by examining the influence of harvest gap size on the ground-layer vascular plant community of a northern hardwood forest. Our novel approach used both observed gap-level data and estimated forest-level simulations. One key finding was that harvest-created gaps increased ground-layer plant diversity compared to closed forest patches and that diversity increased most in medium-sized gaps. Diversity differences among gap sizes was largely attributed to compositional heterogeneity among gap replicates, which captured uncommon species, and suggested that stochastic processes may be important to structuring gap diversity. Another key finding was that, at the forest-level, changing gap size increased richness. We found that harvest scenarios with larger gaps that emulated natural disturbance increased species and trait diversity from uncut forest conditions. Our findings also suggest that the effect of harvest-created gaps on ground-layer plant diversity were not transient, as the gap size effects presented here are the effects in

Table 3. Harvest scenario and characteristics of ground-layer plants 13 years after harvest based a canopy gap field experiment in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin.

Variable	Description	Scenario				
		No cutting	Thinning	Mod. single-tree	Group	Multicohort
Coefficient of conservatism	*Affinity for unaltered habitat*	..........................(Relative proportion of community cover)				
	High (>6)	0.23 (0.02)	0.22 (0.01)	0.22 (0.01)	0.21 (0.02)	0.19 (0.01)
	Intermediate (4–6)	0.50 (0.03)	0.49 (0.02)	0.47 (0.02)	0.45 (0.02)	0.44 (0.02)
	Low (<4)	0.27 (0.01)	0.28 (0.01)	0.32 (0.02)	0.34 (0.02)	0.37 (0.02)
Origin	*Status in northern Wisconsin*	..........................(Relative proportion of community cover)				
	Native	1.00 (<0.01)	1.00 (<0.01)	0.99 (<0.01)	0.99 (<0.01)	0.99 (<0.01)
	Introduced	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)
Diversity	*Species group–transformed index*	..............................(Number of species)				
	Dominant ($1/H_{obs}$)	12.6 (0.6)	14.4 (1.1)	15.8 (1.0)	16.4 (1.1)	16.7 (1.0)
	Very dominant ($1/\lambda_{obs}$)	7.3 (0.4)	8.5 (0.6)	9.3 (0.6)	9.8 (0.6)	10.4 (0.5)

Values are means (standard deviation) of resampling ($N = 1,000$) the gap sizes randomly to a common sampling effort (175 plots) according to the overstory conditions specifications (see Table 1).
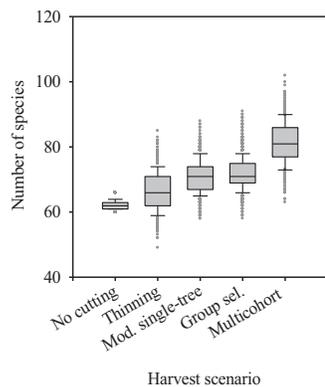

Figure 4. Harvest scenario and estimated species richness of ground-layer plants 13 years after harvest based a canopy gap field experiment in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin. Jackknife procedures estimated forest species richness (γ^*, ~136 ha) at equal sampling effort (175 sample plots stratified by replicate and randomly selected without replacement; $N = 1,000$) according to the overstory conditions (noted in Table 1). The richness distributions are denoted with box and whiskers indicating the 10th percentile, lower quartile, median, upper quartile, and 90th percentile and with individual points indicating the outliers.

Figure 5. Estimated species richness and SD (or Shannon diversity) of trait values of ground-layer plants 13 years after harvest by harvest scenario based on a canopy gap field experiment in a northern hardwood forest on the Chequamegon–Nicolet National Forest, Wisconsin. (A) Potential maximum height. (B) Potential initial bloom. (C) Potential maximum leaf length. (D) Potential maximum leaf length. (E) Shade tolerance index (Humbert et al. 2007). (F) Number of life-forms. Symbols represent the mean (SD) of resampling ($N = 1,000$) the gap sizes randomly to a common sampling effort (175 plots) according to the overstory conditions (noted in Table 1).

the 13th year post initial harvest. We further discuss these findings in the following subsections.

Species and Trait Diversity Among Gap Sizes

Our field experiment clearly showed nonlinear effects of gap size on species diversity. Overall, gaps increased species richness from closed forest or reference conditions, but the degree of increase depended on gap size. Other studies have found that gaps increase the number of species by providing space and resources unavailable under closed forest canopy (Schumann et al. 2003, Galhidy et al. 2006, Naaf and Wulf 2007). In some contexts, gap size was important to species diversity; for example, diversity increased with gap size in European beech forests (Naaf and Wulf 2007) and Florida scrubland communities (Menges et al. 2008). However, the effect of gap size on species richness has been negligible in other contexts due to resilience of preexisting vegetation (Collins and Pickett 1988), gap treatments convoluted in shape (Schumann et al. 2003), or examination of a narrow range of gap sizes (Moore and Vankat 1986). Our study did not have these confounding factors: Our study
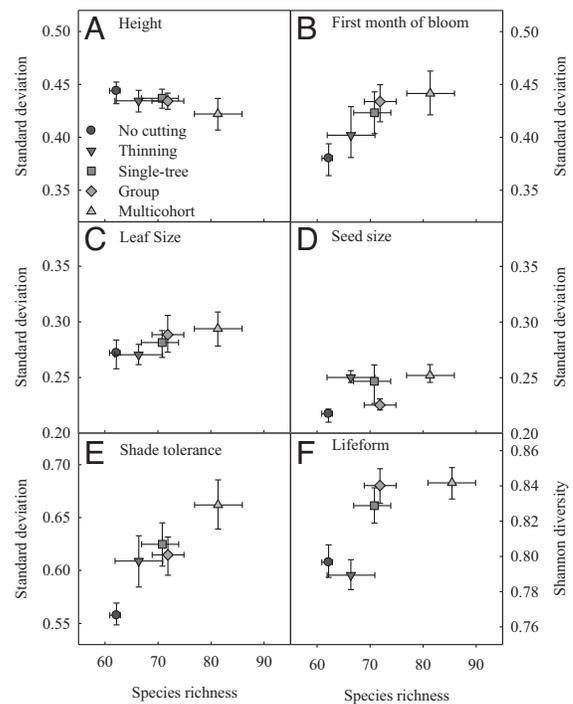
gaps were clear felled (to > 2.54 dbh), circular, and ranged widely in gap size. In contrast to past studies, we found that medium gap sizes were most species rich; as gap size increased, species diversity increased from small to medium gaps and decreased from medium to large gaps. The difference in species diversity between medium and large gaps was likely due to the fewer number of dominant species in large gaps; a few species increased abundance at the cost of other species presence, thereby decreasing species diversity.

Species diversity displayed a unimodal pattern that increased

then decreased with increasing gap size. In our study site, larger gaps tended to have high *Rubus idaeus* abundance (Kern et al. 2013). This shrub regenerates from persistent seed banks and grows at high densities that limit persistence of competing species (Donoso and Nyland 2006), thus, has the potential characteristics to decrease diversity (Strong et al. 1998, Decocq et al. 2004). Furthermore, microclimate was extremely variable in large gaps (Strong et al. 1997) and potentially lethal to some preexisting vegetation. As a result, species colonization was likely limited to those species with wind or animal seed dispersal, ability to reproduce from belowground plant parts, or persistent seed banks (Naaf and Wulf 2007) (e.g., *Rubus*).

Trait diversity showed some linear patterns as gap size increased. At one extreme, we found that closed forest patches had narrower ranges of initial bloom, shade tolerance, life-forms, and leaf size and greater range of heights. At the other extreme, large gaps had the opposite effect: Ground-layer plants were characterized by wider range of initial bloom, shade tolerance, life-forms, and leaf size and narrow range of heights.

Our additive partitioning results highlight that gap diversity was partly structured by stochastic processes. Gap diversity was composed, in part, of uncommon species, regardless of gap size (Figures 1 and 2), which were likely to be present as the result of dispersal or recruitment limitations. This finding supports the idea of species neutrality and randomness structuring species assemblages (Hubbell et al. 1999, Hubbell 2001). Gap studies in unmanaged forests have also detected the importance of uncommon species but with little support for niche-related processes (Grau 2002, Obiri and Lawes 2004). Therefore, our research highlights that gap diversity is not completely a result of deterministic or stochastic processes, rather our study supports multiple, concurrent mechanisms structuring ground-layer plant diversity in canopy gaps as found in other studies (Fahey and Puettmann 2007, Burton et al. 2011).

Species and Trait Diversity Among Harvest Scenarios

Our study also highlighted that the relationship between species and trait diversity varied with scale. Gap-level effects on trait diversity were evident at the forest scale. More intense harvest scenarios, which included larger gaps and a greater proportion of forest in gaps, had similar effects as increasing gap size on trait variability, except for height. Height variability was similar among the scenarios, likely because trees were the predominant life-form among all scenarios. In terms of species diversity, our harvest scenario results are similar to results from other stand-level applications of selection, where ground-layer species diversity did not differ between single-tree or group selection (Jenkins and Parker 1999, Falk et al. 2008, Smith et al. 2008). However, studies of stand-level silvicultural systems have suggested that treatments intermediate in intensity result in high diversity (Battles et al. 2001, Haeussler et al. 2002, Wang and Chen 2010), while others have detected a threshold effect (Pawson et al. 2006, Zenner et al. 2006). Across our gradient of harvest scenario intensity, species diversity increased. The gap-based, multicohort approach had the widest range of gap sizes and greatest proportion of forest in gap, likely providing a wide range of conditions for many species to exist. This supports the coarse filter approach to ecosystem management, where managing for heterogeneous conditions will create a range of niches and support a greater number of species than managing for homogeneous conditions that creates few niches supporting few species (Seymour and Hunter 1999).

One novel aspect of our study was that we examined both species

and trait diversity among forest management alternatives. As the intensity of harvest scenario increased from no cutting, thinning (small gap creation) to multicohort (thinning + gap creation [small to large gap creation]), we observed not only increased species diversity but also increased trait variation for initial bloom time and shade tolerance and to a lesser degree for seed size and life-form. Thus, harvesting removed dominant, overstory trees and created more available niche space allowing colonization from the regional species pool of species that span a greater range of trait values (Tilman et al. 1997, Mayfield et al. 2010). On the other hand, increasing species diversity with increasing harvest scenario did not further diversify the trait values of height and leaf size already found in the plant community, supporting the idea of functional redundancy. Redundant traits in a community increase reliability of an ecosystem to respond to change (Diaz and Cabido 2001). The relationships between species and trait diversity suggest that several ecosystem functions such as productivity should persist under some degree of change. This supports the "resistance strategy" to managing for change; abundant, diverse range of trait values in a native plant community enhance the capacity of ecosystems to withstand or absorb increasing effects without irreversible changes in important processes and functionality (Millar et al. 2007).

Implications and Limitations of Study

Although these species and trait diversity results highlight patterns that support ecological concepts within this particular managed forest setting, the floristic quality of these plant communities must be noted for context. More intense harvest scenarios had a greater number of introduced species and a higher abundance of species with strong affinity for disturbed habitats than less intense scenarios. The influx of ruderal and exotic species after harvest has been noted in some studies (e.g., Wolf et al. 2008, Burnham and Lee 2010), but not others (e.g., McDonald et al. 2008). Although the abundance of introduced species was low among the harvest scenarios, their establishment could lead to expansion with future harvest entries (Buckley et al. 2003) and decrease ecosystem function (Peltzer et al. 2010). This illustrates the importance of additional precautions to evaluate species pool and seed sources prior to harvest, which will be important to maintain or restore the many functions of ground-layer plant communities of managed forests.

Our study also depicted harvest-created gaps 13 years after a single entry into a closed forest composed primarily of native species. Stands managed with multiple entries, which result in gaps of different age, have at some sites homogenized the plant community to species that thrive on regular disturbance (Scheller and Mladenoff 2002, Decocq et al. 2004). We were not able to test the effects of multiple harvests. However, maintaining undisturbed forest patches through multiple entries may maintain many elements of biodiversity (Battles et al. 2001, Smith et al. 2008). Reserve patches ~1 ha in size were important to preserving late successional species and those slow to colonize in structural retention harvests of *Pseudotsuga menziesii* forests (Nelson and Halpern 2005). Nonetheless, our results illustrate that the effects of canopy gaps are not transient and influence ground-layer species diversity for at least 13 years after an initial harvest.

Lastly, we examined only a few values (diversity, trait variation, origin, etc.) of plant communities among a range of experimental gap sizes. In practice, managers would likely consider numerous factors in addition to gap size and proportion of forest in gaps such as spatial location and arrangement of gaps in relation to site features

(e.g., topography) and residual tree vigor, stem quality, and crown development. In addition, other values besides ground-layer plant diversity may require additional tools and attributes to design management practices. For instance, recent work on selection system modifications for a range of goods and services include retention of gap seed trees (Shields and Webster 2007) and various sources of large woody debris (Smith et al. 2008). Our results provide an ecological context to common forest management practices that can be used to meet a wide range of objectives related to delivery of diverse goods and services from forest ecosystems.

Literature Cited

BATTLES, J.J., A.J. SHLISKY, R.H. BARRETT, R.C. HEALD, AND B.H. ALLEN-DIAZ. 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. *For. Ecol. Manage.* 146(1–3): 211–222.

BISWAS, S.R., AND A.U. MALLIK. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology* 91(1):28–35.

BUCKLEY, D.S., T.R. CROW, E.A. NAUERTZ, AND K.E. SCHULZ. 2003. Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in Upper Michigan, USA. *For. Ecol. Manage.* 175:509–520.

BURGER, J.A. 2009. Management effects on growth, production and sustainability of managed forest ecosystems: Past trends and future directions. *For. Ecol. Manage.* 258(10):2335–2346.

BURNHAM, K.M., AND T.D. LEE. 2010. Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. *Biol. Invasions* 12(6):1509–1520.

BURTON, J.I., D.J. MLADENOFF, M.K. CLAYTON, AND J.A. FORRESTER. 2011. The roles of environmental filtering and colonization in the fine-scale spatial patterning of ground-layer plant communities in north temperate deciduous forests. *J. Ecol.* 99(3):764–776.

CADOTTE, M.W. 2011. The new diversity: Management gains through insights into the functional diversity of communities. *J. Appl. Ecol.* 48(5):1067–1069.

CADOTTE, M.W., K. CARSCADDEN, AND N. MIROTCHNICK. 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48(5):1079–1087.

CHANDY, S., D.J. GIBSON, AND P.A. ROBERTSON. 2006. Additive partitioning of diversity across hierarchical spatial scales in a forested landscape. *J. Appl. Ecol.* 43(4):792–801.

COATES, K.D., AND P.J. BURTON. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manage.* 99(3):337–354.

COLLINS, B.S., AND S.T.A. PICKETT. 1988. Response of herb layer cover to experimental canopy gaps. *Am. Midl. Nat.* 119(2):282–290.

COLWELL, R.K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples, version 8. Available online at http://viceroy.eeb.uconn.edu/estimates; last accessed July 22, 2013.

CONNELL, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199(4335):1302–1310.

CROW, T.R., D.S. BUCKLEY, E.A. NAUERTZ, AND J.C. ZASADA. 2002. Effects of management on the composition and structure of northern hardwood forests in Upper Michigan. *For. Sci.* 48:129–145.

DAHIR, S., AND C. LORIMER. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Can. J. For. Res.* 26(10):1875–1892.

DECOCQ, G., B. VALENTIN, B. TOUSSAINT, F. HENDOUX, R. SAGUEZ, AND J. BARDAT. 2004. Soil seed bank composition and diversity in a managed temperate deciduous forest. *Biodivers. Conserv.* 13:2485–2509.

DENSLOW, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica.* 12(2):47–55.

DIAZ, S., AND M. CABIDO. 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16(11): 646–655.

DONOSO, P.J., AND R.D. NYLAND. 2006. Interference to hardwood regeneration in northeastern North America: The effects of raspberries (*Rubus* sp.) following clearcutting and shelterwood methods. *North. J. Appl. For.* 23(4):288–296.

ERDMANN, G.G. 1986. Developing quality in second-growth stands. P. 206–222 in *The northern hardwood resource: Management and potential*, Mroz, G.D., and D.D. Reed (eds.). Michigan Technological University, Houghton, MI.

FAHEY, R.T., AND K.J. PUETTMANN. 2007. Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *J. Ecol.* 95:1098–1109.

FALK, K.J., D.M. BURKE, K.A. ELLIOTT, AND S.B. HOLMES. 2008. Effects of single-tree and group selection harvesting on the diversity and abundance of spring forest herbs in deciduous forests in southwestern Ontario. *For. Ecol. Manage.* 255(7):2486–2494.

FOX, J., WITH CONTRIBUTIONS FROM L. ANDRONIC, M. ASH, T. BOYE, S. CALZA, A. CHANG, ET AL. 2011. Rcmdr: R Commander. R package version 1.6–3. Available online at http://CRAN.R-project.org/package=Rcmdr; last accessed July 22, 2013.

FRANKLIN, J.F., D.R. BERG, D.A. THORNBURGH, AND J.C. TAPPEINER. 1997. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. P. 111–140 in *Creating a forestry for the 21st century*, Kohm, K.A., and J.F. Franklin (eds.). Island Press, Seattle, WA.

FRELICH, L.E., AND C.G. LORIMER. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. *Ecol. Monogr.* 61(2):145–164.

GALHIDY, L., B. MIHOK, A. HAGYO, K. RAJKAI, AND T. STANDOVAR. 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecol.* 183(1):133–145.

GRAU, H.R. 2002. Scale-dependent relationships between treefalls and species richness in a neotropical montane forest. *Ecology* 83(9):2591–2601.

HAEUSSLER, S., L. BEDFORD, A. LEDUC, Y. BERGERON, AND J.M. KRANABETTER. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva. Fenn.* 36(1):307–327.

HANSON, J., AND C. LORIMER. 2007. Forest structure and light regimes following moderate wind storms: Implications for multi-cohort management. *Ecol. Appl.* 17(5):1325–1340.

HUBBELL, S.P. 2001. *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton, NJ. 377 p.

HUBBELL, S.P., R.B. FOSTER, S.T. O'BRIEN, K.E. HARMS, R. CONDIT, B. WECHSLER, ET AL. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557.

HUMBERT, L., D. GAGNON, D. KNEESHAW, AND C. MESSIER. 2007. A shade tolerance index for common understory species of northeastern North America. *Ecol. Indic.* 7(1):195–207.

ISBELL, F., V. CALCAGNO, A. HECTOR, J. CONNOLLY, W.S. HARPOLE, P.B. REICH, ET AL. 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477(7363):199–202.

JENKINS, M.A., AND G.R. PARKER. 1999. Composition and diversity of ground-layer vegetation in silvicultural openings of southern Indiana forests. *Am. Midl. Nat.* 142(1):1–16.

JOST, L., P. DEVRIES, T. WALLA, H. GREENEY, A. CHAO, AND C. RICOTTA. 2010. Partitioning diversity for conservation analyses. *Divers. Distrib.* 16(1):65–76.

KERN, C.C., R.A. MONTGOMERY, P.B. REICH, AND T.F. STRONG. 2013. Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest. *J. Plant Ecol.* 6(1):101–112.

KINDT, R., AND R. COE. 2005. *Tree diversity analysis: A manual and software for common statistical methods for ecological and biodiversity studies.* World Agroforestry Centre (ICRAF), Nairobi.

KOTAR, J., J.A. KOVACH, AND T.L. BURGER. 2002. *A guide to forest communities and habitat types of northern Wisconsin.* University of Wisconsin, Madison, WI. 488 p.

LANDE, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76(1):5–13.

LEAK, W.B., AND S.M. FILIP. 1977. 38 years of group selection in New England northern hardwoods. *J. For.* 75(10):641–643.

MAYFIELD, M.M., S.P. BONSER, J.W. MORGAN, I. AUBIN, S. MCNAMARA, AND P.A. VESK. 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecol. Biogeograph.* 19(4):423–431.

MCDONALD, R.I., G. MOTZKIN, AND D.R. FOSTER. 2008. The effect of logging on vegetation composition in western Massachusetts. *For. Ecol. Manage.* 255:4021–4031.

MENGES, E.S., A. CRADDOCK, J. SALO, R. ZINTHEFER, AND C.W. WEEKLEY. 2008. Gap ecology in Florida scrub: Species occurrence, diversity and gap properties. *J. Veg. Sci.* 19(4):503–514.

MILLAR, C.I., N.L. STEPHENSON, AND S.L. STEPHENS. 2007. Climate change and forests of the future: Managing in the face of uncertainty. *Ecol. Appl.* 17(8):2145–2151.

MITCHELL, R.J., B.J. PALIK, AND M.L. HUNTER. 2002. Natural disturbance as a guide to silviculture. *For. Ecol. Manage.* 155 (1–3):315–317.

MOORE, M.R., AND J.L. VANKAT. 1986. Responses of the herb layer to the gap dynamics of mature beech-maple forest. *Am. Midl. Nat.* 115(2):336–347.

NAAF, T., AND M. WULF. 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. *For. Ecol. Manage.* 244 (1–3):141–149.

NELSON, C.R., AND C.B. HALPERN. 2005. Edge-related responses of understory plants to aggregated retention harvest in the Pacific Northwest. *Ecolo. Appl.* 15:196–209.

OBIRI, J.F., AND M.J. LAWES. 2004. Chance versus determinism in canopy gap regeneration in coastal scarp forest in South Africa. *J. Veg. Sci.* 15(4):539–547.

OKSANEN, J., F.G. BLANCHET, R. KINDT, P. LEGENDRE, R.B. O'HARA, G.L. SIMPSON, ET AL. 2011. Vegan: Community Ecology Package, version 1.17–8. Available online at http://CRAN.R-project.org/package=vegan; last accessed July 22, 2013.

PAWSON, S.M., E.G. BROCKERHOFF, D.A. NORTON, AND R.K. DIDHAM. 2006. Clear-fell harvest impacts on biodiversity: Past research and the search for harvest size thresholds. *Can. J. For. Res.* 36(4):1035–1046.

PELTZER, D.A., R.B. ALLEN, G.M. LOVETT, D. WHITEHEAD, AND D.A. WARDLE. 2010. Effects of biological invasions on forest carbon sequestration. *Glob. Change Biol.* 16(2):732–746.

R DEVELOPMENT CORE TEAM. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

REICH, P.B., D. TILMAN, F. ISBELL, K. MUELLER, S.E. HOBBIE, D.F.B. FLYNN, ET AL. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336:589–592.

RICKLEFS, R.E. 1977. Environmental heterogeneity and plant species diversity: A hypothesis. *Am. Nat.* 111(978):376–381.

ROBERTS, M.R., AND F.S. GILLIAM. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. *Ecol. Appl.* 5(4):969–977.

SAS INSTITUTE, INC. 2008. SAS version 9.2, Cary, NC.

SCHELLER, R.M., AND D.J. MLADENOFF. 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecol. Appl.* 12(5):1329–1343.

SCHUMANN, M.E., A.S. WHITE, AND J.W. WITHAM. 2003. The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. *For. Ecol. Manage.* 176 (1–3):543–561.

SEYMOUR, R.S., AND M. HUNTER. 1999. Principles of ecological forestry. P. 22–61 in *Maintaining biodiversity in forest ecosystems.* Cambridge University Press, Cambridge, UK.

SEYMOUR, R.S., A.S. WHITE, AND P.G. DEMAYNADIER. 2002. Natural disturbance regimes in northeastern North America—Evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manage.* 155:357–367.

SHIELDS, J.M., AND C.R. WEBSTER. 2007. Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. *Can. J. For. Res.* 37:1797–1807.

SMITH, K.J., W.S. KEETON, M.J. TWERY, AND D.R. TOBI. 2008. Understory plant responses to uneven-aged forestry alternatives in northern hardwood–Conifer forests. *Can. J. For. Res.* 38(6):1303–1318.

STRONG, T.F., R.M. TECLAW, AND J.C. ZASADA. 1997. Monitoring the effects of partial cutting and gap size on microclimate and vegetation responses in northern hardwood forests in Wisconsin. P. 42–47 in *Proceedings of the national silviculture workshop.* USDA For. Serv., Gen. Tech. Rep. NE-238, Northeastern Research Station, Radnor, PA.

STRONG, T.F., J.C. ZASADA, AND A.H. WIESE. 1998. The effects of canopy gap size on the microclimate and understory vegetation in a northern hardwood forest. P. 323–325 in *Third international conference on forest vegetation management: Popular summaries.* Ontario Ministry of Natural Resources, For. Res. Info. Paper No. 141, Sault Ste. Marie, Ontario.

SWINK, F., AND G. WILHELM. 1994. *Plants of the Chicago Region,* 4th ed. Indiana Academy of Science, Indianapolis, IN. 932 p.

TILMAN, D., J. KNOPS, D. WEDIN, P. REICH, M. RITCHIE, AND E. SIEMANN. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277(5330):1300–1302.

TYRRELL, L.E., AND T.R. CROW. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75(2):370–386.

USDA FOREST SERVICE. 2011. *National report on sustainable forests—2010.* USDA For. Serv., FS-979, Washington, DC. 212 p.

USDA NRCS. 2009. The PLANTS Database. USDA NRCS, National Plant Data Center, Baton Rouge, LA. Available online at http://plants.usda.gov; last accessed Oct. 16, 2009.

VEECH, J.A., AND T.O. CRIST. 2009. PARTITION: Software for hierarchical partitioning of species diversity, version 3.0.

VEECH, J.A., K.S. SUMMERVILLE, T.O. CRIST, AND J.C. GERING. 2002. The additive partitioning of species diversity: Recent revival of an old idea. *Oikos* 99(1):3–9.

WANG, S., AND H.Y.H. CHEN. 2010. Diversity of northern plantations peaks at intermediate management intensity. *For. Ecol. Manage.* 259(3):360–366.

WISCONSIN DEPARTMENT OF NATURAL RESOURCES. 2008. *Northern hardwood cover type—Silvics and silviculture.* State of Wisconsin Department of Natural Resources Publ. 2431.5, Chapter 40.

WISCONSIN STATE HERBARIUM. 2011. *WISFLORA.* University of Wisconsin—Madison, Madison, WI. Available online at http://www.wisflora.org; last accessed Oct. 16, 2009.

WOLF, A.T., L. PARKER, G. FEWLESS, K. CORIO, J. SUNDANCE, R. HOWE, ET AL. 2008. Impacts of summer versus winter logging on understory vegetation in the Chequamegon-Nicolet National Forest. *For. Ecol. Manage.* 254(1):35–45.

ZENNER, E.K., J.M. KABRICK, R.G. JENSEN, J.L.E. PECK, AND J.K. GRABNER. 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. *For. Ecol. Manage.* 222:326–334.

ZHANG, Y., H.Y. CHEN, AND P.B. REICH. 2012. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *J. Ecol.* 100(3):742–749.