



# Functional diversity of ground-layer plant communities in old-growth and managed northern hardwood forests

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## Keywords

forest management; fourth-corner analysis; functional divergence; functional evenness; functional richness; life-history traits; mixed-effect models; spring ephemerals

## Abbreviations

SLA = Specific leaf area; %T = % of light transmittance; PCoA = Principal coordinate analysis

## Nomenclature

Gleason & Cronquist (1991)

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## Abstract

**Questions:** Do ecological sorting processes and functional diversity of forest ground-layer plant communities vary among mature (65–85-yr-old) even-aged, managed uneven-aged and old-growth forest stands? How does functional diversity relate to environmental variables within stands?

**Location:** Northern temperate deciduous forests of Wisconsin and the Upper Peninsula of Michigan, USA.

**Methods:** Ground-layer species cover and light availability were measured at each of four old-growth, even-aged second-growth, and managed uneven-aged stands ( $n = 12$  stands total). We used mixed-effect models and fourth-corner analysis to assess relationships among forest structure, species traits and the three components of functional diversity (functional richness, evenness, divergence) based on 32 leaf, reproductive and whole plant traits from 111 species.

**Results:** We identified differences in leaf phenology and morphology, life form and dispersal among stand types at the community level. Ground-layer plant communities of even-aged and uneven-aged stands were at opposite ends of a spectrum of strategies aimed at tolerating stressful vs competitive environments, respectively. In even-aged stands, communities were characterized by species adapted to relatively dark and closed conditions (heavy-seeded tree saplings, spring ephemerals). In contrast, managed uneven-aged stands were characterized by species with potential for quick returns on investment of nutrients and dry mass in leaves (i.e. early summer species with high specific leaf area, low leaf dry matter content and high phosphorus concentration). Old-growth stands had fewer trait associations than managed stands, and were characterized by ferns and species with either ballistic or wind-assisted seed dispersal. Functional diversity metrics were related in complex ways to light, management and soil texture. Managed stands had higher functional richness and divergence than old-growth stands, which, instead, showed higher functional evenness.

**Conclusions:** Even-aged and managed stands support ground-layer species with a distinct set of traits relative to those found in old-growth forests. Although there is broad interest in uneven-aged management as a means to restore the structures and functions of old-growth forests, uneven-aged management does not, at least initially, produce ground-layer plant communities more similar to old-growth forests than even-aged management.

## Introduction

Anthropogenic changes in disturbance regimes have altered the structure of temperate forests worldwide (Burscano et al. 2013). In the northern temperate deciduous forests of the upper Great Lakes region of the United States

timber harvesting has become the dominant disturbance within the last century. The widespread clear-cut logging following Euroamerican settlement resulted in a contemporary landscape dominated by ca. 80–100-yr-old second-growth stands (Frelich 1995). In contrast, light to moderately severe wind was the prevalent disturbance prior to

Euroamerican settlement (ca. 1850), resulting in a region dominated by old, multi-aged forests (Schulte & Mladenoff 2005).

Beyond timber production, forest management objectives increasingly include provisions for biodiversity and wildlife habitat, as well as other ecosystem, cultural and aesthetic services (Neill & Puettmann 2013). Presently, there is broad interest in using partial overstorey harvests typically associated with intermediate thinning or uneven-aged management systems to restore the structures of old-growth forests and to recreate a full range of early- and late-successional species and associated functions in younger second-growth stands. Remaining primary forests provide a reference to better understand the effects of forest management upon biodiversity and ecosystem function, and provide guidance for restoration strategies (Scheller & Mladenoff 2002; Burton et al. 2009; Burrascano et al. 2013).

The majority of vascular plant species in temperate forests are restricted to the ground layer, providing habitat and forage for many wildlife species (Gilliam 2007). Ground-layer plant communities also play an important role in forest ecosystem functioning, influencing nutrient cycles and successional pathways in the overstorey (Royo & Carson 2006; Mabry et al. 2008). In turn, overstorey structure affects environmental conditions at the ground level, controlling light availability and exerting an influence on the composition, diversity and spatial pattern of ground-layer plant communities (Scheller & Mladenoff 2002; Burrascano et al. 2011; Burton et al. 2011).

Studies have demonstrated that even-aged second-growth stands exhibit simplified stand structures, with both relatively lower resource levels and a more homogeneous distribution of resources for plants in the ground layer, compared to old-growth and managed uneven-aged stands (e.g. Scheller & Mladenoff 2002; Burton et al. 2009; Burrascano et al. 2013). Yet little is known about how observed differences relate to sorting processes (e.g. habitat filtering and niche differentiation) and functions in the ground layer. Indeed, the detailed mechanisms that link the species present in an ecosystem to its functioning are often system specific, making generalizations difficult. The need to shift the focus from species composition and diversity *per se* to a more mechanistic view based on functional diversity, i.e. the value, range and relative abundance of functional traits of co-existing species, is now generally accepted (Hooper et al. 2005; Diaz et al. 2007; de Bello et al. 2013).

Such a shift in perspective has a twofold importance. Life history and functional traits mediate ground-layer species response to disturbance (Mayfield et al. 2010; Pakeman 2011). For instance, plant species have been classified along a continuum, from species with a fast return on carbon investment, to species with more

conservative behaviour reflecting the economics of gas exchange, support and biotic interactions (Givnish 1987; Wright et al. 2004). Furthermore, functional traits have been shown to be directly relevant to several important ecosystem services related, for instance, to productivity, food availability for wildlife, litter decomposition and biogeochemical cycles (Diaz et al. 2007; Cornwell et al. 2008; Mouillot et al. 2011; Neill & Puettmann 2013).

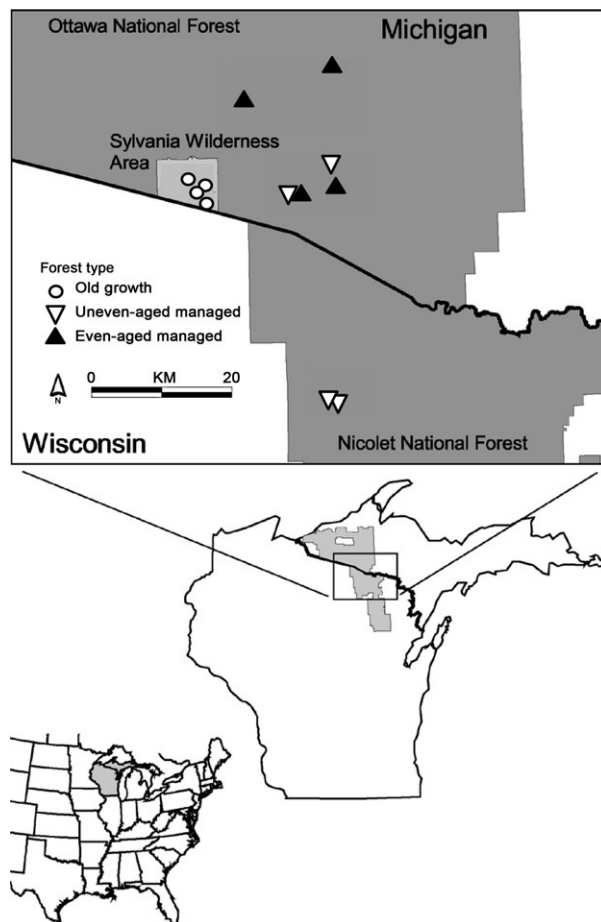
In this paper, we examine functional trait associations among: (1) old-growth stands with a history of natural disturbance and regeneration; (2) even-aged stands originating from clearcut logging (ca. 65–85 yr old); and (3) second-growth managed uneven-aged stands with recent selective logging. Then we compare and contrast associated patterns of functional diversity in ground-layer plant communities. We focused primarily on the effects of differences in forest structure on functional diversity based on different subsets of traits related to strategies for light acquisition, regeneration and plant growth, since different traits can simultaneously converge and diverge under the same environmental pressure (Grime 2006).

We hypothesized that associations of plant functional traits with stand types reflect different ecological sorting processes related to stand structure and light transmittance, resulting in differences in functional diversity. We expected (1) species with a fast return on carbon investment to be associated with uneven-aged, and species characterized by conservative growth strategies prevail in even-aged stands. With respect to functional diversity, we expected: (2) functional richness to be higher in species-rich uneven-aged stands as a result of weaker habitat filters, and given higher species richness observed by Scheller & Mladenoff (2002) and known correlations between species and functional richness; and (3) functional divergence to increase in uneven-aged stands due to higher competition among understorey species that is expected to limit their similarity and increase niche differentiation. Although these predictions relate to light acquisition traits, we expected patterns based on regenerative traits to be similar, since correspondences have been observed between reproductive and dispersal behaviour and phenological guilds (Mason et al. 2012), especially in ground-layer species of northern hardwood forests (Aubin et al. 2007).

## Methods

### Study area

We analysed data collected from 12 forest stands in northern Wisconsin and the Upper Peninsula of Michigan (Fig. 1, App. S1, Table S1.1) chosen from a set of 24 northern hardwood stands studied in a large, multidisciplinary project (Bockheim 1997; Goodburn & Lorimer 1998, 1999; Miller et al. 2002; Scheller & Mladenoff 2002). The area is



**Figure 1.** Locations of 12 northern hardwood study sites in northern Wisconsin and Michigan, USA (from Scheller & Mladenoff 2002)

situated on the Laurentian shield bedrock and overlain with glacial deposits of the Winegar terminal moraine. Topography is gently rolling, with elevations ranging from 517 to 567 m a.s.l. Soils vary from sandy to coarse loamy (Table S1.2; Bockheim 1997). The study area has a continental climate, with cold winters and moderate summers. Average temperature (1971–2000) was 4.5 °C and annual precipitation 752 mm, more than half of this falls during the growing season, which lasts ca. 123 days (Midwestern Regional Climate Center: <http://mcc.sws.uiuc.edu>).

Four forest stands were chosen within each of three disturbance histories: (1) old-growth stands that were never clearcut; (2) even-aged stands resulting from clearcut logging; and (3) recently harvested uneven-aged stands. Stands were selected to be as similar as possible in soil types, site quality (Table S1.1) and overstorey composition. All 12 chosen stands are dominated by sugar maple (*Acer saccharum*) with basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*) and eastern hemlock (*Tsuga canadensis*) as co-dominants.

Even-aged stands resulted from clearcut logging in the first half of the 20th century and, with the exception of limited thinning, have not been logged for 65–85 yr. The managed uneven-aged stands have been harvested under a single tree selection system in the late 1980s under wildlife tree retention guidelines (Goodburn & Lorimer 1998), but unfortunately their long-term management history is not completely known. All the old-growth forest stands were located inside the 74 km<sup>2</sup> Sylvania Wilderness Area (ca. 89°W, 46°N), encompassing a mosaic of forest stands with different species composition and age. Although the selection of our old-growth stands from this restricted area may create pseudoreplication and weaken any inferences drawn from this study, this should not be an issue, given the similarities in climate and underlying geology across stands. Additionally, all the sites were located between 2 and 5 km, a distance well beyond the reported spatial autocorrelation distances for most understorey species in Sylvania forest (Miller et al. 2002). Furthermore, these were the only old-growth stands occurring locally that respected the selection criteria of similarity in soil, site quality and overstorey composition, and thus there was no alternative.

### Sampling design

In each stand, communities were sampled along two transects that overlapped at a 60° angle. Along each transect 2 m × 2 m quadrats were placed with unequal spacing between quadrats, following a cyclic sampling scheme. Transects extended up to the scale (width) of the forest stand (up to a maximum of 520 m in length with 80 quadrats in 20 cycles). A total of 1155 quadrats were sampled, accounting for a total area ranging from 248 to 512 m<sup>2</sup> per stand (Scheller & Mladenoff 2002).

In each quadrat, the presence and cover of all ground-layer vascular plants and tree seedlings <2 m in height were recorded. Flora was sampled in summer 1998 or 1999; spring ephemerals were sampled once from mid-May to mid-June 1999 or 2000. All tree saplings <10 cm DBH occurring in each quadrat were tallied. The species and DBH of the three trees >10 cm DBH closest to quadrat centre were measured for overstorey basal area calculations (Scheller & Mladenoff 2002). Three measurements of diffuse light transmittance (%T), i.e. the photosynthetically active radiation reaching the ground layer, were collected at each quadrat using Decagon AccuPAR ceptometer (Decagon Devices, Pullman, Washington, WA, US), under uniformly cloudy conditions. The average %T at each quadrat was then normalized on a percentage basis through comparison to independent measurements taken in a nearby opening (Scheller & Mladenoff 2002). Light transmittance data are summarized in Table S1.2.

### Plant functional trait collection

We collected a total of 32 species traits from multiple sources (App. S2, Table S2.1). Most of the traits were collected from the literature (mostly from Gleason & Cronquist 1991; traits 1–19 in Table S2.1). Remaining quantitative traits (traits 20–32 in Table S2.1) were collected following standard protocols; see App. S2 for additional information. After excluding taxa not identified at species level (12 taxa, <2% of total occurrences, especially genera *Carex*, *Viola* and *Hieracium*), we obtained a final matrix of 111 species by 32 traits.

### Fourth-corner analysis

To examine how disturbance history affects the composition of understorey plant communities, we applied the fourth-corner analysis (Dray & Legendre 2008), calculating species abundance as the proportion of quadrats in which a species occurred per stand. We ran the analysis using management system as an environmental variable with three states: old-growth, even-aged and uneven-aged.

Exploratory analysis suggested that soil type may have a significant confounding effect on the relationship between plant functional traits and management system. For this reason, the analysis was run also for each soil type separately. Results were mostly consistent across soil types and only those related to all stands pooled together are shown.

### Reducing collinearity and dimensionality of the species-by-traits matrix

Functional traits that were significant in fourth-corner analysis ( $n = 19$ ) were classified in three subsets, i.e. 'leaf traits' (ten traits), 'regenerative traits' (three traits) and 'whole plant traits' (six traits), corresponding to the primary trade-offs described in the Leaf–Height–Seed (LHS) scheme (Westoby et al. 2002; Table S2.1). We adopted the distance-based approach suggested by Laliberté & Legendre (2010), and performed principal coordinate analysis (PCoA) ordinations both on all the selected traits, and for each leaf, regenerative and whole-plant subset separately, using Gower's dissimilarity measure. After the ordinations, we retained, respectively, 14 (total), ten (leaf), three (regenerative) and four (whole plant) ordination axes (always >90% of explained variation).

### Selection and calculation of diversity indices

We used the species axes scores resulting from PCoA ordinations to calculate functional indices on the basis of each set of traits (see above). We selected at least two indices for

each of the three facets of functional diversity from the literature (Mason et al. 2005; Villéger et al. 2008). Functional richness represents the range of functional space occupied by a species assemblage and was calculated through  $F_{Ric}$  (Cornwell et al. 2006) and  $FD_{Petchey}$  (Petchey & Gaston 2002). Functional evenness measures how regularly species abundances are distributed in the functional space, with low values indicating an increasing importance of competitively dominant species. We measured this facet through the indices  $F_{Eve}$  (Villéger et al. 2008) and the overall functional regularity index (OFRO), the multivariate extension of the functional regularity index (Mouillot et al. 2005). We developed an *ad hoc* R-script to calculate OFRO (App. S3).

Finally, functional divergence measures how far highly abundant species are from the centre of the functional space, and should increase when niche complementarity enhances species' relative abundances (Mouchet et al. 2010; Mason et al. 2013). We calculated two indices of functional divergence:  $F_{Div}$  (Villéger et al. 2008) and RaoQ (Botta-Dukat 2005), although the latter was shown to also be related to functional richness (Mouchet et al. 2010). A non-parametric correlation analysis among indices is reported in App. S4, Fig. S4.1. For a review of most of these indices and how they are calculated, see Mouchet et al. (2010).

Departures of functional indices from random expectations were evaluated using null models, permuting site vectors 999 times in the species  $\times$  site table (permutation method 2 in Dray & Legendre 2008). In this way, we were able to test whether functional diversity of observed communities significantly deviated from that of permuted communities that were unaffected by management systems. We also calculated functional indices using each subset of traits (leaf, regenerative, whole plant) separately.

All analyses were performed using R v 2.12.0 (R Foundation for Statistical Computing, Vienna, AT). When not specified, functional indices were calculated using the R function dbFD in the *FD* package (Laliberté & Legendre 2010).

### Mixed models: Environmental correlates of functional diversity metrics

For each facet of functional diversity, we selected a functional index that could be computed for each individual quadrat, notwithstanding the number of species in the quadrat (i.e.  $FD_{Petchey}$ , OFRO and RaoQ). Quadrats with missing environmental data ( $n = 30$  of 1155 total) were excluded from further analysis.

The responses of the three facets of functional diversity (both for the complete set of traits and for the three sub-



sets) were modelled through linear mixed effect models, using stand as random effect. We also tested whether stands differed in the slopes of their responses to different environmental variables, testing different random intercept and slope models for significance. Seven environmental variables were used as explanatory variables: (1) diffuse light transmittance (%T); (2) overstorey basal area; (3) sapling basal area; (4) percentage of basal area of evergreen species in the overstorey; (5) overstorey tree richness; (6) management system; and (7) soil texture. Variables 1–5 were measured at quadrat scale; variable 6 and 7 were categorical.

To find best fitting models, we followed the protocol suggested in Zuur et al. (2009). We accounted for heterogeneity in residuals modelling for multiple variances and for their spatial autocorrelation by selecting the best-fitting autocorrelation structure. Mixed-effect models were computed in R using *nlme* package (v 3.1-105).

## Results

### Fourth-corner analysis

Results from the fourth-corner analysis indicate that most traits examined are associated with one or more stand types (Table S5.1). Even-aged stands were characterized by species with low specific leaf area (SLA), high leaf dry matter content and low nutrient concentration in leaves. A higher than expected proportion of heavy-seeded species, tree seedlings and spring ephemerals was also associated with even-aged stands. Conversely, hemi-cryptophytes, species with palmate leaves and species capable of producing multiple flushes of leaves within a growing season (e.g. *Viola pubescens*, *Hydrophyllum virginianum* and *Osmorhiza* spp.) were negatively associated with even-aged stands.

The functional traits significantly associated to uneven-aged stands were: early summer phenology, nutrient-rich leaves with high SLA, spinescence and adhesively dispersed propagules. We noted also a higher than expected presence of shrubs and of insect-pollinated species, with pubescent and/or compound leaves. However, tree seedlings, spring ephemerals and species with simple leaves were disproportionately uncommon in uneven-aged stands.

Old-growth stands were positively associated both with light-seeded, wind-dispersed species, such as ferns and club mosses (the latter association is only marginally significant in the global data set,  $P = 0.072$ , but becomes highly significant on loamy soils,  $P = 0.002$ ) and with ballistically dispersed species. We also observed a negative association with stem dry matter content and a lower than expected occurrence of graminoids, spiny and alternate-leaved species.

### Functional richness, evenness and divergence

Both indices of functional richness (i.e.  $F_{Ric}$  and  $FD_{Petchy}$ ) showed the same pattern (Table 1): uneven-aged stands averaged higher than the even-aged stands, which, in turn, averaged more than old-growth stands. Functional richness in uneven-aged stands departed positively from random expectations, while in old-growth stands it departed negatively. The two indices of functional evenness were inconsistent and ranked the stands differently. OFRO departed positively from random expectations in old-growth stands and even-aged stands, and negatively in uneven-aged stands.  $F_{Eve}$  instead departed positively from random expectations in even-aged and negatively in old-growth stands. Regarding functional divergence,  $F_{Div}$  in even- and uneven-aged stands were significantly higher than expected, while in old-growth stands it was significantly lower. There was no significant difference from random among stand types when calculating functional divergence using RaoQ.

### Mixed effect models and functional diversity

The mixed effect models relating functional diversity indices to environmental variables were substantially consistent across different subsets of functional traits (i.e. leaf, regenerative and whole-plant traits), with respect to significance, direction and relative strength of fixed and random effects (App. S6). Therefore, we report results from models of functional diversity based on all traits combined. Results from separate models of functional diversity indices of leaf, height and seed traits are reported in App. S6.

For functional richness ( $FD_{Petchy}$ ), the best fitting model included a random intercept (stand) and slope (% T); for functional evenness (OFRO) and divergence (RaoQ), instead, stand was the only random effect (random intercept model, Table S6.2). The final variance

**Table 1.** Mean functional indices for the three management systems (E – Even aged, U – Uneven aged, OG – Old-growth). Asterisks indicate a significant deviation from a random expectation. \*:  $0.01 < P < 0.05$ ; \*\*:  $0.01 < P < 0.001$ ; \*\*\*:  $P < 0.001$ .

	E	UE	OG
Functional richness			
$F_{Ric}$	0.010	0.017***	0.006***
$FD_{Petchy}$	35.50	48.65***	24.84***
Functional evenness			
$F_{Eve}$	0.52***	0.50	0.44***
OFRO	0.598***	0.532***	0.623***
Functional divergence			
$F_{Div}$	0.76*	0.78***	0.66***
RaoQ	0.33	0.32	0.31

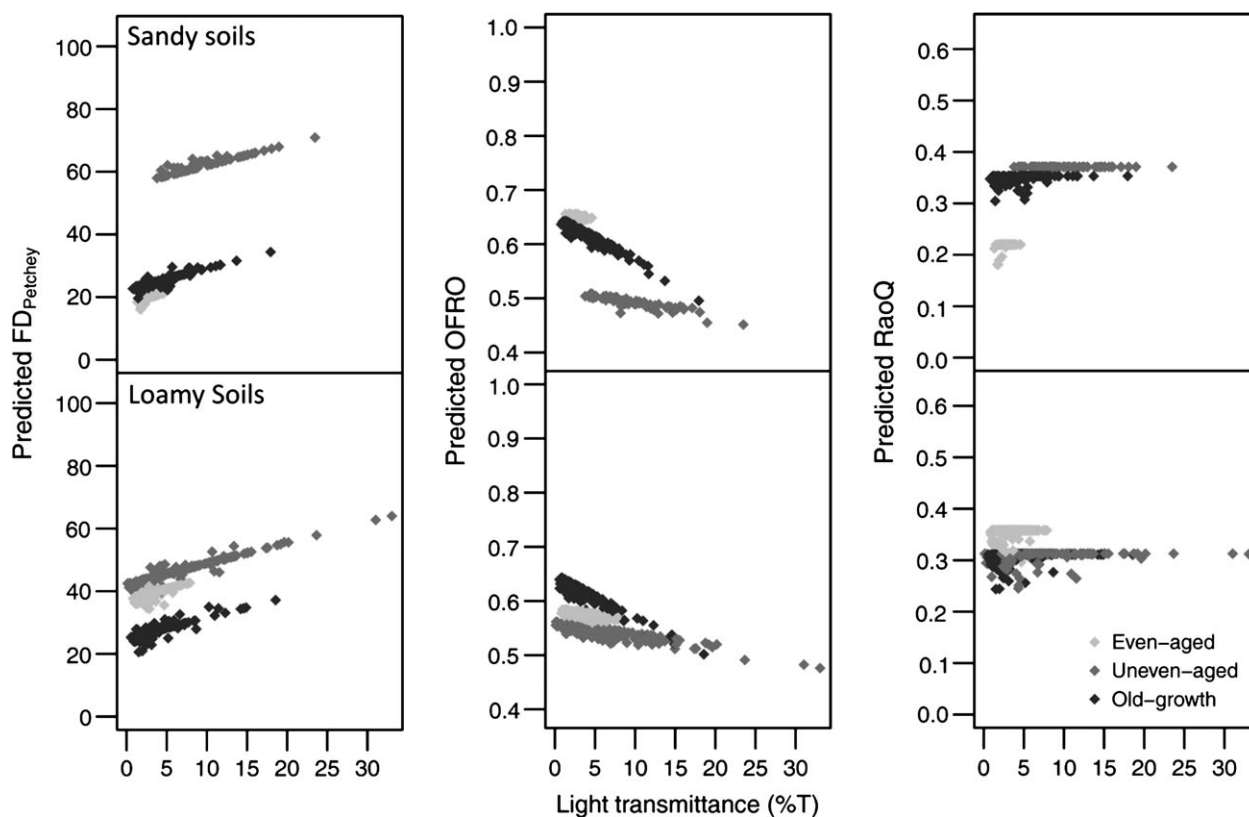
structure was the same for all three models, allowing for one variance parameter for each stand type–soil type combination. When the residuals of the final models showed some degree of spatial autocorrelation they were modelled through an exponential variogram. Parameters of the final mixed effect models are reported in Table S6.1 and S6.2.

Both functional richness and evenness were significantly related to light transmittance (%T; Fig. 2), but while functional richness had a positive relationship, OFRO was negatively related to %T. Functional evenness (OFRO) was the only functional diversity index that was related to an interaction between stand type and %T (LRT = 6.22,  $P = 0.044$ ; Table S6.1, Fig. 2). Sapling basal area was negatively related to both  $FD_{Petchey}$  (LRT = 8.38,  $P = 0.004$ ) and RaoQ (LRT = 8.22,  $P = 0.016$ ). Functional evenness was negatively related to overstorey basal area (LRT = 8.26,  $P = 0.004$ ). Furthermore, stand type, soil texture and the interaction thereof significantly affected all three facets of functional diversity (LRT of the interaction term –  $FD_{Petchey}$ : 11.98,  $P = 0.003$ ; OFRO: 7.93,  $P = 0.019$ , RaoQ: 8.22,  $P = 0.016$ ).

## Discussion

### Functional traits respond to forest management

Our study demonstrates that different overstorey structures create distinct environmental filters that result in ground-layer communities composed of species that sit at opposite ends of a spectrum of strategies aimed at tolerating stressful vs competitive, resource-rich environments (Wright et al. 2004). The relatively homogeneous, closed canopy, even-aged stands favour species associated with low light levels (i.e. species with slow return rates on carbon invested, low SLA leaf construction and low leaf nutrient concentrations), as well as species that are able to avoid stress due to their phenological adaptation (i.e. spring ephemerals). In contrast to even-aged stands, uneven-aged stands have relatively high light availability after overstorey leaf-out, which provides favourable growing conditions for early summer species. Additionally, the association of species that are protected against herbivory (i.e. spinescent), dispersed adhesively by birds and mammals, and biologically pollinated with uneven-aged stands show how interactions between the occurrence of canopy



**Figure 2.** Scatterplots of predicted values of functional richness (left), evenness (centre) and divergence (right) estimated by linear mixed effect models to light transmittance by stand type (top: stands on sandy soils, bottom: stands on loamy soils) in 12 forest stands in northern Wisconsin and Michigan, USA. We plotted predicted values to emphasize relationships with fixed effects. Random effects are not shown.

gaps and wildlife and insect pollinators can result in selection for such traits during community assembly (Neill & Puettmann 2013).

The significant association between even-aged stands and spring ephemerals is consistent with the results of Aubin et al. (2007), who showed that spring ephemerals were associated with second-growth stands lacking recent human disturbance. Spring ephemerals (e.g. *Claytonia caroliniana*, *Dicentra cucullaria*, *Erythronium americanum*) are characterized by relatively high leaf nutrient content and short-lived leaves that emerge early in the spring and senesce before the overstorey canopy reaches its maximum leaf area (Givnish 1987). In even-aged stands, the growth of early-summer forbs and woody species is limited by the uniformly low mid-summer light levels, and, in their absence, spring ephemerals are predicted to succeed. However, the association between spring ephemerals and even-aged stands may also be related to a decreased importance of evergreen hemlock trees in the even-aged stands, as evergreen overstorey species reduce spring light availability and soil nutrients (Burton et al. 2011).

We expected ground-layer plant communities in old-growth stands would be comprised of a suite of traits more similar to uneven- than even-aged stands, but old-growth stands generally lacked strong trait associations. Our study highlights the co-occurrence of wind-dispersed species (especially ferns and club mosses) together with species with low dispersal ability (e.g. some ballistically dispersed species including *Scutellaria lateriflora* and *Cardamine concatenata*), as already noted in previous studies (Aubin et al. 2007; Mabry & Fraterrigo 2009). Such patterns are usually related either to the occurrence of small- to intermediate-sized gaps, promoting the establishment of wind-dispersed species, or to the ecological continuity of old-growth forests that favours the persistence of low dispersal species (Ricotta et al. 2010).

### Disturbance and functional diversity

The relationship between functional diversity and disturbance is still a matter of concern. According to the general model proposed by Mayfield et al. (2010), an increase in functional diversity with species richness is expected when an anthropogenic impact (such as land-use change or harvest) releases environmentally compatible species from strong or dominant competitors. Indeed, disturbance is considered the most potent mechanism creating and sustaining trait variation in plant communities (Grime 2006), although evidence is accumulating that disturbance can also be a driver of convergence (Pakeman 2011).

In our study functional richness was higher than expected in uneven-aged stands, but lower than expected in undisturbed old-growth stands. Biswas & Mallik (2010)

reported understorey functional richness peaked at intermediate levels of disturbance in temperate forests, but other studies suggest that the relationship between disturbance and functional richness is either negative (Mayfield et al. 2010; Pakeman 2011) or not significant (Flynn et al. 2009). The highest functional richness we observed in species-rich, uneven-aged stands was expected, given the correlation between species richness and functional richness (Fig. S4.1). In our case, however, we were not able to discern whether the high functional richness in uneven-aged stands was driven by the 'sampling effect' alone (Hooper et al. 2005) or by more variable light conditions allowing for the presence of species adapted to a wider range of environmental conditions or disturbance events (Kern et al. 2013; Neill & Puettmann 2013).

Functional evenness is generally used to indicate under- or over-utilization of resources. From this perspective, the low functional evenness found in uneven-aged stands may be interpreted either as resulting from the increase in suitable niche space not yet filled by the arrival of species with adequate characteristics, or to the arrival of competitive species that may exclude other guilds due to their higher metabolic rates. However,  $F_{Eve}$  has the disadvantage of being potentially maximized at low levels of  $F_{Ric}$  (as lower ranges will result in artificially more even trait spacing) and, although it has proven to be useful in some situations (Pakeman 2011), some authors recommend that its use should be subordinated to a better understanding of its relevance for community structure (de Bello et al. 2013).

Functional divergence may be a proxy for the degree of niche differentiation in the community (Mason et al. 2005), and it was reported to be a good proxy of ecosystem multifunctionality (Mouillot et al. 2011). The indices of functional divergence we used returned inconsistent results.  $F_{Div}$  was reported to have only moderate power to detect assembly processes (Mouchet et al. 2010; Mason et al. 2013). RaoQ, on the other hand, is related both to functional richness and divergence, and this may have created some noise in our results. RaoQ becomes a pure index of functional divergence when it is compared to null models that randomize species abundances (but not occurrences) within communities (Mason et al. 2012). We calculated randomized RaoQ and the results were qualitatively comparable to those reported in Table 1 (data not shown), suggesting our results were not confounded by functional richness. The relatively high functional divergence observed in even-aged stands contrasted with our expectation, and is possibly related to the co-occurrence of different phenological guilds (evergreen and spring ephemerals) that diverge in light capture strategies and have different suites of functional traits. These two guilds of species have recently been noted for their nutrient uptake and retention capacity, and are considered really important for

ecosystem biogeochemical cycling (Cornwell et al. 2008; Mabry et al. 2008; Mouillot et al. 2011).

### Complex relationship between light and functional diversity

Our results suggest that light performs an important role in shaping ground-layer species assemblages, not only when considering functional traits related to light acquisition (i.e. 'leaf' subset), but also when calculating functional indices based on plant reproductive and architectural traits (Mason et al. 2012). We expected functional diversity to be related to the light regime since, in forest systems, light is often reported to increase species richness (Thomas et al. 1999) and consequently functional richness (Fig. 2, Fig. S4.1). The effect of management on functional diversity also varied with soil properties. Indeed, canopy openness and spatial heterogeneity may differ with soil texture, modifying interactions among ground-layer plant communities, sapling and shrub density, litter, humidity and resource distribution (Miller et al. 2002; Burton et al. 2011). Given the low number of stands on sandy soil that we sampled, our results should be interpreted with caution. Our study did not consider either microtopography or important soil properties that may vary at the quadrat level. However, our variables related to overstorey composition and structure likely accounted for some of the effects of these missing variables, given that soil, ground-layer and overstorey composition are tightly related through several direct and indirect relationships (Burrascano et al. 2011; Burton et al. 2011).

In conclusion, our work demonstrated that different forest management systems modify the distribution of functional traits of herb-layer assemblages via effects on stand structure. We observed a strong human-induced change in the functional structure of communities that may have a strong impact on key ecosystem processes, such as biogeochemical cycles, decomposition rates and food availability for wildlife and insect pollinators. These changes should receive more attention when developing and implementing forest management practices aimed at maintaining (or restoring) biodiversity and associated functions in northern hardwood forests.

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### Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Soil and morphology characteristics of study sites.

**Appendix S2.** Species functional traits description.

**Appendix S3.** R script ‘OFRO.calc’ for the calculation of overall functional regularity index.

**Appendix S4.** Calculation of FD indices and correlation among FD and environmental conditions.

**Appendix S5.** Results of the fourth corner analysis

**Appendix S6.** Results of the mixed effect models on functional diversity indices based on leaf, regenerative and whole-plant functional traits subsets.