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ARTICLE

Increasing ground-layer plant taxonomic diversity masks declining phylogenetic diversity along a silvicultural disturbance gradient

Stefan F. Hupperts, Christopher R. Webster, Robert E. Froese, Erik A. Lilleskov, Amy M. Marcarelli, and Yvette L. Dickinson

Abstract: Most plant diversity in temperate deciduous forests is found in the ground layer, but nearly all studies comparing plant community assembly using taxonomic, trait, and phylogenetic diversity indices are limited to woody plants. To examine the relationship between short-term ground-layer plant community assembly and disturbance severity, we leveraged a silvicultural experiment that applied a combination of harvest and site preparation treatments in a northern hardwood forest in Michigan, USA. We predicted that after two growing seasons, plant communities would be less sensitive to harvest treatments when compared with site preparation treatments that disturb the rhizosphere and modify rooting substrate. We also predicted that an increase in taxonomic diversity would accompany a decline in trait diversity and phylogenetic diversity. Instead, plant species composition responded similarly to harvest treatment and site preparation treatment. However, our measure of disturbance severity was positively correlated with both trait diversity and taxonomic diversity but negatively correlated with phylogenetic diversity, indicating that increasingly diverse traits and taxonomies along this disturbance severity gradient were comprised of more phylogenetically simple plant communities. Informed management decisions should therefore consider the underlying value of each diversity measure, as taxonomic diversity alone may not be the best metric for assessing plant community assembly.

Key words: community assembly, northern hardwoods, silviculture, conservation, functional ecology.

Résumé : La plus grande partie de la diversité végétale des forêts feuillues tempérées se trouve dans la strate près du sol, mais presque toutes les études comparant l'assemblage des communautés végétales à l'aide d'indices de diversité taxonomique, phylogénétique et caractérielle se limitent aux plantes ligneuses. Pour étudier la relation à court terme entre l'assemblage des communautés végétales de la strate près du sol et l'intensité des perturbations, nous avons utilisé une expérience sylvicole combinant des traitements de récolte et de préparation de terrain dans une forêt feuillue du nord du Michigan, aux États-Unis. Nous avons anticipé qu'après deux saisons de croissance, les communautés végétales seraient moins sensibles aux traitements de récolte qu'aux traitements de préparation de terrain qui perturbent la rhizosphère et modifient le substrat d'enracinement. Nous avons également anticipé qu'une augmentation de la diversité taxonomique serait associée à une baisse de la diversité phylogénétique et caractérielle. Nous avons plutôt observé que la composition des espèces végétales a réagi de façon similaire aux traitements de récolte et de préparation de terrain. Cependant, notre mesure de l'intensité des perturbations était positivement corrélée à la diversité taxonomique et caractérielle, mais négativement reliée à la diversité phylogénétique. Ces résultats indiquent que l'augmentation de la diversité des caractères et des taxons le long du gradient d'intensité des perturbations se traduisait par des communautés végétales plus simples sur le plan phylogénétique. Des décisions d'aménagement éclairées doivent donc tenir compte de la valeur sous-jacente de chaque mesure de diversité, puisque la seule diversité taxonomique pourrait ne pas être la meilleure mesure pour évaluer l'assemblage des communautés végétales. [Traduit par la Rédaction]

Mots-clés : assemblage des communautés, feuillus nordiques, sylviculture, conservation, écologie fonctionnelle.

1. Introduction

The ground layer typically contributes the majority of compositional diversity in temperate deciduous forest communities (Gilliam 2014). Consequently, disentangling the effects of canopy and forest floor disturbances on the taxonomic, trait, and phylogenetic diversities of ground-layer plant communities may be important for determining the mechanisms by which disturbances influence plant community assembly. The intermediate disturbance hypothesis suggests a unimodal response of taxonomic diversity to disturbance severity because intermediate-severity disturbances often promote colonization by disturbance-adapted species but are not severe enough to eliminate disturbance-intolerant species and may consequently yield communities with higher taxonomic diversity (Grime 1973). For example, previous work in northern hardwood forests has found higher taxonomic and trait diversities in medium-sized gaps compared with small

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and large gaps (e.g., Kern et al. 2014). On the other hand, many studies have demonstrated little evidence of the classic unimodal response, and fewer than 20% of studies found maximum diversity at intermediate disturbance levels (Fox 2013). Regardless, quantifying disturbance severity depends on the ecosystem, spatial scale, temporal scale, and objectives. In the context of the herbaceous layer, Roberts and Gilliam (2014) defined disturbance severity as "the amount of forest overstory removed and the amount of understory vegetation, forest floor, and soil destroyed." Accordingly, assessing taxonomic, trait, and phylogenetic diversities along a gradient of postdisturbance canopy and forest floor conditions may be a useful way to assess ground-layer plant community responses to disturbance.

Few studies have concomitantly assessed the response of taxonomic, trait, and phylogenetic diversities of ground-layer plant communities to variations in disturbance severity. Explicitly testing whether these three diversity indices respond similarly to disturbances could provide a more comprehensive understanding of disturbance effects than taxonomic diversity alone (Cavender-Bares et al. 2009). For example, greater taxonomic diversity following a disturbance may simply be driven by the addition of generalist species (Battles et al. 2001). Consequently, trait and phylogenetic diversity indices may provide additional insight into plant community dynamics. High trait diversity usually implies more filled niche space and competitive filtering processes, while low trait diversity typically implies trait redundancy and more environmental filtering processes (Liu et al. 2018). Despite its recent popularity in community ecology and its ability to detect convergent evolutionary processes, trait diversity indices depend on the quantity and types of measured traits and may consequently be inconsistent among different studies (Pakeman 2014). Phylogenetic diversity, on the other hand, is a simple and robust measure of evolutionary relatedness that can provide an important component of community responses to disturbance not fully captured by taxonomic or trait diversity alone (Faith 1992). More recently, phylogenetic diversity has been used to gauge vulnerability to invasion (Gerhold et al. 2011) and infer assembly mechanisms following disturbance (Cavender-Bares et al. 2009). For example, one study found that phylogenetically simple plant communities were more susceptible to introduced species when compared with phylogenetically diverse plant communities (Gerhold et al. 2011), and another reported higher colonization in a manipulated grassland community of low phylogenetic diversity despite high trait diversity (Galland et al. 2019).

The relationship between disturbance severity and plant community assembly can be used to inform management decisions. Contemporary silvicultural research focuses on disturbance-based management systems to better emulate historical natural disturbance regimes and restore historical species diversity (Webster et al. 2018). Along with variations in harvesting intensity to emulate windthrow severity (Kern et al. 2017), mechanical duff layer removal to expose mineral soil has been used to emulate windthrow effects by favoring traits of desired species that are typically less competitive in sites with thick duff layers such as rapid growth and low-mass fruit production (Willis et al. 2015). Though canopy disturbances such as harvesting drastically alter light and temperature, site preparation techniques including mechanical scarification and tip-up mound creation may disrupt the rhizosphere and alter the rooting substrate (Pec et al. 2019), in addition to modifying ground-layer temperature, light, and forest floor insulation capacity (Landhäusser 2009). However, tip-up mounds can also foster unique plant communities in both the short term (Beatty 2014) and long term (Kern et al. 2019) and elevate stand-level diversity (Smith et al. 2008). Disentangling the effects of harvest and site preparation disturbances on plant community composition and comparing the responses of diversity indices to these disturbances could therefore provide valuable insight into how such processes structure plant community assembly following silvicultural disturbances.

In this study, we assess the short-term responses of ground-layer plant taxonomic, trait, and phylogenetic diversities to silvicultural disturbances of varying severity and, further, attempt to disentangle the effects of harvest and site preparation treatments on plant community composition. To our knowledge, this is among the first studies to include phylogenetic diversity when comparing ground-layer plant diversity indices along a silvicultural disturbance gradient. We hypothesized that (1) taxonomic plant community composition would be more sensitive to site preparation treatments when compared with harvest treatments owing to disruption of the rhizophere and rooting substrate; (2) increasing disturbance severity would be correlated with increasing taxonomic diversity, declining trait diversity, and declining phylogenetic diversity, resulting in more trait and phylogenetically simple communities; and (3) the heterogeneity of plant community taxonomic and phylogenetic composition would increase following disturbances. To test our hypotheses, we leveraged a silvicultural disturbance that applied a range of harvesting and site preparation treatments in a northern hardwood forest. Plant community composition was assessed before and one or two consecutive growing seasons after treatment application and compared with environmental variables such as canopy openness, leaf litter depth, and soil water content.

2. Materials and methods

2.1. Site description

Study plots are part of the Northern Hardwood Silvicultural Experiment to Enhance Diversity (NHSEED) near Alberta, Michigan (46°37′39.4″N, 88°28′24.9″W), within the northern hardwood forest type. Average daily temperatures (1981–2010) in Alberta range from –10.8 °C in January to 18.1 °C in July for a yearly average of 4.7 °C (National Oceanic and Atmospheric Administration (NOAA) 2016). Precipitation averages 88.9 cm annually, including 390.1 cm of snowfall (NOAA 2016). Mean daily maximum temperature and total precipitation from May through September in Alberta for 2016 and 2018 are reported in Supplementary Table S1[1]. Soils are moderately well drained, primarily consisting of cobbly silt loam overlaying Precambrian bedrock with isolated low-lying areas (Albert 1995). A pine–hardwood forest type dominated the site prior to extensive harvesting ca. 1900 to 1938 (Erickson et al. 1990). Subsequently, single-tree selection management, which harvests individual trees across a range of diameter sizes, has been applied since the 1960s, resulting in uneven-structured stands that are heavily dominated (~80% of total basal area) by a canopy of sugar maple (*Acer saccharum* Marsh.). Other canopy species include red maple (*Acer rubrum* L.) and yellow birch (*Betula alleghaniensis* Britton), with 8% and 5% of total basal area, respectively.

2.2. Experimental design

The experiment is a split-plot design involving a factorial combination of three ~1.0 ha site preparation treatments within each of four ~3.0 ha harvest treatments, replicated across three blocks (Supplementary Fig. S1[1]). Harvest treatments include single-tree selection (n = 3 harvest treatment units), irregular shelterwood with high (60%) canopy cover retention (irregular shelterwood – high, n = 6 harvest treatment units), irregular shelterwood with low (30%) canopy cover retention (irregular shelterwood – low, n = 6 harvest treatment units), and patch clearcut (n = 3 harvest treat-

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2020-0055.

ment units). Irregular shelterwood harvests remove canopy and midcanopy trees but retain relatively continuous canopy cover to buffer new seedlings against harsh environmental fluctuations (Nyland et al. 2016). Half of the irregular shelterwood – high and irregular shelterwood – low treatments will undergo a final harvest once seedlings have established (~5 years). Owing to its historical and continuing widespread application throughout the Great Lakes hardwood forests (Pond et al. 2014), we use single-tree selection as our experimental control to represent the "business as usual" model. Sites were harvested in February and March 2017 when snow cover and cold soil minimized soil disturbances during the harvest treatment. Small diameter trees (<5 cm diameter at breast height (dbh)) were cut by brush saw in August 2017 and left on-site.

Each harvest treatment unit is split into three ~1.0 ha site preparation treatments (Supplementary Fig. S1[1]), including untreated reference, creation of artificial pit–mound topography, and mechanical scarification. To emulate windthrow damage, artificial pit–mound topography was created during initial harvest by removing the tree and attached root ball from the soil and placing them within ~5 m of the residual pit (Supplementary Fig. S1[1]). Owing to challenges of operational-scale experiments, average mound density (±1 SE) was inconsistent among treatments but not statistically different, ranging from 12.0 (±1.0) mounds·ha^{-1} in single-tree selection treatments to 17.1 (±5.6) mounds·ha^{-1} in clearcut treatments. No measurement plots were located on pits or mounds, but nearby pits or mounds likely provide refugia and seed sources that may influence local biodiversity (Kern et al. 2019). Mechanical scarification was implemented in October 2017 using a salmon blade to mix the A and O horizons, including the duff layer. Two 15 m^2 circular plots were placed in each site preparation unit and randomly located greater than 20 m from the edge of the unit (n = 108).

2.3. Environmental variables

Roberts and Gilliam (2014) defined disturbance severity as "the amount of forest overstory removed and the amount of understory vegetation, forest floor, and soil destroyed." Accordingly, to quantify disturbance severity, we measured factors that may indicate the degree of overstory and understory disturbances: canopy openness; average soil water content; intraseasonal variation in soil water content; average leaf litter depth; and spatial variation of leaf litter depth. Canopy openness was measured at each plot with hemispherical photography during the 2015 and 2018 field seasons using a Sigma 4.5 mm F2.8 EX HSM fisheye lens (Sigma Corporation, Ronkonkoma, N.Y., USA) attached to a Nikon D3200 digital camera (Nikon Inc., Melville, N.Y., USA) at 1 m height pointed directly vertical. Photographs were taken once during the growing season when canopy leaves were fully expanded, overcast conditions prevailed, exposure was uniform, and solar disc was not visible. Though other pretreatment measurements were taken one year following pretreatment photographs, canopy conditions were relatively unchanged. Soil water content was recorded once per month during the second week of each growing season month (June, July, August) in 2016 and 2018 with a ThetaProbe Soil Moisture Sensor (Delta-T Devices Ltd., Cambridge, U.K.) in each plot, calibrated for mineral soil. Measurements were taken in two consecutive days and at least 36 h following a precipitation event. Seventeen measurements were taken in each plot: one measurement at plot center and four along each cardinal direction at intervals of 50 cm. Intraseasonal variation in soil water content was measured by calculating the coefficient of variation (CV; calculated as (standard deviation/mean) × 100 and expressed as a percentage) of the three-month plot-level average. Litter (Oi layer) depth was measured with a ruler at 10 randomly chosen locations within each 15 m^2 plot. Spatial variation in litter depth was quantified using the within-plot litter depth CV, calculated with the 10 measurements per plot.

2.4. Plant community assessment

To assess plant community dynamics, all vascular plant species less than 1.37 m in height were surveyed during 2016 and 2018 in each 15 m^2 plot using eight cover classes: 1%; 2%–5%; 6%–10%; 11%–25%; 26%–50%; 51%–75%; 76%–95%; and 96%–100%. Surveys took place from mid-June to mid-September, and the majority of plots were surveyed during July and August. Most plants were identified to species level, but 14 of 111 taxa were identified to genus or family level, owing to challenges in identifying to species level given their phenology and the timing of sampling (Supplementary Table S2[1]). Due to the narrow survey window required to accurately assess spring ephemerals, they were not included in the present study. Cover classes were then converted to midpoints of respective cover ranges prior to all analyses.

2.5. Diversity indices

For a comprehensive assessment of diversity responses, we calculated taxonomic, trait, and phylogenetic α-diversity for 2016 and 2018. Taxonomic α-diversity was calculated using Shannon's diversity index. All taxa, including those not identified to species level, were included in taxonomic and phylogenetic diversity indices to avoid underestimating the influence of abundant taxa. As such, our reported values do not represent true species diversity but rather relative taxonomic diversity.

Trait α-diversity was assessed using several life history traits post hoc to capture a range of above- and below-ground traits: fruit type, growth form, mycorrhizae type, and coefficient of conservatism (Supplementary Table S2[1]). Growth forms were compiled using the USDA PLANTS Database and the Kew Seed Information Database (http://data.kew.org/sid/). Fruit types were compiled using the USDA PLANTS Database, Gleason and Cronquist (1991), and several online sources. Mycorrhizal type (e.g., arbuscular mycorrhizal, ectomycorrhizal, or nonmycorrhizal) was compiled using Brundrett and Tedersoo (2019). Coefficient of conservatism, a regionally specific measure of species affinity for disturbance, was compiled using Chadde (2014). On a 0–10 scale, a coefficient of zero corresponds to a high affinity for disturbance, while a coefficient of 10 corresponds to a low affinity for disturbance. Introduced species were given a coefficient of zero. For taxa not identified to species level, the coefficient was averaged among all possible regionally identified species within the genus that could naturally occur in the given conditions. Trait diversity was quantified by calculating functional dispersion, which measures the distribution of traits in niche space based on the relative abundance of each trait and is independent of species richness (Laliberté et al. 2014). A high abundance of similar traits will decrease dispersion, while a moderate abundance of unique or similar traits will increase dispersion (Mason et al. 2005). Analyses were conducted using the dbFD function in the FD package of R 3.5.0 software (R Core Team 2018).

Phylogenetic α-diversity was quantified by first constructing a phylogenetic tree of all recorded taxa using the phylo.maker function in the V.Phylomaker package of R (Jin and Qian 2019). The total branch length of each taxon was measured to produce an index of phylogenetic diversity, which is positively correlated with species richness and therefore cannot be accurately compared among samples of varying richness (Kembel et al. 2010). To account for this, our reported value of phylogenetic diversity is a standardized effect size, calculated by comparing observed phylogenetic diversity with a null model of random taxa from the total pool. A negative value corresponds to more clustered phylogenies when compared with the null model of phylogenetic diversity, while a positive value corresponds to overdispersion. The standardized effect size was calculated using the ses.pd function in the picante package of R 3.5.0 software, with taxa.labels specified as the null model at 999 runs and 1000 iterations (Kembel et al. 2010).

To assess the heterogeneity of plant communities across spatial scales, we calculated β-dispersion as a measure of β-diversity at

Table 1. Permutational multivariate analysis of variance (PERMANOVA) effects of (*a*) environmental variables ($n = 212$) and (*b*) silvicultural treatments ($n = 54$) on ground-layer plant species composition in 15 m^2 plots in a managed northern hardwood forest of Upper Michigan, USA.

	df	SS	MS	*F* value	R^2	*p* value
(*a*) Environmental variables						
Canopy openness	1	2.806	2.806	17.135	0.072	0.001*
Litter depth	1	0.803	0.803	4.906	0.021	0.001*
Soil water content (SWC)	1	0.820	0.820	5.006	0.021	0.001*
SWC intraseasonal variation (CV)	1	0.470	0.470	2.872	0.012	0.003*
Litter depth within plot variation (CV)	1	0.283	0.283	1.729	0.007	0.029*
Residuals	206	33.730	0.164		0.867	
Total	211	39.134			1.000	
(*b*) Silvicultural treatments						
Harvest	3	1.081	0.360	1.602	0.086	0.006*
Site preparation	2	0.729	0.365	1.621	0.058	0.023*
Residuals	48	10.797	0.225		0.856	
Total	53	12.607			1.000	

Note: df, degrees of freedom; SS, sum of squares; MS, mean squares; CV, coefficient of variation. Treatment effects were tested on composition gain scores (absolute value of 2018 minus 2016 cover) to account for repeated measures, and permutations were constrained within blocks. No treatment interactions were detected and therefore they were removed from the final model. Asterisks indicate statistical significance ($p < 0.05$).

the treatment level (i.e., turnover among plots within a treatment combination) for each year. Lower β-dispersion corresponds to less compositional turnover among plots. Taxonomic β-dispersion was calculated with the betadisper function in the vegan package of R 3.5.0 software, using the Bray–Curtis dissimilarity measure. Phylogenetic β-dispersion was calculated by first using the phylosor function in the picante package of R 3.5.0 software to create a distance matrix of the fraction of branch length shared between the constructed phylogenetic tree and a pruned phylogenetic tree. We then calculated β-dispersion using the betadisper function in the vegan package.

2.6. Data analysis

To test our first hypothesis comparing silvicultural treatment effects on taxonomic plant community composition, the relationships among continuous environmental variables and species composition in 2016 and 2018 ($n = 212$) were assessed with permutational multivariate analysis of variance (ANOVA) (PERMANOVA; the adonis function in the vegan package of R 3.5.0; Oksanen et al. 2018) using Bray–Curtis distance matrices constrained within blocks. Rare species were retained in the analysis, but four plots with incomplete environmental data were removed. The effects of silvicultural treatment on species composition were similarly assessed with PERMANOVA; however, to account for repeated measures, we used the average change in cover (2018 minus 2016, $n = 54$) for each species in the community matrix and then calculated Bray–Curtis distances constrained within blocks and included harvest and site preparation treatments as predictor variables. Models first included all treatment interactions and then were simplified if no interaction effect was detected. Pairwise multiple comparisons were conducted with the pairwise.perm.manova function in the RVAideMemoire package (Hervé 2019) using Holm's multiple comparison adjustment. Changes in composition were visualized with nonmetric multidimensional scaling (NMDS) ordination using Bray–Curtis distances. Ordinations were constructed with the metaMDS function in the vegan package of R 3.5.0, with 999 iterations. Rare species were included in the matrix, and environmental variables were relativized by maximum value of each variable, along with all species. Average point scores from the first two axes of each silvicultural treatment were graphed, with environmental variables and species fitted as vectors onto the community ordination using the envfit function. Indicator species and traits were identified using the multi-patt function in the indicspecies package of R 3.5.0 with 999 permutations (De Cáceres and Legendre 2009). To identify indicators of silvicultural treatments, we only included posttreatment species cover.

To test our second hypothesis, we tested the effect of silvicultural treatment on plot-level environmental variables with mixed-effects models. We then tested the effect of silvicultural treatment on plot-level diversity indices, also with mixed-effects models. To account for restricted randomization imposed by the experimental layout, we included a random effect of site preparation unit nested within harvest unit and block. Response variables were then Box–Cox transformed as necessary to meet assumptions. Mixed-effects models were conducted using the lme function in the nlme package in R 3.5.0 software (Pinheiro et al. 2018) and fitted by the Satterthwaite test. Pairwise multiple comparisons were conducted with the emmeans package (Lenth 2018) using Tukey's honestly significant difference (HSD) test.

To further quantify disturbance severity while accounting for multicollinearity, we created a synthetic variable, "disturbance severity", using ordination scores from the first axis of a principal component analysis of correlated variables, including canopy openness, litter depth, within-plot litter depth variation, and intraseasonal soil water content variation (Supplementary Table S3[1] and Fig. S2[1]). We then tested the relationship between diversity indices and disturbance severity using simple linear regression and second-order polynomial regression, but selected simple linear regressions based on the Akaike information criterion (AIC) and adjusted R^2 values. To confirm that mixed taxa resolution did not skew diversity–disturbance relationships, we tested the relationship at the family and species levels. Family-level binning allowed us to include all taxa. In contrast, testing at the species level provided greater resolution but required us to remove lower-resolution taxa, resulting in fewer taxa (97 species remaining out of 111 taxa).

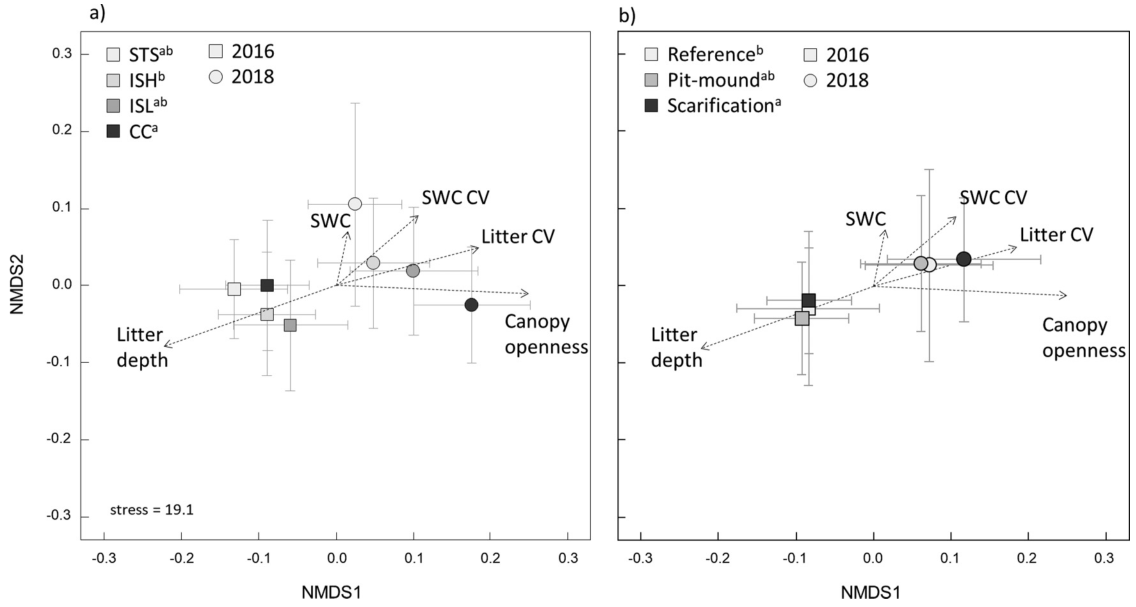
To test our third hypothesis, we compared pre- and post-treatment β-dispersion among plots within each treatment combination ($n = 6$ plots) using Tukey's HSD test.

3. Results

3.1. Species composition

The largest gains in cover were in clearcut and irregular shelterwood – high treatments, but these varied among site preparation treatments (Supplementary Table S4[1]). Sedges had the highest gains in cover from pre- to post-treatment, along with *Galeopsis tetrahit*, *Veronica officinalis*, *Rubus idaeus*, and grasses. In contrast, the greatest losses in cover from pre- to post-treatment

Fig. 1. Nonmetric multidimensional scaling (NMDS) ordination comparing pretreatment (2016) and posttreatment (2018) plot-level ground-layer plant species composition (n = 212) among (*a*) harvest treatments and (*b*) site preparation treatments. Each point represents average plant community composition (±SD) using the first two ordination axes. Distance between points represents the similarity of average treatment composition. The direction and length of each vector indicate the relative influence of environmental variables on composition. Lowercase letters denote significant differences in compositional change from 2016 to 2018 among harvest treatments or site preparation treatments with Holm's adjustment (α = 0.05). STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut. SWC, soil water content; SWC CV, intraseasonal SWC variation; litter CV, within-plot litter depth variation.



were from *Dryopteris carthusiana*, *Lonicera canadensis*, *Maianthemum canadense*, and *Hieracium* spp. Decreases among these taxa were generally equally distributed among harvest and site preparation treatments, but *M. canadense* decreased most in clearcut and irregular shelterwood – high treatments.

Environmental variables and silvicultural treatments predicted species composition (Table 1). Species composition was related to all measured environmental variables, but more related to canopy openness (R^2 = 0.072, p = 0.001; Table 1), which increased with greater harvest disturbance (F = 51.71, p < 0.001; Supplementary Table S5[1] and Fig. S3[1]). Translating to treatment effects, the change in species composition was similarly related to harvest treatment (R^2 = 0.086, p = 0.006; Table 1) and site preparation treatment (R^2 = 0.058, p = 0.023; Table 1), but there was no interaction among treatments.

NMDS ordination illustrated overall effects of silvicultural disturbance treatments in driving species dissimilarity of plots across years, mediated by changes in environmental variables (Fig. 1). The ordination illustrates an overall shift in plot-level composition along an opposing canopy openness – litter depth gradient. Grouping plots by harvest treatment demonstrates the increasing dissimilarity among treatments from pre- to posttreatment, though considerable overlap remains. Grouping plots by site preparation treatment also illustrates marginally increasing dissimilarity among treatments, though considerable overlap remains despite statistically significant differences in the change in species composition among site preparation treatments.

Several species and traits were indicators of year or silvicultural treatment. Ten species, three growth forms, four fruit types, and two mycorrhizal types were 2018 indicators, likely due to the overall disturbances (Supplementary Table S6[1]). Nine species and two fruit types were indicators of harvest treatment. For example, *Eplilobium leptophyllum*, *Hieracium* spp., *Onoclea sensibilis*, *Rubus idaeus*, drupelets, and pyxis were indicators of the highest severity harvest treatment. In contrast, only three species and no fruit types were indicators of site preparation treatment: *Epilobium ciliatum*, *Fallopia cilinodis*, and *Onoclea sensibilis*.

3.2. Diversity indices

Diversity indices were better predicted by pretreatment diversity values than by silvicultural treatments (Table 2; Fig. 2). Taxonomic diversity and phylogenetic diversity were marginally related to site preparation treatment, but taxonomic diversity tended to increase while phylogenetic diversity tended to decline (Supplementary Table S7[1]; Fig. 2). Trait diversity, however, was most related to a harvest × site preparation × pretreatment diversity interaction effect (F = 2.77, p = 0.023; Table 2; Fig. 2), suggesting that treatment effects depended on existing phylogenetic diversity and interactions with each other. For example, phylogenetic diversity tended to increase in single-tree selection and irregular shelterwood – high treatments with no site preparation treatment, but decrease in all other treatment combinations (Fig. 2).

All three diversity indices were correlated with disturbance severity and best explained by simple linear regression (Table 3; Fig. 3; Supplementary Fig. S4[1]). Increasing disturbance severity was positively correlated with taxonomic diversity (r^2 = 0.04, p = 0.003; Table 3; Fig. 3) and trait diversity (r^2 = 0.03, p = 0.008; Table 3; Fig. 3), while negatively correlated with phylogenetic diversity (r^2 = 0.03, p = 0.004; Table 3; Fig. 3), demonstrating that increasing taxonomic and trait diversities was mirrored by a concurrent decline in phylogenetic diversity in our study. Trends among diversity indices and disturbance severity persisted at both the family and species levels (Supplementary Table S8[1] and Fig. S5[1]).

Taxonomic and phylogenetic β-diversities within each treatment combination remained unchanged from 2016 to 2018 (Table 4; Supplementary Table S9[1]).

4. Discussion

This study revealed a short-term decline in ground-layer plant phylogenetic diversity, despite an increase in taxonomic diver-

Table 2. Mixed-effects models of harvest treatment, site preparation treatment, and year on taxonomic, phylogenetic, and trait α-diversity in a managed northern hardwood forest of Upper Michigan, USA.

	Taxonomic diversity ($n = 108$)				Phylogenetic diversity ($n = 108$)				Trait diversity ($n = 108$)			
	R^2_M (0.138)		R^2_C (0.216)		R^2_M (0.101)		R^2_C (0.252)		R^2_M (0.326)		R^2_C (0.440)	
Predictor	df_{num}	df_{den}	F value	p value	df_{num}	df_{den}	F value	p value	df_{num}	df_{den}	F value	p value
Intercept	1	53	3048.554	<0.001*	1	53	49.535	<0.001*	1	42	1333301.09	<0.001*
Harvest	3	12	1.241	0.338	3	12	0.981	0.434	3	12	0.37	0.777
Site preparation	2	34	2.759	*0.078*	2	34	2.546	*0.093*	2	28	1.95	0.160
Pretreatment diversity	1	53	5.923	0.018*	1	53	3.009	*0.089*	1	42	7.75	0.008*
Harvest × site preparation disturbance	—	—	—	—	—	—	—	—	6	28	0.82	0.561
Harvest × pretreatment diversity	—	—	—	—	—	—	—	—	3	42	1.02	0.393
Site preparation × pretreatment diversity	—	—	—	—	—	—	—	—	2	42	2.62	*0.085*
Harvest × site preparation × pretreatment diversity	—	—	—	—	—	—	—	—	6	42	2.77	0.023*

Note: R^2_M, marginal R^2 (fixed effects only); R^2_C, conditional R^2 (fixed and random effects); df, degrees of freedom. Models first included all treatment interactions and were simplified if no interaction effect was detected. Asterisks denote statistical significance ($p < 0.05$). Italicized values denote marginal significance ($0.05 < p < 0.10$).

Fig. 2. Taxonomic, trait, and phylogenetic diversities among harvest and site preparation treatments in 15 m² plots of a northern hardwood forest in Upper Michigan, USA. Values reported for phylogenetic diversity are standardized effect sizes. Note index-specific *y*-axes ranges. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

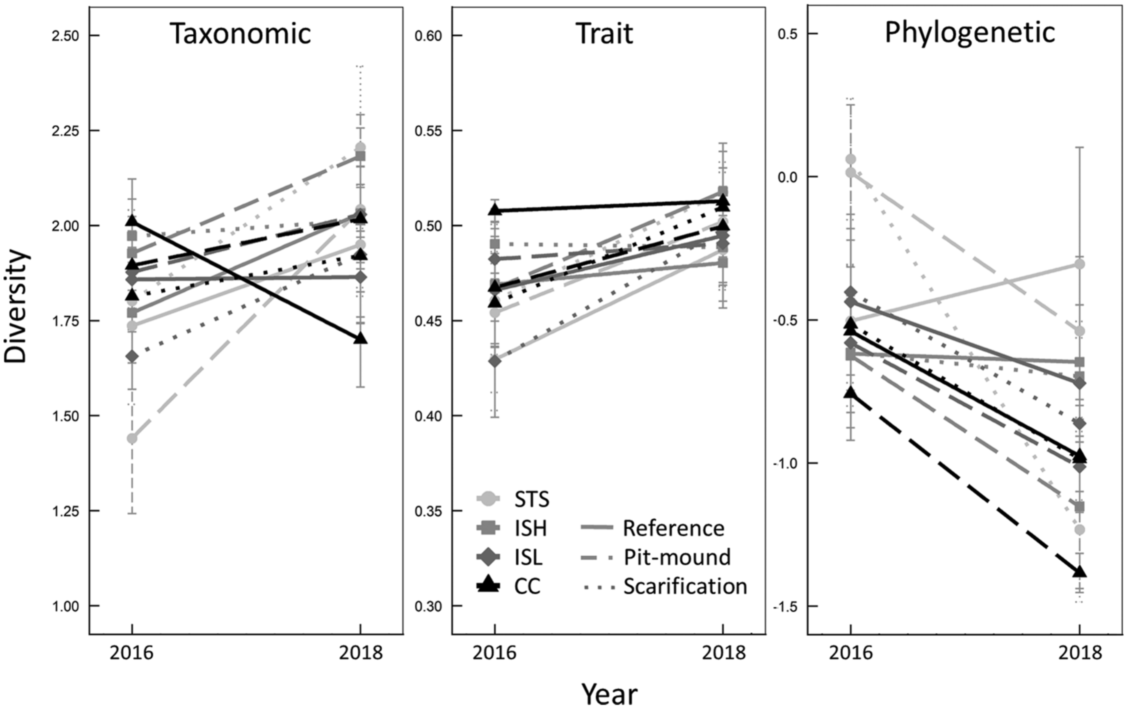


Table 3. Linear model relationships between disturbance severity and α-diversity indices ($n = 212$ plots).

	Disturbance severity					
Response	Estimate	SE	df	t value	p value	r^2_{Adj}
Taxonomic diversity	0.053	0.018	210	2.968	0.003	0.036
Trait diversity	0.001	<0.001	210	2.698	0.008	0.030
Phylogenetic diversity	–0.098	0.034	210	–2.877	0.004	0.033

Note: SE, standard error; df, degrees of freedom; r^2_{Adj}, adjusted r^2. Disturbance severity denotes ordination scores from the first axis of a principle components analysis of canopy openness, litter depth, within-plot litter depth variation, and intraseasonal soil water content variation.

sity, along a silvicultural disturbance gradient. Many studies have also documented increasing taxonomic diversity immediately following disturbances owing to an influx of generalist species, but we further discovered that resulting ground-layer plant communities are more phylogenetically simple. Moreover, previous studies have measured phylogenetic diversity but were primarily limited to woody plants. Hence, this is a particularly new and informative contribution to plant community ecology in silvicultural systems and has important implications for plant community conservation in managed forests. While these responses are notable, they capture the short term and may not necessarily persist; longer term assessments will be necessary to fully understand the community response to disturbance. Regardless, informed management decisions should consider the underlying value of preserving each type of diversity (i.e., taxonomic vs. trait vs. phylogenetic) if they do not respond similarly to silvicultural treatments.

4.1. Treatment effects on species composition

In contrast to our hypothesis that taxonomic composition would be more sensitive to site preparation treatments than to harvest treatments, we found that composition was similarly sensitive to both. Ordinations illustrated that increasing canopy

Fig. 3. Relationship between taxonomic (TD), trait (TrD), and phylogenetic (PD) diversity and disturbance severity (n = 212 plots). Diversity indices are standardized to range from 0 to 1. Disturbance severity denotes ordination scores from the first axis of a principle components analysis of canopy openness, litter depth, within-plot litter depth variation, and intraseasonal soil water content variation.

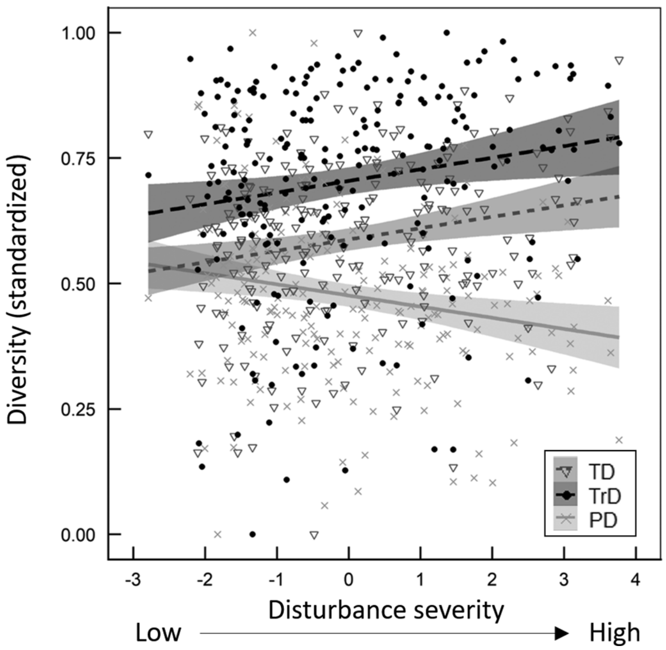


Table 4. Pairwise comparisons of β-diversity within each treatment combination between 2016 and 2018 using Tukey's HSD correction test.

Harvest treatment	Site preparation treatment	Taxonomic β-diversity p value	Phylogenetic β-diversity p value
STS	Reference	0.153	0.365
	Pit–mound	0.433	0.979
	Scarification	0.583	0.811
ISH	Reference	0.777	0.437
	Pit–mound	0.581	0.815
	Scarification	0.715	0.601
ISL	Reference	0.679	0.873
	Pit–mound	0.421	0.541
	Scarification	*0.095*	0.407
CC	Reference	0.749	0.489
	Pit–mound	0.781	0.943
	Scarification	0.645	0.379

Note: Italicized values denote marginal significance (0.05 < p < 0.10). STS, single-tree selection; ISH, irregular shelterwood–high residual; ISL, irregular shelterwood–low residual; CC, clearcut.

openness and declining litter depth were associated with, and likely driving, plot dissimilarity over time by favoring species with suitable life history traits. For example, fruit type reflects dispersal strategy and is also associated with disturbance adaptations (Lavorel and Garnier 2002). Low-mass fruit types (e.g., achenes, schizocarps, and capsules) are typically wind-dispersed and more readily colonize a recently disturbed site when compared with high-mass fruit types (e.g., berries, drupes, and pomes), which tend to rely on animals for dispersal (Westoby et al. 1996). Moreover, species with low-mass fruits may have consistently low population abundances in undisturbed forests but can quickly colonize recently disturbed sites via high propagule pressure of wind-dispersed seeds and ultimately dominate the site (Williamson 1996). In our study, *Epilobium leptophyllum*, *Hieracium* spp., *Onoclea sensibilis*, and *Rubus idaeus* were indicators of the highest severity harvest treatment, while increasing canopy openness also favored Cyperaceae, *Viola* spp., *Solidago* spp., and the introduced herb *Galeopsis tetrahit*. Excluding *R. idaeus*, these species are characterized by small fruit types such as capsules, cypselae, and schizocarps, which allow them to disperse and quickly colonize recently disturbed sites (Kern et al. 2017). Though drupelets produced by *R. idaeus* are larger and fleshy, they contain seeds that can remain viable for up to 60 years when buried and are commonly dispersed by birds and mammals (Donoso and Nyland 2006), traits that may allow rapid colonization of recently disturbed sites (Kern et al. 2017).

Site preparation treatment effects on species composition were less pronounced and driven by the most severe treatment, scarification. The forbs *Epilobium ciliatum* and *Fallopia cilinodis* were indicators of scarification likely because their low-mass, wind-dispersed fruit led to rapid colonization of exposed soil. The rhizomatous growth strategy of another indicator of scarification, *Onoclea sensibilis*, may benefit from the removal of nonrhizomatous herbaceous plants during scarification. In contrast, the shrub *Lonicera canadensis* was an indicator for reference and pit–mound treatments, suggesting little tolerance for soil disturbance, and has been previously reported as a disturbance-sensitive species (Smith et al. 2008). Though the effects of site preparation treatments on species composition were less pronounced than those of harvest treatments, non-native earthworms have already substantially modified seedbed conditions and soil properties in the region (Bal et al. 2017). Consequently, further disturbances in this forest could be dampened when compared with uninvaded forests (Holdsworth et al. 2007).

Treatments also favored certain mycorrhizal types. Species with typically nonmycorrhizal roots, along with ectomycorrhizal species, were indicators of posttreatment communities and generally had only neutral or positive gains in cover from before treatment to after treatment. For example, sedges are typically nonmycorrhizal (Brundrett and Tedersoo 2019), a flexibility that could allow sedges to allocate photosynthates toward rapid growth, rather than mycorrhizal symbionts, in recently disturbed sites with high nutrient availability.

The observed compositional shifts in response to silvicultural treatments are consistent with other studies in northern hardwoods (e.g., Burton et al. 2014). Harvesting and site preparation may favor the life history traits of generalists such as graminoids and introduced species (Kern et al. 2013), which often respond positively to canopy and soil disturbances and may subsequently drive compositional shifts (Kraft et al. 2004). In our study, generalists and introduced species had the greatest gains in cover from pre- to post-treatment, while forbs indicative of mature Great Lakes northern hardwood forests (Kotar et al. 2002), including *Dryopteris carthusiana* and *Maianthemum canadense*, had the greatest losses in cover from before treatment to after treatment. On the other hand, Smith et al. (2008) found no difference in understory composition four years after silvicultural treatments in a New England northern hardwood forest, and Kern et al. (2006) similarly found no ground-layer compositional differences in a long-term silvicultural study.

4.2. Contrasting insights from diversity indices

Our second hypothesis was partially supported: though we found no difference among treatments, disturbance severity had a positive relationship with taxonomic diversity and trait diversity and a negative relationship with phylogenetic diversity. Converging phylogenies along the disturbance severity gradient were comprised of increasingly diverse traits and taxonomies, ultimately providing more support for competitive processes rather than for environmental filtering processes in structuring plant communities under high disturbance severity (Liu et al. 2018).

While this result may seem contradictory, phylogenetically simple communities can still have diverse trait assemblages owing to divergent evolution (Liu et al. 2018). We recognize, however, that the use of categorical traits and mixed taxonomic resolution may not yield similar outcomes in other forest types due to different species pools. Though our suite of traits ultimately does not capture all dimensions of trait diversity, for the range of included traits, our comparisons are striking. Our four life history traits (life form, fruit type, mycorrhizal type, and coefficient of conservatism) capture a range of growth, reproductive, and resource acquisition strategies. Other studies have used as few as four to seven traits, ranging from exclusively categorical traits to exclusively measurable traits (e.g., Mazel et al. 2018), and a 2014 study found that the exclusive use of life history traits provides more reliable results than incomplete sampling of measurable traits (Pakeman 2014). We recognize, however, that making broader inferences to other forests and ecosystems might require the use of more measurable traits such as leaf area, leaf nitrogen, and specific root length. Finally, because we found nearly identical trends at the family and species levels, our use of mixed taxonomic resolution did not appear to skew our results.

The findings of this study have important implications for forest management. Without examining phylogenetic diversity, we could conclude that silvicultural treatments caused a short-term increase in diversity; however, the response of phylogenetic diversity in our study suggests the opposite: taxa following higher severity disturbances were more phylogenetically simple when compared with those under lower severity disturbances. Phylogenetic diversity is often positively correlated with ecosystem properties such as productivity, nutrient cycling, and resilience, and a decline in phylogenetic diversity may jeopardize community resilience to future disturbances (Tucker et al. 2019) or invasion by introduced species (Gerhold et al. 2011). Introduced species, however, partially contributed toward declining phylogenetic diversity in our study. For example, increases in both introduced and native generalist species such as Cyperaceae species, *Galeopsis tetrahit*, *Veronica officinalis*, and *Rubus idaeus* suggest that both introduced and native species contributed toward increasing taxonomic but declining phylogenetic diversity. Many studies have examined disturbance–diversity relationships in northern hardwoods (e.g., Bell et al. 2014) and have shown that an influx of generalist species following silvicultural disturbances temporarily increases plant taxonomic diversity (e.g., Smith et al. 2008). However, this is the first study, to our knowledge, to quantify the consequences of generalist species colonization on the phylogenetic relatedness of resulting ground-layer plant communities in northern hardwoods.

Previous studies in other forest types have found similar responses of plant phylogenetic diversity to disturbance severity but are primarily limited to woody plants. In dry tropical forests, for example, Shivaprakash et al. (2018) found that tree phylogenetic diversity declined with increasing disturbance severity. Arroyo-Rodríguez et al. (2012) and Mo et al. (2013) also found declining stand-level tree phylogenetic diversity with increasing disturbance severity in neotropical and tropical forests, respectively. Our study supports this general trend that stand-level phylogenetic diversity often declines with increasing disturbance severity, and further, our inclusion of ground-layer vascular plants suggests that the trend is not limited to woody plants.

Our third hypothesis was unsupported. Taxonomic and phylogenetic β-diversities remained unaltered from before treatment to after treatment within treatment combinations. These findings suggest that plot-level composition was retained at larger spatial scales and silvicultural treatments had no detectable effect on compositional turnover within a treatment combination. Previous work in other forest types have found that within-disturbance β-diversity is often lower than among-disturbance β-diversity (Gómez-Díaz et al. 2017). Continued measurement will be necessary to determine if environmental and competitive filtering processes increase site-level β-diversity as time progresses from the initial experimental disturbance in this study framework.

5. Conclusions

In one of the first studies to concomitantly measure taxonomic, trait, and phylogenetic diversities of the ground-layer plant community along a silvicultural disturbance gradient, we found that positive correlations among taxonomic diversity, trait diversity, and disturbance severity were mirrored by a negative relationship with phylogenetic diversity. We also found that the shift in taxonomic composition was relatively similar among harvest and site preparation treatments, as implemented in this study. Though increasing trait diversity suggests competitive rather than environmental processes in structuring plant community assembly, declining phylogenetic diversity points toward greater evolutionary relatedness within posttreatment plant communities, which could jeopardize community resilience to future disturbances. While many studies have shown an increase in generalist species immediately following silvicultural disturbances, to our knowledge, this is the first study to quantitatively demonstrate that ground-layer plant communities in northern hardwoods become more phylogenetically simple despite gains in taxonomic diversity. Our findings highlight that informed management decisions should consider the underlying value of each diversity measure, as taxonomic diversity alone may not be the best metric for assessing plant community assembly following silvicultural disturbances.

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