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LETTER

Structural diversity as a predictor of ecosystem function

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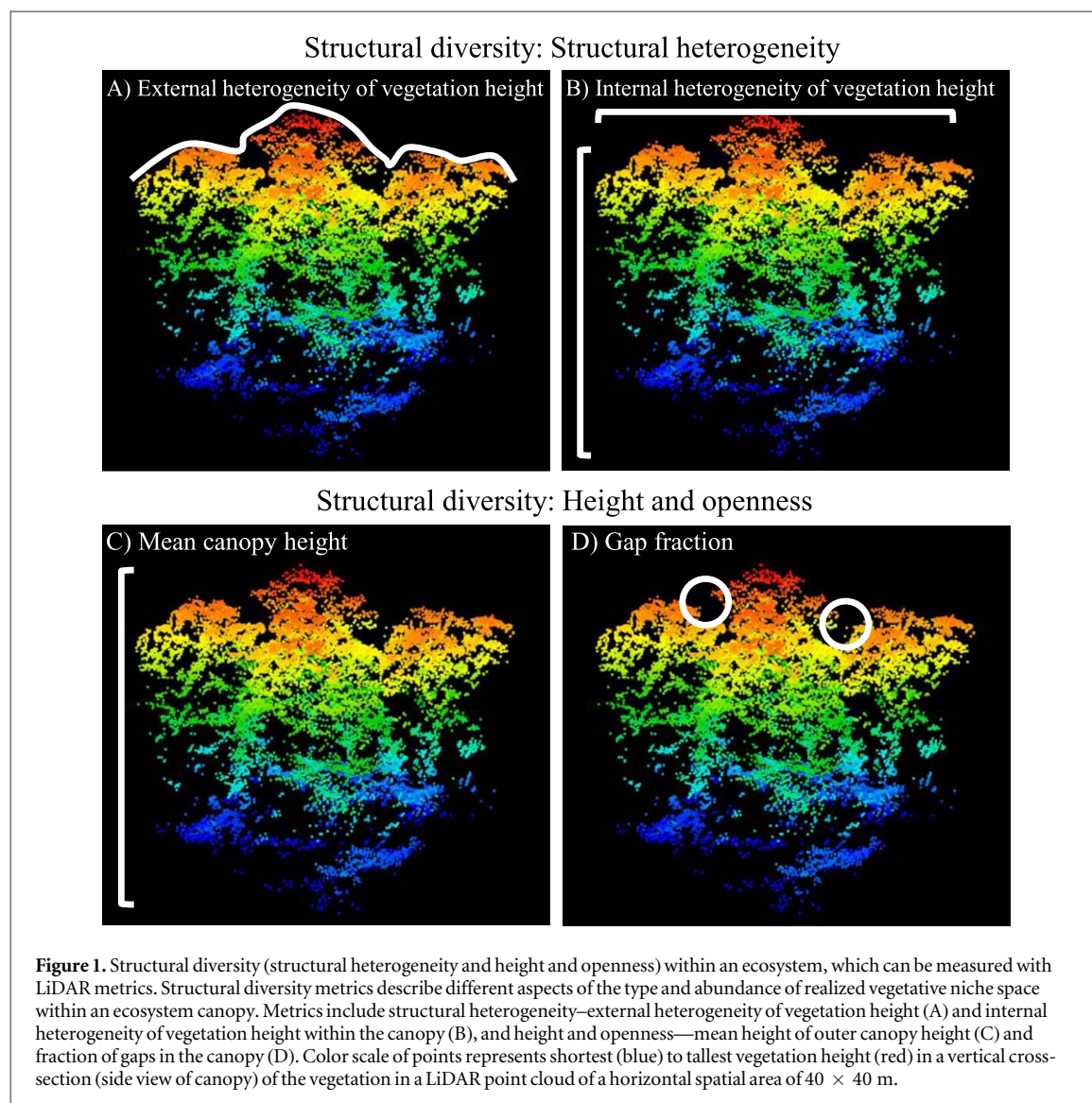
Abstract

Biodiversity is believed to be closely related to ecosystem functions. However, the ability of existing biodiversity measures, such as species richness and phylogenetic diversity, to predict ecosystem functions remains elusive. Here, we propose a new vector of diversity metrics, structural diversity, which directly incorporates niche space in measuring ecosystem structure. We hypothesize that structural diversity will provide better predictive ability of key ecosystem functions than traditional biodiversity measures. Using the new lidar-derived canopy structural diversity metrics on 19 National Ecological Observation Network forested sites across the USA, we show that structural diversity is a better predictor of key ecosystem functions, such as productivity, energy, and nutrient dynamics than existing biodiversity measures (i.e. species richness and phylogenetic diversity). Similar to existing biodiversity measures, we found that the relationships between structural diversity and ecosystem functions are sensitive to environmental context. Our study indicates that structural diversity may be as good or a better predictor of ecosystem functions than species richness and phylogenetic diversity.

Introduction

The relationship between biodiversity and ecosystem functions is a central topic in ecology research, but a consensus over which diversity measures provide the best predictive ability of ecosystem functions remains elusive (Turnbull *et al* 2016). The biodiversity of organisms living within an ecosystem is often measured as species richness and more recently phylogenetic diversity as an estimate of functional trait diversity (Petchey and Gaston 2006, Cadotte *et al* 2009). The number of species living in an ecosystem is assumed to be a proxy for the number of niche spaces filled in the ecosystem (Turnbull *et al* 2016). Niche space (i.e. multi-dimensional axes representing different ecological parameters) is roughly equivalent to the number of unique habitats occupied by different species within a community (Hutchinson 1957). Diversity metrics are assumed to be proxies for the amount of niche space filled (Turnbull *et al* 2016), because higher biodiversity is expected to promote partitioning of resource use between different species

(Silvertown 2004), thereby contributing to higher overall ecosystem function (Loreau *et al* 2002, Tilman and Lehman 2002). Indeed, plant species richness and phylogenetic diversity have been linked to ecosystem functions of productivity (Tillman *et al* 1997, Grace *et al* 2016), resistance to invasion (Iannone *et al* 2016), and nutrient cycling (Gamfeldt *et al* 2013, Ratcliffe *et al* 2017).

However, species richness and phylogenetic diversity are not always accurate proxies for the amount of niche space filled (Turnbull *et al* 2016). This low accuracy of species richness and phylogenetic diversity as proxies for niche space might be responsible for their low predictive ability and inconsistent diversity-ecosystem function relationships (hereafter referred to as D-EF) observed across various studies (Winfree *et al* 2015, Turnbull *et al* 2016). In general, species richness and phylogenetic diversity alone only explain a relatively small portion of the variance (4%–9%) of ecosystem functions at regional to continental scales (Ratcliffe *et al* 2017, Fei *et al* 2018). Furthermore, the strength of D-EF is often inconsistent across spatial

Structural diversity: Structural heterogeneity

Figure 1. Structural diversity (structural heterogeneity and height and openness) within an ecosystem, which can be measured with LiDAR metrics. Structural diversity metrics describe different aspects of the type and abundance of realized vegetative niche space within an ecosystem canopy. Metrics include structural heterogeneity–external heterogeneity of vegetation height (A) and internal heterogeneity of vegetation height within the canopy (B), and height and openness—mean height of outer canopy height (C) and fraction of gaps in the canopy (D). Color scale of points represents shortest (blue) to tallest vegetation height (red) in a vertical cross-section (side view of canopy) of the vegetation in a LiDAR point cloud of a horizontal spatial area of 40 × 40 m.

scales (Griffin *et al* 2009), because they are sensitive to environmental gradients (Cardinale *et al* 2000, Fei *et al* 2018).

Metrics of ecosystem structure and diversity that directly incorporate niche space increase our ability to accurately predict ecosystem functions (Tilman *et al* 1997, Turnbull *et al* 2016). For example, heterogeneity in vegetation height could be a better measure of realized niche space associated with vertical vegetation stratification (e.g. bird habitat, Macarthur and Macarthur 1961) than species richness, which may not reflect variations in tree height due to phenotypic plasticity. Here, we expand upon previous definitions of structural diversity (Staudhammer and LeMay 2001, Storch *et al* 2018), to include the arrangement, complexity, and biological (genetic) variation of vegetation structure within ecosystems (figure 1). Structural diversity has two important aspects that could lead to better predictions of D-EF. First, structural diversity could provide a more direct measure of ecological niche space. Structural diversity within the canopy can represent the availability and occupancy of physical

niche space in the ecosystem and the eco-physiological niche space of resources. For example, complementarity in the vertical overlap of tree crowns leads to greater use of niche space for light in the canopy (Williams *et al* 2017, Zheng *et al* 2019). Furthermore, forest structure is linked to the functional diversity of plant traits (Russell *et al* 2014). This makes it likely that structural diversity is also related to functional traits that result in a unique physical arrangement of vegetation (e.g. branch and leaf architecture) and would also indicate more ecological niche space is filled. Second, as structural diversity measures physical niche space (Mura *et al* 2015), it may better account for variation in some environmental conditions (e.g. water or soil nutrients; Kreuzwieser and Gessler 2010, Levesque *et al* 2015), making the strength of D-EF less variable across environmental gradients (e.g. D-EF and biotope space as a gradient; Dimitrakopoulos and Schmid 2004, Eisenhauer 2012). Structural diversity is able to control conditions such as the availability of light and moisture, that are both critical resources for forest primary production (Baldocchi and

Collineau 1994, Brum *et al* 2019). The ability of structural diversity to predict ecosystem functions may be a stronger and more consistent predictor than traditional measures of diversity across environmental gradients of physical volume and resource availability.

Unfortunately, aspects of structural diversity have been difficult to measure, and, therefore, their ability to predict ecosystem functions at large geographic scales is under explored (Lefsky *et al* 2002, Asner *et al* 2015). Structural diversity can be measured in various ways, such as traditional field-based measures of stand structure, plant functional traits, and new lidar-derived metrics of canopy structural complexity, all of which could have mechanistic links to ecosystem functions. Manual measurements of structural diversity metrics, such as crown complementarity, are known to be drivers of forest carbon at small scales (Williams *et al* 2017, Zheng *et al* 2019). However, emerging frontiers in remote sensing along with advanced computational capabilities allow structural diversity to be measured and computed at larger scales and in greater three-dimensional detail (Lefsky *et al* 2002, Asner *et al* 2015). Indeed, certain remote sensing-based measures with direct links to structural diversity, have been shown to be correlated with certain ecosystem functions such as productivity within a site (Hardiman *et al* 2011, Stark *et al* 2012). Here, we focus on the components of the structural diversity of ecosystems that can be measured rapidly with remote sensing tools over large spatial scales compared to traditional trait-based metrics that are time consuming to measure on a small spatial scale. Overall, the advent of new remote sensing technologies and the computational capacity to handle big datasets such as LiDAR present new opportunities to test how previously unexplored metrics of structural diversity influence ecosystem functions across scales (Martinez *et al* 2016, Cordell *et al* 2017, Tello *et al* 2018).

We explore the feasibility of using our proposed set of structural diversity metrics (figure 1), which were derived from contemporary remote sensing methods as a novel predictor of ecosystem functions across a range of environmental gradients. To do this we leveraged data from 19 sites spanning the National Ecological Observation Network (NEON). We compared the relative abilities of structural diversity versus species richness, and phylogenetic diversity to predict important ecosystem functions across 19 NEON forested sites (figure S1 and table S1 in supplemental data is available online at stacks.iop.org/ERL/14/114011/mmedia). Further, we hypothesized that structural diversity is a more consistent predictor of ecosystem functions than species richness and phylogenetic diversity, in a range of environmental gradients across geographical space. We tested this by asking whether D-EF with structural diversity were less environmentally context-dependent than species richness and phylogenetic diversity.

Methods

Structural diversity

Similar to species richness and phylogenetic diversity, structural diversity is complex and difficult to fully capture by a single metric; various metrics of structural diversity are likely to predict ecosystem functions differently. Here, we proposed four metrics corresponding to different facets of the three-dimensional arrangement of canopy structure to provide an overview of structural diversity within an ecosystem (table 1). There are multiple metrics that can be used to characterize diversity in forest structure (i.e. Parker *et al* 2004, McElhinny *et al* 2005, Atkins *et al* 2018a), however most of these focus on height, openness, or heterogeneity at different points in the canopy (Atkins *et al* 2018a). We chose to focus on a single metric representing each of four dimensions of structural diversity (volume, openness, external and internal heterogeneity), that combined give an overview of realized structural niche space. We included two measures of structural heterogeneity: external heterogeneity as a measure of variation in the height of vegetation at the canopy surface and internal heterogeneity of vegetation height within the canopy (figure 1, table 1). We selected metrics of heterogeneity based primarily on their ease of calculation with the low to medium point density of discrete return LiDAR (e.g. Parker *et al* 2004). We also incorporated two measures of height and openness: mean outer canopy height as a measure of total niche volume and the fraction of canopy gaps as a measure of physical niche openness (figure 1, table 1). Mean canopy height and gap fraction are comparable to the metrics of forest-stand height and openness generated from forest inventory data (see McElhinny *et al* 2005) and can be calculated with discrete return LiDAR (Hopkinson *et al* 2004, Vepakomma *et al* 2008). We recognize that such LiDAR based metrics of structural diversity can be correlated with each other. However, including multiple metrics can explain additional variance (Hardiman *et al* 2011), because they represent different proxies of filled niche space in the environment (e.g. gap fraction is not necessarily caused by the same ecological drivers influencing canopy height and these metrics provide different types of niche space for organisms). In recognition of likely correlations among structural diversity metrics, we conservatively treat these metrics as a 'structural diversity' group when making inferences. We measured structural diversity using Level 1 discrete return LiDAR from the NEON Airborne Observation Platform (NEON 2018) (see table 1 for metric definitions). All data products used in this study were downloaded from the NEON Data Portal in April 2018 (table S2). We developed a workflow in R v.3.5.0 (R Development Core Team 2018) to measure the four structural diversity metrics from the LiDAR point cloud within the area of 40 m × 40 m NEON base plots (1600 m^2, N_{Plots}

Table 1. Structural diversity, species richness, and phylogenetic diversity metrics.

Ecosystem diversity	Metric	Hypothesized proxies of filled niche space	Computational description
Structural diversity: Structural heterogeneity	External heterogeneity	Number of niches occurring at canopy exterior (Macarthur and Macarthur 1961)	Heterogeneity in vegetation height at the top of the canopy (standard deviation of maximum height in a 1 m² raster grid of the plot) (i.e. top rugosity)
	Internal heterogeneity	Number of niches occurring vertically and horizontally within the volume of the canopy vegetation (Macarthur and Macarthur 1961)	Vertical and horizontal heterogeneity of vegetation height within the canopy (standard deviation of height within vertical columns across a 1 m² raster grid and then the horizontal standard deviation taken across entire plot) (i.e. SD SD height)
Structural diversity: Height and openness	Mean canopy height	Number of niches filled within the eco-system volume (Currie *et al* 2004)	Average outer height of the canopy across 1 m² raster grid
	Gap fraction	Number of open niches occurring due to missing vegetation (McElhinny *et al* 2005)	Proportion of 1 m² columns within the canopy lacking vegetation
Biological diversity: Species richness	Native plant species richness	Number of different niche spaces filled by native plant species (Turnbull *et al* 2016)	Number of native species in the plant community
	Tree species richness	Number of niche spaces filled by different tree species (Turnbull *et al* 2016)	Number of tree species in the plant community
Biological diversity: Phylogenetic diversity	Native phylogenetic species richness	Amount of niche space filled by function-ally different species (Helmus *et al* 2007)	Amount of phylogenetic diversity of the plant community
	Native phylogenetic species variability	Divergence in types of niche space filled (Helmus *et al* 2007)	Degree of phylogenetic relatedness of plant species within the community

= 5–32 per site). The point cloud within a 60 m buffer around each plot area was corrected for elevation with an interpolation based on a Delaunay triangulation using the *lasnormalize* function from the *lidR* package (Roussel *et al* 2019).

Species richness and phylogenetic diversity
We calculated two aspects of species richness in the forest plant community (table 1) at each plot from the NEON Terrestrial Observation System plant surveys (NEON 2018). We chose to focus on metrics of total and native tree species richness as predictors of ecosystem functions, which would be independent of invasion measurements. We summed up the total number of native plant species of all growth forms, exotic plants, and trees that were found from an area of 400 m² within each plot (four 100 m² sampling quadrats in large NEON baseplot quadrants; NEON 2018). We estimated phylogenetic diversity using two of the most commonly used metrics (table 1): phylogenetic species richness (PSR) and phylogenetic species variability (PSV) of the plant community at the genus-level in each plot (Helmus *et al* 2007). We used the function *S.PhyloMaker* to create a phylogeny from the Qian and Jin (2016) megaphylogeny of global plant life, where unidentified taxa were added to the backbone of the phylogeny. The *picante* R package (Kembel *et al* 2010) was used to measure PSR and PSV with an unrooted tree from the number of genera found within a given plot. We measured PSV and PSR for the native plant

and PSR for exotic plant species within a plot. PSR and PSV cannot be measured if only one species was found in a plot, therefore plots containing less than two exotic species were removed from the exotic PSR dataset ($N_{Sites} = 8$).

Ecosystem functions
NEON measures several variables at each plot that can be used as proxies for a variety of ecosystem functions, including productivity, energy and nutrient dynamics, and biotic resistance to invasion. The proxies of aboveground productivity were total plot-level basal area (basal area) and leaf area index (LAI) (Paquette and Messier 2011, Reich 2012). Basal area was calculated from diameter at breast height of individual trees (>10 cm) within the 1600 m² plot (m²/plot) from the NEON plant structure surveys (NEON 2018). LAI from within the plot area was extracted from level 3 NEON AOP rasters (NEON 2018), which was derived from spectral data and is an independent measurement from the LiDAR-derived structural diversity. Proxies of energy and nutrient dynamics were coarse woody debris and the fraction of absorbed photosynthetically available radiation (fPAR; a higher value equals more light absorbed by the canopy). fPAR was considered a measure of ecosystem energy use instead of a proxy for productivity, because it is one of many precursors of net primary production (e.g. light use efficiency and species specific photosynthetic rates) (Ishii 2004). We extracted fPAR from within the

plot area from spectral remote sensing imagery data which is provided for the level 3 NEON AOP rasters on a 1 m^2 grid (NEON 2018). The amount of coarse woody debris is indicative of carbon nutrient cycling through forests as an ecosystem function (Ratcliffe *et al* 2017), but can also be altered by local disturbance regime such as fire and influenced by local climate that alters its decomposition rate. Coarse woody debris was calculated as the total cylindrical volume (m^3) of fallen trees greater than 2 cm in diameter sampled in the NEON downed log surveys (NEON 2018). Proxies of biotic resistance to invasion were measured as components of richness (Byers and Noonburg 2003): species richness and PSR of exotic plants in the forest community. We used all data available from each site, but not every data product was available for each ecosystem function for each site at the time of analysis ($N_{Sites} = 12–19$; see table S2).

Environmental gradients

We estimated environmental gradients of resource availability and physical volume at sites to test if they were more important for shaping D-EF based on structural diversity versus the other categories of ecosystem diversity. Plot values of maximum canopy height from LiDAR, mean annual temperature (MAT), and mean annual precipitation (MAP) were each averaged across a site. Maximum canopy height (i.e. physical volume) is representative of the physiological constraints imposed by climate (McDowell *et al* 2008) and is an indicator of environmental harshness (Marks *et al* 2016), which may not be reflected by mean canopy height (i.e. averaging plot-level height across canopy gaps due to disturbance). We extracted MAT and MAP from unique plots within the 800 m × 800 m grid resolution of PRISM climate data in the continental USA (http://prism.oregonstate.edu/). MAT and MAP values for Alaska sites were obtained from their NEON site descriptions. Finally, we estimated the average total soil nitrogen in the O and A horizons using the megapit dug at the construction of each NEON site (NEON 2018).

Statistical analyses

We used a mixed-effects modeling framework to test hypothesis one for D-EF magnitude and direction across NEON sites, because it accounts for cross-scale patterns within our dataset without having to know the underlying causes of spatial heterogeneity (Hamil *et al* 2016). First, we z-score standardized diversity metrics across plots in all sites ($[x − mean(x)/SD(x)]$). Exotic PSR and coarse woody debris were natural log transformed to normalize the data ($log[1 + x]$). Models were constructed with individual ecosystem functions as the response terms of fixed effects diversity metrics and sites as random effects. The site random effect had independent intercept and slope estimates ($N_{Sites} = 8–19$). We used a zero-inflated model and a

negative binomial distribution with a log-link for the response variable of exotic species richness in the R package *glmmADMB* (Skaug *et al* 2018). To determine if the D-EF slope was significant at a national level while controlling for site-level heterogeneity in each analysis, we resampled from separate site slope estimates using a bootstrapping approach for a 95% confidence internal (appendix S1).
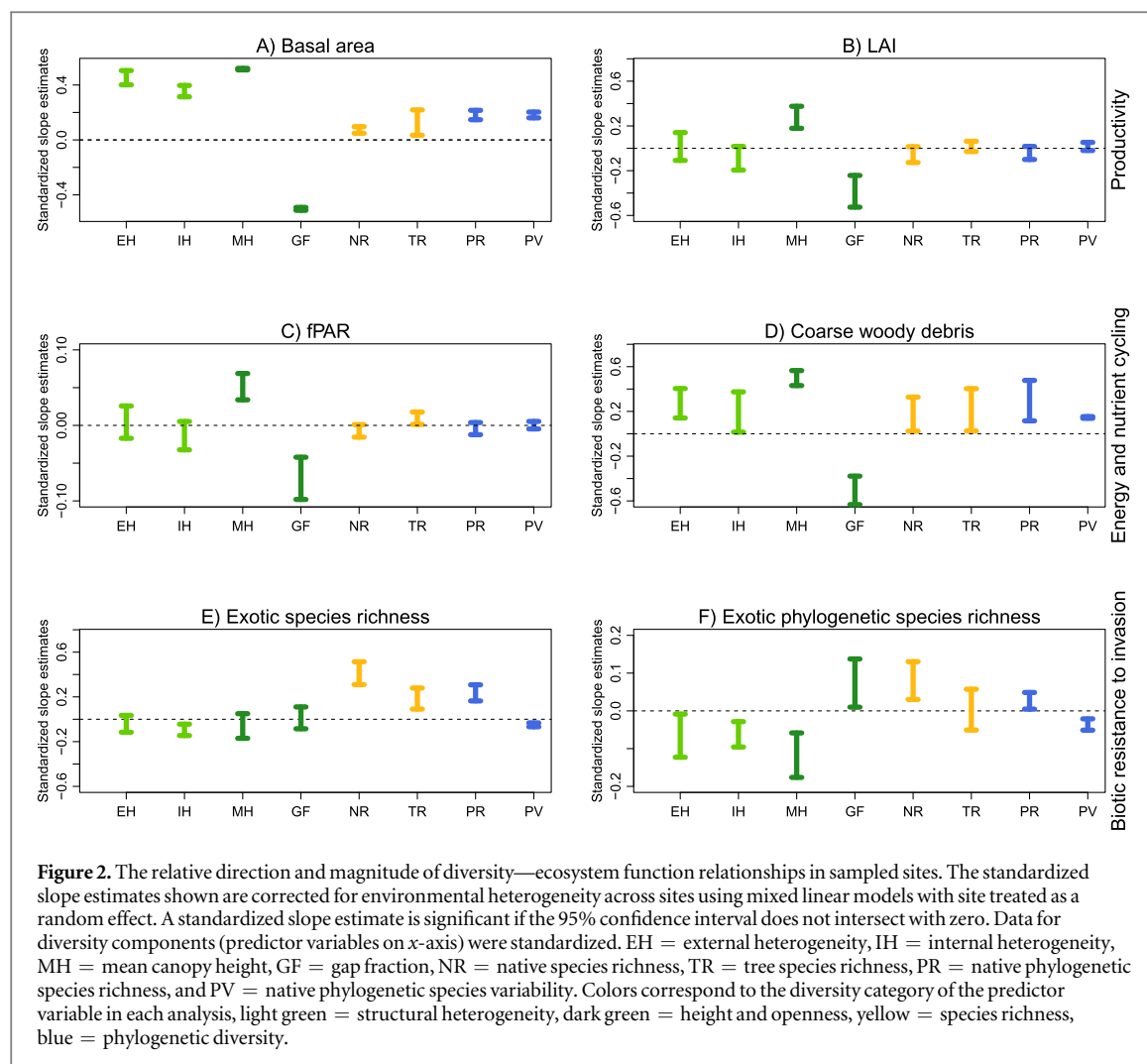
To test hypothesis two, we evaluated whether there were significant linear relationships between environmental gradients and D-EF site slopes. We extracted slopes from simple linear regressions between the D-EF at each site ($N_{Slopes} = 12–19$, table S3). The site-level means for MAT, MAP, and total soil nitrogen, and maximum canopy height were used as the predictors of D-EF slopes for each combination of diversity components and ecosystem functions. To determine whether D-EF slope strength varied with environmental gradients, we resampled the linear slope estimates with a bootstrapping approach for a 95% confidence interval. Exotic PSR was not included in this analysis, because it included only $N_{Sites} = 8$.

Results

Forest diversity components as predictors of ecosystem functions

Structural diversity significantly predicted all ecosystem functions tested (figure 2). Structural heterogeneity significantly predicted four of six ecosystem functions (figure 2). The two metrics of structural diversity that describe internal and external heterogeneity of vegetation heights positively predicted the proxy of wood productivity (basal area; figure 2(A)), with external heterogeneity being the strongest. Meanwhile, external and internal heterogeneity positively predicted carbon nutrient cycling (coarse woody debris; figure 2(D)). Internal heterogeneity negatively predicted two proxies for biotic resistance to invasion (exotic species richness and exotic PSR; figure 2(E)). Finally, external heterogeneity negatively predicted exotic PSR (figure 2(F)). The two metrics of height and openness, mean canopy height and gap fraction, significantly predicted 5 of 6 ecosystem functions (figure 2). Mean canopy height consistently positively predicted two proxies of ecosystem productivity, while gap fraction negatively predicted these two functions (basal area and LAI; figures 2(A) and (B)). Mean canopy height was a positive predictor of energy and nutrient proxies, whereas gap fraction negatively predicted both (coarse woody debris and fPAR; figures 2(C) and (D)). Finally, mean canopy height negatively and gap fraction positively predicted exotic PSR (figure 2(F)).

The ability of structural diversity metrics to predict ecosystem functions was greater than species richness and phylogenetic diversity, for three of the six proxies of ecosystem functions tested (figures 2 and 3). All

Figure 2. The relative direction and magnitude of diversity—ecosystem function relationships in sampled sites. The standardized slope estimates shown are corrected for environmental heterogeneity across sites using mixed linear models with site treated as a random effect. A standardized slope estimate is significant if the 95% confidence interval does not intersect with zero. Data for diversity components (predictor variables on *x*-axis) were standardized. EH = external heterogeneity, IH = internal heterogeneity, MH = mean canopy height, GF = gap fraction, NR = native species richness, TR = tree species richness, PR = native phylogenetic species richness, and PV = native phylogenetic species variability. Colors correspond to the diversity category of the predictor variable in each analysis, light green = structural heterogeneity, dark green = height and openness, yellow = species richness, blue = phylogenetic diversity.

		Productivity		Energy/nutrients		Biotic resistance	
		Basal area	LAI	fPAR	CWD	Exotic richness	Exotic PSR
Structural diversity: **Structural heterogeneity**	External heterogeneity	++	0	0	+	0	–
	Internal heterogeneity	++	0	0	+	–	–
Structural diversity: **Height and openness**	Canopy height	++	++	++	+	0	–
	Gap fraction	– –	– –	– –	– –	0	+
Species richness	Native richness	+	0	0	+	++	+
	Tree richness	+	0	+	+	+	0
Phylogenetic diversity	Native PSR	+	0	0	+	+	+
	Native PSV	+	0	0	–	–	–

Figure 3. Direction and relative ability of different diversity components to predict proxies of ecosystem functions. + refers to a significant positive relationship and − a significant negative relationship, while ++ or −− indicates (and darker shade of color) that this metric was one of strongest predictors of a specific ecosystem function proxy.

Table 2. Significant environmental gradient dependency of diversity—ecosystem function relationships in sampled sites. Only significant linear relationships are shown. The significance of the linear relationships shown were generated from a bootstrapped, bias corrected, accelerated 95% confidence interval and can be found in table S4. Maximum tree height is a proxy for physical volume and mean annual temperature and mean annual precipitation a proxy for resource availability. Nitrogen (N) is the total percent soil nitrogen in the O and A soil horizons. Colors correspond to the diversity category of the predictor variable in each analysis, light green = structural heterogeneity, dark green = height and openness, yellow = species richness, blue = phylogenetic diversity. EH = external heterogeneity, IH = internal heterogeneity, MH = mean canopy height, GF = gap fraction, NR = native species richness, TR = tree species richness, PR = native phylogenetic species richness, and PV = native phylogenetic species variability.

		EH	IH	MH	GF	NR	TR	PS	PV
Basal area	Max height	−0.050		−0.340				−0.031	
	MAT	−0.057						−0.039	
	MAP			−0.007				−0.0007	
	N								
LAI	Max height			−0.106					
	MAT			−0.115					
	MAP					0.0004			
	N						−0.015		−0.031
fPAR	Max height			−0.027					
	MAT			−0.029	0.011				
	MAP					0.00009			
	N								−0.004
Coarse woody debris	Max height								−0.030
	MAT				−0.044		0.077		
	MAP								
	N								
Exotic species richness	Max height			0.088	−0.072				
	MAT								
	MAP			0.001					
	N				0.039				0.036

metrics of structural diversity were stronger predictors of wood productivity and two structural diversity metrics (height and openness) were stronger predictors of productivity (LAI) than species richness and phylogenetic diversity (figures 2(A) and (B)). Two structural diversity metrics (height and openness) were much stronger predictors of energy than tree species richness (fPAR; figure (C)). Structural diversity, species richness, and phylogenetic diversity metrics were equally strong predictors of the carbon nutrient proxy regardless of whether they were positively or negatively related to it (coarse woody debris; figure 2(D)). Native species richness had the strongest relationship with one of the two proxies of biotic resistance (exotic species richness; figure 2(E)). The structural diversity metrics, native species richness, and phylogenetic diversity metrics were equivalent predicators of the other proxy of biotic resistance to invasion (i.e. exotic PSR; figure 2(F)).

Environmental gradients of diversity—ecosystem function relationships

All structural diversity-based D-EF exhibited sensitivity to at least one environmental gradient (table 2), with 17.5% of the structural diversity-based D-EF being sensitive to an environmental gradient. Out of all four structural diversity metrics, mean canopy height D-EF was the most commonly sensitive across resource availability and ecosystem volume gradients, followed by gap fraction, and external heterogeneity. Internal heterogeneity D-EF was not sensitive to environmental gradients. Structural diversity was more sensitive than species richness or phylogenetic diversity-based D-EF to environmental gradients (table 2, table S4), with structure height and openness metrics being the most sensitive. The greatest number of structural diversity-based D-EF relationships were sensitive to environmental gradients at 17.5%, while 13.75% of species richness and phylogenetic diversity-based D-EF combined were sensitive to environmental gradients (table 2). External heterogeneity, mean canopy height, and native PSR D-EF with forest wood productivity varied along environmental gradients (basal area: table 2). Metrics of structural diversity, species richness, and phylogenetic diversity as predictors of forest productivity were sensitive to environmental gradients (LAI; table 2). Gap fraction, native PSV, and tree species richness as predictors of the proxy of carbon nutrient cycling were sensitive to several environmental gradients (coarse woody debris; table 2). Structural diversity, species richness, and phylogenetic diversity as predictors of energy were sensitive to environmental gradients (fPAR; table 2). D-EF with canopy height, gap fraction, and native PSV

as predictors of the proxy of biotic resistance to invasion were sensitive to environmental gradients (exotic species richness; table 2). In all cases, there was at least one structural diversity and one species richness or phylogenetic diversity metric as the predictor of each ecosystem function for which the D-EF slopes were inconsistent along environmental gradients.

Discussion

We hypothesized that as a more direct measure of the availability and occupancy of niche space in the ecosystem, structural diversity would be a better predictor of ecosystem functions than species richness or phylogenetic diversity. Indeed, we found that structural diversity metrics predicted all six measures of ecosystem functions and were better predictors 50% of the time compared to species richness and phylogenetic measures (figure 3). The categories that structural diversity was better at predicting were those of productivity and energy. Specifically, we found that all metrics of structural diversity, structural heterogeneity and height and openness, were better at predicting wood productivity than species richness or phylogenetic diversity. This is consistent with findings within a single site that internal canopy heterogeneity of vegetation density (i.e. rugosity) was correlated with woody primary productivity (Hardiman *et al* 2011). Furthermore, height and openness, canopy height and gap fraction, were better at predicting a proxy of forest productivity (LAI) than any of the biodiversity categories. Canopy height and gap fraction were also better at explaining the amount of light energy in the ecosystem (fPAR) than structural heterogeneity, species richness, or phylogenetic diversity, which is consistent with forest openness being a main driver of light interception (Ishii *et al* 2004). Species richness was only a better predictor of one of the proxies of biotic resistance to invasion; however, we have found no previous work that has investigated the ability for structural diversity to predict biotic resistance to invasion. Our study indicates that structural diversity, which directly measures various aspects of niche space, may provide a more useful predictor of ecosystem functions than simply species richness or phylogenetic diversity in ecological studies alone. A critical next step will be to test if structural diversity remains the best predictor of ecosystem functions in other ecosystem types and in a global suite of ecosystem functions.

Ecosystem functions change as forest stands age, and changes in structural diversity due to distinct successional stages can have some predictive power on the relationship between structural diversity and ecosystem functions (Franklin *et al* 1981, McElhinny *et al* 2005). However climate (Mao *et al* 2019), microhabitat heterogeneity in resources (Aber *et al* 1982), and species diversity (Ehbrecht *et al* 2017) all have

important additional impacts on structural diversity, making structural diversity—function predictions at large scales challenging. Later successional stages are often characterized by taller trees, vertical stratification of vegetation, and can develop canopy gaps due to single tree mortality events (Franklin *et al* 1981, McElhinny *et al* 2005), which are linked to higher ecosystem productivity (Hardiman *et al* 2011), light absorption (Atkins *et al* 2018b), and biotic resistance to invasion (Iannone *et al* 2016). Our results support these stand-level observations of forest structure driving productivity, energy and nutrient cycling, and biotic resistances at a large-scale. However, structural diversity metrics varied with one or more climate variables at the site-level in our study (table S5). We have used new remote sensing technology to improve the ease of measuring fine-scale variation in structural diversity at a continental extent compared to measurements that have only been historically tested at the stand-stand scale in forest ecology. Thereby, we have provided a new test of the relationship between different aspects of forest structural diversity and ecosystem functions at a continental-scale.

We did not find that structural diversity metrics would be less variable across environmental gradients in predicting ecosystem functions. Instead we found that the strength of structural diversity D-EF was just as likely to vary across environmental gradients of resource availability and physical volume as richness or phylogenetic diversity. Therefore, the ability for structural diversity to provide a stronger predictive ability of forest productivity and energy than richness or phylogenetic diversity in our study was not due to a lack of sensitivity to environmental gradients. More interestingly, the D-EF of specific diversity metrics from each category were not always sensitive to environmental gradients, indicating that there may be some variation in the sensitivity of individual metrics to environmental conditions. For example, there was no evidence for environmentally context dependent relationships found between internal heterogeneity, mean canopy height, or gap fraction and wood productivity in our study (table 2), which may be a result of climate and soil nitrogen being strong determinants of tree growth (Kreuzwieser and Gessler 2010, Levesque *et al* 2015). Greater structural diversity in forests is known to increase resource partitioning of light use among species (Kohyama 1993, Yachi and Loreau 2007, Álvarez-Yépiz *et al* 2017, Atkins *et al* 2018b), which may explain why internal heterogeneity, height, or gap fraction as a predictor of wood productivity were less sensitive to environmental gradients. Therefore, the sensitivity of structural diversity as a predictor of ecosystem functions in our case study using forested NEON sites may in part depend upon the sensitivity of certain D-EF relationships to environmental gradients.

Metrics of structural diversity versus species richness or phylogenetic diversity exhibited divergent

relationships to invasion, indicating opposing ecological mechanisms, whereas the direction of other D-EF was often the same between metrics of structural diversity and species richness or phylogenetic diversity. Our results indicated that three of four structural diversity metrics and phylogenetic variability promoted biotic resistance to invasion, while species and phylogenetic richness and gap fraction were positively associated with exotic invasion across sites. In our study, species richness as the number of native plant species, was the strongest predictor and was positively associated with exotic plant diversity. This is consistent with both facilitation at a large spatial extent (Byers and Noonburg 2003) and with mixed support for the biotic resistance hypothesis (Jeschke *et al* 2012). Conversely, structural diversity was negatively related to exotic plant diversity, which indicates that structural diversity is associated with biotic resistance to invasion in recipient forest ecosystems. Although native species richness was better at predicting variation in invasion across space, structural diversity predicted biotic resistance to invasion, indicating it may be more useful in predicting this ecosystem function. Indeed, more heterogeneous (rugose) canopies absorb a greater fraction of available light (Atkins *et al* 2018b), which may exclude shade intolerant exotic plants at locations with high structural heterogeneity. Furthermore, the size and frequencies of canopy gaps might influence invasion dynamics at scales larger than the gap size (1 m^2) we measured here. Our study provides a new avenue in invasion ecology, i.e. structural diversity promotes the resistance of invasive species, which warrants further study to understand the underlying mechanisms.

Our study showed that it is necessary to include multiple metrics of structural diversity in studies on ecosystem structure and function, despite correlations among metrics, because no one metric of structural diversity could collectively characterize the strength and direction of all relationships between different metrics and ecosystem functions. The aspects of forest structural diversity studied here are interrelated (table S6), and therefore neither statistically or ecologically independent, however they do contribute to explanatory power for understanding realized structural niche space that cannot be ecologically understood by one metric alone. We also note that we used new remote sensing tools to characterize structural diversity at a large-scale with metrics that can be intercorrelated, but that are complementary to those from traditional stand-level metrics in forest ecology. Height and openness, mean canopy height (a proxy of niche volume) and gap fraction (a proxy of open niche availability), were consistently among the strongest predictors across ecosystem functions compared to metrics of internal and external heterogeneity of vegetation height (proxies of niche space at the canopy surface and interior, respectively). In addition, gap fraction always had the opposite relationship with each proxy

of ecosystem functions compared to the other three metrics of structural diversity. Taller and more heterogenous vegetation heights in forests were associated with greater ecosystem function, while larger gap fractions had a negative impact on ecosystem function. Gap fraction is therefore an aspect of structural diversity that is more reflective of niche openness associated with ecosystem disturbance (Schliemann and Bockheim 2011) than other metrics of structural diversity that promote ecosystem functions by promoting high niche occupancy. We therefore recommend that multiple metrics be used to represent different aspects of structural diversity, as illustrated here, when using them to predict ecosystem functions in future studies.

Conclusion

All components of diversity are related to ecosystem functions, but in some ecological contexts, structural diversity is more important than species richness and phylogenetic diversity in supporting higher levels of ecosystem functions. Therefore, management practitioners should consider the importance of conserving ecosystems that are structurally diverse in their physical arrangement, because they may result in differential levels of ecosystem functions. Finally, as a measure of niche space in the ecosystem, structural diversity is likely to be related to the diversity of functional traits within the plant community. The ability to describe functional trait diversity with remote sensing of structural diversity could provide a new direction for understanding structure and function at large spatial scales. Critical future research should consider the relationships between structural diversity and functional trait diversity. In the future, emerging frontiers in remote sensing will provide many exciting opportunities to further understand the mechanistic underpinnings for how and why structural diversity is associated with ecosystem functions.

Statement of authorship

EAL and SF conceived the idea. EAL performed the data acquisition and analyses and wrote the first draft of the manuscript. JME assisted in data acquisition and analyses. SF and BSH provided substantial input on analyses, interpretation of results, and writing of subsequent drafts.

Data accessibility statement

All data are available online from the National Ecological Observatory Network (https://neonscience.org/data) or the PRISM climate database (http://prism.oregonstate.edu/).

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