

Both canopy and understory traits act as response–effect traits in fire-managed forests

TYLER K. REFSLAND ^{1,†} AND JENNIFER M. FRATERRIGO^{1,2}

¹Program in Ecology, Evolution and Conservation Biology, University of Illinois, Urbana, Illinois 61801 USA

²Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, Illinois 61801 USA

Citation: Refsland, T. K., and J. M. Fraterrigo. 2017. Both canopy and understory traits act as response–effect traits in fire-managed forests. *Ecosphere* 8(12):e02036. 10.1002/ecs2.2036

Abstract. Community-level shifts in the distributions of plant functional traits associated with environmental change are expected to influence ecosystem functioning. However, few studies have identified traits that both respond to environmental change and affect ecosystem properties, thus limiting potential to scale the effects of environmental change through the community level. We measured canopy and understory plant functional traits, characterizing the most abundant functional trait value (community-weighted mean; CWM) and the functional diversity (FD), across a soil resource gradient in fire-managed mixed-deciduous forests to determine how traits both respond to a disturbance-resource gradient and affect stocks of active and stable soil organic carbon (SOC) fractions. We expected that understory traits would respond mainly to fire and canopy traits would respond mainly to soil resources. We further hypothesized that fire and resource conditions affect SOC stocks (1) through mass-ratio, by influencing trait abundance; (2) through non-additive effects, by influencing the FD of plant communities; or (3) directly, through either combustion or environmental controls on SOC stocks. Understory traits responded to soil resource conditions and fire, whereas only canopy CWM leaf dry matter content (LDMC) varied with resource conditions; no canopy traits varied with fire. Among the response traits, canopy CWM LDMC and diversity in the maximum height of the understory were related to SOC stocks, suggesting they play dual roles as response and effect traits. SOC stocks were primarily associated with mass-ratio effects from canopy leaf traits and secondarily with non-additive effects from the canopy and understory. There were also strong, fraction-dependent patterns in SOC stocks with fire disturbance. Repeatedly burned forests characterized by resource conservative traits (i.e., high canopy CWM LDMC) had a higher relative proportion of active SOC, whereas unburned forests characterized by resource acquisitive traits (i.e., high canopy CWM leaf nitrogen content) had a higher relative proportion of stable SOC. Our results suggest that canopy community-aggregated leaf traits and diversity in understory size traits can act as both response and effect traits in disturbed forests. Predicting forest SOC stocks using a response–effect trait framework will thus require knowledge of both canopy and understory trait distributions, as well as disturbance history.

Key words: environmental filtering; functional diversity; functional traits; limiting similarity; plant community dynamics; prescribed fire; soil carbon; temperate deciduous forest.

Received 28 October 2017; accepted 3 November 2017. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2017 Refsland and Fraterrigo. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** refsland2@illinois.edu

INTRODUCTION

A primary goal of community ecology is to predict the consequences of changing biodiversity

for ecosystem function (Chapin et al. 2000). Plant functional traits are important to this goal as traits can determine species' responses to resource gradients and disturbance (response

traits) as well as their effects on ecosystem function (effect traits; Díaz and Cabido 2001, Lavorel and Garnier 2002). Certain traits may be deemed dual response–effect traits if those traits favored by the environment are those that also influence ecosystem function. Because such linked traits provide a direct means of scaling community-level changes to changes in ecosystem functioning (Suding et al. 2008), identifying them could enhance capacity to predict future ecosystem services (Lavorel et al. 2011).

Despite increasing adoption of the response–effect trait framework (Garnier et al. 2004, Laliberté and Tylianakis 2012), few empirical studies have tested for the existence of response–effect traits, especially in forest ecosystems (but see Conti and Díaz 2013). To fully implement the response–effect framework for scaling ecosystem-level consequences of environmental change through the community level, studies must not only examine the degree of overlap between response and effect traits (Suding et al. 2008), but also acknowledge the potential contribution of forest canopy and understory plant communities to ecosystem functioning, such as soil carbon (C) storage (Conti and Díaz 2013). These stratified communities are comprised of species with different growth forms and sensitivities to environmental change. For instance, while rarely affecting canopy trees, surface fires can kill sub-canopy trees and increase light availability in the understory, which in turn may promote perennial grass cover and enhance soil C stocks through increased belowground litter inputs (Post and Kwon 2000, Rasse et al. 2005). Few studies, however, have examined the response–effect trait linkages of canopy and understory communities and compared their contribution to ecosystem function.

Fire is one of the most widespread disturbances in forests, with natural and prescriptive fires impacting millions of hectares of forest per year (Ruiz et al. 2007). Although fire can act as a filter that selects species based on the suitability of traits (White 1983, Knapp et al. 2015), it is unknown whether its effects on trait composition are consistent across resource gradients where fire intensity and vegetation recovery can strongly vary (Wimberly and Reilly 2007, Iverson et al. 2008). Previous research shows that resource availability and disturbance operate

simultaneously to shape community assembly and functional trait composition (de Bello et al. 2013, Ames et al. 2016). Additionally, forest understory and canopy plant communities may respond to disturbance and resource availability through multiple but not necessarily mutually exclusive assembly processes, specifically environmental filtering (Grime 2006) and limiting similarity (i.e., niche partitioning; MacArthur and Levins 1967). This could result in the convergence or divergence of response trait values, respectively. For example, leaf traits are expected to show convergence in more productive habitats but increased competition in such habitats may instead promote divergence in traits to limit similarity. Consequently, the distribution of response traits may vary across disturbed forests that encompass steep gradients of resource availability.

Soil organic carbon (SOC) storage is a key ecosystem function of interest, given that forest soils store approximately one-third of Earth's terrestrial C (787 Gt C) and serve a critical role in climate regulation (Ciais et al. 2013). Predicting SOC storage is difficult due to highly variable stocks and a complex interplay of drivers (Bird et al. 2001). The response–effect trait framework provides a promising approach to predict SOC stocks at local scales, where disturbance, soil properties, and vegetation should be major drivers of C (Cornwell et al. 2008, De Deyn et al. 2008). Detecting such response–effect trait linkages, however, may require resolving soil C into component pools. Soil C varies greatly in its size and origin, from large particles originating from recent plant inputs (active fraction), to small, physically, and chemically protected particles associated with microbial byproducts (stable fraction; Schmidt et al. 2011). The active soil C fraction may be better associated with vegetation-mediated effects of fire; however, most studies focus on total soil C rather than its composition (Nave et al. 2011).

There are two primary hypotheses on how forest plant community composition may affect SOC stocks: (1) mass-ratio hypothesis (Grime 1998) and (2) non-additive, functional diversity (FD) effects (Tilman et al. 1997). Plant functional traits have been widely linked to C cycling through the mass-ratio hypothesis, which posits that the most abundant trait values (i.e., community-weighted mean,

CWM) should determine C storage patterns (Grime 1998). Traits associated with resource acquisition, such as high specific leaf area (SLA), low leaf dry matter content (LDMC), and high leaf nitrogen concentration (LNC), promote fast C accumulation and fast decomposition, whereas the opposite trait values are associated with resource conservation and favor slow C accumulation but high storage (Wright et al. 2004, Cornwell et al. 2008). Size-related traits such as leaf area (LA) or maximum height (H_{\max}) can also be important: Larger plants that produce and shed a higher quantity of litter per unit area are expected to contribute more C to the organic soil horizon (Moles et al. 2009, Falster et al. 2010). Thus, fire might enhance soil C stocks by favoring communities dominated by species with conservative leaf traits or reduce SOC by favoring shorter species (Lavorel et al. 1997, Garnier et al. 2004, De Deyn et al. 2008).

In contrast, the non-additive FD effects hypothesis posits that the presence of diverging functional trait values (e.g., conservative and acquisitive leaf traits) should lead to greater resource exploitation and production by the plant community and thus higher litter inputs and SOC storage (Fornara and Tilman 2008). Functional diversity is composed of the variety of trait values present in the community, weighed by their abundance (i.e., community-weighted trait variance, CWV). If fire reduces competitive dominance and promotes divergence in traits, in either the canopy, understory, or both, then non-additive effects should result in higher SOC stocks than in unburned communities with convergent trait values.

Our aim was to elucidate relationships among fire, plant functional traits, and SOC stocks across a soil resource gradient (xeric to mesic) in mixed-deciduous forests of the central United States to determine whether prospective response–effect traits are correlated with soil C storage. We addressed three specific questions pertaining to the response–effect trait framework: (1) To what extent do fire history and soil resources affect functional trait distributions and drive assembly processes? (2) How are functional trait distributions related to soil C storage? (3) What is the overlap between response and effect traits? We examined trait distributions in forest understory and canopy communities, expecting that understory traits

would respond mainly to the low-intensity fires characteristic of this region (Knapp et al. 2015) and canopy traits would respond mainly to soil resources. We hypothesized that disturbance and resource conditions affect SOC stocks (1) through mass-ratio, by influencing trait abundance; (2) through non-additive effects, by influencing the FD of plant communities; or (3) directly, through either combustion or environmental controls on SOC stocks, regardless of changes in functional traits.

METHODS

Study site and experimental design

This study was conducted within the Shawnee National Forest, a 1100-km² federally protected area in extreme southern Illinois, USA (37°44' N, 88°67' W). The climate is humid subtropical with a mean annual temperature of 15°C and a mean annual precipitation of 1250 mm distributed evenly throughout the year. The differences in soil properties and moisture availability with topographic position drive tree species distributions in the Shawnee region (Fralish 1988).

We selected three mature, upland forest sites that contained both burned and unburned stands and were at least 12 km apart (Appendix S1: Table S1). Within each site, we established paired 0.1-ha (50 × 20 m) plots consisting of a burn treatment and nearby (<1 km) unburned control. Burned stands experienced three to four low-intensity, prescribed fires between 2002 and 2013, including a spring 2013 burn six months prior to the study, whereas unburned stands had no record of fire activity in the past three decades, according to United States Forest Service records dating back to 1980 (S. Crist, *personal communication*). Given that fires were prescriptive, we assume fire treatment does not depend on environmental conditions and community traits.

To investigate response–effect trait linkages after fire disturbance under contrasting environmental conditions, we replicated the paired plots in xeric and mesic habitat types within each site, resulting in six sets of paired plots ($n = 12$ plots in total). Xeric and mesic habitat types were identified a priori from an integrated moisture index calculated in ArcGIS (version 10.3, ESRI, Redlands, California, USA) based on inputs of aspect, slope, curvature, and flow accumulation

(Iverson et al. 1997). Because topography can influence fire behavior in this region, we explore both the additive and interactive effects of fire and resource conditions on functional traits.

Soil sampling and resource gradient

In August 2013, we collected soil from three subplots per plot, spaced 12.5 m apart. Within each subplot, we randomly selected two 228-cm² areas from which we removed all leaf litter and organic soil (i.e., the O horizon) prior to collecting two cores (0–10 cm depth) of mineral soil using a 5 cm diameter soil corer. We chose to focus on the 0–10 cm depth to avoid bedrock and because only shallow soils experience heating during low-intensity fires (DeBano 2000). Samples were composited by subplot, resulting in three replicates per plot (3 × 12 plots = 36 total samples). Composited samples were weighed for field-moist and air-dried mass, sieved to 2 mm, and stored at 20°C until analysis (Appendix S2). Replicate samples were processed separately, and values were averaged for each plot for the purposes of statistical analysis.

Six soil parameters were measured using standard procedures (Appendix S2) to characterize the contrasting environmental conditions across all plots: soil water content, soil texture (clay, silt, and sand gravimetric content), pH, ion-exchangeable inorganic nitrogen (N) and phosphorus (P), and soil C:N ratio (summarized in Appendix S1: Table S1). Soil parameters were analyzed using principal component analysis (PCA; Appendix S3: Fig. S1) on the correlation matrix by scaling and centering all parameters. We refer to plot scores along first PCA axis (PC1) as the resource gradient and use PC1 for all subsequent statistical analyses as a single variable representing soil conditions across xeric and mesic habitat types.

SOC fractionation

To evaluate associations among the soil resource gradient, fire treatment, and community traits on SOC pools with different turnover times, we physically fractionated mineral soil C from each composite soil sample using a modified wet-sieving method (Craig et al. 2015). This method separates SOC into large, recently plant-derived particles (i.e., particulate organic matter, >53 μm) and small, physicochemically protected

particles associated with microbial byproducts (i.e., mineral-associated organic matter, ≤53 μm), hereafter referred to as the active and stable fractions, respectively (details in Appendix S2).

Trait measurements

After surveying the percent cover of understory species (Appendix S2), we sampled traits of only those species ($n = 24$) that represented approximately 85% of the cumulative cover for each plot in order to achieve a representative sample of the most abundant species in the community (Pakeman and Quested 2007). For the canopy tree community, the abundance of each tree species was based on its share of the total basal area per plot.

We selected five functional traits known or expected to both respond to disturbance-driven changes to resource availability (Cavender-Bares and Reich 2012, Forrestel et al. 2014) and affect ecosystem C dynamics and storage (De Deyn et al. 2008). Leaf dry matter content (LDMC; mg g⁻¹), specific leaf area (SLA; mm⁻² mg⁻¹), and leaf N content per dry mass (LNC; mg N g⁻¹) are key traits along the leaf economics spectrum (Wright et al. 2004), whereas leaf area (LA; cm²) and maximum height (H_{\max} ; meters) constitute key components of the size axis and are associated with large woody species that are intermediate along the leaf economics spectrum (Pierce et al. 2013, Díaz et al. 2016). For the understory, LA, LDMC, and SLA were measured on ten individuals per species per plot by averaging values from two mature, undamaged sun-lit leaves per individual using standard methodology (Pérez-Harguindeguy et al. 2013). H_{\max} and LNC were obtained for species or congeners using the TRY global database (Kattge et al. 2011). Due to the difficulty of sampling canopy leaves, we did not collect in situ trait data for canopy species, but rather used region-specific average values of LA, SLA, and LDMC collected from adult trees (Spasojevic et al. 2014) and retrieved LNC and H_{\max} using TRY. We acknowledge database values can be imperfect surrogates for in situ trait values (Cordlandwehr et al. 2013), but including database-derived understory and canopy traits in our analyses significantly improved model fit, so they were retained.

To assess the response of understory and canopy community traits to fire and the resource

gradient, as well as their association with SOC stocks, we calculated the CWM and CWV of trait values, weighted by species abundance (Appendix S2). We performed separate calculations for the understory and canopy communities because we hypothesized they would respond differently to fire.

Modeling mean trait responses and dispersion

To investigate the response of trait distributions to environmental conditions and fire, we modeled relationships between the CWM of each trait, the soil resource gradient defined by PC1 axes, fire, and their interaction using multiple linear regression.

We evaluated how fire history and soil resources influenced functional trait dispersion and community assembly processes using a null model approach. Specifically, we generated a null model where the observed species and associated trait values in each plot remained unchanged but abundance was shuffled randomly among species, thus breaking the relationship between trait values and abundance while maintaining richness and evenness of abundances within plots. Based on a distribution generated by 9999 runs of the null model, we calculated an effect size (ES) based on the probability of obtaining an observed value lower or higher than expected by chance (i.e., the quantile of the null distribution in which the observed value is found; Chase et al. 2011, Bernard-Verdier et al. 2012; Appendix S2). We used a two-tailed Wilcoxon signed-ranks test to examine whether CWV ES values were significantly greater or less than zero across all communities. Lower CWV values than expected (i.e., negative ES) provide evidence of convergence toward a common trait value, and larger CWV values (i.e., positive ES) provide evidence of a divergent trait distribution. Values close to zero (i.e., the null expectation) indicated random dispersion of abundance among species trait values. To explore relationships between community structure and the soil resource gradient, we plotted CWV ES values against the resource gradient and used Spearman's rank correlations to test for significant trends along the gradient. Partial correlation was used to assess the association between CWV ES values and fire treatment while controlling for the effect of the resource gradient.

Modeling trait effects

We evaluated the correlation between our predictors and SOC stocks using multiple linear regression and an information-theoretic approach (Burnham and Anderson 2002). We chose a multi-modal approach because it allowed us to compare the relative support for each of our competing hypotheses. For each SOC pool, we performed separate analyses where we developed a set of linear models constructed by adding explanatory variables and their interactions in fixed sequential order according to a hierarchy of controls (Diaz et al. 2007, Manning et al. 2015). Specifically, we first added the resource gradient, fire treatment, and forest basal area terms followed by canopy trait CWMs and CWVs and finally, understory trait CWMs and CWVs. Fire frequency (fires/decade) was also considered as a predictor, but was not found to be significant for any SOC pool, so it was not considered in the final models. If predictor variables were correlated ($|r| > 0.5$), no more than one of the correlated variables was included in the model, with preference given to terms that were higher in the hierarchy (e.g., canopy traits over understory traits). To further minimize multi-collinearity among variables, only those models with variance inflation factors < 5 were retained. We also limited the maximum number of predictors in a single model to four terms to avoid overfitting the data.

In order to quantify the relative importance (RI) of each predictor across the resulting set of competing models, we ranked each model according to Akaike Information Criterion, adjusted for small sample size (AICc), and the relative support was evaluated with AICc weight (Burnham and Anderson 2002). We retained a confidence set of models with a cumulative AICc weight of 0.95 (Johnson and Omland 2004). The RI of each predictor in the confidence set was calculated as the sum of Akaike weights over all models in which it appeared. We calculated the model-averaged estimates of the predictors over the confidence set (Burnham and Anderson 2002). To facilitate comparison of effect sizes, standardized parameter estimates were calculated by scaling all continuous variables to mean of zero and standard deviation of one. All analyses were performed using R version 3.4.1 (R Core Development Team 2017) and the package MuMIn (Bartoń 2016).

RESULTS

Soil resource gradient

Of the original seven soil parameters, only phosphorus availability was significantly correlated with fire treatment ($P = 0.04$) and therefore was excluded from the PCA. Most of the six remaining soil parameters were collinear, with the first axis of the PCA explaining 42.8% of the variance and indicating that soils varied from dry and sandy with low pH and N availability (xeric) to moist and clay-rich with high pH and N availability (mesic; Appendix S2: Fig. S1). The second axis of the PCA explained 27.7% of the variability, capturing differences in primarily silt and clay content caused by an outlier plot with unusually high clay and low silt content. Therefore, we used the first axis of the PCA (the resource gradient) and fire treatment as independent predictors in our analyses. Species turnover in the understory did not occur along the resource gradient (Mantel $r = 0.15$, $P = 0.13$; Appendix S3: Fig. S1). In canopy communities, however, species turnover did occur along the gradient, as indicated by the positive correlation between Bray-Curtis dissimilarities and differences in soil conditions (Mantel $r = 0.23$, $P = 0.04$).

Understory trait means and divergence with fire and soil conditions

Understory CWM trait values varied with soil resources or fire treatment. Averaging over fire treatment, CWM SLA increased ($P = 0.02$) and CWM LA ($P < 0.01$), LDMC ($P = 0.04$), and H_{\max} decreased ($P = 0.02$) along the resource gradient from xeric to mesic habitats (Fig. 1). Averaging over the resource gradient, burned communities had significantly lower CWM LA ($P = 0.04$) and H_{\max} ($P = 0.02$; Fig. 1) and similar CWM SLA and LDMC ($P > 0.3$) compared to unburned communities. Community-weighted mean LNC was the only trait that did not vary with soil resource conditions or fire treatment.

Understory trait diversity also varied with soil resources or fire treatment. Fire was associated with less diversity in understory LA, as indicated by a lower CWV in LA than expected from the null model (Wilcoxon test toward lower values: $P = 0.04$; Fig. 2). By contrast, unburned understory communities showed less diversity in SLA

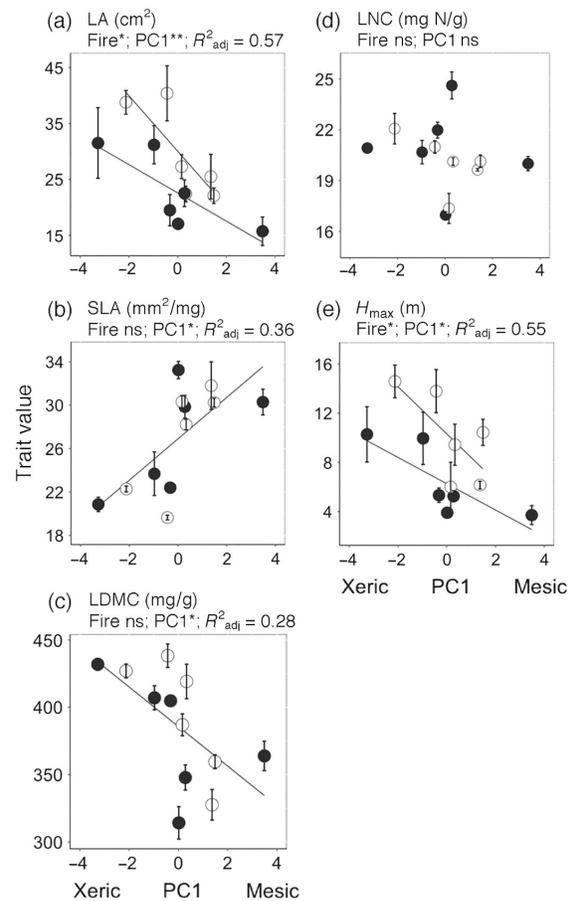


Fig. 1. Community-weighted mean (CWM) trait values (\pm SE) of understory plant communities in burned (black symbols) and unburned stands (white symbols) along a resource gradient (PC1). Black lines represent significant regressions, and statistics are indicated above panels (ns: $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). CWM, community-weighted mean; CWV, community-weighted variance; LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf N content; H_{\max} , maximum attainable height.

than expected from random (Wilcoxon toward lower values: $P = 0.02$; Fig. 2).

Examination of the values of ES in relation to the soil resource gradient demonstrated that the diversity of SLA and H_{\max} in the understory decreased from xeric to mesic habitats ($\rho < -0.50$, $P < 0.05$), whereas LDMC diversity increased from xeric to mesic habitats ($\rho = 0.68$, $P = 0.01$; Fig. 2). In contrast to all other traits, diversity in LNC did not vary with soil resources

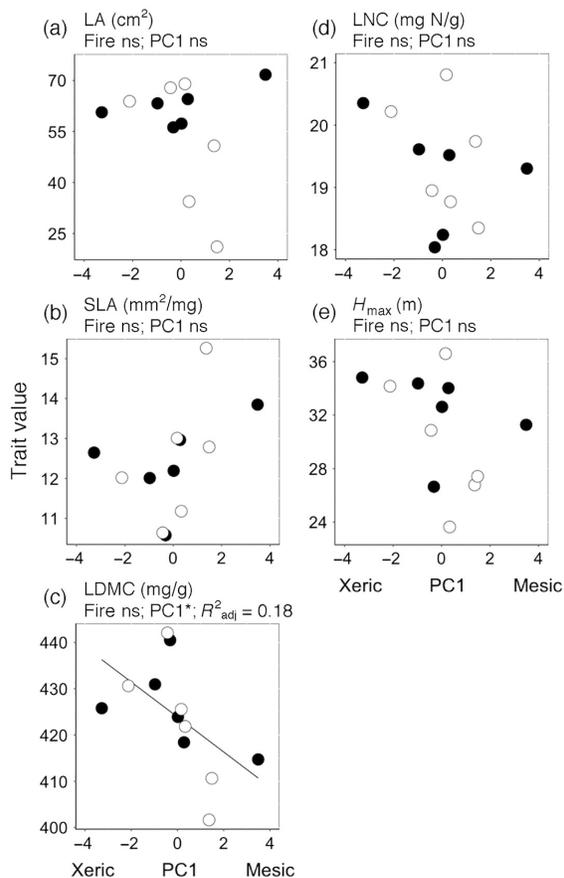


Fig. 2. Community-weighted trait variance (CWV) of understory plant communities in burned (black symbols) and unburned stands (white symbols) along a resource gradient (PC1). Effect sizes (ES) of CWV were calculated by comparing observed CWV to a null distribution (see *Methods*). Negative ES values represent a lower CWV than expected, suggesting trait convergence, whereas positive ES values suggest trait divergence. One-sided Wilcoxon (W) tests were used to compare observed values to the null expectation (ES = 0), represented by the solid horizontal line. Spearman's rank correlations (ρ) were used to assess patterns of divergence along the resource gradient. Statistics are indicated above panels (ns: $P \geq 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

or fire treatment, but instead showed greater divergence than expected from random across all plots (Wilcoxon toward higher values: $P = 0.04$; Fig. 2). Fire treatment did not interact with the resource gradient to determine trait diversity (for all traits: partial correlation, $P > 0.05$).

Canopy trait means and divergence with fire and soil conditions

Canopy CWM LDMC decreased significantly along the resource gradient ($P = 0.04$), whereas CWM SLA increased from xeric to mesic habitats ($P = 0.01$; Fig. 3). There was no relationship between canopy CWM LA or SLA and the resource gradient ($P > 0.1$), and none of the canopy CWM trait values differed with fire treatment ($P > 0.6$).

Although canopy communities displayed higher CWV in LA, SLA, and LDMC than expected from the null model (Wilcoxon toward higher values: $P < 0.01$), there was no relationship between the values of ES and the resource

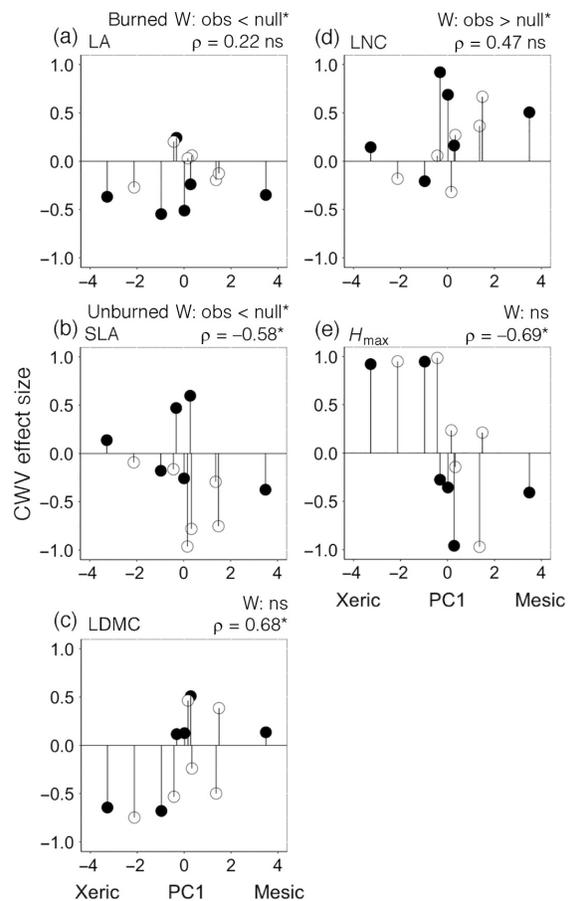


Fig. 3. Community-weighted mean (CWM) trait values of canopy communities in burned (black symbols) and unburned stands (white symbols) along a resource gradient (PC1). Black lines represent significant or marginally significant regressions, with statistics indicated above panels (ns: $P \geq 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

gradient or fire (for all traits: partial correlation, $P > 0.05$; Appendix S3: Fig. S2). Canopy CWV LNC and H_{\max} were randomly distributed and unrelated to the resource gradient and fire (Appendix S3: Fig. S2).

Linkages between disturbance-resource gradient, traits, and SOC stocks

Total mineral soil C stocks ranged from 16.4 to 31.8 Mg/ha and were most strongly related to canopy community-aggregated leaf traits and diversity in canopy H_{\max} (Fig. 4a). The single best-performing model included canopy CWM LA and LDMC as significant predictors (AIC weight = 0.23, $R^2 = 0.66$; Appendix S4: Tables S1 and S2). Across all supported models, mineral SOC stocks were significantly lower in communities with greater canopy CWM LA (Appendix S4: Fig. S1), whereas stocks were significantly greater in communities with greater canopy CWM LDMC and CWV H_{\max} . Mineral SOC stocks decreased significantly with increasing understory CWV LNC and marginally increased with canopy CWM LNC (Fig. 4a; Appendix S4: Table S2).

We found that fire had strong effects when analyzing the active and stable SOC fractions separately (Fig. 4b, c; Appendix S4: Table S1). Specifically, burned stands had 25% higher stocks of the active fraction and 23% lower stocks of the stable fraction than unburned stands, resulting in no net difference in total mineral soil C stocks with fire (lsmean difference = -0.56 Mg/ha \pm 3.21).

Stocks of the active and stable fraction were strongly related to canopy CWM LDMC and LA, respectively, and shared no significant predictors aside from canopy CWM LA. In general, the active fraction was positively related to conservative resource-use traits, whereas stocks of the stable fraction were positively related to acquisitive resource-use traits in the canopy. For the active fraction, the single best-performing model included fire, canopy CWV SLA and H_{\max} , and understory CWV H_{\max} as significant predictors (AIC weight = 0.27, $R^2 = 0.92$; Appendix S4: Tables S1 and S2). Across all supported models, the active fraction also showed a significant positive relationship with canopy and understory CWM LDMC and a negative relationship with canopy CWM LA and CWV H_{\max} (Fig. 4b; Appendix S4: Fig. S1). Stocks of this fraction

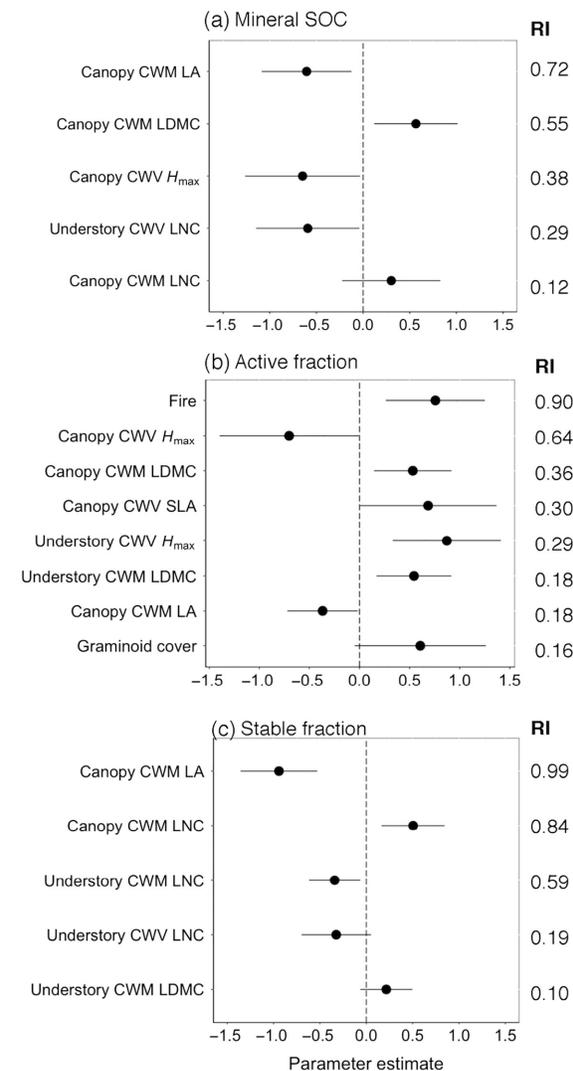


Fig. 4. Model-averaged coefficient estimates and 95% confidence intervals for predictors included in the confidence set of simple linear regression models explaining (a) total mineral soil organic carbon, (b) active fraction (>53 μm particle size), and (c) stable fraction (≤ 53 μm particle size) C stocks. Continuous predictors were standardized (mean = 0, SD = 1) to make effect sizes comparable. Relative importance (RI) is the sum of AICc weights of models in which the predictor appears. Only those predictors with RI > 0.10 are shown.

increased marginally in communities with higher canopy CWV SLA and increased graminoid cover (Fig. 4b; Appendix S4: Table S2).

Stocks of the stable fraction were best predicted by canopy CWM LA and LNC and understory

CWM LNC (AIC weight = 0.29, $R^2 = 0.86$; Appendix S4: Tables S1 and S2). Across all supported models, stable fraction stocks were positively related to canopy CWM LNC and negatively related to understory CWM LNC and canopy CWM LA (Fig. 4c; Appendix S4: Fig. S1). We also found that stocks of this fraction decreased marginally with understory CWV LNC and increased marginally with understory CWM LDMC (Fig. 4c; Appendix S4: Table S2).

DISCUSSION

Years after establishment of response–effect trait framework, we still lack empirical evidence for response–effect traits, especially in forests. Our observational approach of examining trait distributions and their relationship to SOC stocks along a resource gradient in a disturbed, mixed-deciduous forest allowed us to empirically test for evidence of response–effect traits that mediate plant community effects on SOC storage. We found that canopy and understory CWM LDMC varied along the resource gradient, but not with fire, and that the positive association among these traits and SOC stocks was fraction dependent. We also found evidence that variation in the maximum height of the understory responded to the resource gradient and was positively associated with the active soil C fraction. Most traits, however, including canopy CWM LA, CWM LNC, and CWV Hmax, that were associated with effects on SOC stocks did not respond to fire or the resource gradient. Furthermore, while canopy traits are the primary “effect” traits influencing SOC stocks, understory traits are also associated with soil C storage in forests experiencing fire.

Trait response to soil conditions and fire

There was a trait-specific functional response of the understory and canopy community to the resource gradient, as evidenced by trends in community-weighted means for four of the five traits we examined. We also found that fire and the resource gradient were associated with distinct rather than interactive effects on understory trait distributions. Leaf traits associated with the leaf economics spectrum (Wright et al. 2004) responded only to the resource gradient, with more slow-growing and nutrient conservative

species on dry, N-limited soils and fast-growing and less resource-efficient species on moist, N-rich soils. This result is consistent with past studies showing leaf traits, unlike regenerative traits, respond primarily to resource availability rather than disturbance directly (Shipley et al. 1989, Lavorel and Garnier 2002, Peltzer et al. 2016). Although long-term, fire-induced N limitation can result in communities characterized by resource conservative traits (Cavender-Bares and Reich 2012, Forrester et al. 2014), our results show that in forests with relatively brief fire histories and limited changes to N (Appendix S1: Table S1), leaf economic traits respond mainly to existing soil conditions. In contrast, the size-related traits of understory LA and H_{\max} both responded to fire and the resource gradient. Together, these results support the idea that functional traits respond to specific environmental changes, with leaf economic traits primarily responsive to soil gradients, while size-based traits may respond to both soil gradients and disturbance (Lavorel et al. 1997, Pausas et al. 2004).

Functional divergence response to soil conditions and fire

Our results suggest that abiotic controls lead to convergence toward high SLA for understory communities in mesic habitats and high LDMC for those in xeric habitats (Figs. 1, 2). This finding is consistent with environmental filtering which predicts that traits related to resource acquisition will be under-dispersed along environmental gradients (Grime 2006). We also observed convergence in understory H_{\max} along the resource gradient, suggesting increased competition for light from mesic to xeric habitats. In mesic habitats, dense canopy cover competitively excludes otherwise dominant, shade-intolerant tree species (*Quercus* and *Carya* spp.), but not shorter, shade-tolerant herbs (e.g., *Acalypha rhomboidea*) and shrubs (e.g., *Toxicodendron radicans*), resulting in convergence toward low H_{\max} . In contrast, shallow soils and limited moisture in xeric habitats prevent dense canopy cover in the study region (Fralish 1994, Iverson et al. 1997), allowing the formation of functionally divergent communities where light-demanding perennial grasses and forbs (e.g., *Dicanthelium* spp., *Helianthus divaricatus*) coexist with tree species and potentially partition light resources in a complementary way

(Vojtech et al. 2008). This finding is consistent with the theory of limiting similarity, which predicts that plant traits within a community will show divergence to reflect strategies to reduce competition (MacArthur and Levins 1967). Together, these results suggest that multiple assembly processes—environmental filtering and limiting similarity—can operate simultaneously to structure plant communities along disturbance-resource gradients (Spasojevic and Suding 2012, Laliberté et al. 2013).

Although functional divergence did not differ with fire across the resource gradient, fire disturbance was associated with convergence in LA and a random distribution of SLA for understory communities across the gradient. We suggest that these differences in leaf trait diversity reflect regenerative, rather than leaf traits, directly responding to fire. For example, the herbaceous species with the greatest increase in abundance from unburned to burned plots (*A. rhomboidea*, *Amphicarpaea bracteata*, *H. divaricatus*, and *Viola sororia*) have lower LA and have more diverse SLA values than the average values of unburned plots, as with our general results (Fig. 2). These herbaceous species, however, also represent a wide array of regenerative strategies ranging from annuals with small, transient seeds to perennial herbs that reproduce asexually and sexually (Kattge et al. 2011). Therefore, the observed patterns in leaf trait diversity with fire may be a consequence of disturbance influencing variation in regenerative traits by increasing the range of regenerative niches (Grubb 1977, Crawley and May 1987).

Response–effect trait linkages with SOC stocks

Trait combinations are not only a useful way for identifying different strategies of resource use, but are also expected to describe the relationship between plant community and ecosystem function (Díaz and Cabido 2001, Lavorel and Garnier 2002). Yet empirical evidence of such relationships is scant for temperate forests. We found that SOC stocks were primarily associated with a subset of canopy traits that represented effect, but not response traits (e.g., canopy CWM LA, canopy CWV H_{\max}). There were a small number of response traits, notably canopy and understory CWM LDMC, that both varied with the resource gradient and were associated with

effects on total mineral SOC and the active SOC fraction.

We found that fire was associated with significant opposite effects on C stocks in the active and stable fractions, resulting in no net change in total mineral SOC with fire. After controlling for the soil gradient and vegetation, however, we found that fire was associated with a direct, positive effect on stocks of the active soil C fraction but no effect on the stable soil C fraction. This is consistent with past studies that found fire to directly increase C stocks in the active fraction by promoting the incorporation of litter into the mineral soil (González-Pérez et al. 2004, Kane et al. 2007). Our results also agree with past studies that find prescribed fire to have little to no consistent effect on mineral SOC stocks, especially in hardwood forests (Eivazi and Bayan 1996, Boerner et al. 2005, Nave et al. 2011). Specifically, our study showed that the association between burning and mineral soil C stocks can range from positive to negative depending on the balance between fire-induced gains in soil C in the plant-derived, active fraction and losses in microbe-derived, stable fraction. These contrasting, fraction-dependent changes in SOC highlight the complexity of factors that influence SOC stocks in forests disturbed by fire.

Canopy community-weighted LDMC was positively associated with total mineral and active fraction C stocks, in support of the leaf economy spectrum comprising key response–effect traits that influence SOC stocks through mass-ratio. This result is consistent with the prevailing view that acquisitive syndromes are associated with higher C fluxes (Díaz et al. 2004, Freschet et al. 2012), while conservative syndromes should promote higher C stocks overall (De Deyn et al. 2008). This mass-ratio effect on SOC stocks, however, was contingent on SOC fraction. For the stable fraction, we found canopy CWM LA to be the dominant response–effect trait, in support of size-related traits being important in determining mass-ratio effects on ecosystem C storage (De Deyn et al. 2008, Conti and Díaz 2013). Additionally, we found that canopy and understory CWM LNC were positively and negatively associated with stable SOC stocks, respectively. The canopy results support the emerging view that, unlike the plant-derived active fraction, stocks in the stable soil C fraction should increase under

higher-quality litter (i.e., high LNC) due to greater microbial C-use efficiency and thus greater formation of microbially derived products that are primary constituents of the stable soil C fraction (Cotrufo et al. 2013). We attribute the negative association between understory litter quality and stable SOC stocks to the change in understory (but not canopy) vegetation immediately after fire disturbance. Stable SOC stocks were lower in burned than in unburned plots, where understories had shifted from woody species dominance (i.e., low LNC) toward herbaceous species dominance (i.e., high LNC). This change in understory but not canopy species composition immediately after fire produces a mismatch in the litter quality of the understory vs. canopy. Of the few empirical studies to link functional trait composition to size-fractionated SOC stocks, Manning et al. (2015) found that C stocks in the stable fraction were greater in grassland communities with high LNC. Given that root inputs are a dominant contributor to SOC, data on root traits and exudation rates would be needed to address these contradictory findings (Schmidt et al. 2011).

We found that diversity in canopy and understory H_{\max} were associated with negative and positive effects on SOC stocks, respectively, in support of non-additive (FD) effects having important consequences for ecosystem function. Only understory CWV H_{\max} was found to be a response–effect trait: CWV H_{\max} declined from xeric to mesic habitats and was in turn associated with positive effects on the active soil C fraction (Figs. 1, 4b). After accounting for the effect of fire, C stocks in the active fraction increased with increased divergence in H_{\max} as communities transitioned from short, shade-tolerant herbs and shrubs in mesic habitats to the co-existence of light-demanding herbaceous and tree species in xeric habitats (Appendix S5: Fig. S1). In other words, by reducing subcanopy tree cover, especially in xeric habitats where relatively low basal area allows for greater light penetration, fire promotes the abundance of light-demanding herbaceous species (Appendix S5: Fig. S1), resulting in an extra layer of productivity in the understory and an additional C input to the soil (De Deyn et al. 2008). Relative to shrubs and trees, herbaceous species tend to have a shallow rooting zone, which after fire-induced dieback of fine

roots (Day et al. 2006) can contribute substantial C inputs below ground (Kelly et al. 1996, Ansley et al. 2006, Poeplau et al. 2011), where conditions for decomposition are less favorable than the soil surface (Post and Kwon 2000, Rasse et al. 2005). These results highlight that fire may help determine response–effect trait linkages across soil resource gradients.

Although canopy CWV H_{\max} did not vary with fire disturbance, it was negatively related to both total mineral and active fraction C stocks. Canopy CWV H_{\max} was inversely related to basal area; stands with high basal area had lower CWV H_{\max} (Appendix S5: Fig. S2). Therefore, variance in H_{\max} may correlate with stand age and productivity with lower CWV H_{\max} , indicating older and more productive forest canopies with higher rates of litterfall, and in turn high rates of aboveground C input to soil (Pregitzer and Euskirchen 2004, Jandl et al. 2007).

Limitations

There are some key limitations to our study that may have influenced the results. First, the response–effect trait linkages reported here are correlative and should not be interpreted as cause effect. Second, although LNC can be highly variable depending on N-supply, our use of database-derived LNC values does not account for potential intraspecific variation in LNC. Third, sampling was limited to the top 10 cm of the mineral soil and thus did not capture patterns present at greater depths. Other studies have found the effects of plant functional types on SOC stocks to depend on soil depth (Jobbágy and Jackson 2000, Fornara and Tilman 2008). Third, our study lacked information on root traits, such as specific root length and root N, which have recently been shown to be important for belowground C dynamics (Bardgett et al. 2014). Incorporating disturbance effects on belowground trait composition could further elucidate how community assembly influences SOC storage.

CONCLUSIONS

Overall, we found support for dual response–effect traits in the context of predicting SOC stocks: There was a distinct overlap between those forest canopy and understory functional

traits that responded to abiotic conditions and those found to be associated with SOC stocks. Abiotic-driven mass-ratio (canopy or understory LDMC) effects were associated with all SOC fractions, whereas abiotic-driven non-additive (understory divergence in height) effects and direct fire effects were associated with C stocks of the active fraction. Our results suggest that fire disturbance may increase total mineral SOC stocks by promoting an extra layer of vegetation in the understory, notably shallow-rooted perennial grass and forb species with high belowground C inputs. Consistent with this, repeatedly burned forests had a higher relative proportion of SOC derived from recent plant inputs than unburned forests. Incorporating trait-based vegetation characteristics into ecosystem models that currently use climate and land cover data may thus help improve estimates of SOC storage across disturbance-resource gradients, therefore aiding in our ability to manage forests for ecosystem services.

ACKNOWLEDGMENTS

This study was supported by the USDA McIntire-Stennis Cooperative Forestry Program Project Number 875-303. We thank the USDA Forest Service for permits and access to Shawnee National Forest and Scott Crist for assistance with selecting field sites and logistical help. We thank two anonymous referees for greatly improving the quality of the manuscript.

LITERATURE CITED

- Ames, G. M., S. M. Anderson, and J. P. Wright. 2016. Multiple environmental drivers structure plant traits at the community level in a pyrogenic ecosystem. *Functional Ecology* 30:789–798.
- Ansley, R. J., T. W. Boutton, and J. O. Skjemstad. 2006. Soil organic carbon and black carbon storage and dynamics under different fire regimes in temperate mixed-grass savanna. *Global Biogeochemical Cycles* 20:1–11.
- Bardgett, R. D., L. Mommer, and F. T. De Vries. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology and Evolution* 29:692–699.
- Bartoń, K. 2016. MuMIn: multi-model inference. R package version 1.15.6.
- Bernard-Verdier, M., M.-L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology* 100:1422–1433.
- Bird, M., J. Lloyd, and H. Santrůcková. 2001. Global soil organic carbon pool. Pages 185–199 in E. D. Schulze, editor. *Global biogeochemical cycles in the climate system*. Academic Press, London, UK.
- Boerner, R. E. J., J. A. Brinkman, and A. Smith. 2005. Seasonal variations in enzyme activity and organic carbon in soil of a burned and unburned hardwood forest. *Soil Biology and Biochemistry* 37: 1419–1426.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA.
- Cavender-Bares, J., and P. B. Reich. 2012. Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment. *Ecology* 93: 52–69.
- Chapin, F. S., et al. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere* 2:1–11.
- Ciais, P., et al. 2013. Carbon and other biogeochemical cycles. Pages 465–570 in T. F. Stocker, D. Qin, G. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Conti, G., and S. Diaz. 2013. Plant functional diversity and carbon storage—an empirical test in semi-arid forest ecosystems. *Journal of Ecology* 101:18–28.
- Cordlandwehr, V., R. L. Meredith, W. A. Ozinga, R. M. Bekker, J. M. van Groenendael, and J. P. Bakker. 2013. Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology* 101:662–670.
- Cornwell, W. K., et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11: 1065–1071.
- Cotrufo, M. F., M. D. Wallenstein, C. M. Boot, K. Deneff, and E. Paul. 2013. The microbial efficiency-matrix stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology* 19:988–995.

- Craig, M. E., S. M. Pearson, and J. M. Fraterrigo. 2015. Grass invasion effects on forest soil carbon depend on landscape-level land use patterns. *Ecology* 96:2265–2279.
- Crawley, M. J., and R. M. May. 1987. Population-dynamics and plant community structure – competition between annuals and perennials. *Journal of Theoretical Biology* 125:475–489.
- Day, F. P., D. B. Stover, A. L. Pagel, B. A. Hungate, J. J. Dilustro, B. T. Herbert, B. G. Drake, and C. R. Hinkle. 2006. Rapid root closure after fire limits fine root responses to elevated atmospheric CO₂ in a scrub oak ecosystem in central Florida, USA. *Global Change Biology* 12:1047–1053.
- de Bello, F., M. Vandewalle, T. Reitalu, J. Lepš, H. C. Prentice, S. Lavorel, and M. T. Sykes. 2013. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology* 101:1237–1244.
- De Deyn, G. B., J. H. Cornelissen, and R. D. Bardgett. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* 11:516–531.
- DeBano, L. F. 2000. The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* 231–232:195–206.
- Díaz, S., and M. Cabido. 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16: 646–655.
- Díaz, S., et al. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15:295–304.
- Díaz, S., et al. 2016. The global spectrum of plant form and function. *Nature* 529:167–171.
- Díaz, S., S. Lavorel, F. de Bello, F. Quétier, K. Grigulis, and T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences USA* 104:20684–20689.
- Eivazi, F., and M. R. Bayan. 1996. Effects of long-term prescribed burning on the activity of select soil enzymes in an oak-hickory forest. *Canadian Journal of Forest Research* 26:1799–1804.
- Falster, D. S., Å. Brännström, U. Dieckmann, and M. Westoby. 2010. Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: a theoretical investigation. *Journal of Ecology* 99:148–164.
- Fornara, D. A., and D. Tilman. 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology* 96: 314–322.
- Forrestel, E. J., M. J. Donoghue, and M. D. Smith. 2014. Convergent phylogenetic and functional responses to altered fire regimes in mesic savanna grasslands of North America and South Africa. *New Phytologist* 203:1000–1011.
- Fralish, J. S. 1988. Predicting potential stand composition from site characteristics in the Shawnee Hills forest of Illinois. *American Midland Naturalist* 120:79–101.
- Fralish, J. S. 1994. The effect of site environment on forest productivity in the Illinois Shawnee Hills. *Ecological Applications* 4:134–143.
- Freschet, G. T., R. Aerts, and J. H. C. Cornelissen. 2012. A plant economics spectrum of litter decomposability. *Functional Ecology* 26:56–65.
- Garnier, E., J. Cortez, G. Billès, M. L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, and A. Bellmann. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637.
- González-Pérez, J. A., F. J. González-Vila, G. Almen-dros, and H. Knicker. 2004. The effect of fire on soil organic matter—a review. *Environment International* 30:855–870.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86:902–910.
- Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17:255–260.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145.
- Iverson, L. R., M. E. Dale, C. T. Scott, and A. Prasad. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.). *Landscape Ecology* 12:331–348.
- Iverson, L. R., T. F. Hutchinson, A. M. Prasad, and M. P. Peters. 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *Forest Ecology and Management* 255:3035–3050.
- Jandl, R., M. Lindner, L. Vesterdal, B. Bauwens, R. Baritz, F. Hagedorn, D. W. Johnson, K. Minkinen, and K. A. Byrne. 2007. How strongly can forest management influence soil carbon sequestration? *Geoderma* 137:253–268.
- Jobbágy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10:423–436.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101–108.

- Kane, E. S., E. S. Kasischke, D. W. Valentine, M. R. Turetsky, and A. D. McGuire. 2007. Topographic influences on wildfire consumption of soil organic carbon in interior Alaska: implications for black carbon accumulation. *Journal of Geophysical Research* 112:1–11.
- Kattge, J., et al. 2011. TRY – a global database of plant traits. *Global Change Biology* 17:2905–2935.
- Kelly, R. H., I. C. Burke, and W. K. Lauenroth. 1996. Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. *Ecology* 77:2516–2527.
- Knapp, B. O., K. Stephan, and J. A. Hubbart. 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. *Forest Ecology and Management* 344:95–109.
- Laliberté, E., D. A. Norton, and D. Scott. 2013. Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. *Journal of Vegetation Science* 24: 834–842.
- Laliberté, E., and J. M. Tylianakis. 2012. Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. *Ecology* 93:145–155.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Lavorel, S., K. Grigulis, P. Lamarque, M.-P. Colace, D. Garden, J. Girel, G. Pellet, and R. Douzet. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* 99:135–147.
- Lavorel, S., S. McIntyre, J. Landsberg, and T. Forbes. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* 12: 474–478.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- Manning, P., et al. 2015. Simple measures of climate, soil properties and plant traits predict national-scale grassland soil carbon stocks. *Journal of Applied Ecology* 52:1188–1196.
- Moles, A. T., D. I. Warton, L. Warman, N. G. Swenson, S. W. Laffan, A. E. Zanne, A. Pitman, F. A. Hemmings, and M. R. Leishman. 2009. Global patterns in plant height. *Journal of Ecology* 97:923–932.
- Nave, L. E., E. D. Vance, C. W. Swanston, and P. S. Curtis. 2011. Fire effects on temperate forest soil C and N storage. *Ecological Applications* 21:1189–1201.
- Pakeman, R. J., and H. M. Queded. 2007. Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science* 10:91–96.
- Pausas, J. G., R. A. Bradstock, D. A. Keith, and J. E. Keeley. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85:1085–1100.
- Peltzer, D. A., H. Kurokawa, and D. A. Wardle. 2016. Soil fertility and disturbance interact to drive contrasting responses of co-occurring native and non-native species. *Ecology* 97:515–529.
- Pérez-Harguindeguy, N., et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61:167.
- Pierce, S., G. Brusa, I. Vagge, and B. E. L. Cerabolini. 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology* 27:1002–1010.
- Poeplau, C., A. Don, L. Vesterdal, J. Leifeld, B. van Wesemael, J. Schumacher, and A. Gensior. 2011. Temporal dynamics of soil organic carbon after land-use change in the temperate zone – carbon response functions as a model approach. *Global Change Biology* 17:2415–2427.
- Post, W. M., and K. C. Kwon. 2000. Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology* 6:317–327.
- Pregitzer, K. S., and E. S. Euskirchen. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology* 10:2052–2077.
- R Core Development Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rasse, D. P., C. Rumpel, and M.-F. Dignac. 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil* 269:341–356.
- Ruiz, E. M., R. Vélez, C. L. Tot, and F. Hernández. 2007. Fire management – global assessment 2006. FAO Forestry Paper 151. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Schmidt, M. W. I., et al. 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478:49–56.
- Shiple, B., P. A. Keddy, D. R. J. Moore, and K. Lemky. 1989. Regeneration and establishment strategies of emergent macrophytes. *Journal of Ecology* 77:1093–1110.
- Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of

- multiple assembly processes. *Journal of Ecology* 100:652–661.
- Spasojevic, M. J., E. A. Yablon, B. Oberle, and J. A. Myers. 2014. Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* 5:1–20.
- Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Díaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M.-L. Navas. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14:1125–1140.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Vojtech, E., M. Loreau, S. Yachi, E. M. Spehn, and A. Hector. 2008. Light partitioning in experimental grass communities. *Oikos* 117:1351–1361.
- White, A. S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. *Ecology* 64:1081–1085.
- Wimberly, M., and M. Reilly. 2007. Assessment of fire severity and species diversity in the southern Appalachians using Landsat TM and ETM+ imagery. *Remote Sensing of Environment* 108:189–197.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2036/full>