Trait integration and functional differentiation among co-existing plant species

Julia I. Burton[1,5] (iD) , Steven S. Perakis[2], J. Renée Brooks[3], and Klaus J. Puettmann[4]

PREMISE: Determining which traits characterize strategies of coexisting species is important to developing trait-based models of plant communities. First, global dimensions may not exist locally. Second, the degree to which traits and trait spectra constitute independent dimensions of functional variation at various scales continues to be refined. Finally, traits may be associated with existing categorical groupings.

METHODS: We assessed trait integration and differentiation across 57 forest understory plant species in Douglas-fir forests of western Oregon, United States. We combined measurements for a range of traits with literature-based estimates of seed mass and species groupings. We used network analysis and nonmetric multidimensional scaling ordination (NMS) to determine the degree of integration.

RESULTS: We observed a strong leaf economics spectrum (LES) integrated with stem but not root traits. However, stem traits and intrinsic water-use efficiency integrated LES and root traits. Network analyses indicated a modest grouping of a priori trait dimensions. NMS indicated that multivariate differences among species were related primarily to (1) rooting depth and plant height vs. specific root length, (2) the LES, and (3) leaf size vs. seed mass. These differences were related to species groupings associated with growth and life form, leaf lifespan and seed dispersal mechanisms.

CONCLUSIONS: The strategies of coexisting understory plant species could not be reduced to a single dimension. Yet, species can be characterized efficiently and effectively for trait-based studies of plant communities by measuring four common traits: plant height, specific leaf area, leaf size, and seed mass.

KEY WORDS ecophysiology; functional ecology; herbaceous layer; leaf economics spectrum; network analysis; specific root length; stem-specific density; trait-based analysis.

Ecologists are increasingly developing trait-based models to mechanistically project how plant communities and ecosystem functions and services will respond to environmental change (Lavorel and Garnier, 2002; Laughlin et al., 2011; Madani et al., 2018). Given the diversity of traits that can potentially influence plant performance, a primary challenge lies in identifying traits that best represent the strategies of species in the community (Weiher et al., 1999; Shipley et al., 2016; Funk et al., 2017). Evolutionary and biophysical constraints can result in trait correlations, such as the worldwide leaf economics spectrum (LES) and analogous stem and root spectra (Eissenstat and Yanai, 1997; Wright et al., 2004; Chave et al., 2009; Ma et al., 2018). These dimensions may be further integrated in a single "fast–slow" plant economics spectrum reflecting a coordinated strategy for dealing with multiple forms of stress and resource limitation (Grace, 1990; Grime, 2001; Reich, 2014). Alternatively, strategies may be high-dimensional as a result of interactions among multiple resource limitations (Tilman, 1982; Westoby et al., 2002; Kraft et al., 2015). However, global-scale relationships may not be evident in local communities (Funk and Cornwell, 2013; Kraft et al., 2015; Messier et al., 2017). Moreover, measuring multiple correlated traits and/or traits that do not function to differentiate species locally can lead to diminishing returns (Laughlin, 2014). Therefore, an understanding of the relationship of trait integration and functional differentiation among species within local communities is required to determine which traits are necessary to represent ecological strategies in trait-based models.

Integration of traits and trait spectra across resources (i.e., light, water, carbon, and nutrients) and organs suggest that strategies of plants can be quantified using a relatively small number of traits (Reich et al., 2014). Global dimensions of trait

differentiation include the LES (Wright et al., 2004), wood/stem (Chave et al., 2009), and root (Eissenstat and Yanai, 1997; Ma et al., 2018) economics spectra, "size-dimension"-associated architectural constraints (Corner's rule, Corner, 1949; White, 1983; Díaz et al., 2016; Messier et al., 2017), and seed size–seed number trade-off (Moles and Westoby, 2004; Shipley and Dion, 1992). In addition to organ-based trait spectra, characterization of whole-plant traits with stable isotopes (i.e., intrinsic water-use efficiency [iWUE] and δ^{15}N) is increasingly contributing to our understanding of ecological strategies of plants (Evans, 2001; Dawson et al., 2002; Cornwell et al., 2018). Wright et al. (2004) noted that the LES represented in local communities generally mirrors that represented worldwide, but global scale trait relationships may not be present if community-level analyses are completed along short gradients or in taxonomically or functionally restricted study systems (Funk and Cornwell, 2013; Messier et al., 2017; Anderegg et al., 2018). Therefore, determining how traits and trait spectra differentiate species locally is key to selecting which traits to measure.

Recent studies have improved our understanding of relationships among a broad range of traits, organs, and trait spectra. Díaz et al. (2016) recently identified two principal independent global dimensions of trait variation related to plant size and construction costs for photosynthetic leaf area (i.e., the LES), suggesting high levels of integration among traits and a relatively small trait hypervolume. However, it is unclear whether and how these traits and trait spectra are integrated with other functionally important aspects of trait variation such as root traits (Tjoelker et al., 2005; Liu et al., 2010; Kramer-Walter et al., 2016), iWUE (Bonal et al., 2007; Li et al., 2015), and nitrogen discrimination (Laliberté, 2017). More studies are required to determine the degree to which these traits and trait spectra are integrated or constitute independent dimensions of functional variation among species.

There is a plethora of traits that may be important to community assembly, but continuous trait data are expensive to collect and/or time consuming (e.g., gas exchange). Indeed, project constraints frequently limit investigators to the use of functional groupings and literature-based traits (Aubin et al., 2009; Neill and Puettmann, 2013; Kern et al., 2014). Therefore, understanding how trait syndromes vary among species groupings can inform not only trait selection for a given community, but also interpretations of species groupings for studies lacking continuous trait data.

Here we assess trait integration and multivariate strategies of coexisting forest understory plant species. Understory species vary in growth and life form, leaf lifespan, clonality, successional status, and seed dispersal, and therefore represent a range of ecological strategies. Our first objective was to determine whether or not species were differentiated along a leaf economics spectrum. Then we quantified the degree to which LES traits were integrated with analogous stem and root economics traits, and stable isotope-based whole plant traits. Finally, we determined which continuous and categorical traits best distinguish species at the multivariate level. We hypothesized that (1) leaf traits differentiating species with acquisitive rather than conservative strategies are linked to analogous stem and root traits (e.g., Reich et al., 2014), and as a result, (2) species differentiate in low-dimensional space relative to the number of quantitative traits assessed ($n = 12$), and (3) quantitative trait dimensions are related to categorical species groupings.

MATERIALS AND METHODS

Study system

We collected trait data from seven sites composed of 60- to 80-yr-old Douglas-fir [*Pseudotsuga menziesii* (Mirbel) Franco, Pinaceae] stands with varying abundances of western hemlock [*Tsuga heterophylla* (Rafinesque) Sargent, Pinaceae; 0.4–53.3% basal area, Dodson et al., 2014] that have been commercially thinned twice. Sites are distributed across the western hemlock zone in Oregon, United States (Franklin and Dyrness, 1988), spanning a broad geographic (sites range between 10 and 245 km apart) and climatic gradient (across sites average 2001–2010 mean annual temperatures range from 8.6 to 11.7°C, mean annual precipitation ranges from 1274 to 2080 mm; Wang et al., 2016). The climate is Mediterranean with mild, wet winters and warm, dry summers (Franklin and Dyrness, 1988). Soils are well to poorly drained (highly weathered) Ultisols and (younger, less structured) Inceptisols and vary widely among sites in nitrogen availability (soil mineralization rates range from 80 to 207 mg N m^{-2}·30 d^{-1}; Thiel and Perakis, 2009). Thinning treatments were applied in a randomized complete block design with one replicate of four density treatments at each of seven 94–131-ha sites (Cissel et al., 2006). However, this experimental structure did not factor explicitly into the sampling design or analysis, except for the fact that treatments resulted in heterogeneous overstory conditions. Instead, we stratified our sampling not across treatments but across a range of overstory tree density (measured as basal area) and associated resources and environmental conditions. We used data collected from permanent plots (Ares et al., 2009) to select dominant understory species and characterize local overstory conditions. More detailed information about the experiment, history, soils, and climate has been described by Cissel et al. (2006) and Puettmann et al. (2016).

Field data collection

We focused on 12 whole-plant, leaf, stem, and root traits commonly used to infer ecological strategies of plants (Table 1). Plant traits were sampled in 2015, 3 years following that most recent experimental thinning treatment. The mass ratio hypothesis predicts that the contribution of species to ecosystem functions is proportional to their relative abundances (Grime, 1998). Therefore, we measured traits of species contributing to ≥80% of the cumulative importance (the average of the relative frequency and relative abundance, measured here as percent cover, Curtis and McIntosh, 1951). Plants were sampled in plots characterized by high (60+ m²/ha), intermediate (20–60 m²/ha) and low (0–20 m²/ha) levels of overstory basal area (a measure of overstory cover) at each site. We followed standard protocols (Pérez-Harguindeguy et al., 2013). Rooting depth was estimated as the vertical distance between the surface of the forest floor and the bottom of the excavation hole. For specimens with straight, robust roots, rooting depth was measured as the shortest distance between caudex and the deepest root segment. All depths were measured to the nearest 1 cm using a measuring tape. Rooting depth was estimated as 25+ cm for specimens with rooting depths >25 cm (e.g., most shrubs). Seed mass data were obtained from the Seed Information Database (Kew Royal Botanic Gardens, 2018). For more details on trait data collection procedures, see Appendix S1.

From foliar δ^{13}C values, we calculated iWUE, accounting for effects of vertical variation in the atmospheric CO_2 isotopic composition (Buchmann et al., 2002; Burton et al., 2017). Soil δ^{15}N values

TABLE 1. Quantitative whole-plant, leaf, stem, root and seed traits assessed in this study, abbreviation, units, ecological strategy, key resources/environmental conditions and references for theory and significance. The ratio of the maximum to minimum observed values indicates the range variation in our data.

Trait	Abbreviation	Units	Max/Min	Function(s)	Key resources/ environmental conditions	References
Whole plant						
N discrimination	$\Delta^{15}N$	‰	1.9[†]	N-use strategy	Soil N	1–3
Intrinsic water-use efficiency	iWUE	$\mu mol\ CO_2\ /mol\ H_2O$	2.4	Resource acquisition vs. conservation, energy balance	Water	4
Leaf						
Specific leaf area	SLA		9.9	Leaf economics	Soil nutrients, light, water	5, 6
Leaf N content	LNC	mg/g	2.8	Leaf economics	Soil nutrients, light, water	5, 6
Leaf N per unit area	N_{area}	g/m^3	8.8	Leaf economics	Soil nutrients, light, water	5, 6
Leaf dry matter content	LDMC	mg dry wt/g fresh wt	5.4	Leaf economics	Soil nutrients, light, water	5, 6
Leaf size	None	cm^2	445.0	Architectural constraints, energy balance	Soil nutrients, light, water, temperature	7–9
Stem						
Stem specific density	SSD	mg/mm^3	10.0	Stem economics	Water	10
Height	Ht	cm	38.1	Architectural constraints	Light	11, 17
Root						
Specific root length	SRL	m/g	33.5	Root economics	Soil nutrients, water	12, 13
Root depth	Depth	cm	3.5	Root economics	Water	14, 15
Seed						
Seed mass	None	g	340,000	Architectural constraints seed size vs. seed number	N/A	7, 16, 17

References:
(1) Evans, 2001; (2) Nadelhoffer et al., 1996; (3) Gubsch et al., 2011; (4) Farquhar et al., 1989; (5) Díaz et al., 2004; (6) Wright et al., 2004; (7) Corner, 1949; (8) Ackerly et al., 2002; (9) Wright et al., 2017; (10) Chave et al., 2009; (11) Givnish, 1982; (12) Eissenstat and Yanai, 1997; (13) Eissenstat, 2000; (14) Antos and Halpern, 1997; (15) Casper and Jackson, 1997; (16) Moles and Westoby, 2004; (17) Westoby et al., 2002.
Reflects absolute range in values spanning positive and negative values.

in forests vary widely in response to local topography, N fixation, and disturbance history, which can contribute to variation in plant tissue $\delta^{15}N$ among sites (Perakis et al., 2011, 2015). To control for background soil variation and enable comparisons of $\delta^{15}N$ as a trait-based measure of plant N use, we calculated $\Delta^{15}N$ as $\delta^{15}N_{soil}$ subtracted from leaf $\delta^{15}N$ before statistical analysis (e.g., Gubsch et al., 2011).

Data analyses

Integration of traits and trait spectra—All analyses were based on model-estimated species trait values for a common set of resources and environmental conditions (Appendix S2; Burton et al., 2017). First, we examined bivariate correlations among individual whole-plant, architectural, leaf, stem, and root traits (Table 1). Relationships among variables were nonlinear, even after log-transformation. Therefore, relationship strength was quantified using Spearman's rank correlation coefficients (ρ) and associated p-values. We used network analyses to visualize and quantify trait integration by constructing and analyzing our network graph using correlations with $\rho \geq 0.5$ (Appendix 1; Wright et al., 2006; Poorter et al., 2014; Messier et al., 2017). We excluded statistically significant correlations with $\rho < 0.5$ from our network because they are generally not expected to have a strong mechanistic basis (e.g., Poorter et al., 2014). Next, we used the Fruchterman–Reingold layout algorithm to determine the locations of nodes and edges (Fruchterman and Reingold, 1991). We tested whether predefined groups of traits (i.e., Table 1) formed distinct modules in the graph using the modularity function (Clauset et al., 2004). Modularity

(Q) is estimated as the fraction of edges within the defined modules minus the expected fraction if edges were random. Edges were weighted by their correlations (ρ). Q values can range from −1 to 1 and are positive when the observed number or weights of edges within groups exceeds a value expected by chance. We compared Q values assessing modulation among a priori trait groupings for the observed network (Q_A) to three alternative models. First, we calculated Q for a fully modulated network with perfect correlations ($\rho = 1$) among traits within each trait group (Q_M, Fig. 1B). Similarly, we compared Q_A to a completely integrated network (Q_I) with equal, but relatively weak, correlations among all traits ($\rho = 0.5$, Fig. 1A). To examine whether or not the a priori trait groupings (i.e., modules) were consistent with the observed trait groupings, we calculated Q_P for a network with modules identified post hoc using the cluster walktrap function. This function uses random walks to find densely connected subgraphs; short random walks between traits with shorter and thicker edges that are located near one another tend to stay in the same group or module. Finally, we quantified network centrality for traits using the degree and betweenness functions. The degree function yields a count of the number of edges connected to each node; in other words, how many other traits are connected to a given trait. Betweenness measures the position of a trait between several modules as the number of times a node acts as a bridge along the shortest path between two other nodes (Brandes, 2001). For example, a trait such as SLA can act as a bridge if it connects two other traits that are not directly connected (e.g., leaf dry matter content and stem specific density [SSD]). Hub traits with high centrality scores can be interpreted to have strong effects on plant strategies. All network analyses were
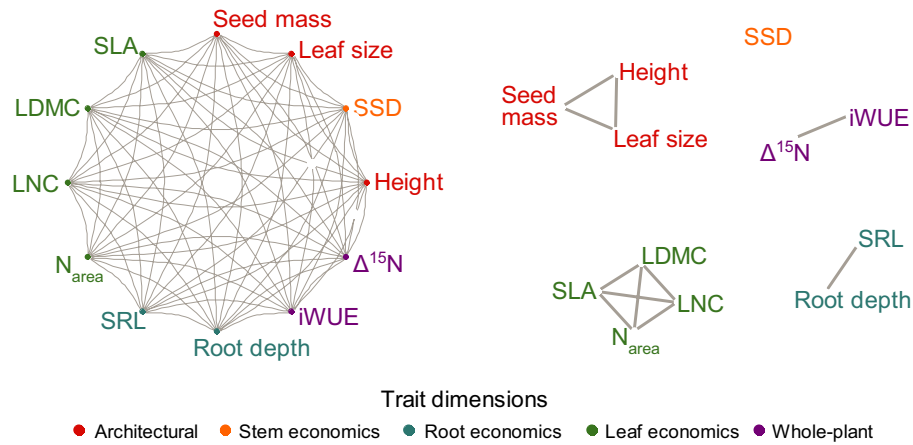
FIGURE 1. Hypothetical fully integrated (A) and completely modulated (B) trait networks for traits measured in this study. Modularity statistics (Q_I and Q_M, respectively) from these models were compared to the observed network in Fig. 3 (Q_A). Note that distances between nodes in fully integrated network (A) are meaningless in circular layout. Traits are color-coded according to a priori groupings and defined in Table 1.

performed using the igraph package (Csardi and Nepusz, 2006) in R version 3.4.3 (R Core Team, 2018).

Multivariate functional differentiation among species—To assess trait dimensionality and multivariate differences among species, we used nonmetric multidimensional scaling (NMDS). Even after transformation, many variables showed a lack of normality and nonlinear relationships. Therefore, we chose NMDS because it does not assume linear relationships among variables (Minchin, 1987; McCune and Grace, 2002). While principal component analysis (PCA) is the most common approach, NMDS is increasingly applied to analyze species-trait matrices (e.g., Cadotte et al., 2009; Apgaua et al., 2015; Miller et al., 2018). So that all traits were on the same scale, each trait was relativized to vary between zero and one. Then, values were transformed using an arcsine square-root transformation to reduce multivariate skewness and kurtosis and thus any influence on outlying observations. The Bray–Curtis distance for continuous data was used to measure trait similarity among species. We determined the number of axes by comparing stress from multiple runs with a range of dimensions. An additional axis was considered to improve the solution if it reduced stress by at least 0.05 and a randomization test showed that the proportion of runs with stress less than or equal to the observed stress was less than 0.05 (McCune and Grace, 2002). The final ordination configuration was rotated to maximize the variability along axis one. We fit biplot overlays using the envfit function. We also used Pearson correlations between species axis scores and traits to assess trait relationships with ordination axes (McCune and Grace, 2002). To quantify the degree to which a reduced set of indicator traits can be used to indicate multivariate strategies, we used a Mantel test (McCune and Grace, 2002) to assess the relationship between the full trait matrix, and a reduced matrix containing only indicator traits, i.e., traits with the strongest correlations with each axis.

We examined whether or not species groupings (i.e., Appendix S1a) reflected multivariate variation in quantitative traits using permutational, distance-based multivariate analysis of variance (PERMANOVA; Anderson, 2001; McCune and Grace, 2002). First, we used a simple separate 1-way test to examine

simple relationships between individual groupings and multivariate differences among species. Then, we used a multifactor analysis to assess how all species groupings collectively relate to multivariate differences in continuous traits. Post hoc pairwise comparisons were assessed in the event the null hypothesis of no differences among groups was rejected ($p < 0.05$). In that case, we corrected p-values for multiple comparisons using the sequential Bonferroni procedure (Holm, 1979). The relationship between species groupings and multivariate differences among species traits was visualized using ordination ellipses. Ordination, Mantel tests and PerMANOVA analyses were performed using the vegan package version 2.5-3 (Oksanen et al., 2018) in R version 3.5.1 (R Core Team, 2018). The randomization test on the ordination was performed in PC-ORD (McCune and Mefford, 2018).

RESULTS

Global LES generalization to the temperate forest understory plant community

The most interrelated traits were those associated with the LES. Relationships among SLA, LDMC, and LNC were consistent with those observed in the worldwide leaf economics spectrum (Appendix 3a). Leaf size was not related to traits in the leaf economics spectrum. Traits such as N discrimination (Δ^{15}N) and seed mass generally varied independently from the other traits at this local scale (Fig. S1). Stem traits were correlated with each other and with many LES traits (SLA, LDMC, and N_{area}). Plant height and SSD were correlated because a greater investment in mechanical stability is required to support taller plants (Appendix 3a). However, this correlation does not hold true when considering woody species alone ($\rho = 0.40$, $p = 0.10$). Within the root traits, rooting depth was more highly correlated with LES traits (LDMC and N_{area}) and stem economics (SSD) than was root economics (SRL; Appendix 3a). For the whole-plant isotopic traits, intrinsic water-use efficiency (iWUE) decreased with SLA and LNC, but increased with LDMC, N_{area}, leaf size, height, SSD, and root depth. Nitrogen discrimination (Δ^{15}N) was not related to any other continuous trait.

Integration of LES with root, stem, and whole-plant traits

Our network analyses revealed a high level of integration among traits (Fig. 2). Modulation of our a priori trait groupings ($Q_A = 0.01$) was lower than modulation of groupings identified post hoc using random walks ($Q_P = 0.11$), suggesting these post hoc groupings were superior to our a priori groupings. Four groupings were identified, the first included leaf economics traits, stem specific density, plant height, and iWUE. The second group included root traits and leaf size. Seed mass and Δ^{15}N were sole indicators of their groups. Results from the modularity test on the observed network
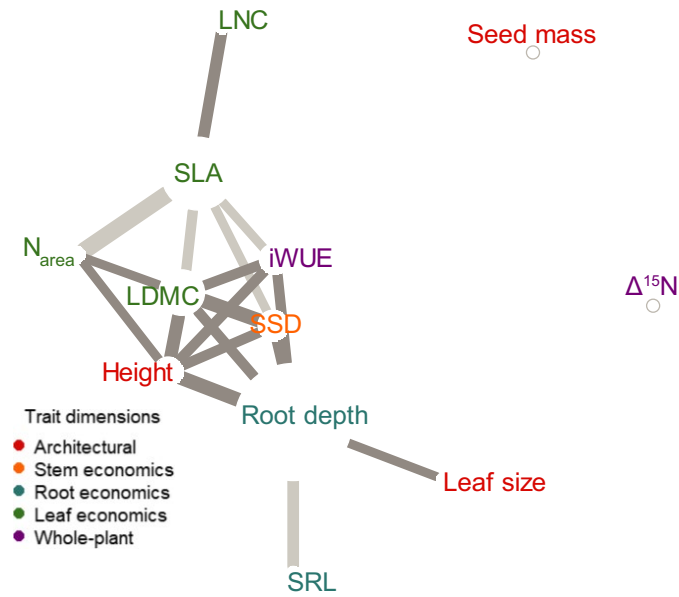
FIGURE 2. Observed correlation network showing interspecific correlations among whole-plant, leaf economics, stem, root and architectural traits ($\rho > 0.5$). The locations of traits were optimized using network analysis tools (igraph package, R), and reflect correlation strength. Nodes (white circles) are scaled to betweenness statistics, where larger nodes indicate greater centrality. Correlation strength is indicated by the thickness of edge lines. Positive correlations are shown as dark, and negative light, gray lines. Trait abbreviations are defined in Table 1.

$(Q_A = 0.01)$ showed that modulation, i.e., clustering of groups of traits, was weak but greater than expected by chance. In contrast, Q statistics for a fully modulated network (Q_M) with perfect correlations within groups and no correlations among traits in differing groups (Fig. 1B) and completely integrated networks (i.e., all traits are correlated equally, Q_I) with equal correlations among all traits (Fig. 1A) were 0.61 and −0.07, respectively. Thus, modularity of the observed network with the a priori groupings was only 1.6% of its potential.

The observed trait correlation network showed integration of iWUE with leaf economics traits (SLA and LDMC), height, and rooting depth (Fig. 2). In contrast, LNC, specific root length, seed mass, leaf size, and $\Delta^{15}N$ were weakly linked, if at all, to other traits in this network (Fig. 2). As the most central trait with the largest centrality statistics, rooting depth integrated SRL and leaf size with the rest of the traits in the network (Appendix S3b). SLA connected LNC to N_{area} and LDMC within the leaf economics spectrum. As a result, it had the second largest betweenness value. With the exception of LNC, leaf economics traits were highly integrated with each other (Fig. 2), resulting in high-degree measures (Appendix S3b).

Differentiation among species

Our results suggested that three dimensions were required to adequately capture multivariate differences among species (final stress = 0.10; Appendix S3c). Biplot overlays fit with the envfit function showed that with the exception of $\Delta^{15}N$, all traits were correlated with the ordination (Fig. 3). The majority of variation was captured by axis 1, which characterized a trade-off between large size (height,

TABLE 2. Multifactor PERMANOVA results relating species groupings to multivariate variation in continuous leaf, stem, and root traits.

Source	df	SS	MS	F	R^2	P
Growth form	4	0.27	0.07	7.86	0.32	0.001
Leaf lifespan	1	0.04	0.04	5.17	0.05	0.001
Life form	5	0.09	0.02	2.04	0.1	0.009
Clonality	1	0.02	0.02	1.83	0.02	0.114
Seral status	2	0.03	0.01	1.59	0.03	0.126
Primary seed dispersal mechanism	5	0.08	0.02	1.76	0.09	0.022
Residuals	37	0.32	0.01		0.38	

$r = -0.79$; rooting depth, $r = -0.88$; high LDMC, $r = -0.66$; iWUE, $r = -0.64$; SSD, $r = -0.59$; seed mass, $r = -0.48$; leaf size, $r = -0.41$) vs. high specific root length ($r = 0.61$). The second dimension differentiated species by leaf economics traits and seed mass. On the acquisitive end of the LES, species with higher SLA ($r = 0.75$) and LNC ($r = 0.55$) tended to have larger seeds ($r = 0.41$) and relatively low N_{area} ($r = -0.76$) and LDMC ($r = -0.47$). The third dimension characterizes a multivariate trade-off between leaf size ($r = -0.66$) and seed mass ($r = -0.61$). Our Mantel test revealed that four "indicator" traits from these three dimensions—plant height (axis 1), SLA (axis 2), leaf size (axis 3) and seed mass (axis 3)—explained a large percentage of variability in the full trait matrix ($r^2 = 0.82$, $p = 0.001$).

Results from our simple, single-factor PerMANOVA analysis showed that at the multivariate level, trait differences among species were related to selected species groups, including growth form ($F_{4, 51} = 6.06$, $p = 0.001$, $r^2 = 0.32$), Raunkiær's life forms ($F_{5, 50} = 3.68$, $p = 0.001$, $r^2 = 0.27$), seed dispersal mechanism ($F_{5, 50} = 3.25$, $p < 0.001$, $r^2 = 0.25$), and leaf lifespan (i.e., evergreen vs. deciduous; $F_{1, 54} = 3.47$, $p = 0.004$, $r^2 = 0.07$). Our multifactor model including all categorical traits, explained 62% of the variation in the distance matrix (Table 2). Reductions in R^2 between the single and multifactor models for life form and seed dispersal mechanism suggest that much of the variation explained by these traits was related to covariation with growth form ($F_{4, 37} = 7.86$, $p = 0.001$, $r^2 = 0.32$). Growth forms, life forms, and dispersal mechanisms were distinguished primarily along axis 1 reflecting differences in plant height and rooting depth (Fig. 4). Post hoc pairwise comparisons showed strong evidence traits of tall shrubs differed from low shrubs, forbs and graminoids, but not ferns ($p < 0.05$). Forbs also differed from ferns, graminoids, and low clonal shrubs ($p < 0.05$). Ferns did not differ from graminoids or low clonal shrubs, and graminoids did not differ from low clonal shrubs, but the number of species representing these groups was admittedly small (Appendix S1a). Differences among Raunkiær's life forms were related primarily to differences between phanerophytes and geophytes, rosettes and hemicryptophytes ($p < 0.05$). Differences among species with different seed dispersal mechanisms were related to differences between ingested and all other mechanisms of dispersal (i.e., wind, ant-dispersed, adhesive, ballistic, and gravity; $p < 0.05$). In contrast, evergreen and deciduous species were distinguished along axis 2, in association with leaf traits characteristic of slow (high LDMC and N_{area}) vs. fast (high SLA and LNC) returns on investments along the leaf economics spectrum (Fig. 4C, D). Interspecific trait variation among species was not related to clonality ($F_{1, 54} = 0.33$, $p = 0.878$) or seral stage ($F_{2, 53} = 1.60$, df = 1, $p = 0.120$).
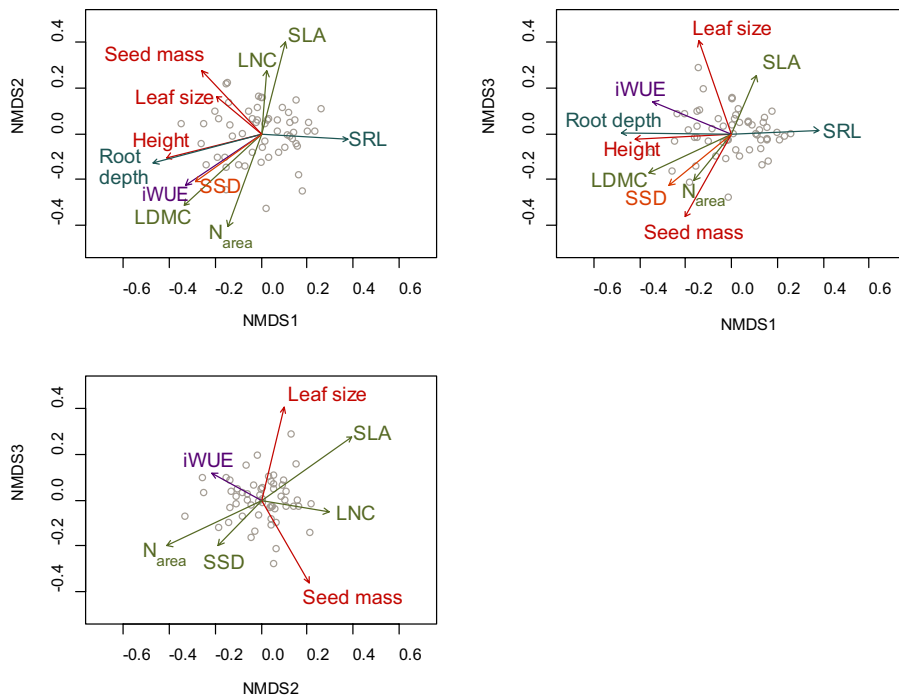
FIGURE 3. Nonmetric multidimensional scaling ordination of 56 species described by 11 leaf, stem, and whole-plant traits. Biplot overlay shows joint correlations between traits in the main matrix and ordination axis scores ($p < 0.05$). Colors are coded as in Figs. 1 and 2; trait abbreviations are defined in Table 1.

DISCUSSION

Our results show forest understory plant species were differentiated along the leaf economics spectrum; however, the ecological strategies of coexisting understory plant species cannot be reduced to a single integrated dimension (e.g., Reich, 2014). Intrinsic water-use efficiency (iWUE), stem specific density (SSD), and plant height integrated above- and belowground traits of temperate forest understory species. However, root traits, including rooting depth and specific root length (SRL) were generally independent of leaf economics. At the multivariate level, species were differentiated by three key dimensions, or trait spectra: (1) plant height and rooting depth vs. specific root length, (2) leaf economics, and (3) seed size vs. leaf size. Plant growth forms and life forms were differentiated along the first dimension, while the second dimension contrasted evergreen and deciduous species. "Indicator" traits from these two dimensions (i.e., plant height, SLA, leaf size, and seed mass) explained 82% of the variability in the trait matrix. Measuring these four traits alone may be sufficient for characterizing the strategies of coexisting species in trait-based models both efficiently and accurately.

Forest understory species differentiate along leaf economics spectrum

Consistent with Laughlin et al. (2010), results from this study provide strong evidence for a leaf economics spectrum in forest understory plant communities. Worldwide, leaf economics variation within a single community is larger than across biomes (Wright et al., 2004), highlighting the large number of successful strategies for plant coexistence in a given environment. However, Kraft et al. (2015) and Messier et al. (2017) observed weak leaf economics relationships locally in communities of annual herbs and deciduous trees, respectively, suggesting the LES is context dependent. These context dependencies result from differences in the range of strategies in local communities, with plant communities composed of just herbaceous or deciduous species with a narrow range of leaf lifespans exhibiting weak or no leaf economics relationships (Funk and Cornwell, 2013). Inclusion of species with both evergreen and deciduous leaf lifespans (Neufeld and Young, 2003) in temperate forest understory plant communities increases the likelihood of a local leaf economics spectrum relative to communities composed on deciduous species exclusively (e.g., Kraft et al., 2015; Messier et al., 2017). With the exception of Laughlin et al. (2010), we are not aware of any other studies of quantitative trait syndromes in temperate forest understory plant communities of this scope.

Network analyses show low levels of modularity among traits

Traits spanning organs and global spectra generally exhibited a large degree of integration; however, modulation of this network (i.e., correlations between groups of traits) was greater than expected by chance. The degree analysis identified a large number of traits with relatively high centrality scores. In contrast, the betweenness analysis identified two key traits that functioned to modulate the network: SLA and rooting depth. Thus, the degree analysis might be more useful for identifying traits central to modules within a more modulated network. In contrast, the betweenness statistic may be more useful for identifying key traits within a relatively integrated network. Although network analysis is increasingly recommended and used to analyze trait networks (e.g., Poorter et al., 2014), it has rarely been used to assess the range of traits examined here. The centrality of SLA and rooting depth in understory species contrasts with results of Messier et al. (2017), who found that the architectural trait leaf size was central to integrating a trait network in temperate deciduous tree species. Potential differences in overstory vs. understory communities and/or our examination of more species (Messier et al., 2017: $N = 57$ vs. $N = 24$) may be responsible for the different results. Our network analysis suggested a modest level of modulation of our trait network, with SLA and rooting depth functioning as central traits in the dominant modules.

Leaf economics spectrum is integrated with stem, but not root, economics

Integration of leaf and stem economics suggests trade-offs between hydraulic conductivity and mechanical stability are coordinated with trade-offs between carbon acquisition and conservation underlying the LES in understory plant communities (Chave, 2009; Reich, 2014). Leaf and stem trait integration may result when high rates of photosynthesis in plants with high SLA are supported by greater rates of hydraulic conductivity in plants with low SSD at the expense
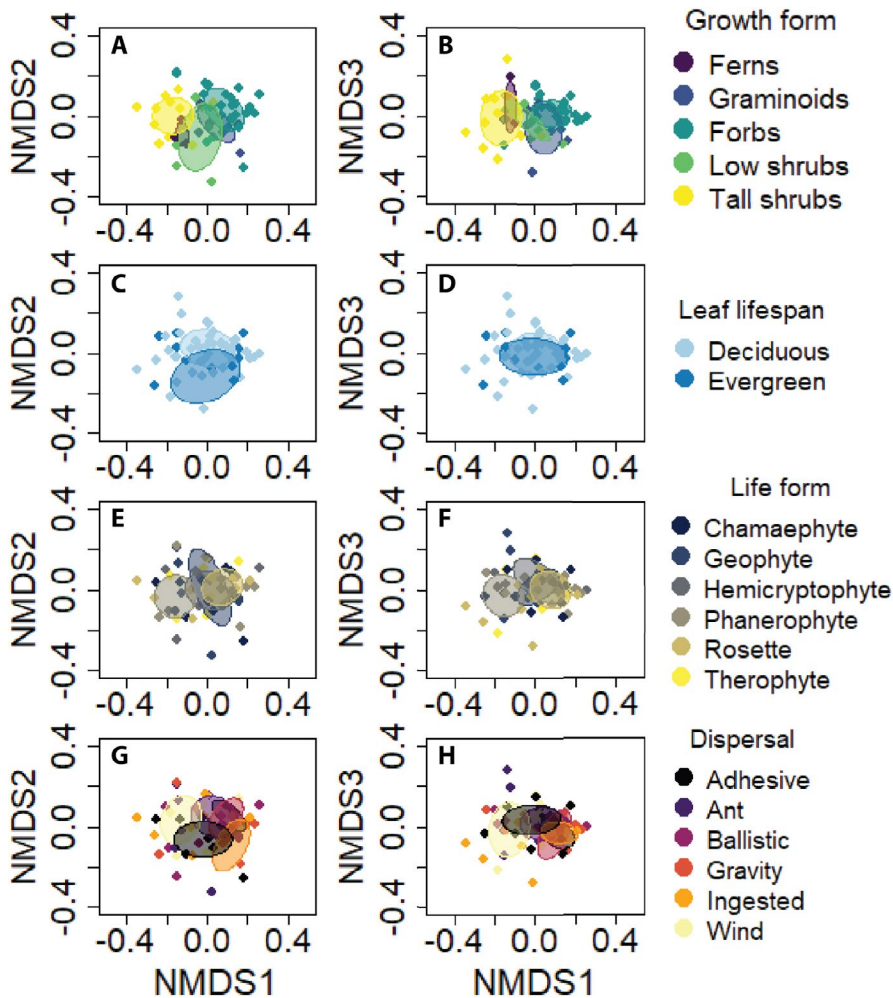
Growth form
- Ferns
- Graminoids
- Forbs
- Low shrubs
- Tall shrubs

Leaf lifespan
- Deciduous
- Evergreen

Life form
- Chamaephyte
- Geophyte
- Hemicryptophyte
- Phanerophyte
- Rosette
- Therophyte

Dispersal
- Adhesive
- Ant
- Ballistic
- Gravity
- Ingested
- Wind

FIGURE 4. Ellipses showing the distribution of species groupings in ordination space (Fig. 3) based on (A, B) growth form, (C, D) phenology, (E, F) Raunkiær's life forms, and (G, H) seed dispersal. Plots of NMDS ordination for 57 species described by 11 leaf, stem, root, and whole-plant traits.

branching order (e.g., McCormack et al., 2015), may reveal more dimensions of root trait variability to compare with the LES.

iWUE integrates leaf economics with size, stem, and root traits

Relationships between LES traits and iWUE observed here suggest strong integration of water, C, and N economies. Consistent with previous studies (e.g., Bonal et al., 2007; Li et al., 2015; Messier et al., 2017), iWUE decreased with SLA and LNC and increased with LDMC and N_{area}. Increased N_{area} is associated with higher photosynthetic enzyme content, which increases leaf C demand (e.g., Cornwell et al., 2018). Hence, plants can increase carbon assimilation per unit water transpired by adjusting leaf morphology and biochemistry. Intrinsic water-use efficiency was also positively related to height and rooting depth and negatively related to SRL. These relationships indicate that increases in iWUE owing to greater stature and access to light, and associated increased demand for water are more important than decreases in iWUE associated with increases in stomatal conductance and access to available soil water in deeper horizons (Ehleringer and Dawson, 1992; Schwinning and Ehleringer, 2001; Warren et al., 2005). Our estimates of iWUE account for spatial (e.g., Buchmann et al., 2002) and temporal variation in atmospheric $\delta^{13}C$, as well as climate and soil N (Cornwell et al., 2018). However, a relatively large proportion of variability in this trait occurs within species compared to other morphological traits (Table 1; Burton et al., 2017). Moreover, $\delta^{13}C$ and related traits (iWUE, $\Delta^{13}C$) may only differ among species in semi-arid or Mediterranean ecosystems where gradients in moisture deficit structure plant communities. Thus, the usefulness of iWUE in trait-based models of plant communities may hinge not only on how well it functions to differentiate coexisting species, but also on how the various mechanisms underlying iWUE interact to influence plant performance.

N discrimination was not related to other traits

Despite its potential to integrate across trait spectra and organs (e.g., especially leaf nitrogen and root traits; Laliberte, 2017), N discrimination ($\Delta^{15}N$) was not related to any other traits. Our results are consistent with high intraspecific variation and low levels of interspecific variation in $\Delta^{15}N$ (Burton et al., 2017), as well as patterns of overstory $\delta^{15}N$ in these forests (Perakis and Sinkhorn, 2011; Perakis et al., 2015). The lack of a relationship between $\Delta^{15}N$ and LNC may also reflect greater reliance on NH_4^+

of longer returns on investments in leaf mass, mechanical stability and resistance to moisture stress (e.g., Santiago et al., 2004; Mendez-Alonzo et al., 2012). In contrast, consistent with Tjoelker et al. (2005) and Kramer-Walter et al. (2016), our results showed that specific root length (SRL, m mg^{-1}) was independent from LES traits and stem economics (i.e., as captured by SSD). Specific root length was negatively correlated with rooting depth, suggesting a trade-off between constructing short-lived roots with high SRL and longer-lived roots with low SRL (Eissenstat and Yanai, 1997) that root deeper in the soil profile. Reducing SRL may allow plants growing in dry soil to penetrate deeper soil layers to access more consistently available soil water (Nicotra et al., 2002; Larson and Funk, 2016; Ma et al., 2018). This belowground trade-off between SRL and rooting depth does not appear to constrain strategies associated with the LES and SSD aboveground. However, we only considered a limited suite of root traits and the particular traits underlying root economics vary among studies and do not always include SRL (Tjoelker et al., 2005; Kramer-Walter et al., 2016; Roumet et al., 2016). Studies assessing a broader range of functional, morphological, and architectural traits associated with diversity in resource uptake strategies, including mycorrhizal associations (e.g., Weemstra et al., 2016) and the degree of

uptake and/or greater mycorrhizal $\delta^{15}N$ discrimination by species with low LNC (Evans, 2001; Gubsch et al., 2011). However, it also highlights the complex network of relationships affecting $\Delta^{15}N$ in plants. This complexity can limit the utility of $\delta^{15}N$ as a trait beyond specific case studies.

Multivariate differences among species suggest three principal ecological dimensions

Our ordination provided evidence for three independent dimensions of ecological variation among species described by 11 continuous traits. The first dimension primarily contrasts taller species with deep rooting depths from species with high specific root length (SRL). Disturbance and structural development commonly result in heterogeneity in light and soil resources in forest understory ecosystems. Increases in plant height reflect light competition (e.g., Givnish, 1982; Westoby et al., 2002). The integration of rooting depth and height may therefore reflect the integration of above- and belowground competition (e.g., Antos and Halpern, 1997; Semchenko et al., 2008; Violle et al., 2009). In contrast, high SRL may benefit shorter forb and graminoid species with shallow roots that occupy the relatively shady portions of the understory. High SRL may allow plants to capitalize on abundant soil moisture and available nutrients early in the growing season or on resource pulses in shallow soil layers later in the summer dry season (Eissenstat, 1991; Schwinning and Ehleringer, 2001). Measurements of height alone may be sufficient for characterizing this size dimension for trait-based analyses of understory communities (Violle et al., 2009).

The second dimension contrasting species with high SLA and LNC from species with high N_{area}, LDMC, and iWUE, was consistent with the global LES, which reflects an evolutionary trade-off between fast and slow returns on investments of dry mass (Wright et al., 2004). The LES dimension was orthogonal to the first dimension, suggesting this trade-off is ubiquitous across growth and life forms. The relationship between our LES dimension and leaf lifespan (i.e., evergreen vs. deciduous) was relatively weak, explaining only 7% of the variation among species. Nevertheless, leaf lifespan varies continuously and the dichotomy between evergreen and deciduous leaves is relatively simple. At the multivariate level, continuous variation in traits associated with the global LES is clearly important to distinguishing species. This variation is likely associated with species distributions along gradients in resources associated with canopy disturbance and edaphic condition. Thus, measuring traits that characterize the LES is important for characterizing this second dimension of functional differentiation in temperate forest understory plant communities.

Finally, the third dimension separated species with large leaves from species with large seed masses. This third dimension contrasted with Corner's rules, which predicts positive relationships between leaf size, branching angle, and fruit and seed size (Corner, 1949) and evidence supporting this rule in neotropical forests (Wright et al., 2006) and eastern deciduous tree communities (White, 1983; Messier et al., 2017). The discrepancy between these studies and our results may suggest that Corner's rule may apply to fruit, rather than seed mass. Seed mass does not necessarily reflect fruit size in temperate forest understory species. Species with large leaves can have large aggregate fruits containing hundreds of small seeds. However, these traits are correlated at only the multivariate level (i.e., a relationship is only shown in ordination), and this relationship is not evident in our analysis of bivariate correlations. Therefore, the relationship between leaf size and seed mass here is an indirect result of correlations with other traits, rather than the result of architectural constraints. Our results suggest that variation in leaf area may reflect energy balance and functional differentiation along temperature gradients (Wright et al., 2017), consistent with the findings of Ackerly et al. (2002) that LES and leaf size dimensions in Mediterranean chaparral communities were independent. Therefore, rather than architectural constraints, this axis may reflect non-resource conditions (e.g., Grace, 1990). However, including measurements of a larger suite of architectural traits may elucidate a stronger architectural dimension.

Multivariate dimensions were generally consistent with the results from the network analysis. Both analyses identified rooting depth and LES traits as differentiating different aspects of functional variation among species. However, traits in the emergent (post hoc) modules (i.e., groups of correlated traits) identified in the network analysis were not consistent with trait spectra identified in the ordination. Differences suggest that functional differentiation at the multivariate level may not necessarily represent physiological constraints underlying species differences. Thus, multivariate differences among species may change in unpredictable ways as environmental changes exert selective pressures on trait networks. Bivariate correlations, network analysis, and structural equation modeling (e.g., Grace et al., 2012) are useful for understanding these constraints, whereas multivariate ordinations may prove most useful for differentiating species in local communities and understanding broader strategies.

CONCLUSIONS

This study contributes to evidence for a local leaf economics spectrum in temperate forest understory plant communities. Our results provide support for the integration of stem economics with the LES, but not root economics as represented by SRL. Rather, SRL was negatively related to plant height and rooting depth at the multivariate level and independent of the LES. In contrast, iWUE integrated leaf economics and stem and root traits likely through various mechanisms. Consistent with those of Laughlin et al. (2010), our results provide quantitative support a leaf–height–seed scheme similar to that proposed by Westoby et al. (2002). However, we highlight a role for root traits, which were correlated with plant height. Rooting depth may be relatively more important than height in our study system characterized by summer-dry Mediterranean climates where water and other belowground resources are limiting at least during part of the year (Franklin and Dyrness, 1988; Beedlow et al., 2013; Perakis et al., 2015). Height may be relatively more important than root traits for distinguishing species in other locations where light competition is relatively more severe (Givnish, 1982). Integration of a priori species groupings with multidimensional variation in continuous traits suggests the LES generalizes across growth and life forms and permits a functional interpretation of these groupings in the absence of continuous trait data. Additional studies are required to confirm the generality of patterns observed here in other communities and the function of these traits in determining community responses to variation in disturbance and environmental gradients (e.g., Laughlin et al., 2011; Shipley et al.,

2016). While strategies are multidimensional, resulting from a complex network of trait–trait relationships, our results suggest that including traits beyond those most representative of these dimensions in models of understory plant communities can lead to inefficiencies.

CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

AUTHOR CONTRIBUTIONS

J.I.B., S.S.P., J.R.B., and K.J.P. conceived and designed the study. J.I.B. conducted the field work, analyzed the data, and wrote the first draft of the manuscript. All authors contributed to revisions.

DATA AVAILABILITY

The final data sets used in this study are available at Figshare: https://figshare.com/account/articles/11605398 (Burton et al., 2020).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Details related to plant trait measurements.

APPENDIX S2. Details related to analytical methods.

APPENDIX S3. Supplementary results.

LITERATURE CITED

Ackerly, D. D., C. A. Knight, S. B. Weiss, K. Barton, and K. P. Starmer. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130: 449–457.

Anderegg, L. D. L., L. T. Berner, G. Badgley, M. L. Sethi, B. E. Law, J. HilleRisLambers, and J. Penuelas. 2018. Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* 21: 734–744.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.

Antos, J. A., and C. B. Halpern. 1997. Root system differences among species: implications for early successional changes in forest of western Oregon. *American Midland Naturalist* 138: 97–108.

Apgaua, D. M., F. Y. Ishida, D. Y. Tng, M. J. Laidlaw, R. M. Santos, R. Rumman, D. Eamus, et al. 2015. Functional traits and water transport strategies in lowland tropical rainforest trees. *PLOS One* 10: e0130799.

Ares, A., S. D. Berryman, and K. J. Puettmann. 2009. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. *Applied Vegetation Science* 12: 472–487.

Aubin, I., M. H. Ouellette, P. Legendre, C. Messier, and A. Bouchard. 2009. Comparison of two plant functional approaches to evaluate natural restoration along an old-field–deciduous forest chronosequence. *Journal of Vegetation Science* 20: 185–198.

Beedlow, P. A., E. H. Lee, D. T. Tingey, R. S. Waschmann, and C. A. Burdick. 2013. The importance of seasonal temperature and moisture patterns on growth of Douglas-fir in western Oregon, USA. *Agricultural and Forest Meteorology* 169: 174–185.

Bonal, D., C. Born, C. Brechet, S. Coste, E. Marcon, J.-C. Roggy, and J.-M. Guehl. 2007. The successional status of tropical rainforest tree species is associated with differences in leaf carbon isotope discrimination and functional traits. *Annals of Forest Science* 64: 169–176.

Brandes, U. 2001. A faster algorithm for betweenness centrality. *Journal of Mathematical Sociology* 25: 163–177.

Buchmann, N., J. R. Brooks, and J. R. Ehleringer. 2002. Predicting daytime carbon isotope ratios of atmospheric CO_2 within forest canopies. *Functional Ecology* 16: 49–57.

Burton, J. I., S. S. Perakis, S. C. McKenzie, C. E. Lawrence, and K. J. Puettmann. 2017. Intraspecific variability and reaction norms of forest understorey plant species traits. *Functional Ecology* 31: 1881–1893.

Burton, J. I., S. S. Perakis, J. R. Brooks, and K. J. Puettmann. 2020. Trait integration and functional differentiation among co-existing plant species. figshare [data set]. https://doi.org/10.6084/m9.figshare.11605398.

Cadotte, M. W., J. Cavender-Bares, D. Tilman, and T. H. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PloS One* 4: e5695.

Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28: 545–570.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Cissel, J. H., P. D. Anderson, D. Olson, K. J. Puettmann, S. D. Berryman, S. Chan, and C. Thompson. 2006. BLM density management and riparian buffer study: establishment report and study plan. Scientific Investigations Report 2006-5087. U.S. Geologial Survey, Reston, VA, USA.

Clauset, A., M. E. Newman, and C. Moore. 2004. Finding community structure in very large networks. *Physical Review E* 70: 066111.

Corner, E. J. H. 1949. The durian theory or the origin of the modern tree. *Annals of Botany* 13: 367–414.

Cornwell, W. K., I. J. Wright, J. Turner, V. Maire, M. M. Barbour, L. A. Cernusak, T. Dawson, et al. 2018. Climate and soils together regulate photosynthetic carbon isotope discrimination within C_3 plants worldwide. *Global Ecology and Biogeography* 27: 1056–1067.

Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. *InterJournal 2006*: Complex Systems 1695: 1–9.

Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie–forest border region of Wisconsin. *Ecology* 32: 476–496.

Dawson, T. E., S. Mambelli, A. H. Plamboeck, P. H. Templer, and K. P. Tu. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507–559.

Díaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Marti, et al. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* 15: 295–304.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, et al. 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.

Dodson, E. K., J. I. Burton, and K. J. Puettmann. 2014. Multiscale controls on natural regeneration dynamics after partial overstory removal in Douglas-fir forests in western Oregon, USA. *Forest Science* 60: 953–961.

Ehleringer, J., and T. Dawson. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell & Environment* 15: 1073–1082.

Eissenstat, D. M. 1991. On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. *New Phytologist* 118: 63–68.

Eissenstat, D. 2000. Root structure and function in an ecological context. *New Phytologist* 148: 353–354.

Eissenstat, D., and R. Yanai. 1997. The ecology of root lifespan. *Advances in Ecological Research* 27: 1–60.

Evans, R. D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends in Plant Science* 6: 121–126.

Farquhar, G., K. Hubick, A. Condon, and R. Richards. 1989. Carbon isotope fractionation and plant water-use efficiency. *In* P. W. Rundel, J. R. Ehleringer, and K. A. Nagy [eds.], Stable isotopes in ecological research, 21–40. Springer, New York, NY, USA.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR, USA.

Fruchterman, T. M., and E. M. Reingold. 1991. Graph drawing by force-directed placement. *Software: Practice and Experience* 21: 1129–1164.

Funk, J. L., and W. K. Cornwell. 2013. Leaf traits within communities: Context may affect the mapping of traits to function. *Ecology* 94: 1893–1897.

Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C. Laughlin, et al. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews* 92: 1156–1173.

Givnish, T. J. 1982. On the adaptive significance of leaf height in forest herbs. *American Naturalist* 120: 353–381.

Grace, J. B. 1990. On the relationship between plant traits and competitive ability. *In* J. B. Grace and D. Tilman [eds.], Perspectives on plant competition, 51–65. Academic Press, New York, NY, USA.

Grace, J. B., D. R. Schoolmaster, G. R. Guntenspergen, A. M. Little, B. R. Mitchell, K. M. Miller, and E. W. Schweiger. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere* 3: 1–44.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.

Grime, J. P. 2001. Plant strategies and vegetational processes, 2nd ed. Wiley & Sons, New York, NY, USA.

Gubsch, M., C. Roscher, G. Gleixner, M. Habekost, A. Lipowsky, B. Schmid, E. D. Schulze, et al. 2011. Foliar and soil $\delta^{15}N$ values reveal increased nitrogen partitioning among species in diverse grassland communities. *Plant, Cell & Environment* 34: 895–908.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6: 65–70.

Kern, C. C., R. A. Montgomery, P. B. Reich, and T. F. Strong. 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. *Forest Science* 60: 335–344.

Kew Royal Botanic Gardens. 2018. Seed Information Database—SID, version 7.1. Website http://data.kew.org/sid/ [accessed February 2017].

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences, USA* 112: 797–802.

Kramer-Walter, K. R., P. J. Bellingham, T. R. Millar, R. D. Smissen, S. J. Richardson, and D. C. Laughlin. 2016. Root traits are multidimensional: Specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* 104: 1299–1310.

Laliberté, E. 2017. Below-ground frontiers in trait-based plant ecology. *New Phytologist* 213: 1597–1603.

Larson, J. E., and J. L. Funk. 2016. Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. *New Phytologist* 210: 827–838.

Laughlin, D. C. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* 102: 186–193.

Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf–height– seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* 24: 493–501.

Laughlin, D. C., P. Z. Fule, D. W. Huffman, J. Crouse, and E. Laliberté. 2011. Climatic constraints on trait-based forest assembly. *Journal of Ecology* 99: 1489–1499.

Lavorel, S., and É. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.

Li, L., M. L. McCormack, C. Ma, D. Kong, Q. Zhang, X. Chen, H. Zeng, et al. 2015. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecology Letters* 18: 899–906.

Liu, G., G. T. Freschet, X. Pan, J. H. Cornelissen, Y. Li, and M. Dong. 2010. Coordinated variation in leaf and root traits across multiple spatial scales in Chinese semi-arid and arid ecosystems. *New Phytologist* 188: 543–553.

Ma, Z., D. Guo, X. Xu, M. Lu, R. D. Bardgett, D. M. Eissenstat, M. L. McCormack, and L. O. Hedin. 2018. Evolutionary history resolves global organization of root functional traits. *Nature* 555: 94–97.

Madani, N., J. S. Kimball, A. P. Ballantyne, D. L. Affleck, P. M. Bodegom, P. B. Reich, J. Kattge, et al. 2018. Future global productivity will be affected by plant trait response to climate. *Scientific Reports* 8: 2870.

McCormack, M. L., I. A. Dickie, D. M. Eissenstat, T. J. Fahey, C. W. Fernandez, D. Guo, H. S. Helmisaari, et al. 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207: 505–518.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR, USA.

McCune, B., and M. J. Mefford. 2018. PC-ORD. Multivariate analysis of ecological data, version 7.08.. MjM Software Design, Gleneden Beach, OR, USA.

Méndez-Alonzo, R., H. Paz, R. C. Zuluaga, J. A. Rosell, and M. E. Olson. 2012. Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93: 2397–2406.

Messier, J., M. J. Lechowicz, B. J. McGill, C. Violle, and B. J. Enquist. 2017. Interspecific integration of trait dimensions at local scales: The plant phenotype as an integrated network. *Journal of Ecology* 105: 1775–1790.

Miller, J. A., R. Gillman, J. T. Carlton, C. C. Murray, J. C. Nelson, M. Otani, and G. M. Ruiz. 2018. Trait-based characterization of species transported on Japanese tsunami marine debris: effect of prior invasion history on trait distribution. *Marine Pollution Bulletin* 132: 90–101.

Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89–107.

Moles, A. T., and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92: 372–383.

Nadelhoffer, K., G. Shaver, B. Fry, A. Giblin, L. Johnson, and R. McKane. 1996. ^{15}N natural abundances and N use by tundra plants. *Oecologia* 107: 386–394.

Neill, A. R., and K. J. Puettmann. 2013. Managing for adaptive capacity: thinning improves food availability for wildlife and insect pollinators under climate change conditions. *Canadian Journal of Forest Research* 43: 428–440.

Neufeld, H. S., and D. R. Young. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. *In* F. S. Gilliam and M. R. Roberts [eds.], The herbaceous layer in forests of eastern North America, 38–90. Oxford University Press, New York, NY, USA.

Nicotra, A., N. Babicka, and M. Westoby. 2002. Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phylogenetically independent contrasts. *Oecologia* 130: 136–145.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2018. vegan: community ecology package. R package version 2.5-3. Website: https://CRAN.R-project.org/package=vegan.

Perakis, S. S., and E. R. Sinkhorn. 2011. Biogeochemistry of a temperate forest nitrogen gradient. *Ecology* 92: 1481–1491.

Perakis, S. S., A. J. Tepley, and J. E. Compton. 2015. Disturbance and topography shape nitrogen availability and δ^{15}N over long-term forest succession. *Ecosystems* 18: 573–588.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. Bret-Harte, et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.

Poorter, H., H. Lambers, and J. R. Evans. 2014. Trait correlation networks: a whole-plant perspective on the recently criticized leaf economic spectrum. *New Phytologist* 201: 378–382.

Puettmann, K. J., A. Ares, J. I. Burton, and E. K. Dodson. 2016. Forest Restoration using variable density thinning: lessons from Douglas-fir stands in western Oregon. *Forests* 7: 14.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P. B. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

Roumet, C., M. Birouste, C. Picon-Cochard, M. Ghestem, N. Osman, S. Vrignon-Brenas, K. F. Cao, and A. Stokes. 2016. Root structure–function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist* 210: 815–826.

Santiago, L. S., G. Goldstein, F. C. Meinzer, J. B. Fisher, K. Machado, D. Woodruff, and T. Jones. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140: 543–550.

Schwinning, S., and J. R. Ehleringer. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* 89: 464–480.

Semchenko, M., K. Zobel, A. Heinemeyer, and M. J. Hutchings. 2008. Foraging for space and avoidance of physical obstructions by plant roots: a comparative study of grasses from contrasting habitats. *New Phytologist* 179: 1162–1170.

Shipley, B., and J. Dion. 1992. The allometry of seed production in herbaceous angiosperms. *The American Naturalist* 139: 467–483.

Shipley, B., F. Bello, J. H. C. Cornelissen, E. Laliberté, D. C. Laughlin, and P. B. Reich. 2016. Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* 180: 923–931.

Thiel, A. L., and S. S. Perakis. 2009. Nitrogen dynamics across silvicultural canopy gaps in young forests of western Oregon. *Forest Ecology and Management* 258: 273–287.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ, USA.

Tjoelker, M., J. M. Craine, D. Wedin, P. B. Reich, and D. Tilman. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* 167: 493–508.

Violle, C., E. Garnier, J. Lecoeur, C. Roumet, C. Podeur, A. Blanchard, and M.-L. Navas. 2009. Competition, traits and resource depletion in plant communities. *Oecologia* 160: 747–755.

Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLOS One* 11: e0156720.

Warren, J. M., F. C. Meinzer, J. R. Brooks, and J. C. Domec. 2005. Vertical stratification of soil water storage and release dynamics in Pacific Northwest coniferous forests. *Agricultural and Forest Meteorology* 130: 39–58.

Weemstra, M., L. Mommer, E. J. W. Visser, J. Ruijven, T. W. Kuyper, G. M. J. Mohren, and F. J. Sterck. 2016. Towards a multidimensional root trait framework: a tree root review. *New Phytologist* 211: 1159–1169.

Weiher, E., A. van der Werf, K. Thompson, M. Roderick, E. Garnier, and O. Eriksson. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

White, P. S. 1983. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. *Bulletin of the Torrey Botanical Club* 110: 203–212.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, et al. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Wright, I. J., D. D. Ackerly, F. Bongers, K. E. Harms, G. Ibarra-Manriquez, M. Martinez-Ramos, S. J. Mazer, et al. 2006. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99: 1003–1015.

Wright, I. J., N. Dong, V. Maire, I. C. Prentice, M. Westoby, S. Díaz, M. R. Gallagher, et al. 2017. Global climatic drivers of leaf size. *Science* 357: 917–921.