

Covariance as constraint: Leveraging leaf economic relationships to constrain plant functional type trait estimates

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introduction	1215	18.4
methods	1747	26.5
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conclusions	324	4.9
total	6598	100.0

Summary

- We investigated whether global leaf economic relationships across plant functional types (PFTs) are also present within-PFTs, and the extent to which this hierarchical structure can be used to constrain trait estimates.
- We developed a hierarchical multivariate Bayesian model that assumes separate means and covariance structures within and across PFTs and fit this model to seven leaf traits from the TRY database: longevity, specific leaf area, nitrogen and phosphorus contents, and rates of dark respiration, maximum

Rubisco carboxylation, and maximum electron transport. We evaluated the ability of this model to estimate trait means and reproduce leaf economic trade-offs.

- Leveraging covariance in multivariate models reduced uncertainties in mean trait estimates, particularly for undersampled trait-PFT combinations. However, additional constraint from the across-PFT hierarchy was limited compared to the simple multivariate models.
- Trait correlations were generally consistent in direction within and across PFTs, and consistent with predictions of the leaf economic spectrum. However, correlation strength varied substantially across PFTs indicating that leaf economic relationships within PFTs are often confounded by other biotic and abiotic factors.

1 Introduction

The diversity and dimensionality of the terrestrial biosphere is vast and complex, and therefore there has been a recurring debate in ecology about the utility of reductionist approaches for capturing this variability. In particular, the use of functional groups with common characteristics has been widely applied in biodiversity studies (Naeem & Wright, 2003) and is essential to the structure of many ecosystem models (Lavorel *et al.*, 1997; Wullschleger *et al.*, 2014). However, ecologists have long recognized the importance of individual variability and stochasticity in shaping ecosystems (Gleason, 1926; Bolnick *et al.*, 2011; Rosindell *et al.*, 2011; Clark, 2016), and the benefits of more finely-resolved representation of functional diversity for predictive ecology are supported by an increasing body of trait ecology literature (Mayfield *et al.*, 2006; McMahon *et al.*, 2011; Van Bodegom *et al.*, 2012; Reichstein *et al.*, 2014; Violle *et al.*, 2014; Medlyn *et al.*, 2015; Moran *et al.*, 2016).

Plant functional traits can be used to link directly measurable features of individuals to their fitness within an ecosystem and, by extension, ecosystem performance as a whole (Violle *et al.*, 2007). Recent syntheses of global trait databases have revealed that although the functional diversity among plant species is immense, this diversity is constrained by allometries and trade-offs between plant strategies (Wright *et al.*, 2004; Kattge *et al.*, 2011; Kleyer & Minden, 2015; Díaz *et al.*, 2016). One axis of trait covariation currently receiving attention is the ‘leaf economic spectrum’, which defines a trade-off between plant investment in productive but short-lived leaves versus less productive but sturdy and long-lived leaves (Wright *et al.*, 2004; Shipley *et al.*, 2006; Reich, 2014; Díaz *et al.*, 2016). Leaf economic traits are well-correlated with plant ecophysiology (Shipley *et al.*, 2005; Niinemets, 2016; Wu *et al.*, 2016b) community composition (Cavender-Bares *et al.*, 2004; Burns, 2004), ecosystem functioning (Diaz *et al.*, 2004; Musavi *et al.*, 2015), and landscape biogeochemistry (Bakker *et al.*, 2011; Hobbie, 2015). The relative position of plant species along the primary axis of the leaf economic spectrum has been shown to be influenced by climate and soil conditions (Wright *et al.*, 2004, 2005b; Cornwell & Ackerly, 2009; Ordoñez *et al.*, 2009; Wigley *et al.*, 2016). As a result, relationships between leaf economic traits and climate have been incorporated into ecosystem models to allow for continuous variation in plant function and environmental responses (Sakschewski *et al.*, 2015; Verheijen *et al.*, 2015).

However, the use of among-trait and trait-environment correlations at the global scale, for both qualitative ecological inference and land surface modeling, has several important caveats. First, observed correlations at the global scale do not always hold at smaller scales (such as sites, species, and individuals). For example, some studies suggested consistent correlations across scales (Wright *et al.*, 2004; Albert *et al.*, 2010a; Asner *et al.*, 2014) whereas others showed no or even opposite correlations (Albert *et al.*, 2010b; Messier *et al.*, 2010, 2017; Wright & Sutton-Grier, 2012; Kichenin *et al.*, 2013; Feng & Dietze, 2013; Grubb *et al.*, 2015; Wigley *et al.*, 2016). Many mechanisms have been suggested for deviation from global trait relationships at smaller scales. Trade-offs between strategies may only be applicable when multiple competing strategies co-occur, and in cases where strong environmental filters allow only a narrow range of strategies, alternative processes can drive community assembly (Rosado & Mattos, 2010, 2017; Grime & Pierce, 2012). Different selective pressures dominate at different scales, particularly within versus among species (Albert *et al.*, 2010b; Messier *et al.*, 2010; Kichenin *et al.*, 2013), and the large variability in the variance structures of traits suggests that different traits have contrasting sensitivity to these different pressures (Messier *et al.*, 2016). Experimental

evidence shows that species can alter different aspects of their leaf economy in a relatively uncoordinated fashion, even when the direction of univariate trait responses to environmental change is consistent (Wright & Sutton-Grier, 2012). Meanwhile, across different plant functional types, resource allocation patterns, for instance of nutrients to photosynthesis versus structure and defense, differ substantially, suggesting different investment strategies and varying relationships among traits (Ghimire *et al.*, 2017). Second, among-trait correlations at any scale do not provide causal evidence for functional trade-offs or even similarity in response to external stimuli (Messier *et al.*, 2016). Therefore, ascribing too much leverage to trait correlations can lead to an underestimation of plant functional diversity (Grubb, 2015). Third, plants maintain their fitness in a given environment through multiple independent strategies (corresponding to multiple mutually orthogonal axes of trait variability). As a consequence, changes in key leaf economic traits such as nitrogen content and mass per unit area may not affect other aspects of plant function, such as hydraulics (Li *et al.*, 2015), overall plant carbon budget (Edwards *et al.*, 2014), and dispersal (Westoby *et al.*, 2002). Finally, modeling ecosystem function based on trait correlations with abiotic factors is sampling from the hypothetical space of potential species and communities that could have evolved, rather than constraining models to forecast the actual vegetation we have today as the result of spatial separation and constraints on convergent evolution. Among other problems, this approach fails to account for the timescales required for adaptation as well as actual limitations of the physiology of different species and community assembly.

An alternative approach is to preserve existing PFT classifications (though potentially with finer taxonomic or functional resolution, e.g. Boulangeat *et al.*, 2012) while using statistical analyses to account for uncertainty and variability in the aggregated trait values. For example, the Predictive Ecosystem Analyzer (PEcAn, pecanproject.org), an ecosystem modeling workflow and ecoinformatics toolbox, parameterizes PFTs using trait probability distributions from a Bayesian meta-analysis of plant trait data across many studies (LeBauer *et al.*, 2013; Dietze *et al.*, 2013). This approach explicitly separates the processes driving PFT-level differentiation from processes that drive finer-scale functional variability, and is useful for quantitatively assessing the validity of PFT definitions and guiding future data collection and efforts addressing ecological modelling (Dietze *et al.*, 2014). However, a univariate meta-analysis, like the one currently in PEcAn, is limited by its failure to account for trait correlations at any scale, therefore neglecting useful knowledge about relationships across PFTs and between traits. At the other extreme, existing regional and global scale analyses (e.g. Van Bodegom *et al.*, 2012; Sakschewski *et al.*, 2015) ignore variability within PFTs, often resulting in macroecological, evolutionary, and ecological trade-offs across PFTs being used to drive both acclimation and instantaneous responses within PFTs.

The above discussion culminates in the following question: Can the constraint on average functional characteristics across PFTs provided by the leaf economic spectrum be reconciled with trait relationships within each PFT? The answer to this question has relevant implications for ecosystem modelling and functional ecology. Here we hypothesize that leaf economic relationships represent a biome-level environmental filter that regulates variability among PFTs and has little to no bearing on trait correlations within PFTs. To evaluate this hypothesis, we develop a hierarchical multivariate Bayesian model that explicitly accounts for across- and within-PFT variability in trait correlations. We then fit this model to a global database of foliar traits to estimate mean trait values and variance-covariance matrices for PFTs as defined in a major earth system model (Community Land Model, CLM, Oleson *et al.*, 2013). We evaluate the ability of this model to reduce uncertainties in trait estimates and reproduce observed patterns of global trait variation compared to non-hierarchical multivariate and univariate models. Finally, we assess the generality and scale dependence of trait trade-offs by comparing covariance and correlation estimates globally and within each PFT. In particular, our study is novel in its treatment of within- and among-PFT variability simultaneously and with a global dataset.

2 Materials and Methods

2.1 Trait data

Foliar trait data for this analysis comes from the TRY global traits database (Kattge *et al.* (2011); Tab. 1). We focused our research on seven foliar traits: Leaf longevity (months), specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$), leaf nitrogen content (N_{mass} , mg N g^{-1} or N_{area} , g m^{-2}), leaf phosphorus content (P_{mass} , mg P g^{-1} or P_{area} , g m^{-2}), leaf dark respiration at leaf temperature ($R_{d, mass}$, $\mu\text{mol g}^{-1} \text{s}^{-1}$, or $R_{d, area}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum Rubisco carboxylation rate at 25°C ($V_{c, max, mass}$, $\mu\text{mol g}^{-1} \text{s}^{-1}$, or $V_{c, max, area}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), and maximum electron transport rate ($J_{max, mass}$, $\mu\text{mol g}^{-1} \text{s}^{-1}$, or $J_{max, area}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$). We performed analyses separately for both mass- and area-normalized traits to avoid potential artifacts caused by different trait normalization (Lloyd *et al.*, 2013; Osnas *et al.*, 2013). We restricted our analysis to TRY data that have been quality-controlled and for which adequate species information was provided for functional type classification (see Kattge *et al.*, 2011).

Although the light- and CO₂-saturated photosynthetic rate (A_{max}) was an important trait in previous studies, we did not include it in our study for two reasons. First of all, data on raw photosynthetic rates are highly sensitive to measurement methodology and environmental conditions, which were generally inconsistent or unavailable in TRY. Second, A_{max} is not a good measure of photosynthetic capacity because it integrates over variability in many physiologically independent traits such as $V_{c, max}$, J_{max} , and stomatal conductance, and is therefore not used in vegetation models as a photosynthetic parameter (Ali *et al.*, 2015).

Following past studies (e.g. Wright *et al.*, 2004, 2005a; Onoda *et al.*, 2011; Díaz *et al.*, 2016), we log-transformed all trait values to correct for their strong right-skewness.

Table 1: Data sources and observation counts for foliar trait data

Reference	Observations
Kleyer <i>et al.</i> (2008)	79467
Wirth & Lichstein (2009)	69142
Baraloto <i>et al.</i> (2010)	51957
Craine <i>et al.</i> (2009)	32657
Reich <i>et al.</i> (2009)	31414
Veihmeyer (1956)	27674
Cerabolini <i>et al.</i> (2010)	19101
Wright <i>et al.</i> (2010)	18005
Wright <i>et al.</i> (2004)	16432
Ogaya & Peñuelas (2003)	16332
Akhmetzhanova <i>et al.</i> (2012)	15258
Frenette-Dussault <i>et al.</i> (2011)	15119
Medlyn <i>et al.</i> (1999)	14993
Kattge <i>et al.</i> (2009)	13019
Laughlin <i>et al.</i> (2010)	12768
Campetella <i>et al.</i> (2011)	12352
Auger & Shipley (2012)	12292
Fyllas <i>et al.</i> (2009)	11030
Blonder <i>et al.</i> (2012)	9897
Cornelissen <i>et al.</i> (2003)	9545
Cavender-Bares <i>et al.</i> (2006)	9334
Garnier <i>et al.</i> (2007)	8619
Prentice <i>et al.</i> (2010)	8516
Fredrickson (2016)	8409
Schweingruber & Landolt (2005)	8029
Onoda <i>et al.</i> (2011)	7281

Reference	Observations
Han <i>et al.</i> (2011)	6980
Domingues <i>et al.</i> (2010)	6483
Han <i>et al.</i> (2005)	6039
Messier <i>et al.</i> (2010)	5722
Price & Enquist (2007)	5637
Kraft <i>et al.</i> (2008)	5387
Pierce <i>et al.</i> (2013)	5034
Wright <i>et al.</i> (2006)	4493
Reich <i>et al.</i> (2008)	4462
Domingues <i>et al.</i> (2007)	4410
Niinemets (2001)	4380
Cornwell <i>et al.</i> (2008)	4317
Vergutz <i>et al.</i> (2012)	4223
Sandel <i>et al.</i> (2011)	3901
Poorter <i>et al.</i> (2009)	3681
Gallagher & Leishman (2012)	3530
Williams <i>et al.</i> (2012)	3325
Choat <i>et al.</i> (2012)	3219
Fonseca <i>et al.</i> (2000)	3129
Burrascano <i>et al.</i> (2015)	3030
Milla & Reich (2011)	2907
Adriaenssens (2012)	2723
Willis <i>et al.</i> (2009)	2663
Kisel <i>et al.</i> (2012)	2594
Pierce <i>et al.</i> (2012)	2379
Cornelissen (1996)	2355
Yguel <i>et al.</i> (2011)	2301
Xu & Baldocchi (2003)	2294
Bond-Lamberty <i>et al.</i> (2004)	2294
Holle & Simberloff (2004)	2216
Chen <i>et al.</i> (2011)	2146
Byun <i>et al.</i> (2012)	2036
Laughlin <i>et al.</i> (2011)	1999
Ordoñez <i>et al.</i> (2010)	1993
Kerkhoff <i>et al.</i> (2006)	1948
Butterfield & Briggs (2010)	1930
Bond-Lamberty <i>et al.</i> (2002a)	1886
Pierce <i>et al.</i> (2007b)	1857
Gutiérrez & Huth (2012)	1790
Manzoni <i>et al.</i> (2013)	1662
Wright & Sutton-Grier (2012)	1634
Chambers <i>et al.</i> (2004)	1572
Guerin <i>et al.</i> (2012)	1534
Bond-Lamberty <i>et al.</i> (2002b)	1473
Müller <i>et al.</i> (2006)	1408
Pierce <i>et al.</i> (2007a)	1284
Craine <i>et al.</i> (2011)	1258
Craine <i>et al.</i> (2012)	1233
Shipley (2002)	1231
Wohlfahrt <i>et al.</i> (1999)	1098
Rüger <i>et al.</i> (2011a)	1070
Rüger <i>et al.</i> (2009)	970

Reference	Observations
Quested <i>et al.</i> (2003)	968
Choat <i>et al.</i> (2012)	960
Pahl <i>et al.</i> (2013)	888
Shipley & Vu (2002)	857
Minden & Kleyer (2011)	827
Meir <i>et al.</i> (2002)	763
Schererlorenzen <i>et al.</i> (2007)	675
Bakker <i>et al.</i> (2006)	636
Penuelas <i>et al.</i> (2009)	616
Powers & Tiffin (2010)	609
Shiodera <i>et al.</i> (2008)	606
Fitter & Peat (1994)	605
Minden <i>et al.</i> (2012)	603
Bond-Lamberty <i>et al.</i> (2006)	598
Rüger <i>et al.</i> (2011b)	568
Peco <i>et al.</i> (2005)	562
Tucker <i>et al.</i> (2011)	559
Weedon <i>et al.</i> (2009)	522
Blonder <i>et al.</i> (2010a)	485
Spasojevic & Suding (2012)	430
Campbell <i>et al.</i> (2007)	429
Craven <i>et al.</i> (2007)	396
Cornelissen <i>et al.</i> (2004)	373
Pillar & Sosinski (2003)	340
Hickler (1999)	320
Bakker <i>et al.</i> (2005)	312
Vile (2005)	299
Craine <i>et al.</i> (2005)	293
Christopher <i>et al.</i> (2016)	288
Wilson <i>et al.</i> (2000)	287
Preston <i>et al.</i> (2006)	268
Zapata-Cuartas <i>et al.</i> (2012)	266
Blonder <i>et al.</i> (2013)	233
Blonder <i>et al.</i> (2010b)	225
Guy <i>et al.</i> (2013)	225
Kichenin <i>et al.</i> (2013)	217
Louault <i>et al.</i> (2005)	215
Araujo <i>et al.</i> (2011)	211
Bocanegra <i>et al.</i> (2015)	186
Beckmann <i>et al.</i> (2012)	155
Adler <i>et al.</i> (2004)	150
Loveys <i>et al.</i> (2003)	144
Bodegom <i>et al.</i> (2008)	142
Domingues <i>et al.</i> (2013)	140
Shipley & Lechowicz (2000)	120
Loranger <i>et al.</i> (2012)	120
Pyankov <i>et al.</i> (1999)	106
Shipley (1995)	102
Cornelissen <i>et al.</i> (1996)	98
Carswell <i>et al.</i> (2000)	88
Givnish <i>et al.</i> (2004)	88
Meziane & Shipley (1999)	86

Reference	Observations
Meir <i>et al.</i> (2007)	75
Atkin <i>et al.</i> (1997)	62
Atkin <i>et al.</i> (1999)	60
Diaz <i>et al.</i> (2004)	59
Kazakou <i>et al.</i> (2006)	48
Demey <i>et al.</i> (2013)	30

2.2 Plant functional types

Table 2: Names, labels, and species counts for plant functional types (PFTs) used in this analysis.

Label	PFT	Number of species
BlETr	Broadleaf Evergreen Tropical	1201
BlETe	Broadleaf Evergreen Temperate	406
BlDTr	Broadleaf Deciduous Tropical	282
BlDTe	Broadleaf Deciduous Temperate	345
BlDBo	Broadleaf Deciduous Boreal	63
NIETe	Needleleaf Evergreen Temperate	133
NIEBo	Needleleaf Evergreen Boreal	31
NID	Needleleaf Deciduous	18
ShE	Shrub Evergreen	1116
ShDTe	Shrub Deciduous Temperate	332
ShDBo	Shrub Deciduous Boreal	91
C3GAr	C3 Grass Arctic	152
C3GTe	C3 Grass Temperate	619
C4G	C4 Grass	247

We assigned each species to a unique plant functional type (PFT) following the scheme in the Community Land Model [CLM4.5, Oleson *et al.* (2013); Tab. 2, Fig. 1]. We obtained categorical data on growth form, leaf type, phenology, and photosynthetic pathway from the TRY database. Where the same species was reported to have different attributes in different datasets, we assigned the attribute that was observed most frequently, and, in cases of ties, selected the attribute that was more likely based on phylogenetically similar species or more likely to occur in nature. For biome specification, we collected all latitude and longitude data for each species, matched these data to 30 second ($\sim 1km^2$) mean annual temperature (AMT , averaged 1970-2000) data from WorldClim-2 (Fick & Hijmans, 2017), calculated the mean AMT for all sites at which that species was observed, and then binned these species based on the following cutoffs: boreal/arctic ($AMT \leq 5^\circ C$), temperate ($AMT \leq 20^\circ C$), and tropical ($AMT > 20^\circ C$).

2.3 Multivariate analysis

2.3.1 Basic model description

In this study, we compared three different models representing different levels of complexity.

The simplest model was the ‘univariate’ model, in which each trait was modeled independently. For an observation $x_{i,t}$ of trait t and sample i :

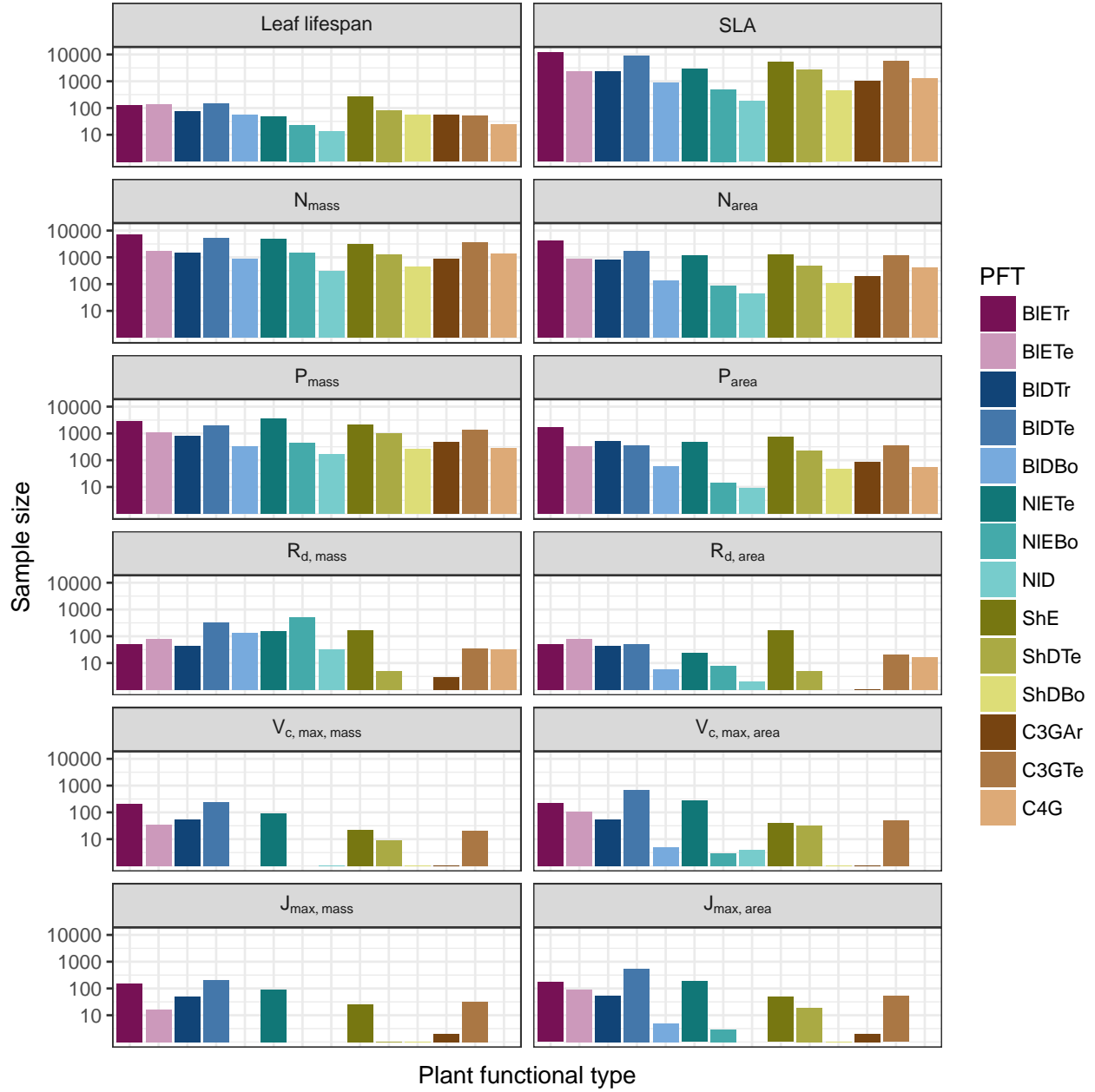


Figure 1: Sample sizes for each trait-PFT pair. y axis is scaled logarithmically.

$$x_{i,t} \sim N(\mu_t, \sigma_t)$$

...where N is the univariate normal (Gaussian) distribution with mean μ_t and standard deviation σ_t for trait t .

The second-simplest model was the ‘multivariate’ model, in which traits were modeled as samples from a multivariate distribution with a single mean vector and covariance matrix. For the observed vector of traits \mathbf{x}_i for sample i ...

$$\mathbf{x}_i \sim mvN(\mu, \Sigma)$$

...where mvN is the multivariate normal (Gaussian) distribution with mean vector μ and variance-covariance matrix Σ . We ran both of these models independently for each PFT as well as for the entire dataset (as if every observation belonged to the same PFT).

The most complex model was the ‘hierarchical’ model, in which observed trait values were drawn from a PFT-specific multivariate normal distribution describing within-PFT variation and whose parameters were themselves sampled from a global multivariate distribution describing the variation among PFTs. For the observed vector of traits $\mathbf{x}_{i,p}$ for sample i belonging to PFT p ...

$$\mathbf{x}_{i,p} \sim mvN(\mu_p, \Sigma_p)$$

$$\mu_p \sim mvN(\mu_g, \Sigma_g)$$

...where μ_p and Σ_p are the mean vector and variance-covariance matrix describing variation within PFT p , and μ_g and Σ_g are the mean vector and variance-covariance matrix describing among-PFT (global) variation.

2.3.2 Model implementation

We fit the above models using a Gibbs sampling algorithm that leveraged known conjugate prior relationships for efficient exploration of the sampling space. For priors on all multivariate mean vectors (μ), we used normal distributions...

$$P(\mu) \sim mvN(\mu_0, \Sigma_0)$$

...which gives rise to the following expression for the posterior...

$$P(\mu \mid \mathbf{x}, \Sigma, \mu_0, \Sigma_0) \sim mvN(\mu^*, \Sigma^*)$$

...where...

$$\Sigma^* = (\Sigma_0^{-1} + n\Sigma^{-1})^{-1}$$

$$\mu^* = \mu_0\Sigma_0^{-1} + \bar{\mathbf{x}}n\Sigma^{-1}$$

...where $\bar{\mathbf{x}}$ are the sample means of the data and n is the number of rows in the data.

For priors on all multivariate variance-covariance matrices, we used the Wishart distribution (W)...

$$P(\Sigma) \sim W(\nu_0, \mathbf{S}_0)$$

...which gives rise to the following expression for the posterior...

$$P(\Sigma \mid \mathbf{x}, \mu, \nu_0, \Sigma_0) \sim (W(\nu^*, S^*))^{-1}$$

...where...

$$\nu^* = 1 + \nu_0 + n + m$$

$$\mathbf{x}^* = \mathbf{x} - \bar{\mu}$$

$$\mathbf{SS} = \mathbf{x}^{*T} \mathbf{x}^*$$

$$\mathbf{S}^* = (\mathbf{S}_0 + \mathbf{SS})^{-1}$$

...where n is the number of rows and m is the number of columns in data matrix x . For further details on this derivation, see Gelman *et al.* (2003).

The fundamentally multivariate nature of the sampling procedure described above makes it incapable of accommodating partially missing observations. Therefore, our algorithm also included imputation of partially missing data, which proceeded as follows: For a block of data \mathbf{x}' containing missing observations in columns \mathbf{m} and present observations in columns \mathbf{p} , the missing values $\mathbf{x}'[m]$ are drawn randomly from a **marginal** multivariate normal distribution at each iteration of the sampling algorithm...

$$\mathbf{x}'[m] \sim mvN(\mu', \Sigma')$$

...where...

$$\mu' = (\mathbf{x}'[p] - \mu'[p])(\Sigma[p, p]^{-1} \Sigma[p, m])$$

$$\Sigma' = \Sigma[m, m] - \Sigma[m, p](\Sigma[p, p]^{-1} \Sigma[p, m])$$

For each model fit, we ran five parallel MCMC chains, automatically increasing the sample size until the final result achieved convergence as determined by a Gelman-Rubin potential scale reduction statistic less than 1.1 (Gelman & Rubin, 1992). We implemented this sampling algorithm in an open source, publicly available R (version 3.4.2; R Core Team, 2017) package (<http://github.com/ashiklom/mvtraits>).

2.3.3 Analysis of results

To assess the impact of multivariate and hierarchical constraint on trait estimates, we compared the mean and size of the 95% confidence intervals of mean estimates of each trait for each PFT from each model (Fig. 2). In addition, we report the mean and 95% confidence intervals of ~~mean estimates~~ for each trait and PFT from the hierarchical model in tabular form (Tab. 3 and 4).

To test the hypothesis that the multivariate and hierarchical models offer more value in terms of uncertainty constraint at smaller sample sizes, we calculated the relative uncertainty (α) as a function of the mean (μ) and upper ($q_{0.975}$) and lower ($q_{0.025}$) confidence limits of trait estimates.

$$\alpha = \frac{q_{0.975} - q_{0.025}}{\mu}$$

We then fit a generalized linear model relating relative uncertainty to sample size (n) for each of the model types (univariate, multivariate, and hierarchical; Fig. 3).

$$\log \alpha = b_0 + b_1 \log n$$

Table 3: Mean and 95% confidence interval of trait estimates for mass-normalized traits from the hierarchical model.

pft	Leaf lifespan	SLA	N_{mass}	P_{mass}	$R_{d,mass}$	$V_{c,max,mass}$	$J_{max,mass}$
BIETr	13.7 (12.1,15.7)	11.6 (11.6,11.7)	19.8 (19.6, 20)	0.892 (0.876,0.909)	8.17 (6.85,9.97)	0.373 (0.35,0.396)	0.666 (0.623,0.709)
BIETe	22.5 (20.3, 25)	7.28 (7.11,7.45)	14.2 (14,14.4)	0.912 (0.882,0.942)	7.67 (6.8,8.56)	0.299 (0.238,0.365)	0.86 (0.572, 1.2)
BIDTr	6.98 (6.21,7.84)	12.8 (12.5,13.1)	20.9 (20.5,21.2)	1.22 (1.17,1.27)	10.2 (8.29,12.6)	0.568 (0.504,0.641)	0.965 (0.846, 1.1)
BIDTe	5.31 (4.72,5.95)	22.5 (22.3,22.8)	21.9 (21.7,22.1)	1.68 (1.64,1.72)	12.4 (11.7,13.1)	0.579 (0.522,0.642)	1.3 (1.16,1.47)
BIDBo	4.86 (3.97,5.95)	16.1 (15.7,16.5)	23.9 (23.3,24.5)	2.06 (1.96,2.17)	22.1 (20.6,23.7)	0.444 (0.00477,36.9)	0.994 (0.0111,88.4)
NIETe	36.5 (31.1, 43)	5.06 (4.96,5.17)	12.3 (12.2,12.4)	1.21 (1.19,1.22)	4.45 (4.12,4.79)	0.275 (0.248,0.306)	0.587 (0.529,0.654)
NIEBo	48.6 (34.7, 66)	4.57 (4.34,4.82)	11.9 (11.7,12.1)	1.38 (1.33,1.44)	5.57 (5.39,5.75)	0.449 (0.00504,43.5)	—
NID	6.08 (4.35,8.58)	13.3 (12.3,14.3)	19.1 (18.5,19.8)	1.87 (1.74, 2)	19.3 (16.1,23.1)	0.445 (0.111, 2.1)	—
ShE	15.2 (13.9,16.6)	8.18 (8.03,8.33)	13 (12.8,13.3)	0.83 (0.805,0.857)	10.2 (9.29,11.2)	0.266 (0.192,0.343)	0.518 (0.289,0.886)
ShDTe	5.52 (4.89,6.22)	16.8 (16.5,17.2)	21.2 (20.7,21.6)	1.55 (1.49, 1.6)	11.8 (4.85,24.5)	0.344 (0.212,0.598)	0.013 (0.00235,0.0746)
ShDBo	4.26 (3.7,4.91)	14.4 (13.8,14.9)	20.5 (19.8,21.3)	1.68 (1.59,1.77)	—	0.527 (0.109,3.91)	0.0689 (0.00876,0.738)
C3GAr	5.63 (4.73,6.74)	14.3 (13.8,14.8)	17.9 (17.4,18.4)	1.27 (1.22,1.33)	31.4 (10.7,88.3)	0.784 (0.0683,9.02)	0.838 (0.112,5.84)
C3GTe	6.57 (4.96,8.41)	16 (15.7,16.3)	16.4 (16.2,16.7)	1.3 (1.25,1.35)	17.1 (13.8,21.3)	0.972 (0.675,1.46)	0.366 (0.16,0.887)
C4G	3.74 (2.68,5.26)	14.5 (13.9, 15)	14.4 (14.1,14.8)	1.23 (1.14,1.33)	18.2 (14.4,22.9)	—	—

If all three models performed equally well at all sample sizes, their respective slope coefficients would be statistically indistinguishable. On the other hand, models that perform better should have lower slope (b_1) coefficients, indicating a slower increase in the uncertainty (α) with decreasing sample size (n).

To assess the consistency of among- and within-PFT trait trade-offs, we calculated the eigenvalues from pairwise variance-covariance matrix estimates for each trait pair and, where the covariance was significantly different from zero ($p < 0.05$), plotted the dominant eigenvectors centered on the mean estimates (Fig. 4). This figure provides a visual representation of relative positions of PFTs in trait space and both the direction and extent of within-PFT trait covariance, and is directly analogous to conceptual figures describing hierarchical trait variability across environmental gradients as presented in, for instance, Cornwell & Ackerly (2009) and Albert *et al.* (2010b). Due to the small number of points used to estimate across-PFT covariance in the hierarchical model, none of the across-PFT covariances estimated in the hierarchical model were significantly different from zero ($p < 0.05$). For this reason, we compared within-PFT covariances as estimated by the hierarchical model with the covariances estimated by fitting a multivariate model to all of the data.

Besides the consistency in the direction of trait covariance globally and between different PFTs, we also investigated the strength and predictive power of these covariances, which is represented by correlation coefficients (i.e. the pairwise covariance normalized to the variances of the component variables). To do this, we plotted the mean and 95% confidence interval of the pairwise trait correlation coefficients for the global estimate from the pooled multivariate model and PFT-level estimates from the hierarchical model (Fig. 5).

The R code for running these analyses is publicly available online at http://github.com/ashiklom/np_trait_analysis. The TRY data used for this analysis can be requested at <http://try-db.org>.

3 Results

3.1 Estimates of PFT-level means

In general, leaf trait estimates from the univariate, multivariate, and hierarchical models were similar (Fig. 2). Where we observed differences between models, the largest were between the univariate and multivariate models, while the additional constraint from the hierarchical model tended to have a minimal effect on trait estimates. Significant differences in trait estimates between univariate and multivariate models occurred even for traits with relatively large sample sizes, such as leaf nitrogen content.

Evergreen PFTs had by far the largest leaf lifespan, with the longest lifespan observed for temperate and boreal needleleaf evergreen species. Meanwhile, all of deciduous species had lifespans shorter than 7 months. Among deciduous species, lifespan was generally longer in warmer biomes than colder ones.

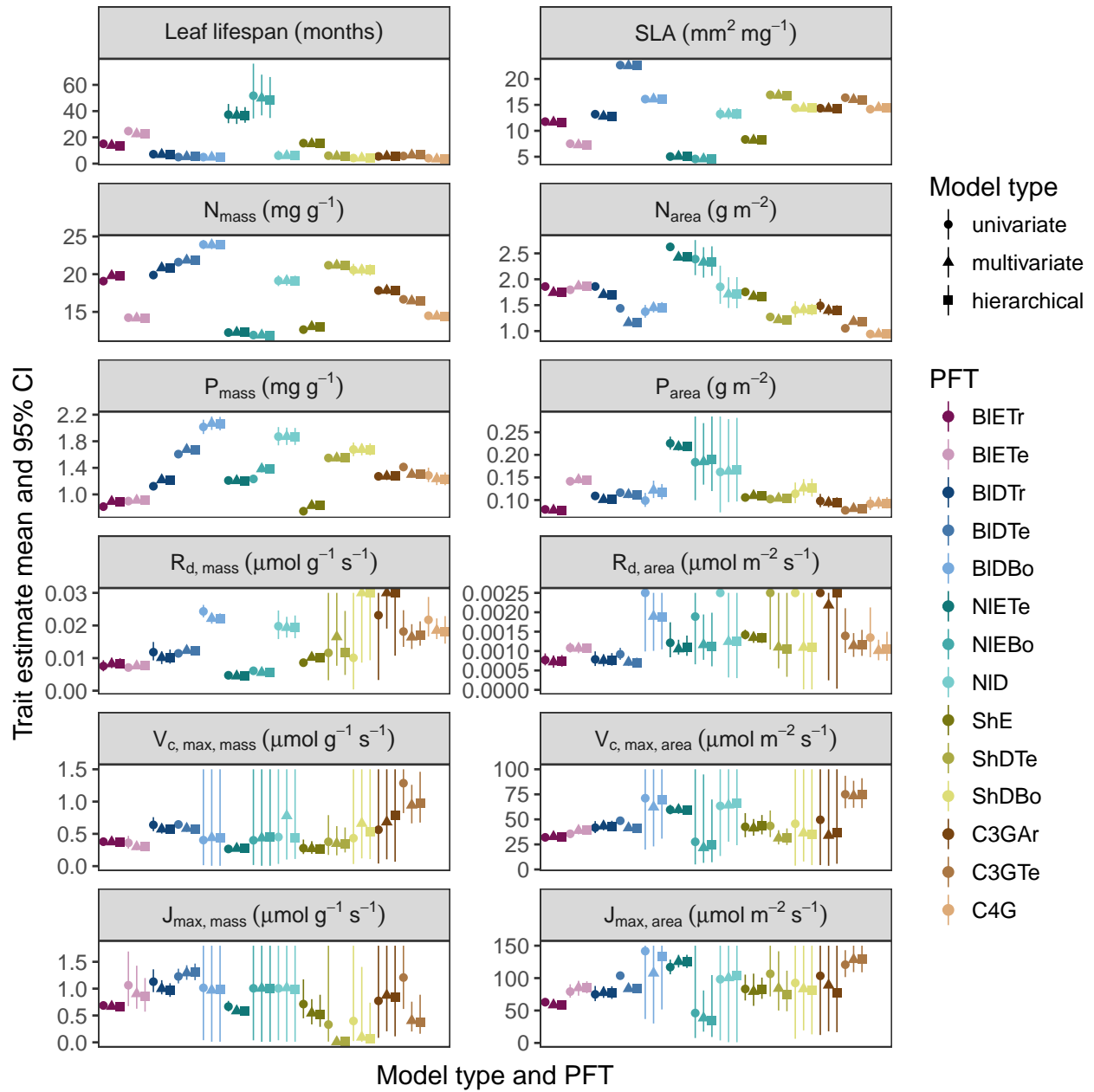


Figure 2: Mean and 95% confidence interval on best estimates of traits for each plant functional type from the univariate, multivariate, and hierarchical models. For leaf lifespan and SLA, results were not significantly different between the mass- and area-based models, so only results from the mass-based model are shown. For some PFT-trait combinations, where large error bars resulting from the relatively uninformative priors are substantially larger than the variability among means, the y axes are constrained to facilitate comparison.



Table 4: Mean and 95% confidence interval of trait estimates for area-normalized traits from the hierarchical model.

pft	Leaf lifespan	SLA	N_{area}	P_{area}	$R_{d,area}$	$V_{c,max,area}$	$J_{max,area}$
BIETr	13.7 (12.1,15.7)	11.6 (11.6,11.7)	1.74 (1.72,1.76)	0.0773 (0.0755,0.0791)	0.739 (0.598,0.898)	32.7 (30.8,34.9)	59.2 (55.6,63.3)
BIETe	22.5 (20.3, 25)	7.28 (7.11,7.45)	1.87 (1.81,1.92)	0.144 (0.136,0.153)	1.08 (0.962, 1.2)	39 (35.3,43.1)	85.5 (76.5,95.1)
BIDTr	6.98 (6.21,7.84)	12.8 (12.5,13.1)	1.7 (1.66,1.74)	0.101 (0.0965,0.106)	0.772 (0.622,0.948)	43.2 (38.2,48.6)	77.2 (67.9,87.5)
BIDTe	5.31 (4.72,5.95)	22.5 (22.3,22.8)	1.16 (1.13,1.19)	0.112 (0.105,0.12)	0.697 (0.595,0.829)	41.5 (39.2,43.9)	83.6 (79.3, 88)
BIDBo	4.86 (3.97,5.95)	16.1 (15.7,16.5)	1.46 (1.36,1.56)	0.118 (0.102,0.135)	1.88 (1.04, 3.6)	69.6 (30.7, 162)	133 (51.6, 275)
NIETe	36.5 (31.1, 43)	5.06 (4.96,5.17)	2.43 (2.37,2.48)	0.219 (0.21,0.228)	1.09 (0.877, 1.4)	59.4 (55.2,63.9)	125 (116, 136)
NIEBo	48.6 (34.7, 66)	4.57 (4.34,4.82)	2.33 (2.07,2.64)	0.189 (0.12,0.307)	1.12 (0.606,1.99)	24.3 (7.21,69.8)	35 (9.15, 105)
NID	6.08 (4.35,8.58)	13.3 (12.3,14.3)	1.72 (1.44,2.04)	0.167 (0.0968,0.282)	1.24 (0.303,4.58)	66.1 (24.2, 189)	—
ShE	15.2 (13.9,16.6)	8.18 (8.03,8.33)	1.67 (1.62,1.71)	0.11 (0.104,0.115)	1.33 (1.21,1.47)	43.4 (35,54.4)	82.9 (68, 101)
ShDTe	5.52 (4.89,6.22)	16.8 (16.5,17.2)	1.22 (1.17,1.26)	0.104 (0.0971,0.111)	1.06 (0.337,2.92)	31.6 (24.4, 41)	75 (48.9, 111)
ShDBo	4.26 (3.7,4.91)	14.4 (13.8,14.9)	1.41 (1.3,1.53)	0.126 (0.107,0.147)	1.09 (0.0122,99.9)	35.1 (4.33, 186)	80.7 (13.3, 504)
C3GAr	5.63 (4.73,6.74)	14.3 (13.8,14.8)	1.4 (1.31, 1.5)	0.0944 (0.0841,0.106)	3.38 (0.0311,49.2)	37.1 (5.71, 158)	77 (16.5, 345)
C3GTe	6.57 (4.96,8.41)	16 (15.7,16.3)	1.18 (1.15,1.21)	0.0807 (0.0741,0.0875)	1.17 (0.877,1.55)	74.6 (61.2,91.1)	129 (109, 153)
C4G	3.74 (2.68,5.26)	14.5 (13.9, 15)	0.944 (0.901,0.989)	0.0929 (0.0814,0.106)	1.05 (0.748, 1.5)	—	—

Across-PFT patterns in SLA and N_{mass} , P_{mass} , and $R_{d,area}$ were similar. Temperate broadleaved deciduous trees and shrubs generally had among the highest values of these traits, while temperate evergreen trees and shrubs had generally among the lowest. However, none of these patterns were universal to all four traits. For example, tropical evergreen trees had relatively high N_{mass} and average SLA and $R_{d,area}$, but among the lowest P_{mass} . Similarly, temperate and boreal shrubs had higher N_{mass} and P_{mass} than any of the grasses, but comparable SLA.

Across-PFT patterns in N_{area} , P_{area} , and $R_{d,area}$ were different from their mass-normalized counterparts. For example, tropical broadleaved evergreen and needleleaf evergreen trees had among the lowest N_{mass} and P_{mass} basis but among the highest N_{area} and P_{area} , while the opposite was true of deciduous temperate trees and shrubs. Species with N contents near the middle of the observed range did not shift as dramatically depending on type of normalization.

C3 grasses had both the highest $V_{c,max,area}$ and $V_{c,max,area}$. Compared to broadleaved trees, temperate needleleaved evergreen trees had lower $V_{c,max,area}$ but higher $V_{c,max,area}$. Among broadleaved trees, deciduous trees had higher $V_{c,max,area}$ and slightly higher $V_{c,max,area}$ than evergreen trees. Between the deciduous and evergreen tree PFTs, we observed no significant trend by climate zone.

C3 grasses and temperate needleleaved evergreen trees had the highest $J_{max,area}$, but temperate broadleaved deciduous trees had the highest $J_{max,area}$. All of the shrub PFTs had the lowest $J_{max,area}$ but average or above-average $J_{max,area}$, while the opposite was true of broadleaved tropical PFTs. Of the tree PFTs, needleleaved evergreen trees had the highest $J_{max,area}$ but the lowest $J_{max,area}$.

We observed clear differences in the relative uncertainties of mean estimates with respect to sample size. All of the high-latitude PFTs consistently had among the largest error bars around their mean estimates relative to other PFTs, while the traits with the largest uncertainties were dark respiration, $V_{c,max}$, and J_{max} . For many of these trait-PFT combinations, the additional constraint from trait covariance provided by the multivariate and hierarchical models substantially reduced error bars, making it possible to compare estimates against those of other PFTs. Our analysis of the relationship between model type, sample size, and estimate relative uncertainty found that this covariance-based constraint from the multivariate model becomes increasingly important at smaller sample sizes (Fig. 3). However, this analysis revealed no consistent significant benefit from the hierarchical model.

3.2 Trait correlation patterns among- and within-PFTs

Where pairwise trait correlations were statistically significant, these correlations were generally consistent in direction both globally and within each PFT (Fig. 4). In particular, mass- and area-normalized traits were all positively correlated with each other and, respectively, positively and negatively correlated with SLA,



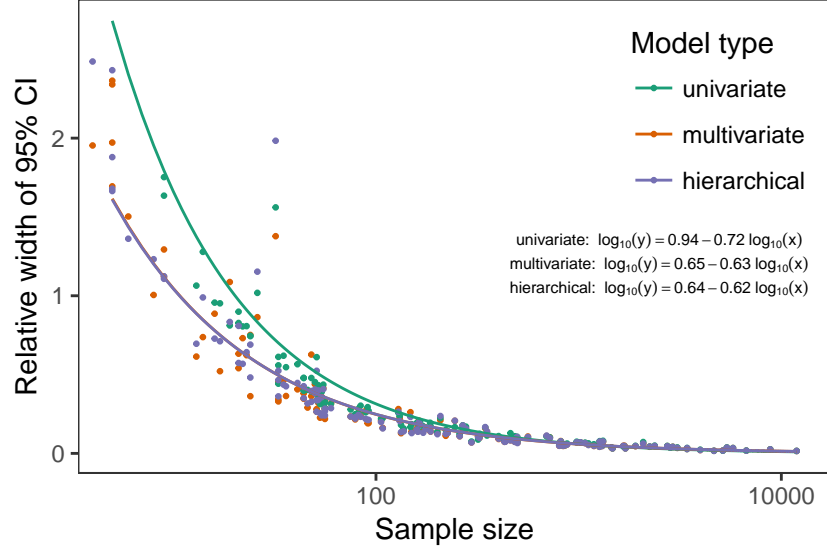


Figure 3: Relative uncertainty in PFT-level trait estimates as a function of sample size for each model type. Lines represent linear models ($\log(y) = b_0 + b_1 \log(x)$) fit independently for each model type. In general, differences in estimate uncertainty between the univariate and multivariate models were minimal at large sample sizes but increasingly important at low sample sizes. However, differences in estimate uncertainty between the multivariate and hierarchical models were consistently negligible.

both globally and within each PFT. The same was generally true of correlations of mass-based traits with leaf lifespan, but correlations of leaf lifespan with area-normalized traits were more variable. The correlation between N_{area} and leaf lifespan was positive globally and for evergreen shrubs but negative for broadleaved deciduous trees and not significant for any other PFTs. Similarly, the correlation between P_{area} and leaf lifespan was positive for temperate broadleaved evergreen trees and needleleaved evergreen trees but negative for evergreen shrubs. The correlation between leaf lifespan and $R_{d,area}$ significant and positive globally, but was not significant within any PFTs. The correlations of leaf lifespan with $V_{c,max,area}$ and $J_{max,area}$ were negative for temperate broadleaved deciduous trees, but not significant for any other PFTs or globally.

A large number of pairwise trait correlations were not significant. In some cases, this was driven by sample size (Fig. 1). For instance, needleleaved deciduous trees were often the only PFT for which a correlation was not statistically significant. In other cases, though, PFTs with smaller sample sizes had significant pairwise correlations while PFTs with much larger sample sizes had none. For example, tropical broadleaved evergreen trees were relatively well-sampled for all traits, but none of their traits were well correlated with leaf lifespan. Meanwhile, temperate broadleaved evergreen trees had significant correlations between leaf lifespan and SLA, P_{area} , and $R_{d,area}$. In general, we observed fewer significant trait correlations among area-normalized traits than mass-normalized traits.

The strength of pairwise trait correlations varied substantially depending on scale, PFT, and trait (Fig. 5). The two pairwise trait correlations that exhibited the most consistent strength globally and within each PFT were the correlation between SLA and N_{area} , and between N_{mass} and P_{mass} . Correlation strength was often, but not always, related to sample size, with well-sampled PFTs exhibiting stronger correlations and undersampled PFTs exhibiting weaker correlations.

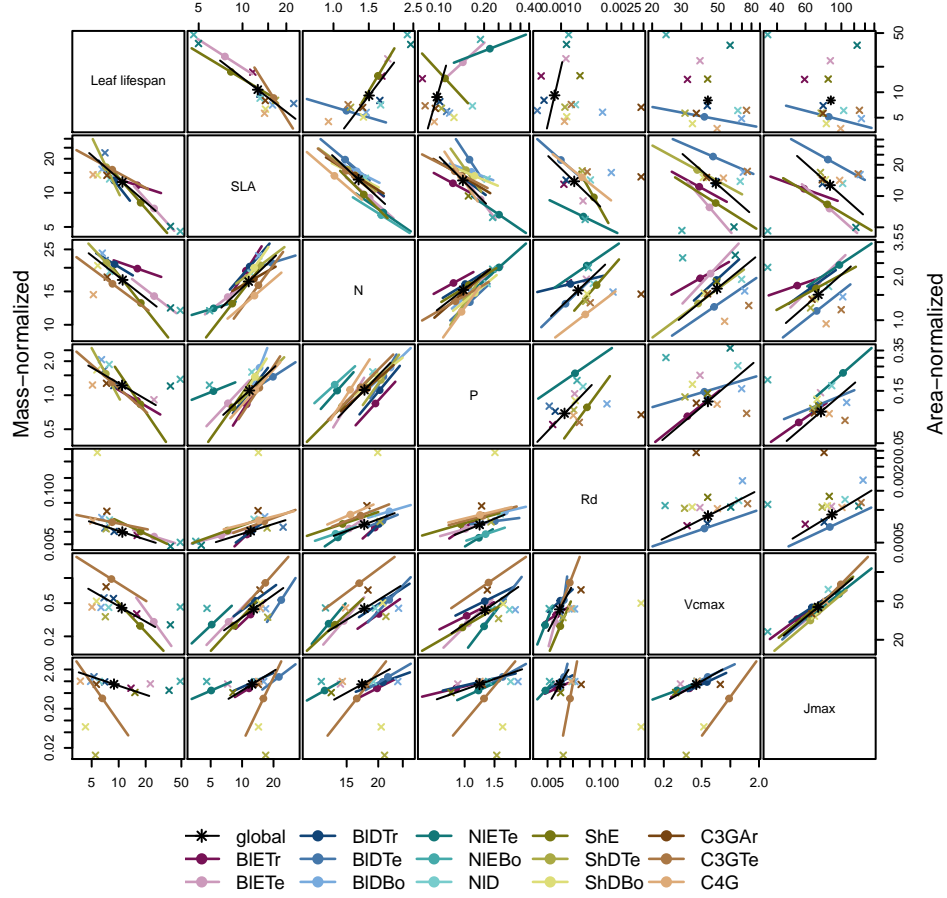


Figure 4: Pairwise trait mean and covariance estimates for all data pooled globally (black) and for each PFT (colored). Covariance estimates not significantly different from zero ($p < 0.05$) are indicated by x symbols at the mean estimate. x and y axes vary on a log scale, reflecting the fact that the model was fit using the base 10 log of all traits. With the exception of leaf lifespan, pairwise covariances are consistent in direction but vary somewhat in magnitude between PFTs, and when comparing PFT-level and global estimates. However, many pairwise covariances are not statistically significant, particularly (but not always) for undersampled traits and PFTs.

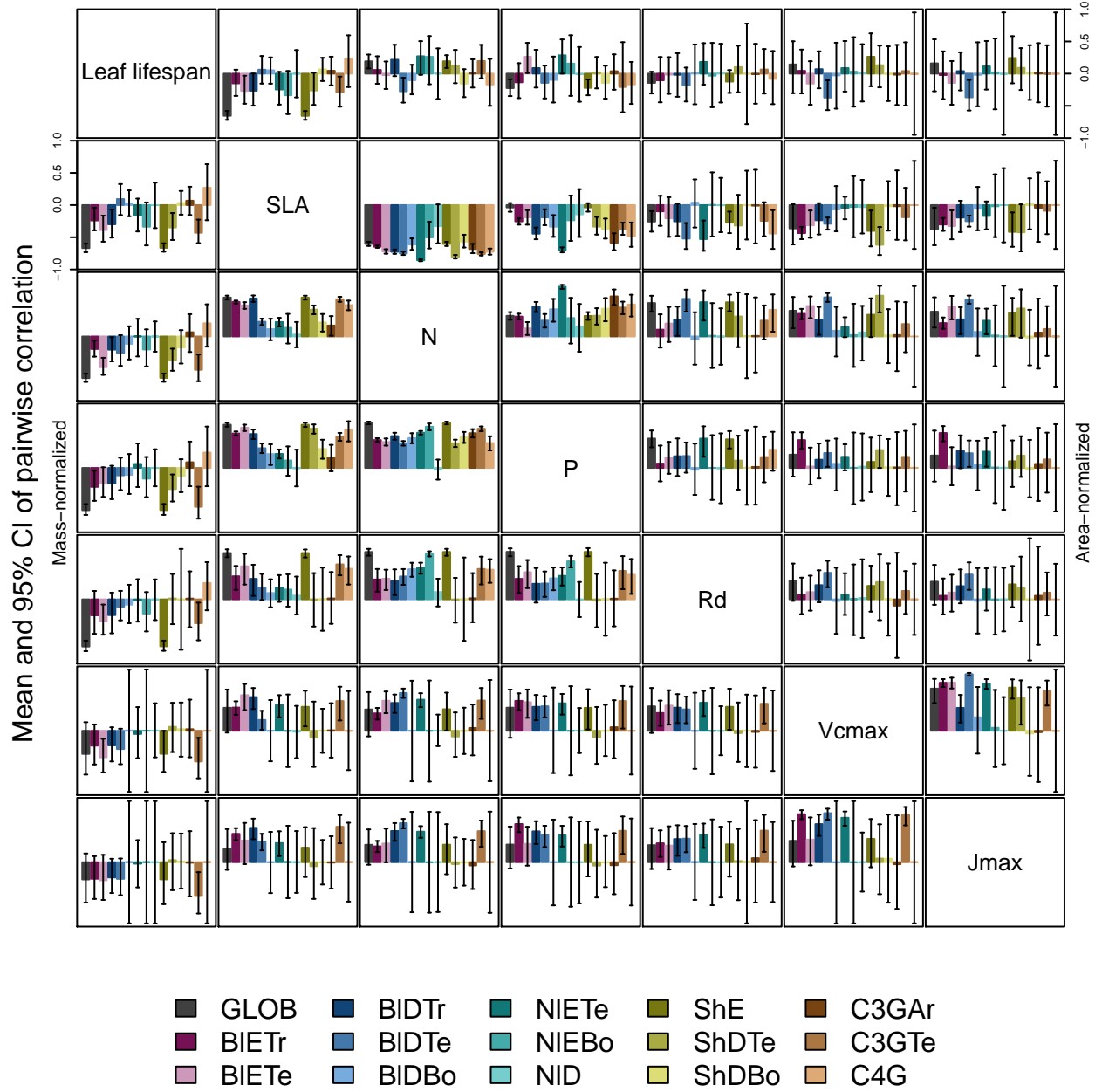


Figure 5: Mean and 95% CI on estimates of pairwise correlation coefficients for all data pooled globally (dark grey) and for each PFT (colored). For most PFT-trait pairs, correlations are mutually consistent in magnitude but vary in strength.

4 Discussion

4.1 Variation in trait means among PFTs

A key application of this study is to provide data-driven parameter estimates for Earth System Models. To this end, we compared our mean parameter estimates (Fig. 2, Tab. 3) with corresponding default parameters in CLM 4.5 (Oleson *et al.*, 2013). Our mean estimates of SLA agreed with CLM's defaults (Oleson *et al.*, 2013, Table 8.1) only for tropical broadleaved evergreen trees, and for all other PFTs, our estimates are significantly lower. We could not directly compare our estimates of N_{mass} to CLM because CLM reports the C to N ratio instead, but we can comment on the relative magnitudes and trends in these respective traits. PFTs in CLM, by default, take on one of three C:N ratios: all grasses and deciduous PFTs have the lowest C:N (i.e. highest N_{mass}), followed by a higher value for all evergreen PFTs except boreal needleleaf evergreen, which has the highest value (i.e. lowest N_{mass}) (Oleson *et al.*, 2013). Our results agree that most evergreen PFTs, particularly needleleaved evergreen species, have lower N_{mass} than deciduous PFTs. However, broadleaved tropical evergreen species N_{mass} was more similar to most deciduous PFTs and significantly higher than other evergreen PFTs. Meanwhile, grasses generally had lower N_{mass} than deciduous trees, and C4 grasses in particular (which comprise many of CLM's agricultural PFTs) had N_{mass} that was nearly as low as the evergreen species. Our mean estimates of $V_{c,max,area}$ (among those that were reasonably constrained by data) were lower than those of CLM for all PFTs except needleleaf evergreen trees and grasses, for which our estimates overlapped CLM's parameters. Kattge *et al.* (2009) also found that $V_{c,max,area}$ was overestimated by Earth System models, but their estimates of $V_{c,max,area}$ and N_{area} are generally slightly higher than ours. This discrepancy may be at least partially due to our use of \log_{10} for all trait values, which weights low values more strongly than high values.

The interaction between growth form and biome in discrete PFT definitions confounds the interpretation of our results with respect to well established ecological and biogeographic patterns. For example, Poorter *et al.* (2009) found variation in SLA by growth form was, from highest to lowest, grasses, deciduous woody plants, evergreen woody plants, and succulents, while the pattern by biome was, again from highest to lowest, grassland, tundra, tropical forest, temperate forest, woodland, shrubland, and desert. We observed as expected that arctic grasses had lower mean SLA than temperate grasses, and that evergreen trees had higher specific leaf area than their deciduous counterparts. However, we observed by far the highest mean specific leaf area values in temperate deciduous broadleaf trees, rather than in grass PFTs as expected. Similarly to Onoda *et al.* (2011), we found no consistent patterns in SLA with temperature: Among broadleaved evergreen PFTs, temperate species had lower SLA than tropical, but among broadleaved deciduous PFTs, temperate species had higher SLA than both tropical and boreal species. With respect to the expected decline in foliar N:P ratios with latitude (Reich & Oleksyn, 2004), we found that N_{mass} was generally higher in PFTs associated with colder biomes compared to warmer ones, but observed biome-related differences in P_{mass} only among deciduous broadleaved and needleleaved evergreen PFTs. Our results for both $R_{d,mass}$ and $R_{d,area}$ failed to show a trend with respect to biome, contrary to the results of Atkin *et al.* (2015) (though this may be partially because our results are for respiration at ambient temperature, whereas Atkin *et al.* found that the climatic gradient was much stronger when respiration rates were standardized to a common temperature).

4.2 Trait correlations and leaf economics

The canonical leaf economic spectrum is defined by a negative correlation of between SLA and leaf lifespan, and a positive correlation of SLA with N_{mass} , P_{mass} , and photosynthesis and respiration rates (Wright *et al.*, 2004). We were able to reproduce the directionality of these relationships for most PFTs in our hierarchical model. Relationships of SLA with N_{mass} and P_{mass} were consistently positive, and relationships of SLA with leaf lifespan were generally negative (though, for some PFTs, correlations were not significantly different from zero). Although we did not include photosynthesis in our analysis, $V_{c,max,mass}$ and $J_{max,mass}$, which are closely related to photosynthesis rates, generally exhibited the expected positive correlations with SLA, as did $R_{d,mass}$, though many correlations were not significant, primarily due to sample size.

While the direction of relationships we observed was largely consistent across different PFTs, the strength of these correlations was more variable. For example, the correlations of SLA with N_{mass} and P_{mass} were significantly weaker in needleleaved PFTs than in broadleaved PFTs. On the other hand, relationships of SLA and N_{area} were strongly negative for all PFTs (except the data-limited needleleaved deciduous trees), and temperate needleleaved species in particular had the strongest SLA- N_{area} and SLA- P_{area} correlations of any PFT. Taken together with the finding that evergreen conifers are relatively unique in their consistently proportional allocation of N to cell walls and Rubisco (Onoda *et al.*, 2017), our results support the idea that needleleaved species primarily adapt to environmental changes through structural changes (i.e. increasing or decreasing SLA) rather than through modulating foliar biochemistry (Robakowski *et al.*, 2004).

We also found that the strength of the correlations of N with photosynthetic parameters $V_{c,max}$ and J_{max} —often used in ecosystem modeling to parameterize photosynthesis (Oleson *et al.*, 2013; Rogers *et al.*, 2017)—varied by plant functional type, whether the traits were normalized by mass or area. Although trait correlations are not necessarily indicative of allocation strategies, this result generally supports the findings of Ghimire *et al.* (2017) that N allocation strategies to photosynthesis vary widely by plant functional type. In particular, the correlations of N_{mass} with traits related to photosynthesis and respiration ($R_{d,mass}$, $V_{c,max,mass}$, and $J_{max,mass}$) were weaker for tropical evergreen broadleaved trees than for most other PFTs, but the correlation of these traits with P_{mass} was comparable or even slightly higher. This suggests that the productivity of tropical species is generally P-limited (Reich & Oleksyn, 2004; Ghimire *et al.*, 2017), that N allocation strategies are more variable under N-poor than N-rich conditions (Ghimire *et al.*, 2017), or more generally that photosynthetic parameters are affected more strongly by environmental covariates than leaf nitrogen contents (Ali *et al.*, 2015). Meanwhile, our result that the N_{area} - $V_{c,max,area}$ correlation is generally weaker for needleleaved than broadleaved species was also found by Kattge *et al.* (2009), and supports the lower allocation of N to photosynthesis found by Ghimire *et al.* (2017). In light of this fact and considering that boreal forests, largely populated by needleleaf species, have the largest influence on global climate of any biome (Snyder *et al.*, 2004; Bonan, 2008), we suggest that parameterization of needleleaf tree productivity based on foliar nitrogen content in Earth System Models be treated with caution.

Correlations of all traits with leaf lifespan was significantly weaker (often to the point of becoming insignificant) within most PFTs than globally. This suggests that leaf economic relationships related to leaf lifespan are dominated by the fundamental differences between deciduous and evergreen PFTs, while the factors driving variability in leaf lifespan within PFTs are more complex and idiosyncratic (Reich *et al.*, 2014; Wu *et al.*, 2016a). That being said, much of this within-PFT variability is known to be driven by variations in shade responses, and a key limitation of our study is that we have no information about the relative canopy positions at which traits were collected (Lusk *et al.*, 2008; Keenan & Niinemets, 2016).

There has been some debate in the trait ecology community about the use of mass- or area-normalized traits in analyses of the leaf economic spectrum. Two studies (Lloyd *et al.*, 2013; Osnas *et al.*, 2013) independently concluded that leaf economic relationships among mass-based traits emerge inevitably out of variation in SLA and are therefore not ecologically meaningful. Responses to these criticisms have suggested that both mass- and area-based normalization have merit, as mass-based traits have a natural interpretation in terms of investment costs and allocation while area-based traits are important due to the fundamentally area-based nature of energy and gas fluxes through leaf surfaces (Westoby *et al.*, 2013; Poorter *et al.*, 2013). Our study suggests the latter, that investigation of trait correlations on both a mass- and area-basis can yield biologically and ecologically meaningful conclusions. For one, our discussion of differences in ecological strategies between broadleaved and needleleaved species fundamentally depends on comparative analysis of mass- and area-normalized nutrient contents. Meanwhile, our discussion of tropical tree productivity with respect to foliar nutrient contents is generally supported by both mass- and area-normalized traits (i.e. the correlation between P and $V_{c,max}$ is stronger than the correlation of N and $V_{c,max}$ for tropical species whether we use the mass- or area-normalized versions of these traits).

4.3 Covariance as constraint

In agreement with our expectations, our results show that accounting for covariance between traits constrained the uncertainty around PFT-level trait means, particularly for trait-PFT combinations with low

sample sizes. Moreover, accounting for trait covariance occasionally also changed the position of trait mean estimates, even for PFT-trait combinations with relatively large sample sizes (e.g. N_{mass} for temperate broadleaved deciduous trees, Fig. 2). This result echoes Díaz *et al.* (2016) in demonstrating the importance of studying the multivariate trait space rather than individual traits. Such shifts suggest that the sampling of these traits in the TRY database is not representative, which is evident from looking at the relative sample sizes of different traits (Fig. 1; see also Kattge *et al.* (2011)). These shifts also indicate that parameter estimates based on univariate trait data (e.g. LeBauer *et al.*, 2013; Dietze *et al.*, 2014) may not only be overestimating uncertainty, but may also be systematically biased. Although our results clearly show that many time- and labor-intensive traits, such as R_d , $V_{c,max}$, and J_{max} for certain PFTs still lack the observations to estimate covariance with other traits, our results also show that the effective sample size of all traits is enhanced when covariance is taken into account, and we therefore suggest that future observational campaigns consider trait covariance when deciding which traits to measure. For example, field and remote sensing studies that estimate only certain traits like SLA and N_{mass} but not others (such as P_{mass} and $R_{d,mass}$) can leverage trait correlations to provide indirect constraint (Serbin *et al.*, 2014; Musavi *et al.*, 2015; Singh *et al.*, 2015; Lepine *et al.*, 2016).

The additional benefit of hierarchical multivariate modeling in our study was limited, largely due to the relatively low number of points used to estimate that across-PFT covariance structure. Therefore, for parameterizing the current generation of ecosystem models we suggest that simple multivariate models fit independently to each PFT are sufficient and that the additional conceptual challenges and computational overhead of hierarchical modeling are not required. However, for modeling work that requires larger numbers of PFTs (Boulangeat *et al.*, 2012), and especially for models that are parameterized on the basis of individual species (e.g. Linkages, Post & Pastor, 2013), the benefits of hierarchical modeling may accumulate (Clark, 2005; Dietze *et al.*, 2008; Cressie *et al.*, 2009; Webb *et al.*, 2010).

5 Conclusions

One aspect of ecology that makes it challenging is that no two organisms are identical and will respond in identical ways to external stimuli. Functional diversity research fundamentally depends on dimensionality reduction through a search for meaningful pattern that can be exploited to take reasonable guesses at average behavior. The trait trade-offs comprising the leaf economic spectrum are one such pattern. In this paper, we reaffirm the existence of the leaf economic spectrum both globally and, with some caveats, within plant functional types, and show how leaf economic relationships can be leveraged to inform trait estimates, particularly at small sample sizes. We also highlight how the strength of leaf economic relationships can be influenced by biotic and abiotic factors specific to certain PFTs.

We foresee tremendous potential of multivariate and hierarchical modeling approaches to elucidating the role of functional traits in organismal and ecosystem function. Besides the many important foliar traits that we did not include (e.g. pigment contents, leaf hydraulic traits), our approach could readily be applied to other plant traits whose relationship to the leaf economic spectrum is less clear. One example is hydraulic traits: While stem and leaf hydraulic traits are correlated (Bartlett *et al.*, 2016), a potential scaling between hydraulic and leaf economic traits is poorly understood (Reich, 2014; Li *et al.*, 2015). Similarly, reexamining the relationships defining wood (Chave *et al.*, 2009; Baraloto *et al.*, 2010; Fortunel *et al.*, 2012) and root (Kramer-Walter *et al.*, 2016; Valverde-Barrantes & Blackwood, 2016) economic spectra, as well as their relationship to the foliar traits, would provide useful information on possible scale-dependence of plant growth and allocation strategies. We emphasize that the relative difficulty of measuring hydraulic and other non-foliar traits (e.g. Jansen *et al.*, 2015) further increases the value of any technique that can fully leverage the information they provide. More generally, multivariate and hierarchical modeling has the potential to reveal functional trade-offs that are mutually confounding at different scales, thereby enhancing our understanding of processes driving functional diversity.

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