ECOLOGY LETTERS

Ecology Letters, (2018) doi: 10.1111/ele.12945

LETTER

Within-species patterns challenge our understanding of the leaf economics spectrum

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Abstract

The utility of plant functional traits for predictive ecology relies on our ability to interpret trait variation across multiple taxonomic and ecological scales. Using extensive data sets of trait variation within species, across species and across communities, we analysed whether and at what scales leaf economics spectrum (LES) traits show predicted trait–trait covariation. We found that most variation in LES traits is often, but not universally, at high taxonomic levels (between families or genera in a family). However, we found that trait covariation shows distinct taxonomic scale dependence, with some trait correlations showing opposite signs within vs. across species. LES traits responded independently to environmental gradients within species, with few shared environmental responses across traits or across scales. We conclude that, at small taxonomic scales, plasticity may obscure or reverse the broad evolutionary linkages between leaf traits, meaning that variation in LES traits cannot always be interpreted as differences in resource use strategy.

Keywords

Functional trait, intra-specific variation, leaf lifespan, leaf mass per area, leaf nitrogen content, taxonomic scale.

Ecology Letters (2018)

INTRODUCTION

Trait-based ecology has the potential to unify ecological disciplines, provide prediction in community ecology and improve ecosystem models. A 'functional' plant trait is an attribute that influences some aspect of plant performance (i.e. growth, reproduction or survival) and that displays different values between species and/or across environmental gradients (Violle *et al*. 2007). As an ecological tool, plant functional traits have proven useful proxies for ecological 'strategies' (e.g. Wright *et al*. 2004; Reich 2014) and have provided insight into demographic outcomes (e.g. Kraft *et al*. 2010; Adler *et al*. 2014; Kunstler *et al*. 2016), climatic stress tolerance (Maherali *et al*. 2004; Skelton *et al*. 2015) and ecosystem function (Finegan *et al*. 2014; Reich *et al*. 2014; Berner & Law 2015; Prado-Junior *et al*. 2016). Yet trait-based approaches have proven less useful in other contexts, limited in their ability to explain observed species range shifts (Angert *et al*. 2011; Buckley & Kingsolver 2012), predict sapling demographic rates (Paine *et al*. 2015), integrate whole-plant resource strategies in local communities (Messier *et al*. 2017a) or explain species coexistence (Kraft *et al*. 2015). The variable success of functional traits suggests a more nuanced understanding is needed of where, when and for what purposes different plant traits are truly functional.

One of the foundational successes of plant functional traits is the global leaf economics spectrum (LES), which explains the majority of among-species variation in leaf morphology and function (Wright *et al*. 2004, 2005). The LES defines a single axis of trait covariation representing a continuum between 'fast' leaves with low leaf mass per area (LMA), short leaf lifespan (LL), high nitrogen per unit leaf mass (N_{mass}) and high photosynthetic and respiration rates; and 'slow' leaves with high LMA, long LL, low N_{mass} and slow physiological rates. The elegance of the LES has led many to interpret variation in simple-to-measure LES traits as variation in leaf resource use strategy across space (Asner *et al*. 2016), through time (Li *et al*. 2015b), between species in communities (Wright *et al*. 2005) and between individuals or populations of the same species (Albert *et al*. 2010b). Others have used LES traits to identify how resource use strategy is abiotically constrained (Maire *et al*. 2015) and related to life-history strategy and resource use efficiency (Adler *et al*. 2014; Kunstler *et al*. 2016). Meanwhile, ecosystem modellers have begun to use empirical trait trade-offs to refine the plant discretisation schemes used in land surface models (Hudiburg *et al*. 2013; Pavlick *et al*. 2013; Scheiter *et al*. 2013; Wullschleger *et al*. 2014).

However, application of the LES has outpaced our understanding of how trait variation should be interpreted at different taxonomic and ecological scales (Messier *et al*. 2010, 2017b; Shipley *et al*. 2016). Can trait variation among populations of a species be interpreted in the same way as variation across plant families (i.e. is the interpretation independent of

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taxonomic scale)? Can variation in community mean trait values be interpreted similarly to variation between individual plants (i.e. is the interpretation independent of ecological scale)? Until we can answer these questions, it remains uncertain in which contexts LES traits can be used to understand resource use strategy. The LES is empirically based on global between-species trait correlations, and its application relies on the assumed but untested universality and scale independence of these correlations arising from physiological or evolutionary trade-offs (Reich *et al.* 1997; Wright *et al.* 2004, 2005; Shipley *et al.* 2006; Blonder *et al.* 2015). Mounting evidence, such as the positive correlations between LL and LMA across land plants vs. sometimes negative correlations within plant canopies, has challenged this assumption (Osada *et al.* 2001; Lusk *et al.* 2008; Russo & Kitajima 2016; Katabuchi *et al.* 2017). Moreover, increasing awareness of within-species trait variation has highlighted the need to understand trait covariation beyond the between-species comparisons from which most trait theory is derived (Albert *et al.* 2010a; Clark *et al.* 2010; Violle *et al.* 2012; Blonder *et al.* 2013, 2015; Niinemets 2014; Siefert *et al.* 2015).

Here we critically examine whether and at what scales leaf traits can be interpreted as variation in resource use strategy. The LES need not hold in all contexts and at all scales to be useful, so long as the limits of its application are known and respected. To identify where and when the LES holds, we explored the variation and covariation of four central LES traits: LMA, leaf lifespan and leaf nitrogen content on both a mass (N_{mass}) and area (N_{area}) basis. Specifically, we aimed to:

1 Decompose global leaf trait variation at different taxonomic levels and test whether the dominant scales of variation depend on the taxonomic breadth of the analysis.
2 Test whether trait covariation of the LES is consistent across taxonomic and ecological scales.
3 Examine trait–environment relationships in a large conifer data set to explore the environmental drivers of LES trait variation within species, between species and across tree communities.

We hypothesised that within-species variation would be small globally, but large in local or taxonomically restricted data sets (Albert *et al.* 2010a,b; Siefert *et al.* 2015; Messier *et al.* 2017b). In addition, we hypothesised that trait covariation would decrease in strength at lower taxonomic scales due to restricted sampling alone, but that the physiological trade-offs assumed to underlie the LES would conserve the general trait–trait relationships within taxa. Moreover, we hypothesised that the mathematical relationship between LMA, N_{area} and N_{mass} (Lloyd *et al.* 2013; Osnas *et al.* 2013) might drive scale-invariant relationships between LMA and mass-based but not area-based nitrogen content. Alternatively, scale dependence of these relationships would suggest a decoupling of leaf structure and leaf economics in certain contexts (e.g. Funk & Cornwell 2013; Niinemets 2014; Li *et al.* 2015a; Muir *et al.* 2016). We also hypothesised that trait covariation across conifer communities would recapitulate the LES, despite suggestions that ecological processes at different scales (e.g. community assembly) might run contrary to the trade-offs driving the global LES (e.g. Messier *et al.* 2010, 2017a,b). Finally, our assumption that the LES is scale invariant drove our expectation of (1) coordinated responses to the same environmental factors among traits and (2) similar trait–environment relationships within-species, between-species and across communities in an example data set of temperate conifers.

METHODS AND MATERIALS

Leaf trait data sets

We collected measurements of LMA, LL, N_{mass} and N_{area} from multiple published and unpublished data sets, comprising 4267 measurements of at least two traits per individual including 2031 species, 962 genera and 216 families. We also compiled data on within-species geographical trait variation of sun leaves for 50 species (17 gymnosperms and 33 angiosperms, minimum of 5 and mean of 36 trait measurements per species). Data sources included GLOPNET, which provided global data primarily on trait variation between species (Wright *et al.* 2004, 2005) and the TERRA-PNW plant trait, productivity, biomass and soil properties database (Law & Berner 2015; Berner & Law 2016), henceforth ‘PNW data’, which provided trait and site environmental data from 239 plots in Oregon and northern California including within-species trait variation for 24 woody species. Additional data on geographical trait variation in five woody and five herbaceous angiosperms were included from published and unpublished studies (Anderegg & HilleRisLambers 2015; Martin *et al.* 2016). See Supplemental Materials: Data Description and Fig. S1.

Variance decomposition

We performed variance decomposition to determine the taxonomic scales of trait variation using linear mixed effects models with a fixed intercept, a random effect for data source and random effects for different taxonomic levels. We compared the size of the random effects variance parameters within-species (i.e. residual variance), within-genus, within-family and between family for $\log_{10}$-transformed LMA, LL, N_{mass} and N_{area} across all measurements and data sets. We also explored how the dominant taxonomic scale of variation differs for two case study analyses, one including all woody species with at least one stem > 10 cm diameter at breast height in the PNW plot network (including 10 plant families) and one with the same plot network including only trees in the evergreen needle-leaf (ENL) plant functional type.

LES-related trait co-variation

We assessed the covariance between $\log_{10}$-transformed LES traits at multiple taxonomic scales by comparing the distributions of within-taxon correlation coefficients and standard major axis (SMA) regression slopes at increasing levels of taxonomic aggregation. First, we created a data set of within-species trait variation including all species in the global data set with more than five trait records ($n = 50$ species, 1803 trait measurements). We then averaged all data to the species level, all species averages to the genus level and all genus averages to the family level. We calculated Pearson correlation coefficients (ρ) and SMA regression slopes for the trait data within each species, genus and family that had at least five measurements (e.g. five measurements within a species, five species within a genus), as well as across family means of families with at least three species and globally across all species means.

We tested for significant differences in correlations and slopes across taxonomic levels using ANOVAs including various weighting schemes (see Table S3). We also assessed sampling effects at lower taxonomic levels using funnel plots and a null model based on the trait distribution at one higher taxonomic level. Because the power to detect significant correlations weakens when sampling less trait space (and trait variances tend to decrease at smaller taxonomic scales, see Fig. 1), we constructed null distributions for within-taxon comparisons by randomly sampling the trait distribution from one higher taxonomic level 10 000 times with the x and y range and sample size set by each taxon. Taxa with correlations significantly different from this null distribution show trait covariance different (in the positive or negative direction) from the taxonomic level above them (see Supplemental Material: Null Models). Finally, we calculated the trait covariation across conifer communities in the PNW data set, where community-weighted mean traits (CWMs, the sum of species mean traits weighted by their basal area fraction, Grime 1998; Garnier *et al.* 2004) could be calculated per plot from species abundances (see below).

Trait–environment relationships

We quantified the effect of site environmental factors on geographical variation in LES traits within-species, between species and across CWMs in conifer forest plots from the PNW data set. Trait–climate relationships within species capture plastic and ecotypic responses to environmental gradients, but across species they represent differences in realised niche along environmental niche dimensions. Meanwhile, trait–climate relationships of CWMs represent variation within species plus changes in species composition and abundance, combining within- and between-species trait variation (Ackerly *et al.* 2002; Lepš *et al.* 2011). LES traits have been found to vary with climate and soil characteristics globally (e.g. Maire *et al.* 2015), stand characteristics (leaf area index (LAI), stand age) and plant characteristics related to probability of self shading (e.g. growth rate, Reich *et al.* 1992).

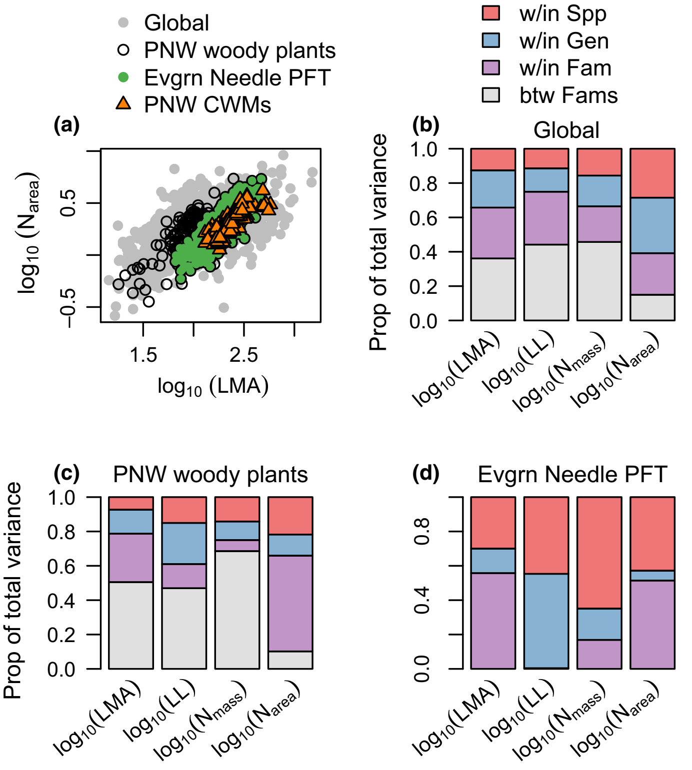

Figure 1 (a) Distribution of $\log_{10}(N_{area})$ and $\log_{10}$(LMA) for land plants globally (grey), all woody plants in the PNW forest plot network (open black), all species from the PNW network in the 'evergreen needle-leaf' Plant Functional Type (green) and PNW plot Community-Weighted Mean traits ('PNW CWMs', orange triangles). (b–d) Variance decomposition of four leaf economics spectrum traits including leaf mass per area (LMA), leaf lifespan (LL), mass-based nitrogen (N_{mass}) and area-based nitrogen (N_{area}) across different taxonomic scales for (b) land plants globally, (c) all woody plants in the PNW plot network (10 plant families) and d) conifers in the 'evergreen needle-leaf' Plant Functional Type (contains only families Pinaceae & Cupressaceae so no family variance component was fit). 'w/in Spp' denotes variance within species, 'w/in Gen' denotes variance between species within a genus, 'w/in Fam' denotes variance between genera within a family and 'btw Fams' denotes variance between plant families.

Specifically, using the PNW data set we fit linear mixed effects models with climate variables (see below), soil nitrogen content, log(plot age), plot LAI (proxy for light availability) and annual above-ground net primary productivity (proxy for rate of self-shading) as fixed effects and a plot level random intercept for the six best-sampled conifer species. We also calculated species mean trait values and mean environmental variables (for the 37 woody species present) and fit linear models relating environmental variables to species mean traits. Finally, we fit linear models relating environmental variables to CWM traits across forest plots. We calculated CWM traits for 165 plots with trait measurements for all species representing at least 75% of plot basal area. If a species representing < 25% of plot basal area lacked measurements, species-level means were used. We removed 39 plots (44 plots for LL) lacking complete environmental data and fit models to the remaining 126 plots (121 for LL).

All traits and predictors were z-score standardised based on the trait mean and standard deviation for each data subset and environmental variable mean and standard deviation for the entire PNW plot network, making effect sizes comparable across traits and predictors. We performed model selection using Akaike information criterion for small sample sizes (AICc) including all possible variable combinations. Multiple models had similar AICcs for many traits and species. To provide robust estimates of predictor importance, we reported the most parsimonious model for each trait and species and calculated model-averaged effect sizes from a model ensemble of all models with a ΔAICc of less than four from the best model.

Before including climate variables as predictors, we performed a PCA of 30yr climatologies (1984–2013) of water year (Oct–Sept) mean temperature, precipitation, cumulative climate moisture index (CMI, precipitation – potential evapotranspiration) and maximum vapour pressure deficit (VPD) from monthly PRISM climate data (Daly *et al.* 2008) plus mean topsoil and full soil column moisture from the Variable Infiltration Capacity hydrology model (Livneh *et al.* 2013). We used the first two principal components, explaining ~ 90% of the variance, as climate predictors. The first ('climPC1', 72% of variance) was interpreted as plot wetness and loaded with precipitation, soil moisture, VPD and CMI (Table S1). The second ('climPC2', 18% of variance) was interpreted as plot warmth and loaded strongly with temperature and slightly with VPD.

All analysis was performed in the R statistical environment (R Core Team 2016, version 3.2.4). We fit SMA regressions using the 'lmodel2' function from the *lmodel2* package (Legendre 2016). Mixed models were fit using the *lme4* and *lmerTest* packages (Bates *et al.* 2015; Kuznetsova *et al.* 2016), and model averaging was performed using the *MuMIn* package (Kamil 2016). Analysis code is available at https://github.com/leanderegg/Anderegg_EcolLet_IntraspecificLES.

RESULTS

Variance decomposition

Analysis of 4267 measurements of $\log_{10}$-transformed leaf lifespan, LMA and leaf nitrogen content from 2031 species showed that inter-specific variation is typically larger than intra-specific variation, with most trait variation occurring between plant families (Fig. 1). Global variation in LL, LMA and N_{mass} was primarily driven by variation between families with a decreasing proportion of total variation at successively lower taxonomic scales (Fig. 1b, Table S2). However, N_{area} showed a different pattern, with 28% of total variation contained within-species and the proportion of variance decreasing at the highest taxonomic scales.

In a regional case study, this pattern held for all woody plants in the PNW data set (including 10 plant families), with between-family variation dominating for all traits except N_{area}. However, when limiting the analysis to conifers in the evergreen needle-leaf (ENL) PFT, within-species trait variation contributed 26–62% of the total trait variation for LMA and N_{mass}, respectively (Fig. 1d, Table S2). Even though the ENL data set covered a large proportion of global trait space (e.g. Figs 1a and S2), within-species variation became important when only two plant families (*Pinaceae* and *Cupressaceae*) were represented.

Trait covariation

We found that LES relationships involving N_{mass} reliably scaled across taxonomic levels (Fig. 2, Tables S3 and S4). The slope between N_{mass} and both LMA and LL did not statistically differ across taxonomic levels with most weighting methods (Fig. 2a,c; Table S3), and was consistent across CWM traits. Correlation strength decreased at lower taxonomic levels, but given the smaller trait variances at lower levels (Fig. 1b) this was likely an artefact of restricted within-taxon N_{mass} variation (see Fig. S3), and few within-species correlations (2 of 35 for LMA-N_{mass}, 1 of 19 for LL-N_{mass}) were less negative than null models simulating restricted sampling alone (Fig. 2, one-tailed $\alpha = 0.05$, Supplemental Material: Null Models).

The similarities between species-level trait correlations and the global LES end there. While the globally strong positive correlation between $\log_{10}$(LL) and $\log_{10}$(LMA) did manifest within genera, within families and between families, it significantly weakened and even reversed within species (Fig. 3, Tables S3 and S4). Moreover, many species, representing both extremes of trait space (long LL and high LMA as well as short LL and low LMA), showed more negative correlations than expected from null models of sampling effects alone (8 of 24 at $\alpha = 0.05$, 12 of 24 at $\alpha = 0.1$, Fig. 3). These negative correlations remained when we controlled for light availability by including only open plots (LAI less than 4) in the PNW data set (Fig. S5). Across conifer communities, the two traits were only weakly positively related ($\rho = 0.139$, $P = 0.08$).

In addition, the relationship between $\log_{10}(N_{area})$ and $\log_{10}$(LMA) was strong within-species and across communities but weak at higher taxonomic levels (Fig. 4a,b; mean slope within-species is 1.08 ± 0.02, but only 0.88 ± 0.01 within genera and 0.65 globally). Slopes differed significantly across taxonomic scale with most weighting methods (Table S3) and 77% of species, 54% of genera and 44% of families showed stronger within-taxon LMA-N_{area} correlations than expected from trait distributions at higher taxonomic levels (Figs 4 and S4). Moreover, because of the reversal of the LL-LMA relationship and strong link between LMA and N_{area} within-species, the globally weak positive relationship between LL and N_{area} became a strong negative relationship within species, with both the slope and correlation differing across taxonomic levels and 8 of 19 species showing more negative correlations than expected from the null model (Figs 4c,d, S3 and Table S4). However, for all trait pairs involving leaf lifespan, our data set only includes temperate species. Across conifer communities, N_{area} and LL were uncorrelated ($P = 0.52$).

Trait–environment relationships

In a regional data set from the NW USA, plot-level environmental characteristics were neither strong nor consistent predictors of trait variation within species, between species or between CWM traits. In six well-sampled conifers, the mean within-species marginal R^2 (within-species variation explained by environment fixed effects) of the best trait–environment model was 0.34 for LL, 0.17 for LMA, 0.24 for N_{mass} and 0.12 for N_{area} (Fig. 5a, Table S5), though the difficulty of quantifying LMA in conifers may influence results for LMA and N_{area}. Environmental variables better predicted trait variation among species (Fig. 5a), perhaps unsurprising given the greater trait variation between than within species (Table S6). CWM traits were also more strongly related to environmental variables than were intraspecific traits, except for N_{mass} (Fig. 5a).

Trait–environment relationships across species and across CWM traits often differed markedly from within-species relationships. LL showed somewhat similar effect sizes and

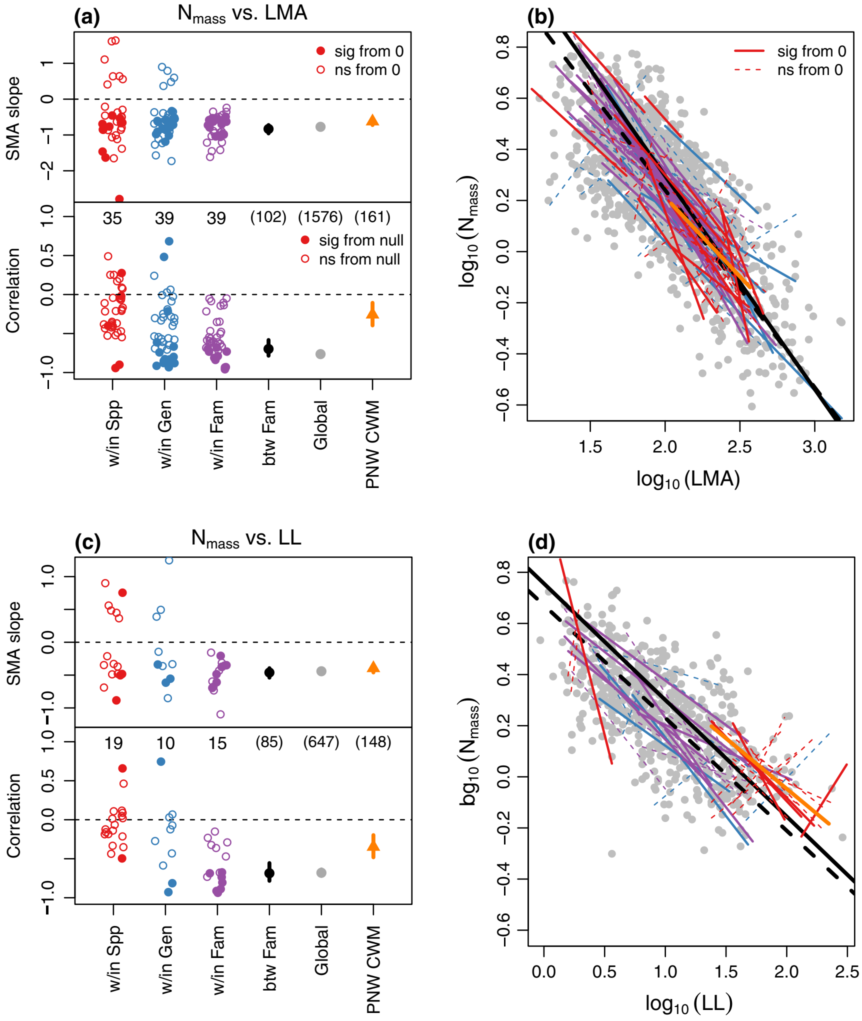

Figure 2 N_{mass} is negatively correlated with leaf mass per area (LMA) (a and b) and leaf lifespan (c and d) at all taxonomic levels and across conifer communities. Points in panels a & c show within-taxon Standard Major Axis regression slopes and Pearson correlations fit to $\log_{10}$ transformed traits from individual species, genera and families, across all plant families ('btw Fam'), globally across all species means ('Global') and across Community-Weighted Mean traits in PNW conifer plots ('PNW CWM'). Filled points show taxa with trait correlations significantly different from zero (upper panel of a and c) or taxa with correlations significantly different from the null model based on resampling the trait distribution at higher taxonomic levels (lower panel of a and c). Numbers indicate the number of within-taxon relationships (parenthetical numbers are number of families, species and plots in the between family, global-between species and between community relationships respectively). (b) Scatterplot of $\log_{10}$(LMA) vs. $\log_{10}$(N_{mass}) or (d) $\log_{10}$(LL) vs. $\log_{10}$(N_{mass}) across global species means (grey points), with the trait relationships for individual species shown as red lines, genera as blue lines and families as purple lines (solid lines indicate significant correlations, dashed lines non-significant correlations). The solid black line is the relationship across families, dashed black line is the global between-species relationship and orange line is the relationship across conifer CWMs.

directions at all scales (Fig. 5). Yet the other three traits all exhibited strong scale-dependent trait–environment relationships along at least one environmental axis, indicating that the drivers of trait variation differed with ecological scale. For example N_{mass} responded positively to soil nitrogen within-species and across CWM traits but not across species, indicating that species do not sort along fertility gradients based on their N_{mass} and that plastic nitrogen allocation within species drives variation in community average N_{mass}. Meanwhile N_{area} showed strong climate responses across species and CWMs, but not within-species, indicating a dominant role of species turnover for CWM N_{area} variation (Fig. 5h,i).

Strikingly, very few LES traits shared environmental responses, with most responding independently to different environmental gradients, particularly within species. LL and LMA did share a common negative response to plot 'warmth' (climate PC2) at all scales, consistent with a shift towards more conservative LES strategies in colder environments within and across species (Fig. 5b–e). Also, LL and LMA slightly increased, whereas N_{mass} decreased with stand age, consistent with a similar shift towards more conservative LES strategies with age (within species), and in late successional species (across species with older mean stand ages). However, little additional trait coordination was discernible. This implies that within-species trait responses to many environmental gradients (e.g. precipitation, soil fertility) may obscure rather than maintain LES trait covariances.

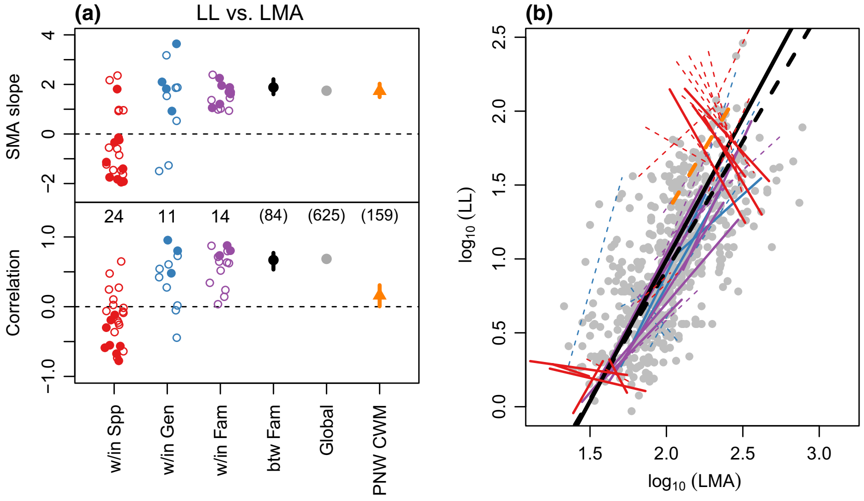

Figure 3 Leaf Lifespan and LMA are strongly positively related across species, genera and families, but negatively related within-species and poorly correlated across conifer communities. (a) SMA slopes (upper panel) and Pearson's correlations (lower panel) between $\log_{10}$(Leaf Lifespan) and $\log_{10}$(LMA). (b) Scatterplot of $\log_{10}$(LMA) vs. $\log_{10}$(Leaf lifespan) across global species means (grey points), with the trait relationships for individual species (red lines), genera (blue) and families (purple), across families (solid black), across species means globally (dashed black) and across conifer communities (orange). Numbers, point types and line types are as in Fig. 2.

DISCUSSION

In total, we found reasons for optimism with regards to the universality of the LES, but also significant areas of caution in its universal application. We found scale-dependent leaf trait covariation, implying that the global LES is maintained by relatively weak evolutionary or physiological trade-offs that can be reversed by plasticity within-species. We also found that, although LES traits vary primarily between plant families, within-species variation can be large for some traits and taxonomically restricted analyses. Thus, the within-species reversal of key trait–trait relationships underpinning the LES indicates that variation in individual LES traits does not directly map to leaf resource use strategy. This supports emerging literature documenting the decoupling of leaf structure and leaf economics (Funk & Cornwell 2013; Li *et al.* 2015a; Mason & Donovan 2015; Muir *et al.* 2016), which may lead to context-dependent relationships between leaf traits and resource use strategy. Finally, the trait- and scale-specific trait–environment relationships documented here suggest little coordination between leaf traits in response to environmental gradients, with the combination of trait plasticity and species sorting driving the contrasting trait–trait and trait–environment patterns across taxonomic and ecological scales.

Small intra-specific trait variation

Our analyses suggest that the relative importance of within-species trait variation depends on the taxonomic diversity of the study system (Fig. 1). While N_{area} was remarkably variable at small taxonomic scales globally, LMA, LL and N_{mass} varied primarily between plant families both globally and regionally, except in conifers. This is consistent with previous context-dependent findings (Jung *et al.* 2010; Messier *et al.* 2010; Lepš *et al.* 2011; Auger & Shipley 2012), where the size of within-species trait variation differed between traits and systems and was not strongly related to species richness, spatial scale or climate (Siefert *et al.* 2015). Taxonomic diversity may thus be a stronger predictor of the relative magnitude of within-species variation than species richness or breadth of sampled trait variation (Fig. 1, Table S2). If so, species-level trait quantification may be sufficient for ecological studies in family rich communities, but insufficient in family poor systems, even if the analysis includes the majority of global trait space. For example discretising within-PFT trait variation in ENL conifers (a naturally family poor PFT) must acknowledge that 30–65% of within-PFT LES variation occurs within species (Fig. 1d, Table S2, Hudiburg *et al.* 2013). For leaf traits to prove functional in such taxonomically restricted scenarios, theoretical frameworks must explain trait variation both within and between species. This will require analysing the variance and covariance patterns of additional functional traits beyond the four considered here.

Scale dependence of the leaf economics spectrum

Some trait correlations, such as the consistent negative relationship between both LMA/LL and N_{mass} across scales (Fig. 2), provided support for the scale independence of the LES. Our results imply that longer lived and thicker/denser leaves tend to have lower photosynthetic capacity per unit mass within-species, between-species and across communities (Fig. 2), if N_{mass} correlates with rubisco content and therefore carboxylation capacity. Variation in leaf nitrogen devoted to photosynthesis (i.e. allocated to rubisco) and rubisco-use efficiency may complicate this interpretation (Hikosaka & Shigeno 2009).

However, the scale independence of N_{mass} relationships proved to be the exception. We observed distinct scale dependence in three of the five trait correlations tested (Figs 3 and 4), including the breakdown and reversal of a central component of the LES: the LL-LMA trade-off (Fig. 3, Tables S3

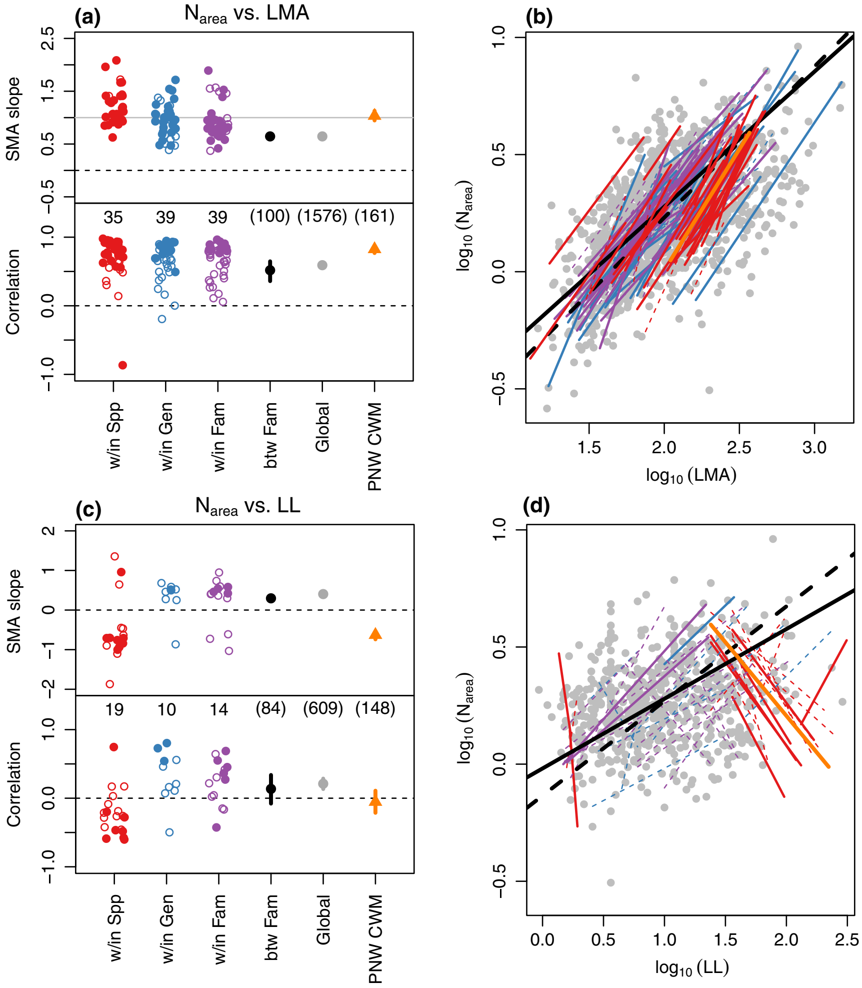

Figure 4 N_{area} is strongly positively correlated with leaf mass per area (LMA) within species, and shows a stronger scaling slope within-species than at higher levels of taxonomic aggregation (a and b). Leaf lifespan shows a weak positive relationship with N_{area} at higher taxonomic scales, but a negative relationship within-species and across conifer communities (b and c). (a and c) SMA slopes (upper panels) and Pearson's correlations (lower panels) between $\log_{10}$(LMA) and $\log_{10}(N_{area})$ (a) or $\log_{10}$(LL) and $\log_{10}(N_{area})$ (c). Scatterplot of $\log_{10}$(LMA) vs. $\log_{10}(N_{area})$ (b) or $\log_{10}$(Leaf lifespan) vs. $\log_{10}(N_{area})$ (d) across global species means (grey points), with the trait relationships for individual species (red lines), genera (blue) and families (purple), across families (solid black), across species means globally (dashed black) and across conifer communities (orange). Numbers, point types and line types are as in Fig. 2. Grey line in panel (a) indicates isometric (1 : 1) scaling.

and S4). At the global scale, the positive correlation between LL and LMA has been interpreted as an evolutionary trade-off: high LMA leaves are costly to build and tend to have low photosynthetic rates, requiring long lifespans to pay off. Yet this relationship breaks down at the scale at which we understand evolution to occur, namely between individuals or populations of a species (Tables S3 and S4).

The within-species reversal of the LL-LMA relationship could be driven by either ecotypic variation (due to genetic differentiation) or plasticity. The first poses an evolutionary conundrum. If within-species patterns are driven by ecotypic/genetic variation between populations, this implies opposing selection pressures at micro-vs. macro-evolutionary scales (e.g. selection for a negative LL-LMA relationship within-species but a positive relationship between species). While there is strong evidence for genetic linkages between LL and LMA in *Arabidopsis thaliana* (L.) Heynh. (Fig. S6, Vasseur *et al.* 2012; Blonder *et al.* 2015), LL has been shown to be decoupled from LMA across species in the herbaceous genera *Viburnum* (Edwards *et al.* 2014) and *Helianthus* (Mason & Donovan 2015). These findings in herbs raise the possibility that macroevolutionary trait relationships may not hold at smaller evolutionary scales (Mason & Donovan 2015), particularly if the LL-LMA relationship is a 'boundary line' relationship (sensu Grubb 2016) that only represents a physiological/evolutionary constraint at trait extremes. Measurements of leaf lifespan in common gardens and experiments will be critical for testing these hypotheses.

A simpler interpretation of the within-species 'counter-gradient' pattern is that LES traits respond plastically to different environmental cues, obscuring or even reversing the soft evolutionary trade-off between leaf longevity and LMA. While we cannot differentiate ecotypic variation vs. plasticity in our analysis, the disparate within-species responses of LL and LMA to environmental gradients support this interpretation (Table S5, Fig. 5). This 'counter-gradient' pattern has

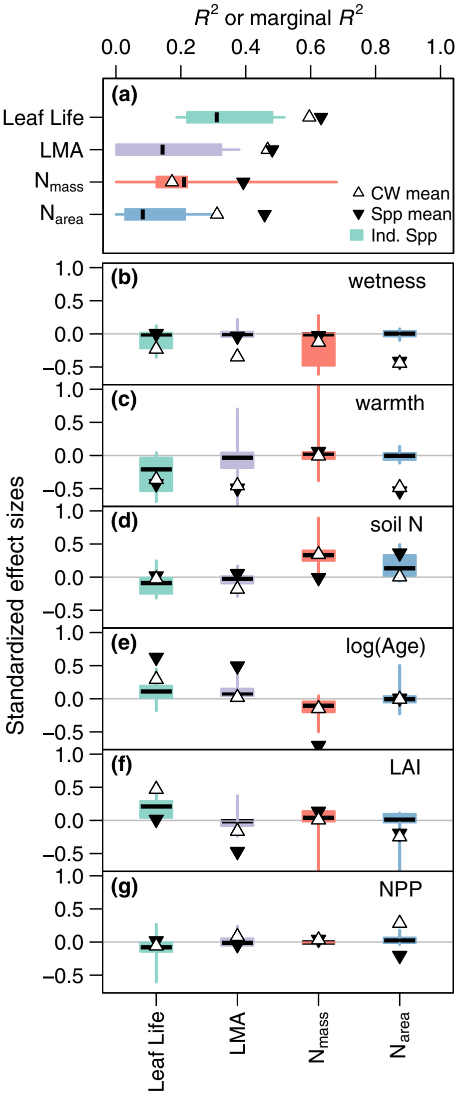

Figure 5 Trait–environment relationships vary considerably between traits and between scales (within-species vs. between species vs. across communities). (a) Best R^2 (or marginal R^2 for within-species models) predicting leaf trait variation from stand environmental variables, either between community-weighted leaf traits (open triangles), between species mean traits (filled triangles) or within individual species for six conifers (boxplots). (b–g) Distribution of standardised, model-averaged effect sizes for six environmental variables from linear mixed effects models relating leaf traits to site environmental factors within species, between species and between communities. Model-averaged effect sizes were derived from the subset of all model formulations that had a ΔAICc of less than 4 from the best model for each species for each trait. Predictor variables included climatic ‘wetness’ (PC1 of climate PCA, see Methods, panel b), climatic ‘warmth’ (PC2 of climate PCA, panel c), soil nitrogen content (soil N, panel d), log-transformed plot age (log(Age), panel e), Leaf Area Index (LAI, panel f) and site Net Primary Productivity (NPP, panel g).

previously been documented in plastic differences between sun and shade leaves of the same species, where structural and functional demands become decoupled (Osada *et al.* 2001; Lusk *et al.* 2013; Katabuchi *et al.* 2017). Our results suggest that the same process can occur in sun leaves across other environmental gradients. The strong effect of temperature on LL found in conifers may indicate that temperature-dependent variation in photosynthetic and respiration rates determines within-species variation in leaf longevity. Variation in construction costs related to changes in LMA – which are not strongly linked to plot-level environmental variables in our analysis (Fig. 5a) – may only weakly influence carbon payback period, at least in cold temperate systems. This is consistent with experimental work showing that resource manipulation alters LL by changing carbon gain rather than construction costs (e.g. Oikawa *et al.* 2006; Pornon *et al.* 2011). We found ‘counter-gradient’ within-species LL-LMA relationships in temperate gymnosperms and angiosperms at the two extremes of LL and LMA, suggesting some generality for this finding. The considerable variation around the average negative LL-LMA relationship may reflect species-specific differences in plasticity. However, we were unable to find within-species LL data from any tropical or subtropical plants. Given that cold stress may place unique demands on leaf structure (Niinemets 2016), expanding this analysis beyond the temperate zone is critical.

We also found that taxonomic scale-dependence can drive ecological scale-dependence in trait–trait relationships. Trait covariation between CWM traits in conifer forests was midway between within-species and between-species patterns (Figs 2, 3 and 4). CWM LL and LMA were only marginally positively correlated (Fig. 2) and showed both stronger (LMA vs. N_{area}) and weaker (LL vs. N_{area}) patterns with N_{area} than the global LES, due to conflicting within- and between-species trait covariation (Fig. 4a,c). Therefore, variation in the ‘dominant’ or mean trait value across conifer communities generally did not recapitulate the LES.

Ultimately, if trait covariation is dependent on taxonomic and ecological scale, variation in LES traits cannot be universally interpreted as variation in leaf resource use strategy in ecological and modelling applications. In particular, considering LMA (probably the single most widely measured plant trait) as the principle proxy for the LES is problematic, as its covariation with both LL and N_{area} differ across taxonomic and ecological scales (Figs 3 and 4). Many LES traits, particularly LMA and leaf nitrogen, are emergent products of multiple underlying physiological and anatomical attributes. For example leaf thickness, mesophyll cell size/number and mesophyll air space jointly determine LMA, yet respond differently to abiotic stresses (Baird *et al.* 2017). Broad application of functional traits will require a mechanistic understanding of the environmental causes and physiological consequences of variation in these underlying attributes.

Even as they challenge our interpretation of the LES, within-species patterns of trait covariation can also inform basic plant physiology. The consistent relationships of both LMA and LL with N_{mass}, yet strong taxonomically dependent patterns with N_{area} imply constraints on nitrogen allocation, regardless of issues of mass vs. area normalisation (Lloyd *et al.* 2013; Osnas *et al.* 2013; Poorter *et al.* 2013; Westoby *et al.* 2013). We found an increasingly tight link between LMA and N_{area} within species, with a 50% change in LMA associated with a 54% change in N_{area} within species but only a 33% change across species. Thus, within-species, increasing LMA requires devoting more leaf nitrogen to leaf structure, likely due to the fixed nitrogen composition of cell walls or structural tissue (Hikosaka & Shigeno 2009; Onoda *et al.* 2017). If nitrogen allocation to photosynthetic and cytosolic pools is plastic within species but the nitrogen content of cell walls is fixed, then the relationship between LMA and N_{mass} should be weaker than the LMA-N_{area} relationship within species as found here (Figs 2a vs. 4a). More research is needed on within-species variation in physiological rates and, critically, leaf anatomy and rubisco content to elucidate the mechanisms behind these patterns.

Inconsistent trait–environment relationships across traits and scales

We found very few coordinated trait responses to environment variables. The LES would predict LMA, LL and N_{area} to respond similarly and N_{mass} to respond in the opposite direction to environmental gradients. Yet within conifer species, three of four LES traits varied only weakly along environmental gradients (Fig. 5a) and traits did not share common environmental responses (Fig. 5b–g). In fact, the most strongly correlated environmental factor differed considerably between traits (Fig. 5) and for the same trait in different species (Table S5).

We also found conflicting trait–environment relationships at different ecological scales. Trait values were generally more predictable between species (and across communities) than within species (Fig. 5a) but often showed environmental responses not seen within species (e.g. Fig. 5c). The contrasting trait–environment relationships between vs. within-species indicate that the ecological drivers of variation in the CWM or 'dominant' trait in a community differ depending on the trait and the gradient. For example changes in CWM N_{mass} in response to soil nitrogen appear to be governed by within-species acclimation/ecotypic variation (Fig. 5d). Meanwhile, changes in CWM LL in response to stand age are primarily driven by species turnover during succession (Fig. 5e). Given that biomass-weighted traits (e.g. CWMs) drive many aspects of ecosystem function (Grime 1998; Fortunel *et al.* 2009; Finegan *et al.* 2014), these results highlight how the link between LES traits and ecosystem function is dependent on within-species trait variation (e.g. Reich *et al.* 2014).

Finally, we found it striking that, despite the strong responses of LES traits to experimental manipulations (e.g. Oikawa *et al.* 2006; Poorter *et al.* 2009; Baird *et al.* 2017), the average within-species explanatory power of environmental variables in natural plots is similar to the trait–environment relationships found between species across multiple biomes: stronger for temperature than precipitation but weak overall (Moles *et al.* 2014; Maire *et al.* 2015). Globally, leaf economics are very weakly related to abiotic constraints; there is much more variation in LES traits within an individual community than across large climate gradients (Wright *et al.* 2004). While trait–environment relationships may prove strong for community-weighted means (i.e. the traits of the dominant species in a community), between species with similar ecologies (i.e. mid to late succession overstory trees, Fig. 5a), or in core vs. transient species (Umaña *et al.* 2017), there are still many ways to be a plant in most environments.

CONCLUSION

Our understanding and application of leaf traits is far from complete, as highlighted by the incongruities between the global leaf economics spectrum and within-species trait data. The weakening/reversal of trait coordination at small scales limits the utility of existing leaf economics theory within species and across communities, particularly where taxonomic diversity is low. The path forward will require mechanistic models of trait variation explicitly built from observations at multiple ecological and taxonomic scales. Our analysis also illustrates how contrasting patterns of trait coordination across ecological and taxonomic scales may themselves help reveal the underlying evolutionary, physiological and ecological mechanisms linking traits to each other and to leaf economics. Understanding the mechanisms that link leaf form and function across scales will both power predictive models of global ecosystems and shed light on the fundamental processes and trade-offs constraining plant physiology.

ACKNOWLEDGEMENTS

We thank P Reich and WRL Anderegg for insightful discussion and comments on the manuscript. We also thank B Blonder and two anonymous reviewers for helpful feedback on the manuscript. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No.s DGE-1256082; DDIG-1500837, an NSF international travel allowance through the Graduate Research Opportunities Worldwide and an NSF Postdoctoral Research Fellowship Grant No. DBI-1711243 (to LDLA). Any opinions, findings and conclusions or recommendations expressed in this material are those of the author (s) and do not necessarily reflect the views of the National Science Foundation.

AUTHORSHIP

BEL, LTB, MLS and LDLA collected and compiled data; LDLA, LTB, GB, BEL and JHRL designed the study; LDLA performed the statistical analysis and wrote the first draft of the manuscript; all authors contributed substantially to revisions.

DATA ACCESSIBILITY STATEMENT

Most data used in the analysis are publicly available (https://doi.org/10.1038/nature02403 for GLOPNET, dx.doi.org/10.3334/ORNLDAAC/1292 for NACP TERR-PNW, https://doi.org/10.1111/1365-2435.12790 for *Coffea Arabica*). Additional, previously unpublished trait data can be found on Dryad, https://doi.org/10.5061/dryad.c1dn34b. Code used to perform analyses is available at https://github.com/leanderegg/Anderegg_EcolLet_IntraspecificLES.

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SUPPORTING INFORMATION

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

Editor, Josep Penuelas
Manuscript received 10 October 2017
First decision made 8 November 2017
Second decision made 5 February 2018
Manuscript accepted 18 February 2018