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## Leaf Traits Within Communities: Context May Affect the Mapping of Traits to Function

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### Comments

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## Leaf traits within communities: Context may affect the mapping of traits to function

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**Abstract.** The leaf economics spectrum (LES) has revolutionized the way many ecologists think about quantifying plant ecological trade-offs. In particular, the LES has connected a clear functional trade-off (long-lived leaves with slow carbon capture vs. short-lived leaves with fast carbon capture) to a handful of easily measured leaf traits. Building on this work, community ecologists are now able to quickly assess species carbon-capture strategies, which may have implications for community-level patterns such as competition or succession. However, there are a number of steps in this logic that require careful examination, and a potential danger arises when interpreting leaf-trait variation among species within communities where trait relationships are weak. Using data from 22 diverse communities, we show that relationships among three common functional traits (photosynthetic rate, leaf nitrogen concentration per mass, leaf mass per area) are weak in communities with low variation in leaf life span (LLS), especially communities dominated by herbaceous or deciduous woody species. However, globally there are few LLS data sets for communities dominated by herbaceous or deciduous species, and more data are needed to confirm this pattern. The context-dependent nature of trait relationships at the community level suggests that leaf-trait variation within communities, especially those dominated by herbaceous and deciduous woody species, should be interpreted with caution.

**Key words:** carbon capture; community ecology; functional trait; GLOPNET database; leaf economics spectrum, LES; leaf life span; leaf mass per unit area, LMA; leaf-trait variation; photosynthesis; trait-based ecology.

### INTRODUCTION

One of the most significant developments within the field of ecology in the last decade was the formalization of the leaf economics spectrum (LES). The LES shows that relationships exist among several key traits across a broad range of species and different climates (Reich et al. 1997, Wright et al. 2004). For example, leaf photosynthetic rate scales negatively with leaf mass per area (LMA) because a high leaf area displayed per unit mass invested leads to more efficient light capture and a shorter distance of CO<sub>2</sub> transport to sites of carboxylation (Parkhurst 1994, Niinemets and Sack 2006). On the other hand, higher LMA allows for a longer leaf life span (LLS), which allows for a leaf's carbon gain to

extend over a longer period of time. These alternative strategies (slow and long vs. fast but short) often co-occur in communities dominated by woody vegetation. For example, in the Californian chaparral community, LLS of woody species varied from 2 to 23 months, and LLS was closely correlated with photosynthetic rates per unit leaf mass ( $A_{\text{mass}}$ ; Ackerly 2004).

One implication of the LES is that evolutionary processes are constrained, with some combinations of leaf traits being either biochemically or competitively unviable (Reich et al. 1997, Donovan et al. 2011). A second implication is that easy-to-measure functional traits, such as LMA or leaf dry-matter content, can be collected from large numbers of species and used to infer processes that are more difficult to measure (e.g., photosynthetic rate, growth rate, life span) but correlate strongly with these functional traits across a broad range of species (Reich et al. 2007). Indeed, new comprehensive trait databases are being assembled with the

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expectation that plant traits will enable a more empirically grounded representation of vegetation in Earth system models (Kattge et al. 2011).

Before making a paradigm shift from species- to trait-based ecology, we should critically evaluate the ability of trait-based approaches such as the LES to meet our goals. When addressing questions at large scales, where a broad diversity of taxa and environmental conditions are represented, functional traits such as LMA, plant height, or phenology may tell us a great deal about plant function. However, a potential danger arises when interpreting leaf-trait variation among species *within* communities where trait relationships do not match the global pattern.

Why might LES relationships be weaker within than across communities? Wright et al. (2005) suggested that the composition of different growth forms (e.g., herbaceous, deciduous woody, evergreen woody) within individual communities would contribute to variation in LES relationships. Abiotic factors may also influence the strength of LES relationships within communities. For example, Wright et al. (2004) found that the slope of the LLS–LMA relationship declines with increased temperature or irradiance, meaning that the duration of carbon assimilation per unit of tissue invested is shorter in hot or high-light environments. Additionally, the strength of LES relationships within communities is driven by sample size and the range of trait variation: relationships will be weaker if there is no variation present (Niinemets and Sack 2006). Lastly, phylogenetic and biogeographic processes such as physical barriers to dispersal and climatic or geological events can lead to different selective pressures within communities that may result in different trait values and trait scaling relationships. For example, Heberling and Fridley (2012) analyzed similar vegetation types with different historical biogeographic influences and found that communities with a history of more intense competition had higher resource-use efficiency resulting in different slopes and intercepts of relationships between  $A_{\text{mass}}$  and  $R_{\text{dmass}}$  (mass-based dark respiration), LMA–LLS, and  $A_{\text{mass}}-N_{\text{mass}}$  (mass-based leaf nitrogen concentration).

While each one of these factors likely contributes to variation in LES relationships within communities, the degree to which variation in LLS affects LES relationships within communities is unknown because relatively few LLS data exist for key vegetation types. The LES was developed on a global scale using a broad range of species with considerable variation in LLS (Reich et al. 1997, Wright et al. 2004). While woody evergreen communities contain significant variation in LLS, many communities do not. Two globally important vegetation types in which variation in LLS is constrained are those dominated by herbaceous and deciduous woody plants (see Plate 1). In these communities, variation in LLS exists but it is markedly reduced compared to woody-dominated communities (Lusk and Warton 2007, Lusk et al. 2008). Because the absence of significant variation

in LLS affects the logic of the LES trade-off, this raises the possibility that the LES does not operate within some communities.

We explored this idea by assembling data for three commonly measured functional traits (LMA,  $N_{\text{mass}}$ ,  $A_{\text{mass}}$ ) across 31 communities that vary in their composition of deciduous woody, evergreen woody, and herbaceous species. We predicted that leaf-trait relationships would be strong within communities containing a broad mix of leaf types; however, trait relationships would be weaker in communities with low variation in LLS. Ecologists are increasingly using leaf trait variation to infer community-level function; many recent studies have used either LMA or leaf dry-matter content as an indicator of “plant function” to interpret community-level patterns (e.g., Brym et al. 2011, Falster et al. 2011, Long et al. 2011) and ecosystem services (Lavorel and Grigulis 2012). Thus, there is a pressing need to understand how the LES can be applied within communities.

#### AN EXPLORATION OF EXISTING DATA

We used data from the GLOPNET data set (Wright et al. 2004), which contains 2548 entries of 2021 plant species from 175 sites. We included data from communities with sample sizes greater than 10 for univariate analysis of leaf life span (LLS) and 15 for bivariate relationships; bivariate relationships require a larger sample size for reliable estimates (see Wright et al. 2005). Phylogenetically restricted data sets (e.g., sampling of only one genus) were excluded. This resulted in 31 communities and a total of 531 observations for 514 species for univariate analysis of leaf life span. For bivariate analysis, we focused on leaf mass per unit area (LMA), leaf nitrogen concentration per mass ( $N_{\text{mass}}$ ), and photosynthesis rate per unit leaf mass ( $A_{\text{mass}}$ ) because these are important leaf economics spectrum (LES) traits and relationships among mass-based traits are stronger than among area-based traits (Wright et al. 2005). For the bivariate analysis, filtering the data set left 22 communities and a total of 673 observations for 580 species. Prior to analysis, all data were log-transformed. Correlation coefficients, linear regression, and ANOVA were conducted in R (version 2.15.1; R Development Core Team 2012). We present variation in LLS as standard deviation (SD), coefficient of variation (CV), and range.

Of the 31 communities containing LLS data, the majority were dominated by evergreen species ( $n = 10$ ) or were a mix of evergreen, herbaceous and woody deciduous species ( $n = 14$ ). Only two communities were dominated by woody deciduous species and five were dominated by herbaceous species (Fig. 1). Thus, our analysis identified a lack of LLS data for communities with relatively short leaf life span. Variation in LLS was smaller in communities dominated by woody deciduous and herbaceous species than those dominated by evergreen woody species or in mixed communities

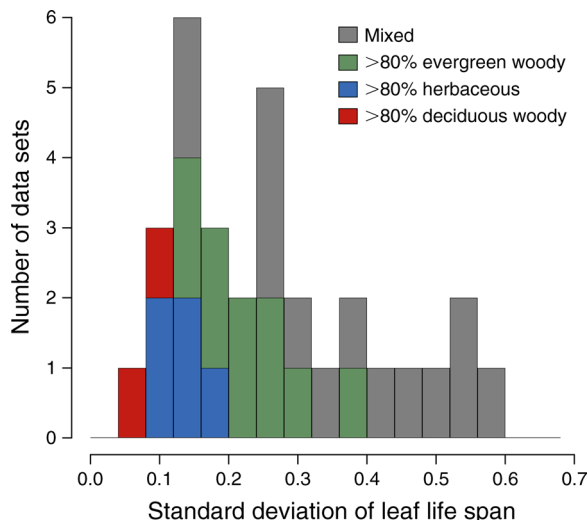


FIG. 1. Histogram of the standard deviation (SD) of log-transformed leaf life span (LLS) for local data sets within GLOPNET (Wright et al. 2004). Only data sets with >10 species observations are shown ( $n = 31$  communities). Data sets are colored by their functional-group composition. We used three functional groups (as defined by Wright et al. [2004]): woody deciduous, woody evergreen, and herbaceous. If a data set consists of >80% of one of those functional groups it is colored in the histogram. Mixed communities are those where no life-form comprised 80% of total species.

(Fig. 1). The greatest variation in LLS was observed in mixed communities. These patterns were qualitatively similar if variation was expressed as SD, CV, or range (Appendix A).

Only a subset of the communities ( $n = 22$ ) contained both LLS data and at least 15 species with LMA,  $N_{\text{mass}}$ , or  $A_{\text{mass}}$  data for the bivariate relationships (see Appendix B for bivariate plots). Most communities had LMA and  $N_{\text{mass}}$  data ( $n = 21$ ), including four herbaceous communities and one deciduous woody community. For LMA- $N_{\text{mass}}$ , correlation coefficients were weaker in herbaceous and deciduous woody communities relative to evergreen and mixed communities ( $F_3 = 6.66$ ,  $P < 0.01$ ). Photosynthetic data only existed for two herbaceous communities and one deciduous woody community; thus, we were unable to statistically evaluate differences in correlation coefficients across community types for  $A_{\text{mass}}$ - $N_{\text{mass}}$  and LMA- $A_{\text{mass}}$ .

Despite the small number of available community data sets, we found significant relationships between the strength of LES relationships and variation in LLS among communities (Fig. 2). Overall, communities dominated by herbaceous and deciduous woody species had lower variation in LLS and correlation coefficients for LES relationships relative to evergreen-dominated and mixed communities. These data support the hypothesis that communities with low variation in LLS have weaker LES relationships. While many studies have found differences in leaf traits, including LLS,

among life-forms (Poorter et al. 2009, Ordóñez et al. 2010) fewer studies have examined LES relationships among life-forms (Reich et al. 1997, Wright et al. 2005). For example, LMA is generally higher in woody species

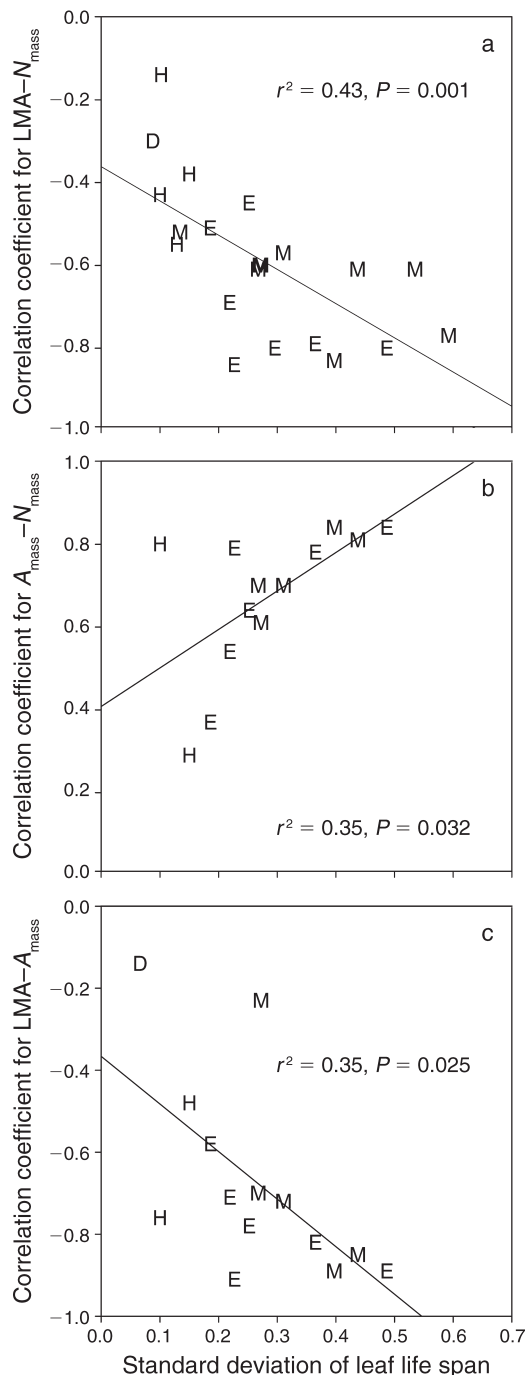


FIG. 2. Plot of the standard deviation (SD) of log-transformed leaf life span (LLS) vs. the correlation coefficient ( $r$ ) for three leaf-trait relationships: (a) LMA- $N_{\text{mass}}$  ( $n = 21$ ), (b)  $A_{\text{mass}}$ - $N_{\text{mass}}$  ( $n = 13$ ), and (c) LMA- $A_{\text{mass}}$  ( $n = 14$ ). Each point is one local data set. Data are grouped together by their functional-group composition: H, >80% herbaceous; D, >80% deciduous woody; E, >80% evergreen woody; M, mixed.



PLATE 1. Few leaf-trait data sets exist for plant communities dominated by herbaceous species such as this serpentine grassland in Edgewood Park and Natural Preserve, California, USA. Photo credit: J. L. Funk.

relative to herbaceous species and, considered in the context of a global species pool, herbaceous species occupy a distinct position on the LES (Reich et al. 1997). However, in the context of co-occurring herbaceous species within a community, the strength of LES trait relationships may depend on the variation in LLS present. Few data sets from communities dominated by herbaceous and woody deciduous species report LLS data; thus, the conclusions from our analysis are suggestive rather than definitive. More data from these communities are needed to thoroughly test the idea that low variation in LLS may weaken LES relationships within communities.

Why should variation in LLS affect the strength of LES relationships? The key part of the LES argument is that variation in LLS exists (e.g., “fast” vs. “slow” carbon gain). Many woody-dominated communities, including the ones where LES theory was developed, contain a wide range of LLS among coexisting evergreen and deciduous species or among coexisting short- and long-lived evergreen species. For example, chaparral communities have a mix of deciduous and evergreen species (Ackerly 2004); Australian sclerophyllous shrublands are exclusively evergreen but contain a wide range of LLS (Wright et al. 2002). However, a large range of LLS within a community is not the rule: in many

herbaceous and woody deciduous communities, LLS is constrained by the seasonality of the climate, and there is only minor variation in LLS among co-occurring species (see Givnish [2002] for theory on climatic constraints on LLS). In this case, within-community variation in  $N_{\text{mass}}$ , LMA, or  $A_{\text{mass}}$  cannot be “economic” in the LES sense because high LMA does not, due to strong climatic constraints, yield a longer LLS.

The functional role of high LMA in communities where LLS is climatically constrained is an interesting and open question. There may be important roles in water-use efficiency (Bartlett et al. 2012) or herbivory defense (Coley 1983, Poorter et al. 2004). Shade-tolerant deciduous species may increase their structural investment in leaves and, consequently, LMA while maintaining low LLS relative to co-occurring shade-tolerant evergreen species (Lusk et al. 2008). Another possibility is that some species with low LLS may invest more heavily in dense tissues. For example, vascular tissue is denser than epidermis and mesophyll tissue and high LMA in some grasses is associated with a higher amount of sclerenchymatic tissue and vascular bundles (Poorter et al. 2009). Alternatively, a lack of selective pressures within communities may result in species with seemingly less efficient leaf function (Heberling and Fridley 2012).

The function of particular traits in communities will always be context dependent, and here we argue that the climatic constraints on *variation in LLS* is a key, and often overlooked, piece of understanding the functional role of leaf-trait variation within many communities. These climatic constraints are highly variable; some communities are composed of species with widely varying LLS while other communities contain species with nearly identical LLS (Fig. 1). This has important implications. While LES trait relationships are upheld in most communities, they are weaker in communities with low variation in LLS (Appendix B). Future analyses including more LLS data from herbaceous and woody deciduous communities are needed. However, if the patterns we observed are upheld, the context-dependent nature of trait relationships at the community level suggests that community ecologists who want to use leaf traits as an indicator of plant or community function should confirm that easy-to-measure traits such as LMA do in fact correlate with functions within their communities, particularly if those communities are composed exclusively or primarily of herbaceous or woody deciduous species.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Histogram of the (A) coefficient of variation (CV) and (B) range of log-transformed leaf life span (LLS) for local data sets within GLOPNET ([Ecological Archives E094-171-A1](#)).

##### Appendix B

Bivariate relationships for GLOPNET data sets with  $N > 25$  for which leaf life-span data are available ([Ecological Archives E094-171-A2](#)).