

LETTER

A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components

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Abstract

Plant functional traits vary both along environmental gradients and among species occupying similar conditions, creating a challenge for the synthesis of functional and community ecology. We present a trait-based approach that provides an additive decomposition of species' trait values into alpha and beta components: beta values refer to a species' position along a gradient defined by community-level mean trait values; alpha values are the difference between a species' trait values and the mean of co-occurring taxa. In woody plant communities of coastal California, beta trait values for specific leaf area, leaf size, wood density and maximum height all covary strongly, reflecting species distributions across a gradient of soil moisture availability. Alpha values, on the other hand, are generally not significantly correlated, suggesting several independent axes of differentiation within communities. This trait-based framework provides a novel approach to integrate functional ecology and gradient analysis with community ecology and coexistence theory.

Keywords

Community assembly, functional diversity, height, leaf size, niche breadth, plant strategies, plasticity, seed size, specific leaf area, wood density.

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INTRODUCTION

The objective of this paper is to develop a quantitative framework integrating two traditions in plant ecology. The first is the study of plant form and function along climatic and edaphic gradients, which has its roots in plant geography (Schimper 1903) and played a central role in the development of plant functional and community ecology (Mooney & Dunn 1970). The second is the development of niche theory (Hutchinson 1957; MacArthur & Levins 1967), and the study of demographic and functional differences among co-occurring species in relation to mechanisms of coexistence (Pacala & Tilman 1994; Tilman 1994; Chesson 2000). Trait-based approaches to community ecology, linking ecological strategies, community assembly theory and functional diversity, have the potential to unify these contrasting viewpoints (Grime 2006; McGill *et al.* 2006; Westoby & Wright 2006).

Global syntheses of plant trait diversity have highlighted two prevalent patterns. On the one hand, mean values of

key plant traits exhibit significant shifts across climatic gradients, at both global and local scales (Bailey & Sinnott 1916; Baker 1972; Dolph & Dilcher 1980; Wright *et al.* 2005; Moles *et al.* 2007). On the other hand, studies at all scales reveal that high levels of trait disparity are observed within communities. For example, > 35% of the global variation in specific leaf area (leaf area/mass, SLA) is found within sites, compared with the variation among sites that may reflect large-scale climatic factors (Wright *et al.* 2004). This partitioning of plant trait diversity into within- and among-site components may be termed alpha and beta trait diversity, by analogy with Whittaker's (1975) distinction between alpha and beta patterns in species diversity.

In this paper, we present a new method for the analysis of trait variation at the community level along environmental gradients, based on a modification of Finlay & Wilkinson's (1963) approach to the analysis of adaptation in plant breeding programmes (also see Garbutt & Zangerl 1983). In this approach, the mean trait value of the species co-occurring in a local community is used to array

communities along a one-dimensional gradient. This gradient reflects the integrated effects of multiple environmental factors, as well as dispersal limitation or other historical factors that may shape the species composition of the communities in question. It also incorporates the contributions of ecotypic variation and phenotypic plasticity to the trait values of each species, and hence to the mean trait value of the community. A key to the subsequent analysis is that the values along the trait-gradient (plot means) are in the same units as the trait values for the individual species within the communities.

Analysis of species distributions and trait variation along this gradient provides an integrated approach to quantify intraspecific variation, niche breadth of individual species, and a novel partitioning of species mean trait values into alpha and beta components. The beta component refers to a species' mean location along the gradient (i.e. a measure of niche position), while the alpha component is the difference between a species' trait value and its beta value, i.e. a measure of how the traits of each species differ from those of co-occurring taxa. The partitioning of trait values into alpha and beta components builds on recent discussions of the alpha and beta niche as species characteristics associated with diversity within (alpha) and across (beta) habitats or communities (Ackerly *et al.* 2006; Silvertown *et al.* 2006a,b). The alpha niche refers to those attributes that differentiate a species from co-occurring taxa, and therefore may contribute to non-neutral maintenance of species diversity. The beta niche, on the other hand, refers to species distributions across habitat or geographic gradients; beta-niche characteristics will tend to be shared among co-occurring species.

There are two important points about these definitions to note at the outset. First, like all ideas in community ecology, they are intrinsically scale-dependent. The partitioning of trait values into alpha vs. beta components will depend on the scale used to define a community. In the effort to better link functional ecology to both gradient analysis and coexistence theories, one advantage of this scale dependence is that the traits can be partitioned at the same scales that are considered important for community processes. Second, the concept of beta diversity (Whittaker 1975) has two components: (i) turnover of species associated with different environmental conditions and (ii) turnover of ecologically similar species in different geographic areas. Cody (1993), and those who have followed his usage, restricted the term beta diversity to the first component, using gamma for the second. Others, following Whittaker, have used beta for both components, at times differentiating the environmental vs. spatial components (Couteron & Pelissier 2004), and used gamma for the total amount of sampled diversity (see Crist *et al.* 2003). In any case, ecologically similar species in similar environments are expected to have similar traits, so there

would be no phenotypic signature associated with contrasting distributions. Thus, the concepts of beta niche (Ackerly *et al.* 2006; Silvertown *et al.* 2006a,b) and species-level beta trait values, discussed here, specifically refer to the first component of beta diversity: the distribution of species in communities that occupy distinct environmental conditions.

OBJECTIVES

We present the method of trait-gradient analysis to partition species traits into alpha (within-community) and beta (among-community) components, and to quantify species niche breadth and the magnitude of intraspecific variation along environmental gradients. Trait-gradient analysis uses a simple data set with four pieces of information: a list of plots or communities, a list of species sampled in each plot, the value for a particular trait measured for each species in each plot, and a measure of relative abundance of each species (or simply presence/absence, if abundance data are not available). We introduce trait-gradient analysis with an empirical data set on five functional traits in woody plant communities in coastal California: SLA, leaf size, wood density, maximum height and seed size (Cornwell 2006). In this landscape, gradients in plot-level means for the first four traits are known to be strongly correlated with underlying gradients in topographic position and soil moisture (Ackerly *et al.* 2002; Cornwell 2006). Here, we develop a quantitative framework to address the following questions: (1) How is variation in species trait values partitioned into alpha vs. beta components? (2) What is the magnitude of intraspecific variation, relative to the overall shift in trait values across communities? (3) Are the beta and alpha components of different traits correlated with each other? We use a simple null model of community structure to determine if observed patterns reflect non-random aspects of community assembly, vs. intrinsic results of our methodology. In the Discussion, we address the significance of these patterns in relation to ecological strategies and potential mechanisms of coexistence across these communities.

The study system

All woody plants were sampled in 44 20 × 20 m plots at the Jasper Ridge Biological Preserve, Stanford University, San Mateo Co., CA, USA (Cornwell *et al.* 2006; Cornwell 2006). The plots were randomly located across the range of communities present, from riparian deciduous woodland to sclerophyll chaparral shrubland. A total of 54 native species were sampled, with alpha diversity ranging from three to 18 species per plot (Table A2; nomenclature follows Hickman 1993). There were a total of 471 species-plot observations that make up our data set for the analyses presented here.

The most important environmental factor underlying these communities is a topographically mediated gradient in soil moisture availability, with drier soils on higher topographic positions and south-facing slopes (Ackerly *et al.* 2002; Cornwell 2006).

The five traits were chosen to represent important features of plant ecological strategies (Westoby *et al.* 2002; Ackerly 2004). SLA is defined as fresh leaf area divided by dry leaf mass, and provides a measure of the allocation of biomass to light harvesting. High SLA values indicate thinner or less dense leaf tissue, and are associated with shorter leaf life span and higher metabolic rates per unit mass. Low SLA values occur in evergreen taxa, with lower instantaneous metabolic rates, but enhanced nutrient and water use efficiency. Leaf size is important for energy balance and hydraulic architecture, with smaller leaves generally observed in drier and more exposed conditions. Wood density is significant in relation to growth and survival rates, and in semi-arid conditions higher wood density is usually associated with greater drought tolerance (Hacke *et al.* 2001; Preston *et al.* 2006). Maximum height provides a basic measure of stature. Seed size is related to life history strategies, dispersal distances and regeneration biology (Leishman *et al.* 2000).

Cornwell (2006) has shown that the mean values of SLA, leaf size and wood density for each plot vary significantly with soil water availability and associated abiotic factors. In addition, the multivariate range of trait values within plots is significantly lower than would be expected based on a null model of community assembly, suggesting strong effects of habitat filtering (Cornwell *et al.* 2006).

The method of trait-gradient analysis

Trait-gradient analysis proceeds as follows, using log₁₀-transformed SLA to illustrate each step. Let t_{ij} = the trait value and a_{ij} = the abundance of species i in plot j . The total number of species and plots in the study is S and P , respectively. Then the abundance-weighted plot mean trait values and species mean trait values are defined, respectively, as

$$\bar{p}_j = \frac{\sum_{i=1}^S a_{ij} t_{ij}}{\sum_{i=1}^S a_{ij}}, \quad (1)$$

$$\bar{t}_i = \frac{\sum_{j=1}^P a_{ij} t_{ij}}{\sum_{j=1}^P a_{ij}}. \quad (2)$$

If abundance values are not available, a_{ij} may be set to 1 or 0 for presence/absence, and these equations simplify to the unweighted mean trait values of plots or species. In our analyses, abundance-weighted and unweighted analyses are

Table 1 Correlations of abiotic measures with plot mean trait values

	April soil water (gravimetric, %)	September soil water (gravimetric, %)	Potential insolation (MJ m ⁻² day ⁻¹)
Leaf area	0.60	0.54	-0.49
SLA	0.71	0.77	-0.22
Wood density	-0.70	-0.67	0.29
Height	-0.04	-0.15	-0.30
Seed mass	-0.13	-0.35	-0.46

Modified from Cornwell (2006); Cornwell and Ackerly (unpublished data).

$n = 44$ in all cases.

similar (results not shown); the generality of this outcome in other data sets merits further exploration. The values of p_j provide a biotic measure of a gradient in community structure, defined by the species traits. Elsewhere, we have shown that plot mean trait values for SLA are significantly correlated with measurements of soil water availability and potential solar insolation (Table 1; Cornwell 2006). The plot trait values provide an integrated measure of these and other aspects of the abiotic and biotic environment that may influence community assembly, and allow us to conduct the subsequent analyses directly on the basis of this gradient of trait values.

A plot of t_{ij} vs. p_j (Fig. 1a) shows the relationship between individual species trait values (including intraspecific variation when available) and plot level means. In this plot, sets of points aligned vertically at a particular value of p_j represent the species that occur together in one plot. For log SLA, t_{ij} varied from 1.51 to 2.83 (range = 1.32) across the entire study, while p_j ranged from 1.78 to 2.46. By definition, the ordinary least squares regression line of t_{ij} vs. p_j (weighting each point by abundance) has slope 1 and intercept zero (the $X = Y$ line).

The plot of t_{ij} vs. p_j provides a template for the calculation of several parameters characterizing each species, as illustrated for *Heteromeles arbutifolia* and two other species in Fig. 1a. *Heteromeles arbutifolia* occurred in 25 of the 44 plots in the study, with $t_i = 1.78$. The plots occupied by *H. arbutifolia* span a range of p_j from 1.78 to 2.26. The species' mean location along the trait gradient is then defined as the abundance-weighted mean of p_j for those plots occupied by the species:

$$\beta_i = \frac{\sum_{j=1}^P \bar{p}_j a_{ij}}{\sum_{j=1}^P a_{ij}}. \quad (3)$$

We call this the beta trait value for the species, as it is a measure of the beta niche position along the gradient

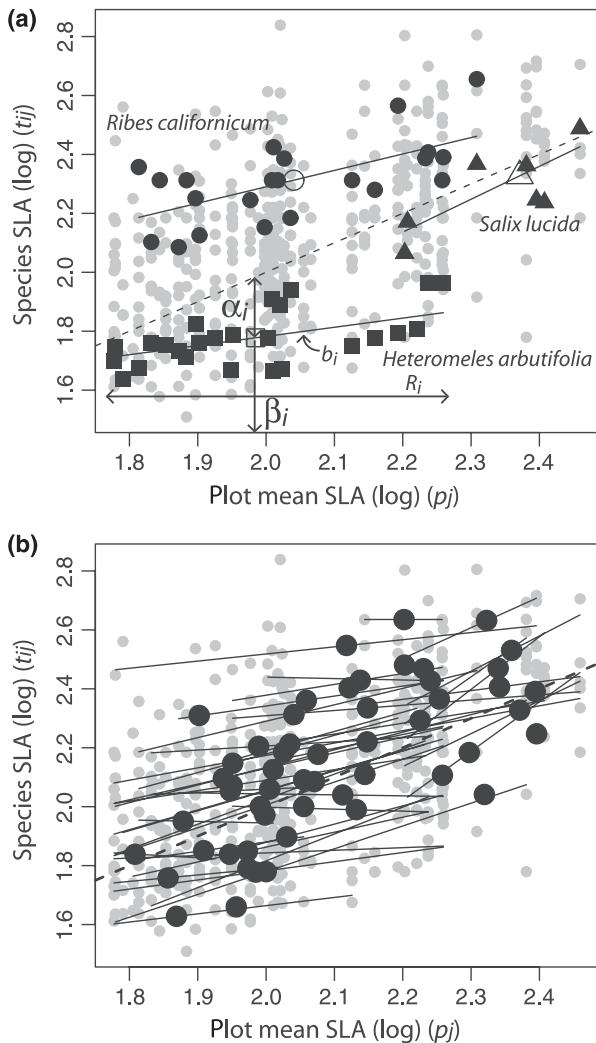


Figure 1 (a) Scatterplot of species trait values (t_{ij}) vs. abundance-weighted plot mean trait values (p_j) for log₁₀ SLA (cm²/g) in 44 woody plant communities of Jasper Ridge Biological Preserve. Dashed line is $X = Y$. Values for three species are highlighted for illustration: *Heteromeles arbutifolia* (squares), *Ribes californicum* (circles), and *Salix lucida* (triangles). For each species, the large open point shows the mean position of occupied plots (β_i on abscissa) and mean species trait value (t_i on ordinate). The difference between these, or the distance from the $X = Y$ line, is α_i . The range of occupied plots on the x -axis is the species niche breadth (R_i). Regression line shows abundance-weighted least squares regression of species trait values relative to plot mean trait values, with slope b_i . See text for further explanation of parameters. (b) Distribution of trait means and regression lines for all 54 woody plant species in study. Distribution of niche breadths (R_i), slopes (b_i) and alpha values (α_i) are shown in Fig. 2.

represented by plot mean SLA values. The open square shows the position of (β_i and t_i), the mean trait value vs. the mean position of *H. arbutifolia* along the gradient.

Now we introduce a novel concept, the alpha trait value of a species, defined as the difference between the species mean trait value and its beta value, such that

$$\bar{t}_i = \beta_i + \alpha_i, \quad (4)$$

where α_i is the deviation of (β_i and t_i) from the $X = Y$ line, and is a measure of the alpha niche position of the species, as it represents its trait value relative to that of co-occurring species. For *H. arbutifolia*, $\beta_i = 1.98$, towards the low end of the gradient, and $\alpha_i = -0.20$. This indicates that the species tends to occupy low SLA plots (mostly chaparral vegetation) and within those plots it has relatively low SLA values (it is an evergreen sclerophyll) (Ackerly 2004). Thus, we now have a decomposition of the species trait value into alpha and beta components (equation 4).

Two other species, *Ribes californicum* and *Salix lucida*, are shown in Fig. 1a to illustrate the insights derived from this analysis. *Ribes californicum* is a deciduous shrub occurring in chaparral and oak woodland. It has a low β_i , similar to *H. arbutifolia*, as it occupies a similar range of habitats; however, it has a positive α_i , reflecting the fact that it has a higher SLA than most of the other species with which it occurs. *Salix lucida*, on the other hand, has a similar mean SLA to *R. californicum*, but this is decomposed into a high β_i and an α_i close to 0. The β_i reflects its distribution in deciduous riparian woodlands, and its SLA is close to the average for these communities.

To characterize the niche breadth of the species along the gradient, let R_i = the range of p_j values of occupied plots (for *H. arbutifolia*, $R_i = 2.26 - 1.78 = 0.48$). The slope of intraspecific variation across this range is then defined as b_i = the slope of t_{ij} vs. p_j for species i (using an abundance-weighted ordinary least squares regression, for consistency with calculation of p_j). For *H. arbutifolia*, $b_i = 0.31$. Note that this slope is dimensionless because the x and y axes are in the same units. It thus expresses the degree of intraspecific variation relative to the overall shift in trait values at the community level. It is weighted by abundance to minimize the overall error in predicting leaf traits of the average individual of a species. We expect that b_i will generally be positive, as intraspecific variation will mirror the overall trend across the gradient, but will be < 1 , as traits are expected to vary less within species compared with the overall shift across communities due to intraspecific variation and species turnover. We also calculated u_i = the unweighted slope of t_{ij} vs. p_j , as a measure of individual trait responses to the environment; this measure is more appropriate to quantify ecotypic and/or plastic responses at the individual level.

Standard errors for the species parameters (β_i , α_i and R_i) were determined by a stratified bootstrap analysis, in which observations (plot–species–trait value) were resampled with replacement within species. This approach ensured that the

number of occurrences per species was held constant, though the diversity of each plot and its mean trait value could vary in each bootstrap replicate. Conventional standard errors of the slopes were obtained from the regression analysis, and meta-analysis methods were used to estimate the mean slope for all species, weighted by the inverse of the standard errors. The plot level trait means are measured with error, due to sampling error in the individual trait values, which will result in attenuation (underestimation) of regression slopes (McArdle 2003; Warton *et al.* 2006); we estimate that this attenuation error is $< 1\%$. This issue, the use of ordinary least squares vs. standardized major axis regression for analysis of slopes, concerns regarding the non-independence of the x and y axes in this analysis, and the possible impacts of edge effects on the analysis, are addressed in detail in the Appendix S1 (see Supplementary Material).

To determine whether any of our observed results arise from the method itself, rather than the distribution of species and traits across this landscape, we examined a null model of community assembly in which species were assembled into communities (i.e. plots) at random with respect to their trait values. This null model serves as a test for a role of habitat filtering in community assembly, because filters lead to co-occurrence of species with similar trait values (Diaz *et al.* 1998). Results of the null model are noted briefly below, and discussed in detail in Appendix S1.

R scripts (R Development Core Team 2006) for all calculations shown here are available in Appendix S1. Note that independent measures of the abiotic environment may be substituted for the plot mean trait values and all of the analyses proceed as described; the values of beta and niche breadth for each species will be in units of the abiotic axis, rather than trait units, so the alpha and beta values will not provide a decomposition of the overall trait value.

RESULTS

The positions and slopes of all species in the Jasper Ridge sample are illustrated in Fig. 1b. Summary statistics for the 54 species are listed in Table A2 (see Appendix S1) and shown in Fig. 2a–c. Niche breadth (R_i) ranged from zero, for species that occur only once, to 0.68 for *Toxicodendron diversilobum* (i.e. it spans virtually the entire gradient; Ackerly 2004). Intraspecific slopes (b_i) were obtained for 39 species in which SLA was measured *in situ* in three or more plots; in 13 of these, slopes were significantly different from 0 (at $P \leq 0.05$), ranging from 0.33 to 0.91. Using standard meta-analysis statistics, the overall estimate of the slope, based on all species, was 0.48 (95% CI: 0.42–0.54). The unweighted slopes (u_i , $N \geq 3$) were similar, with a meta-analysis mean of 0.43 (95% CI: 0.37–0.50).

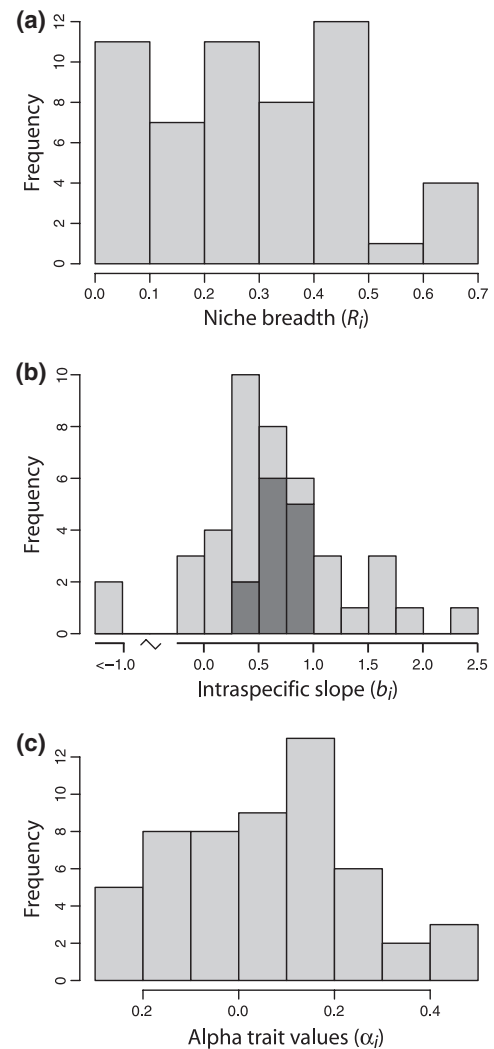


Figure 2 Summary of species parameters for SLA in JRBP data set. (a) niche breadth (R_i), the horizontal extent of species regression lines in Fig. 1b. (b) Abundance-weighted intraspecific slopes (b_i) for species with $N > 3$; shaded bars show slopes that were significantly different from 0 (at $p \leq 0.05$). (c) Alpha trait values (α_i), the distance of the species mean points from the $X = Y$ line in Fig. 1b.

A plot of α_i vs. β_i illustrates the partitioning of species trait values into these two components (Fig. 3). Overall, α_i spanned a range of 0.77 log SLA units, while β_i had a range of 0.58. Under the null model, all species would be expected to have the same β_i value; in contrast, 26 of the 54 species had significantly higher or lower beta than expected. On average, bootstrap standard errors for these parameters (0.052 and 0.055, respectively, for α_i and β_i) were small compared with the range of species means (Table A2). The diagonal isoclines in Fig. 3 indicate species with equivalent average trait values, increasing from low values in the lower left to higher values in the upper right. The three species

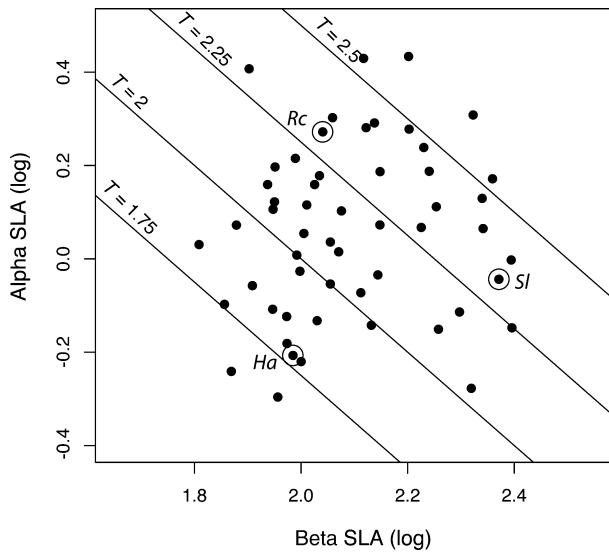


Figure 3 Scatterplot of β_i vs. α_i for SLA of the 54 species in the study. Species trait values (t_i) equal the sum of these two components, so species with equivalent mean SLA fall along diagonal isoclines. Circled points highlight the three species illustrated in Fig. 1a (*Ha* = *Heteromeles arbutifolia*; *Rc* = *Ribes californicum*; *Sl* = *Salix lucida*) (see Discussion in text).

illustrated in Fig. 1a are highlighted. *Heteromeles arbutifolia* and *R. californicum* occupy chaparral and oak woodland, so their β_i values are both fairly low, but *R. californicum* is deciduous and has higher SLA, resulting in positive α_i . *Ribes californicum* and *S. lucida* have similar overall SLA, so they are positioned along the same isocline, but *S. lucida* has a higher β_i and lower α_i value, reflecting its distribution in deciduous woodlands. This decomposition of SLA values illustrates

how each component highlights a distinct aspect of these species' ecology and natural history, one related to its typical habitat (beta niche) and the other to its functional traits relative to other species in its community (alpha niche).

Multivariate patterns

Trait gradient analysis was applied to four other traits in this community: leaf size (cm^2 , log10 transformed), wood density (mg cm^3), maximum height (m, log10 transformed), and seed size (mg, log10 transformed) (results summarized in Table 2). For wood density, seed size and maximum tree height, only species means were available so the intraspecific slopes could not be calculated. For all traits, there was an excess of species with higher or lower β_i values than expected under the null model (see Appendix S1).

Niche breadths (R_i) were comparable for all traits, relative to the overall range in t_p values. The range of α_i values exceeded the range of β_i values for all traits, demonstrating that species vary more in their trait values relative to co-occurring species than they do in the mean trait values of plots in which they occur (Table 2).

Plot level trait means (p_j) exhibited strong positive correlations for SLA and leaf size, and significant negative correlations of each of these traits with wood density ($|r| \geq 0.7$ in all cases; Fig. 4a). p_j for species maximum height was also correlated strongly with leaf size ($r = 0.73$), moderately with wood density ($r = -0.59$), and weakly with SLA ($r = 0.47$). Thus, these traits are generally arrayed along a similar gradient across the Jasper Ridge landscape. Cornwell (2006) has demonstrated that plot mean values for these traits are significantly correlated with an underlying gradient of soil moisture availability. Species β_i values were

Table 2 Summary statistics for five traits measured across 54 species and 44 plots at Jasper Ridge Biological Preserve

Parameter*	Traits (units, transformation)				
	SLA (cm^2/g , log)	Leaf area (cm^2 , log)	Wood density (mg cm^3)	Maximum height (m, log)	Seed mass (mg, log)
Species characteristics					
t_b mean	2.15	0.76	0.62	0.67	1.07
t_b min-max	1.63, 2.64	-1.30, 2.18	0.33, 0.80	-0.52, 1.65	-1.38, 4.55
β_b min-max	1.81, 2.40	-0.27, 1.28	0.50, 0.70	0.50, 1.20	-0.02, 2.61
α_b min-max	-0.34, 0.43	-1.73, 1.33	-0.30, 0.18	-1.32, 0.56	-3.22, 2.21
R_b mean	0.29	0.72	0.092	0.35	1.72
R_b min-max	0, 0.69	0, 1.90	0, 0.23	0, 0.81	0, 3.46
Plot characteristics					
p_p mean	2.06	0.66	0.63	0.76	1.46
p_p min-max	1.78, 2.47	-0.57, 1.33	0.49, 0.73	0.30, 1.11	-0.32, 3.14

SLA, specific leaf area; min, minimum; max, maximum.

t_b , species trait mean; β_b , beta trait value; α_b , alpha trait value; R_b , niche breadth; b_b , intraspecific slope; p_p , plot mean trait value.

*Units for all variables are same as trait units, except for trait slopes (b_b , dimensionless).

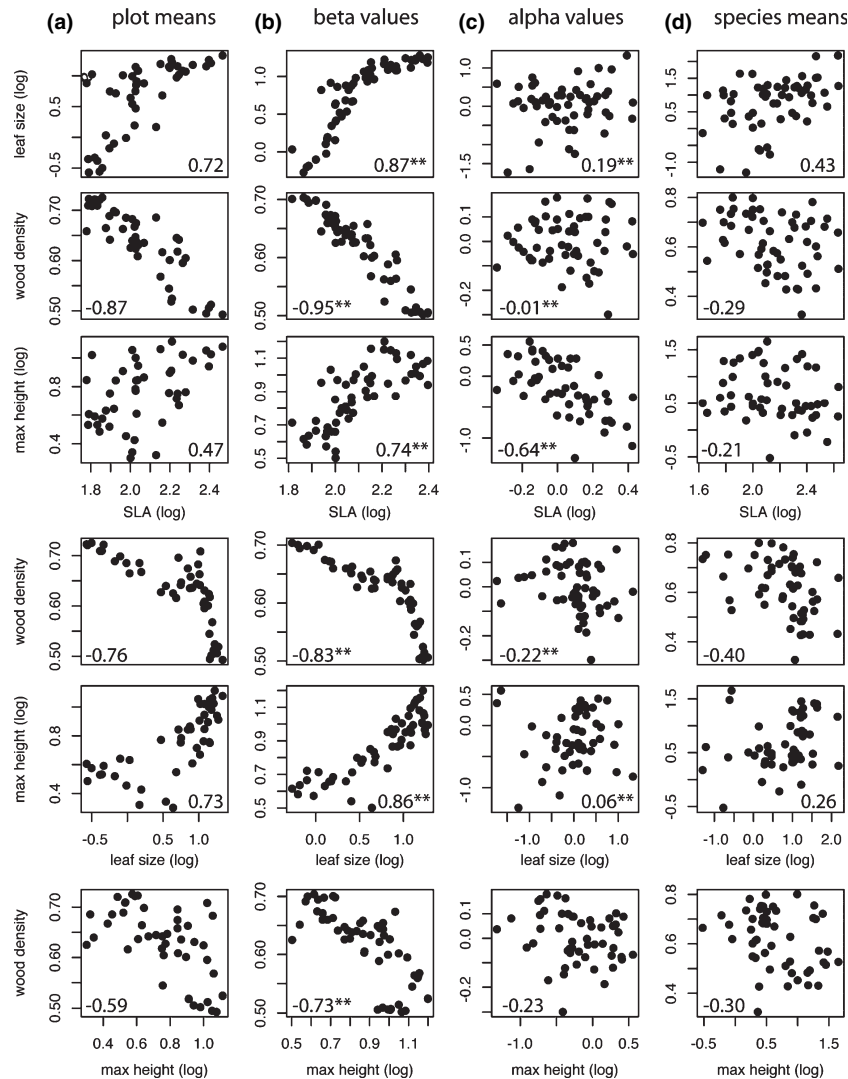


Figure 4 Scatterplots of (a) plot mean trait values (\bar{p}_i), (b) species beta trait values (β_i), (c) species alpha trait values (α_i), and (d) species mean trait values (\bar{t}_i) for all pairwise combinations of specific leaf area, leaf size, wood density, and maximum height. Similar plots for seed size vs. each of these traits are shown in Appendix S1. Trait units and transformations are listed in Table 1. For correlations of β_i and α_i , asterisks indicate significant departure from values expected under a null model of community assembly ($*P \leq 0.01$; $**P \leq 0.001$). These expected correlations of the alpha and beta components, across traits, are generally close to the correlation of the species trait values (column d) (see text).

also strongly correlated among these four traits ($|r| \geq 0.7$ in all cases; Fig. 4b). In contrast, α_i values were not significantly correlated among these traits (Fig. 4c), except for a negative relationship between alpha values for SLA and height ($r = -0.63$, see Discussion). Under our null model, correlations of alpha and beta components are expected to be similar to the overall species trait correlation, and almost all of the observed results for SLA, leaf size, height and wood density were significantly different from this expectation (Fig. 4, Appendix S1). Correlations between alpha and beta components of seed size and the remaining traits were weak or nonlinear, and in general did not diverge from

expectations of the null model based on the underlying correlations of the traits themselves (Fig. A1 in Appendix S1).

DISCUSSION

The development of a trait-based community ecology has attracted considerable interest in recent years (McGill *et al.* 2006; Westoby & Wright 2006). This interest has been motivated in part by the biodiversity-ecosystem function debate, as the functional significance of biodiversity arises primarily from diversity of functional traits among the

species in a community (Hooper *et al.* 2005). The neutral theory of biodiversity, which assumes that species are demographically identical (Hubbell 2001), has also generated renewed interest in the phenotypic structure of communities. Research in community assembly has addressed the dispersion of trait values within communities, relative to appropriate null models (Weiher *et al.* 1998). A restricted range of trait values is viewed as evidence of filtering processes that limit the phenotypic range of coexisting species (usually interpreted in relation to abiotic factors) (Cornwell *et al.* 2006). Phenotypic overdispersion, on the other hand, is interpreted as evidence of niche differentiation among species, reflecting either past or current competitive interactions or small-scale disturbance (Stubbs & Wilson 2004; Grime 2006). The identification of major axes in trait space that differentiate co-occurring species may reflect the primary niche axes associated with resource partitioning and coexistence (Ackerly 2004). This parallel between phenotypic and niche differentiation has been formalized in the idea of the functional niche, defined in terms of the traits of co-occurring species (Rosenfeld 2002).

The decomposition of interspecific trait variation into alpha (within-community) and beta (among-community) components will contribute to the synthesis of functional and community ecology. The beta component (β_j) is based on the mean trait values at the community level, which are then averaged for all the communities occupied by a species. This indicates where a species occurs along the gradient defined by the trait in question. Beta values were more broadly distributed than expected under a simple null model of random assembly, consistent with a significant role for habitat filtering in the assembly of these communities (see Cornwell *et al.* 2006). The beta trait value and niche breadth (R_j) are conceptually similar to the mean and tolerance resulting from correspondence analysis or canonical correspondence analysis (Jongman *et al.* 1995). The key difference and the utility of this method is that the ordination of communities, and the units of the resulting species parameters, are explicitly framed in terms of trait values. As a result, the analysis can be conducted if environmental data are not available or if the factors underlying gradients in particular traits are not known. The alpha component of the trait (α_j) represents the characteristic difference between the species trait value and the mean trait values of the communities it occupies, at the appropriate scale of analysis.

Alpha trait values (α_j) and coexistence

The partitioning of species traits into alpha and beta components provides a link between trait variation and coexistence mechanisms evaluated at comparable scales. Coexistence theories address the mechanisms that maintain a set of species interacting in a certain area; like trait gradient

analysis, they are dependent on the scale at which the community is defined. For example, coexistence mediated by colonization-competition dynamics is based on tradeoffs in dispersal vs. competitive ability (Tilman 1994). If the scale of disturbance is larger than the sampling scale of a community study, plots will be dominated by early or late successional species. Thus, the traits associated with the successional gradient (Bazzaz 1979) will be reflected in species beta trait values. In contrast, small-scale disturbance will lead to within-plot coexistence of early vs. late successional, and the corresponding trait variation will be reflected in alpha trait values (Grime 2006). Similar arguments apply to the partitioning of trait values into alpha and beta components in relation to classical niche partitioning theory, spatial storage effects and temporal storage effects (where 'plots' could be defined temporally). Numerous measures of trait overdispersion or even spacing have been proposed, with associated null models to test for significant patterns of niche differentiation within communities (Weiher *et al.* 1998; Stubbs & Wilson 2004). We propose that future tests applied to alpha trait values will enhance the power of such studies because the alpha values reflect differentiation among co-occurring taxa. Due to space constraints, we were not able to explore such tests in this paper.

Based on previous studies at Jasper Ridge (Ackerly 2004; Cornwell 2006), we believe that alpha trait variation in the woody plant species reflects the effects of small-scale disturbance and within-plot partitioning of vertical gradients of soil moisture (below-ground) and light (above-ground). For example, in the chaparral community, several of the high-SLA species are opportunists that will colonize disturbances such as roadsides, canopy gaps, and small landslips (e.g. *Artemisia californica*). Low-SLA evergreens vary in leaf size and wood density, reflecting differences in effective rooting depth (as measured by pre-dawn water potentials) (Ackerly 2004). There are also important differences in post-fire regeneration strategies and associated traits that may be maintained in the system by fluctuating recruitment opportunities after and between fire events (i.e. temporal storage effects). In the taller, woodland communities, partitioning of the aboveground vertical gradient in light takes on increased importance. Understorey species exhibit characteristics of shade tolerance, such as relatively high wood density and high SLA (e.g. *Symphoricarpos mollis*) (Cornwell 2006). Overall, we believe that both disturbance and resource partitioning are important mechanisms contributing to local coexistence in this system, and these mechanisms are reflected in the range of alpha trait values observed among co-occurring species. However, the long-generation times of woody plants, and the potentially important role of rare wildfires, make it extremely difficult to formally quantify and test the importance of alternative coexistence mechanisms.

An additional factor that may contribute to trait variation is the potential for functional equivalence among species arising from different combinations of ecophysiological and morphological traits (Marks & Lechowicz 2006). True equivalence consists of identical demographic performance under identical abiotic conditions, and thus approaches Hubbell's neutrality assumption (and is also approximated by our null model). If the species are truly identical in performance, they would occupy the same range of environments. Species would then show a narrow range of beta values, and the underlying differences in individual traits would appear as alpha trait variation. However, these alpha trait differences would not be associated with any mechanisms that promote coexistence.

Implications for analysis of functional strategies

There has been considerable interest in recent years in the identification of major axes of ecological strategy variation, based on trait correlations across large numbers of species (e.g. Reich *et al.* 1999; Westoby *et al.* 2002; Ackerly 2004). The decomposition of trait variation into alpha and beta components, as suggested here, will shed additional light on the mechanisms underlying these trait correlations. For example, previous studies have found strong correlations of leaf size and SLA among species distributed along gradients of precipitation and/or nutrients (e.g. Fonseca *et al.* 2000; Ackerly *et al.* 2002). However, within communities, especially if sampling is restricted to herbaceous or woody species, these two traits may exhibit weak or even negative correlations (e.g. Shipley 1995; Grubb 1998). Our results for woody plants at Jasper Ridge demonstrate that the overall correlation between these two traits ($r = 0.43$) is due to a very strong correlation of beta values ($r = 0.87$) but no relationship among alpha values ($r = 0.18$). In other words, each trait is responding to the same underlying abiotic gradient in this community, presumably because both small leaves and low SLA enhance performance in dry sites. However, variation in the two traits is essentially independent at the local scale, when considered relative to co-occurring species. In contrast, comparison of SLA and leaf nitrogen per unit mass, two traits that are known to be tightly linked as part of the leaf economic spectrum (Wright *et al.* 2004), demonstrated significant positive correlations of both alpha and beta components (results not shown).

The results for SLA vs. maximum height are even more striking, as the sign of the correlation switches from positive for beta values to negative for alpha values (Fig. 4, third row). Positive relationships among β_j and β_i values for these traits indicate that taller stature communities, and the species that occur in them, also have higher average SLA, corresponding to more mesic sites in this landscape. However, species that are tall locally have lower SLA,

relative to co-occurring species in the community (negative correlation of α_i values). This reflects the continuum from high-SLA species in the shady understory to low-SLA species that occupy the canopy (Falster & Westoby 2005). The two components cancel each other out, and the species trait values are negatively, but not significantly, correlated. The observed partitioning of trait correlations in this (and several other) cases is highly significant relative to the null model of random assembly with respect to trait values. Thus, negative alpha correlations observed for height vs. SLA, and the weak correlations for several other traits, are not artefacts of the method.

The contrasting correlation structure of the alpha and beta trait components suggests a shift in the dimensionality of ecological strategies at different spatial scales. Among plots, arrayed along a strong abiotic gradient, there is one primary dimension of functional variation related to leaf and wood traits, and a second dimension related to seed size. In contrast, the weak correlations of alpha trait values, with the exception of height and SLA, suggest that each trait defines an independent axis of functional variation in species strategies, relative to co-occurring species. This suggests that traits exhibiting strong correlations at regional and global scales may still be decoupled at a local scale and contribute to independent axes of ecological differentiation and coexistence.

CONCLUSIONS

A central goal of trait-based community ecology is reconciliation of two contrasting research traditions (Westoby & Wright 2006): one has emphasized resource partitioning, disturbance and trait variation among co-occurring species to understand the maintenance of diversity (Tilman 1994; Weiher *et al.* 1998); the other has addressed the convergence of form and function in relation to edaphic and climatic conditions, and the corresponding shifts in physiognomy along environmental gradients that define vegetation types and biomes (Schimper 1903; Wright *et al.* 2005). Although these research traditions have developed independently to a large extent, functional trait variation is important in both contexts. Functional traits influence species distributions along environmental gradients as well as interspecific interactions and resource partitioning within local communities. The trait-gradient method introduced here provides an explicit partitioning of species traits into alpha and beta components, in the context of a specific scale of analysis. This partition provides a clear conceptual basis to address both trait shifts along gradients and variation among co-occurring species, and thus should contribute to a synthesis of these two research traditions. In addition, trait-gradient analysis provides a quantification of niche breadth in units of the trait itself, and a

dimensionless measure of the sensitivity of intraspecific variation relative to gradients in trait means. Both of these should allow for direct comparison across studies, and the latter will allow comparison among traits as well, contributing to a synthesis across diverse study systems. Applying the trait-gradient method in different communities will enhance our understanding of mechanisms underlying functional diversity and the relationship between functional traits and coexistence.

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REFERENCES

- Ackerly, D.D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol. Monogr.*, 75, 25–44.
- Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K. & Starmer, K.P. (2002). Leaf size, specific leaf area and microhabitat distribution of woody plants in a California chaparral: contrasting patterns in species level and community level analyses. *Oecologia*, 130, 449–457.
- Ackerly, D.D., Schwilk, D.W. & Webb, C.O. (2006). Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology*, 87, S50–S61.
- Bailey, I.W. & Sinnott, E.W. (1916). The climatic distribution of certain types of angiosperm leaves. *Am. J. Bot.*, 3, 24–39.
- Baker, H.G. (1972). Seed weight in relation to environmental conditions in California. *Ecology*, 53, 997–1010.
- Bazzaz, F.A. (1979). The physiological ecology of plant succession. *Ann. Rev. Ecol. Syst.*, 10, 351–371.
- Chesson, P.L. (2000). Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol. Syst.*, 31, 343–367.
- Cody, M.L. (1993). Bird diversity patterns and components across Australia. In: *Species Diversity: Historical and Geographical Aspects* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 147–158.
- Cornwell, W. (2006). *Causes and consequences of plant functional diversity*. PhD Thesis. Department of Biological Sciences, Stanford University, Stanford, CA.
- Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87, 1465–1471.
- Couteron, P. & Pelissier, R. (2004). Additive apportioning of species diversity: towards more sophisticated models and analyses. *Oikos*, 107, 215–221.
- Crist, T.O., Veech, J.A., Summerville, K.S. & Gering, J.C. (2003). Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta, and gamma diversity. *Am. Nat.*, 162, 734–743.
- Díaz, S., Cabido, M. & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.*, 9, 113–122.
- Dolph, G.E. & Dilcher, D.L. (1980). Variation in leaf size with respect to climate in the tropics of the Western Hemisphere. *Bull. Torr. Bot. Club*, 107, 154–162.
- Falster, D.S. & Westoby, M. (2005). Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *J. Ecol.*, 93, 521–535.
- Finlay, K. & Wilkinson, G. (1963). The analysis of adaptation in a plant breeding programme. *Aust. J. Agr. Res.*, 14, 742–754.
- Fonseca, C.R., Overton, J.M., Collins, B. & Westoby, M. (2000). Shifts in trait-combinations along rainfall and phosphorous gradients. *J. Ecol.*, 88, 964–977.
- Garbutt, K. & Zangerl, A. (1983). Application of genotype-environment interaction analysis to niche quantification. *Ecology*, 64, 1292–1296.
- Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *J. Veg. Sci.*, 17, 255–260.
- Grubb, P. (1998). A reassessment of the strategies of plants which cope with shortages of resources. *Persp. Plant Ecol. Evol.*, 1, 3–31.
- Hacke, U., Sperry, J., Pockman, W., Davis, S. & McCulloch, K. (2001). Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 126, 457–461.
- Hickman, J.C. (1993). *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Hutchinson, G. (1957). Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.*, 22, 415–427.
- Jongman, R.H.G., ter Braak, C.J.F. & Van Tongeren, O.F.R. (1995). *Data Analysis in Community and Landscape Ecology*, new edn. Cambridge University Press, Cambridge.
- Leishman, M.R., Wright, I., Moles, A.T. & Westoby, M. (2000). The evolutionary ecology of seed size. In: *Seeds: The Ecology of Regeneration in Plant Communities* (ed. Fenner, M). CABI Publishing, Wallingford, UK, pp. 31–57.
- MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, 101, 377–385.
- Marks, C.O. & Lechowicz, M.J. (2006). Alternative designs and the evolution of functional diversity. *Am. Nat.*, 167, 55–66.
- McArdle, B. (2003). Lines, models, and errors: regression in the field. *Limnol. Ocean.*, 48, 1363–1366.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.
- Moles, A.T., Ackerly, D.D., Tweddle, J.C., DiEckie, J.B., Smith, R., Leishman, M. *et al.* (2007). Global patterns in seed size. *Global Ecol. Biogeogr.*, 16, 109–116.
- Mooney, H.A. & Dunn, E.L. (1970). Convergent evolution of Mediterranean-climate evergreen sclerophyllous shrubs. *Evolution*, 24, 292–303.

- Pacala, S.W. & Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.*, 143, 222–257.
- Preston, K.A., Cornwell, W.K. & DeNoyer, J.L. (2006). Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytol.*, 170, 807–818.
- R Development Core Team (2006). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org>.
- Reich, P., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. *et al.* (1999). Generality of leaf trait relationships: a test across six biomes. *Ecology*, 80, 1955–1969.
- Rosenfeld, J. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98, 156–162.
- Schimper, A.F.W. (1903). *Plant Geography Upon a Physiological Basis*. Clarendon Press, Oxford.
- Shipley, B. (1995). Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. *Func. Ecol.*, 9, 312–319.
- Silvertown, J., Dodd, M., Gowing, D. & Lawson, C. (2006a). Phylogeny and the hierarchical organization of plant diversity. *Ecology*, 87, S39–S49.
- Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M.F., Joseph, J.A. *et al.* (2006b). Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. R. Soc. Lond. B*, 273, 39–44.
- Stubbs, W.J. & Wilson, J.B. (2004). Evidence for limiting similarity in a sand dune community. *J. Ecol.*, 92, 557–567.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
- Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biol. Rev.*, 81, 259–291.
- Weiher, E., Clarke, G.D.P. & Keddy, P.A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, 81, 309–322.
- Westoby, M. & Wright, I.J. (2006). Land–plant ecology on the basis of functional traits. *Trends Ecol. Evol.*, 21, 261–268.
- Westoby, M., Falster, D., Moles, A., Vesk, P. & Wright, I. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Ann. Rev. Ecol. Syst.*, 33, 125–159.
- Whittaker, R. (1975). *Communities and Ecosystems*. Macmillan, New York.
- Wright, I.J., Westoby, M., Reich, P.B., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004). The leaf economic spectrum worldwide. *Nature*, 428, 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K. *et al.* (2005). Modulation of leaf economic traits and trait relationships by climate. *Glob. Ecol. Biogeogr.*, 14, 411–421.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Supplementary material.

Appendix S2 R source code: tga.R.

Appendix S3 R source code: tga.script.R.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2006.01006.x>

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