



**SPECIAL FEATURE: FUNCTIONAL DIVERSITY**

**Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude**

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**Keywords**

Community assembly; Intra-specific; Limiting similarity; Niche packing

**Nomenclature**

N/A

**Abbreviations**

SLA = specific leaf area; CWM = community-weighted mean; CWV = community-weighted variance

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**Abstract**

**Questions:** Are patterns of intra- and inter-specific functional trait variation consistent with greater abiotic filtering on community assembly at high latitudes and elevations, and greater biotic filtering at low latitudes and elevations?

**Locations:** Area de Conservación Guanacaste, Costa Rica; Santa Catalina Mountains, Arizona; Siskiyou Mountains, Oregon.

**Methods:** We measured woody plant species abundance and a key functional trait associated with competition for resources and environmental tolerance (specific leaf area, SLA) along elevational gradients in low-latitude tropical (Costa Rica), mid-latitude desert (Arizona) and high latitude mediterranean (southern Oregon) biomes. We explored patterns of abiotic and biotic filtering by comparing observed patterns of community-weighted means and variances along elevational and latitudinal gradients to those expected under random assembly. In addition, we related trait variability to niches and explored how total trait space and breadth vary across broad spatial gradients by quantifying the ratio of intra- to inter-specific variation.

**Results:** Both the community-wide mean and variance of SLA decreased with increasing latitude, consistent with greater abiotic filtering at higher latitudes. Further, low-elevation communities had higher trait variation than expected by chance, consistent with greater biotic filtering at low elevations. Finally, in the tropics and across latitude the ratio of intra- to inter-specific variation was negatively correlated to species richness, which further suggests that biotic interactions influence plant assembly at low latitudes.

**Conclusions:** Intra- and inter-specific patterns of SLA variation appeared broadly consistent with the idea that the relative strength of biotic and abiotic drivers on community assembly changes along elevational and latitudinal gradients; evidence for biotic drivers appeared more prominent at low latitudes and elevations and evidence for abiotic drivers appeared more prominent at high latitudes and elevations.

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## Introduction

Understanding how local processes influence diversity patterns across environmental gradients has been central to the study of plant community ecology (von Humboldt 1849; Kraft et al. 2011). Studies across latitude (e.g. Willig et al. 2003; Schemske et al. 2009; Stegen et al. 2009) and elevation (e.g. Körner 2007; Bryant et al. 2008; McCain & Grytnes 2010) have highlighted both biotic and abiotic mechanisms to explain diversity patterns across these gradients (Dobzhansky 1950; Pianka 1966; MacArthur 1972; Schemske et al. 2009). However, connecting local ecological processes to broad latitudinal and elevational gradients has been challenging. For example, elevational gradients differ from latitudinal gradients in several key ways including smaller species pools and land area and increased isolation (Lomolino 2001). Further, while many of the potential processes invoked to explain latitudinal diversity patterns co-vary along latitudinal gradients (i.e. area, history, climate), they generally do not co-vary across elevation (Körner 2007).

Recently, trait based approaches have been used to understand how multiple mechanisms influence community assembly across environmental gradients (McGill et al. 2006; Weiher et al. 2011), including elevational (Kluge & Kessler 2011; Hoiss et al. 2012; Spasojevic & Suding 2012) and latitudinal (Swenson & Enquist 2007; Swenson & Weiser 2010; Kooyman et al. 2011; Swenson et al. 2012) gradients. These studies often focus on two assembly mechanisms thought to influence diversity patterns along environmental gradients: environmental filtering, which can increase species trait similarity through abiotic constraints (Weiher & Keddy 1995), and competitive interactions (i.e. niche partitioning, limiting similarity) that prevent co-existing species from being too similar (MacArthur & Levins 1967; Chesson 2000). However, these two hypotheses have been difficult to reconcile in species-rich communities in environments that seem to be severe (i.e. the Sonoran desert; Whittaker & Niering 1964; Huston 1979). Thus, making generalizations about how abiotic filtering should influence communities across latitude or elevation has been challenging (Swenson & Enquist 2007). Furthermore, while evidence for greater competitive interactions at lower elevations is more strongly supported (Callaway 1998; Wang et al. 2008; Spasojevic & Suding 2012), the idea of greater competitive interactions at low latitudes is equivocal at best (Vázquez & Stevens 2004; Ricklefs 2009; but see Schemske 2009; Schemske et al. 2009). It has thus been difficult to link the mechanisms that underlie diversity patterns across both elevational and latitudinal gradients (Swenson & Enquist 2007).

One prominent, and seemingly simplistic, hypothesis relating assembly across broad gradients is that abiotic fac-

tors should limit diversity at high latitudes and elevations while biotic factors should underlie diversity patterns at low latitudes and elevations (Pianka 1966). In order to link abiotic and biotic mechanisms to diversity patterns across elevation and latitude, we can begin by assuming that trait variability reflects variation in resource use within a population, thereby reflecting niche space and breadth (Roughgarden 1972; Violle & Jiang 2009; Violle et al. 2012). Recent insights from trait-based ecology, building on classical niche theory, have outlined the use of intra- and inter-specific trait variation for understanding diversity patterns across local to broad spatial scales (Jung et al. 2010; Violle et al. 2012). First, abiotic factors are known to shape the diversity of traits within a community; specifically, a change in the mean (either higher or lower mean values, depending on the trait and environmental gradient considered) and lower variance of trait values across an environmental gradient can indicate whether abiotic filtering is occurring (Weiher & Keddy 1995). In addition, over evolutionary time scales, stronger stabilizing selection in increasingly harsh environments should further filter or reduce the total amount of phenotypic variation within a community (Fischer 1960; Violle et al. 2012). Second, biotic interactions can also shape the diversity of traits within a community. For example, on the one hand, competitive exclusion will eliminate extreme phenotypes so that intra- and inter-specific trait variance is reduced (Grime 1973). On the other hand, if competition imposes limiting similarity with resource partitioning, the diversity of traits will depend on the ratio between species' niche breadth (e.g. intra-specific variation) and total niche space (e.g. inter-specific variation; MacArthur & Levins 1967; MacArthur & Wilson 1967). Thus, for limiting similarity and resource partitioning to occur in a community: (1) the inter-specific packing of traits along a niche or trait axis will tend to be uniformly distributed (e.g. Roughgarden 1972; Brown 1975) and (2) either the ratio of intra- to inter-specific variation should decrease with increasing species richness (MacArthur & Wilson 1967; Violle et al. 2012) and/or (3) the total niche space (phenotypic diversity of the entire community) must increase (Tilman et al. 1997).

Here, we focus on how patterns of one ecologically important trait, specific leaf area (SLA), change along three elevational gradients located in tropical (Costa Rica), desert (Arizona) and mediterranean (southern Oregon) biomes. By quantifying the distribution of intra- and inter-specific trait variation in local communities across broad elevational and latitudinal gradients we address two long-standing questions in plant community ecology. Specifically, we ask: (1) are assembly mechanisms similar across elevational and latitudinal gradients, and (2) are patterns of trait variation consistent with greater abiotic filtering on community assembly at high latitudes and elevations, and

greater biotic pressures on assembly at low latitudes and elevations?

To answer these questions we use three trait-based metrics. First, we determine whether shifts in community trait mean and variance across latitude are similar to those across elevation. Second, we compare the similarity of community trait values relative to random trait similarity, which can further describe the nature of assembly patterns (MacArthur & Levins 1967; Pacala & Tilman 1994; Weiher & Keddy 1995; Grime 2006) where high functional similarity is thought to be a signature of abiotic filtering and low functional similarity is thought to be a signature of limiting similarity (Weiher & Keddy 1995). Third, we describe the relationship between intra- and inter-specific variation and species richness. The ratio of intra- to inter-specific variation expresses the rate at which niche breadth (i.e. intra-specific trait variation) changes relative to total niche space (i.e. inter-specific variation) and can thus be used to determine how total niche space and niche breadth change with increasing species richness across diversity gradients.

## Methods

### Study sites

We conducted our study in three locations that span a 30° latitudinal gradient and an average elevational range of 2000 m a.s.l. (Table 1). Area de Conservación Guanacaste (ACG) in northwestern Costa Rica is characterized by a 6-month dry season in low-elevation (0–300 m a.s.l.) dry tropical forests with a mean annual temperature of 25 °C. However, the length of the dry season decreases, and mean annual precipitation increases with elevation; mean annual precipitation in a rain forest site at 700 m a.s.l. is ca. 3500 mm in comparison with 1500 mm in a lowland dry tropical forest site at 300 m a.s.l. The Santa Catalina Mountains in southern Arizona are characterized by summer and winter monsoons, which together can bring about 330 mm of precipitation annually to lower elevations and 750 mm at the highest elevations (Whittaker & Niering 1964). Finally, the Siskiyou Mountains in southern

Oregon (part of the California Floristic Province) are characterized by mediterranean-type climate with warm, dry summers (mean max. July temperature 27 °C) and cool, wet winters (mean min. January temperature 2 °C); mean annual precipitation ranging from 1400 to 5000 mm, with <15% occurring during May through September (Daly et al. 2002).

### Floristic surveys and plant trait collection

Plant abundance (number of woody individuals) was measured in 20 × 50 m (0.1 ha) plots arrayed across the three elevational gradients in which all stem diameters more than 2.5 cm DBH were measured and species identified. Only woody trees and shrubs were included, as woody plants consistently dominate the total abundance and biomass in each sampled community relative to non-woody species. A total of 25 plots were surveyed in Costa Rica, 22 plots in Arizona and 12 plots were surveyed in Oregon. In Costa Rica, the plots spanned an elevational range of 9–1111 m, 740–2502 m in Arizona and 438–1255 m in Oregon. The location of plots were determined using a stratified sampling regime (Gauch 1982). Using vegetation maps for each site (Oregon: Whittaker 1960; Arizona: Whittaker & Niering 1964; Costa Rica: Holdridge et al. 1971), at least one plot was included in each plant zone across elevation. Locations that had evidence of recent disturbance (e.g. fire, logging) were avoided. Where habitats were more heterogeneous, additional plots per habitat type were included (Gauch 1982). In topographically complex habitats, for example, plots were placed in various slope directions and inclinations in order to represent the continuum of soil moisture availability within a particular habitat type (Whittaker 1960; Whittaker & Niering 1964). This was particularly true in the lowland dry tropical forests of Costa Rica where plant communities differ in deciduousness, ranging from about 20% evergreen hillsides to almost completely evergreen lowlands (Janzen 1986; Powers et al. 2009). After surveying the obvious extreme habitats (e.g. ridge, valley, slope), plots were continually added until the number of new species encountered with increasing area neared zero.

**Table 1.** Site characteristics including latitude (Lat), longitude (Lon), elevational range (m a.s.l.), major vegetation zones and relevant previous studies along each elevational gradient.

Site	Lat/Lon	Elevation (m)	Major vegetation zones	Previous studies
Area de Conservación Guanacaste, Costa Rica	10°51' N	0–1500	Lowland dry tropical forest; transitional moist forest, rain forest, cloud forest	Lowlands: Janzen (1986), Powers et al. (2009)
	85°37' W			
Santa Catalina Mountains, Arizona	32°26' N	740–2790	Sonoran desert scrub; oak woodlands; coniferous forest; sub-alpine forest	Shreve (1915), Whittaker & Niering (1964)
	110°47' W			
Siskiyou Mountains, Oregon	41°49' N	0–2100	Coniferous forest; montane forest; alpine and sub-alpine forests	Whittaker (1960), Damschen et al. (2010) Harrison et al. 2011
	123°40' W			

For all woody species within each plot we measured specific leaf area (SLA), a key functional trait associated with competition for resources and environmental tolerance (Poorter et al. 2009). SLA ( $\text{cm}^2\text{g}^{-1}$ ) is defined as the light capturing surface area per unit of dry biomass and correlates with differences in life-history strategies (e.g. net photosynthetic capacity, leaf longevity, relative growth rate and competitive ability; Reich et al. 1997). For example, SLA is known to reflect a trade-off in plant resource-use strategy from rapid biomass production (high SLA) to efficient nutrient conservation (low SLA; Wright et al. 2004). Further, variation in SLA is tightly coupled with variation in resource gradients such as light and productivity (Grime 1998). For the collection of plant traits, five mature, healthy, sun leaves were collected from five different individuals for each species within a plot (Cornelissen et al. 2003). Once leaves were collected, the fresh area of each leaf was measured within a few hours of collection. Fresh leaf area ( $\text{cm}^2$ ) was measured using a Canon CanoScan LiDE 110 portable electronic scanner (Canon Inc., Lake Success, NY, USA), and leaf area was calculated using the ImageJ imaging software (Abramoff et al. 2004). All leaves were then placed in a drying oven for a minimum of 72 h at 70 °C until a constant mass was reached, and the final dry mass was recorded.

If there were not sufficient individuals within the plot to meet the minimum criteria of five individuals, then leaves were collected from nearby individuals located outside of, but never more than 500 m away from, a plot. Rare species with <5 sampled individuals were not included in the analyses but did not total more than 8% of the total relative abundance in any plot. All individuals in Arizona were sampled during March and April 2010; in Oregon during early May 2010; and in Costa Rica in mid-May through June 2010. These times correspond with the early growing season in each location.

### Statistical analyses

To explore patterns of abiotic filtering across elevation and latitude, we first compared how community-wide trait means and variances change with elevation and latitude. To do this, the abundance-weighted plot mean and variance (community-weighted mean and variance, CWM and CWV, respectively; Violle et al. 2007) of SLA values were calculated for each plot  $k$  as:

$$\text{CWM}_k = \sum a_{ik} t_{ik} \quad (1)$$

$$\text{CWV}_k = \sum a_{ik} (t_{ik} - \text{CWM}_k)^2 \quad (2)$$

where  $a_{ik}$  is the relative abundance of species  $i$  in plot  $k$ , and  $t_{ik}$  is the trait mean of species  $i$  in plot  $k$ . To explore

whether the observed trait patterns differ from random, a null modelling approach is necessary (Gotelli & Graves 1996). A null model compares whether the observed variation in CWM or CWV across elevation is greater than or less than expected given the observed species richness. To create a null community, trait data for each sampling region (i.e. Costa Rica, Arizona or Oregon) were pooled into a regional trait community. For each plot, we calculated the null trait mean and variance value and the 95% confidence interval (CI) based on 999 iterations by shuffling the species-by-plot trait values and thus conserving species richness and abundance within each plot (Gotelli & Graves 1996). This approach avoids averaging the mean and variance of species' SLA values across all plots, which ultimately reduces the observed trait variation both between and within species. Shuffling trait values, as opposed to species' abundances, can also indicate which assembly processes, including abiotic filtering and limiting similarity, structure communities.

First, to understand how plant function varies with elevation and whether abiotic filtering drives assembly at high elevations and latitudes, we performed simple linear regressions of CWM and CWV of SLA against elevation for each community. Second, to determine whether the observed trait values were clustered or over-dispersed compared to random assemblages (and thus the influence of abiotic or biotic drivers), we compared the observed CWM and CWV to random communities. Finally, we explored the central ideas of limiting similarity and niche packing by comparing how the ratio of intra- and inter-specific trait variation changed with increasing species richness. For each plot, we calculated the ratio of intra-specific to inter-specific variation. Plot inter-specific variation was calculated as the variance of all species' mean trait values (i.e. variance of species' means). Plot intra-specific variation was calculated as the mean of all species' intra-specific variances for each trait (i.e. mean of species' variances). We also included a null model to resample trait variation with increasing sample size (i.e. increasing species richness) without replacement using the *sample* package in *R* (R Foundation for Statistical Computing, Vienna, AT). For example, for a sample size of 45 species, we randomly drew 45 values of trait mean and 45 values of intra-specific trait variance. We then calculated the null inter-specific variation as the variance of 45 mean values and the null intra-specific variation as the mean of 45 variance values and calculated the ratio between intra- and inter-specific variance. This was done for each of 999 iterations for each increase in sample size. Finally, we compared the observed and randomized slopes and intercept coefficients from linear regressions between variance (intra-specific, inter-specific and intra:inter) and species richness using the *smatr* package in *R*.

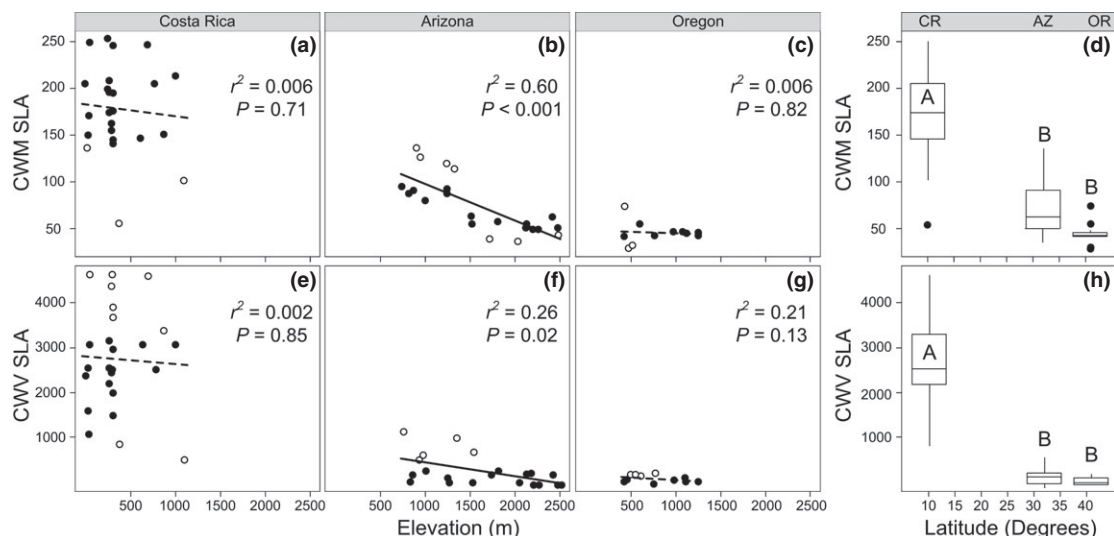
Although variance is often correlated with mean values (Taylor 1961), this ratio is informative for three reasons. First, intra-specific variance includes standardized measurements from a set number of leaves and individuals (five) from each species found within each plot and is thus measured systematically across all plots. Second, calculating the average of intra-specific variances in each plot partially accounts for differences in species richness between plots. Third, by including a resampling model, we can compare the observed patterns of trait variation to those expected under random sampling of trait variation. We used this ratio to explore the biological patterns of variance with increasing species richness (Violle et al. 2012). We regressed intra-specific variation, inter-specific variation and the ratio of intra- to inter-specific variation against species richness. If abiotic and biotic drivers are truly asymmetric across environmental gradients, then a decrease in the ratio of variation with increasing species richness should be evident at low latitudes, suggesting greater limiting similarity in tropical latitudes. All statistical analyses were conducted in *R* (v. 2.15.1).

## Results

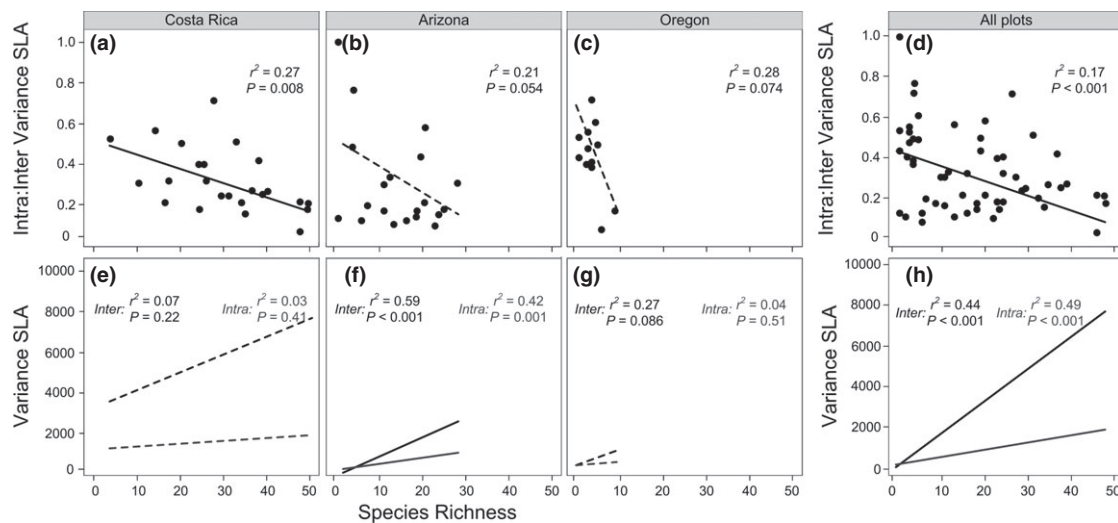
There were a total of 275 woody plant species in our plots in Costa Rica, 65 in Arizona and 18 in Oregon. Species richness decreased with latitude and was not correlated to

elevation in Costa Rica ( $r^2 = 0.089$ ,  $P = 0.14$ ), decreased with increasing elevation in Arizona ( $r^2 = 0.71$ ,  $P < 0.001$ ) and was not correlated to elevation in Oregon ( $r^2 = 0.16$ ,  $P = 0.20$ ; Fig. S1). With increasing latitude, both CWM and CWV of SLA decreased (Fig. 1d,h) and the ratio of intra- to inter-specific variation decreased (Fig. 2d) with increasing species richness. Decomposing this ratio into individual components, both intra- and inter-specific variations increased with increasing species richness at different rates (i.e. slopes; Fig. 2h).

At the lowest latitude (Costa Rica) CWM (Fig. 1a) and CWV (Fig. 1e) of SLA were not correlated to elevation. Compared to a random model of assembly, SLA was more variable than expected at low elevations (Fig. 1e), and the ratio of intra- to inter-specific variation was negatively correlated to species richness ( $r^2 = 0.27$ ,  $P = 0.0083$ ; Fig. 2a) even though the individual components of this ratio were not correlated to species richness (Fig. 2e). At the mid-latitude site (Arizona) CWM ( $r^2 = 0.60$ ,  $P < 0.0001$ ; Fig. 1b) and CWV ( $r^2 = 0.26$ ,  $P = 0.016$ ; Fig. 1f) of SLA decreased with increasing elevation. In comparison with a random model of assembly, community mean SLA was also higher than expected in the low-elevation communities and lower than expected in high-elevation communities (open data points; Fig. 1b). Similarly, CWV SLA was more variable than expected at low elevations (Fig. 1f) compared to a random model of assembly. The ratio of intra- to inter-specific variation of SLA was not significantly correlated to



**Fig. 1.** Community-weighted mean (CWM) and variance (CWV) of specific leaf area (SLA;  $\text{cm}^2\cdot\text{g}^{-1}$ ) against elevation (m a.s.l.) for Costa Rica (CR; a, e), Arizona (AZ; b, f) and Oregon (OR; c, g) and across latitude (d, h). Solid black lines indicate a significant ( $P < 0.05$ ) relationship; dashed black lines indicate a non-significant relationship. Each data point represents a single community (plot). Solid data points indicate communities that are not statistically distinguishable from random communities; open data points indicate communities that are statistically distinguishable from random communities. For latitudinal comparisons, sites separated by letters are statistically distinguishable in a one-way ANOVA. For each site, the lower-elevation communities tend to have increased trait diversity or variance than expected by chance.



**Fig. 2.** The ratio of intra-specific to inter-specific variance (Intra:Inter Variance, upper panel), intra-specific variation (grey lines, lower panel) and inter-specific variation (black lines, lower panel) of specific leaf area (SLA;  $\text{cm}^2 \cdot \text{g}^{-1}$ ) as a function of species richness for elevational gradients in Costa Rica (a, e), Arizona (b, f) and Oregon (c, g) and across latitude (d, h). Each data point represents a single community (plot). Solid lines indicate a significant ( $P < 0.05$ ) relationship; dashed lines indicate a non-significant relationship.

species richness (Fig. 2b) even though the individual components of this ratio were both positively correlated to species richness (Fig. 2f). Finally, at the highest latitude site (Oregon), CWM and CWV of SLA were not correlated to elevation (Fig. 1c,g). Relative to a null model of assembly, CWM and CWV of SLA in the Oregon plots were more variable than expected at low elevations (open data points; Fig. 1c,g), but neither the ratio of intra- to inter-specific variation of SLA nor the individual components were significantly correlated to species richness (Fig. 2c,g). The randomized values of intra-specific variation, inter-specific variation and the trait variation ratio did not increase with increasing species richness (not shown). For each regression analysis between SLA variance and species richness, the observed communities significantly differed in slope from the randomized communities and generally did not differ in intercept (not shown).

## Discussion

The origins of diversity gradients continue to remain a central area of focus and debate (Wiens 2011; Stegen et al. 2012). Few studies, however, have examined whether traits vary in similar ways across gradients of latitude and elevation. Here, we show that at higher latitudes, but not necessarily high elevations, the variance in SLA decreased, consistent with increased abiotic filtering (Weiher & Keddy 1995) at higher latitudes. Further, lower-elevation plots across sites tended to have more variance in SLA than expected by chance, consistent with limiting similarity

(MacArthur & Levins 1967; Chesson 2000). In addition, we found that both intra- and inter-specific variation increased with species diversity but at different rates, so that the total ratio between intra- and inter-specific variations decreased with increasing species richness. This suggests that the total trait space indeed increases towards tropical latitudes; however, because intra-specific variation increases at a slower rate, species are more ‘tightly packed’ in tropical systems. Together, these community-level findings are consistent with the often cited but rarely tested assumption that variation in diversity across broad scale gradients is constrained by available niche space (see Willig et al. 2003; Wiens 2011), but that biotic pressure at lower elevations and latitudes increases the total niche volume and thus phenotypic diversity. These results are consistent with previous findings that both biotic and abiotic forces have likely been important in the evolution of plant function and diversity on contrasting ends of elevational and latitudinal gradients (Shepherd 1998; Stevens et al. 2006; Swenson et al. 2012). We discuss these results in light of both the strengths and current challenges of a trait-based approach for understanding diversity patterns across broad environmental gradients.

## Patterns of trait variation across elevation and latitude

Across latitude, CWM and CWV of SLA decreased with increasing latitude. These patterns are similar to global trends (Reich et al. 1997; Wright et al. 2005). Specifically, SLA has been shown to shift across productivity gradients

(Reich et al. 1997; Grime 2006), and increases in mean annual precipitation and temperature are thought to be the two best predictors of mean SLA across broad geographical gradients (Swenson et al. 2012). Although this study uses a single functional trait, the patterns shown here mirror those found for other plant traits including wood density, maximum height and seed mass (Swenson & Enquist 2007; Swenson & Weiser 2010; Swenson et al. 2012), consistent with the idea that whole-plant level function responds in concert to gradients of elevation and latitude.

Across elevation in Costa Rica, CWM and CWV of SLA were not correlated with elevation (Fig. 1a,e). This pattern suggests that abiotic filtering is a weak driver of trait values across elevation in Costa Rica, the abiotic differences between lowland dry forests and higher elevation communities are reduced during the rainy season (Gotsch et al. 2010), abiotic filtering of SLA is not relevant at this site or spatial scale (see Swenson et al. 2006), or the high habitat heterogeneity characteristic of dry tropical forests obscured our ability to detect patterns in the context of broader environmental gradients (Baraloto & Coutron 2010). For example, the high heterogeneity found in Costa Rica may be related to topographical differences or historical disturbance regimes (i.e. land use, timber extraction, fire; Powers et al. 2009), and each can affect the structure and composition of forest communities. Although areas that had obvious evidence of disturbance were avoided, the long-term legacies of past disturbance events (see Foster et al. 2003) could potentially limit our ability to detect non-random assembly patterns at larger spatial scales. That the community means were similar to random assemblages in Costa Rica may further indicate the opposing effects of both abiotic and biotic filtering at local scales (Swenson et al. 2006) due to either long-term successional processes or the effects of local topographic differences.

In Arizona, the decrease of mean trait values with elevation mirrors the known decrease in SLA with increasing latitude (Reich et al. 1997). This latitudinal trend is thought to be primarily due to the increasing dominance of gymnosperms at high latitudes (McCarthy et al. 2007). Similarly, the increasing dominance of gymnosperms at high elevations in Arizona likely underlies the observed shift in trait mean. Gymnosperms are known to have relatively low values of SLA (Royer et al. 2010) as well as low plasticity compared to angiosperms (Bond 1989). Thus, whether the range of SLA variation is a consistent proxy of functional strategies for gymnosperms and angiosperms requires further exploration.

Similarly, although this study offers the first standardized quantification of how trait variation differs across elevation and latitude, sampling a single functional life form (i.e. woody species) likely underestimates the total observed variation in SLA. Thus, a critical next step for

trait-based ecology will be to determine whether functional strategies of non-woody species respond similarly across environmental gradients compared to woody species. On the one hand, non-woody species can evade harsh abiotic conditions by being non-persistent so that patterns of trait variation across environmental gradients may not reflect patterns of abiotic filtering as seen in woody species. On the other hand, competition between non-woody and woody species may be critical for assembly (see House et al. 2003), particularly during the seedling stage. An emerging research question is thus how patterns of trait variation differ between co-existing life forms and how trait differences may confer competitive and/or fitness differences.

Finally, in Oregon, a gradient dominated by gymnosperms, the lack of clear correspondence between trait mean and variation with elevation may be due to either the stabilizing maritime influence on climate across the Siskiyou Mountains (Whittaker 1960) or that the use of SLA as a proxy for functional strategies is not consistent between gymnosperms and angiosperms. We can thus infer that, first, the processes that influence assembly across elevation are not the same between the three mountain gradients sampled. This is intuitive since elevational gradients reflect the combined effect of regional peculiarities and general altitude phenomena (Körner 2007), and the three mountain gradients sampled here differ in climate, seasonality, topography, age and isolation, among other factors that affect biodiversity along elevational gradients (see Körner 2007). Thus, it would be highly desirable to systematically sample many replicate elevational gradients across a wide spectrum of climatic zones. Although patterns of variation in SLA across environmental gradients provide reasonable support for assembly mechanisms, the use of SLA as a proxy for functional strategies may break down when making comparisons between distinct clades, or even life forms within the same clade. Thus, experimental or simulation approaches may better link differences in SLA to plant function and, ultimately, fitness across environmental gradients.

Despite climatic and topographic differences between elevational gradients, low-elevation communities across all sites had higher trait variance than expected by chance. This finding points to the role of competitive interactions that prevent co-existing species from being too functionally similar. Yet recent debate challenges whether trait variation can be used to infer the relative importance of abiotic vs biotic filters (HilleRisLambers et al. 2012), since competitive exclusion, like abiotic filtering, can also lead to low-trait variation within and between species. Although clear relationships between environmental gradients and traits provide reasonable support that an abiotic filter is important for assembly (HilleRisLambers et al. 2012), experimental approaches that explicitly link abiotic and

biotic factors to the distribution of trait values within communities will further shed light on trait assembly patterns across environmental gradients.

### Trait variation and species richness

In order to determine the relationship between trait variation and species richness we quantified the ratio between intra- and inter-specific variations. By doing so, we were able to test a specific prediction of limiting similarity, namely that the amount of intra-specific variation (niche breadth) compared with inter-specific variation (total niche space) does indeed vary with community species richness. The limiting similarity hypothesis predicts that (1) niche breadth, or intra-specific variation in resource use, should decrease with increased richness (MacArthur & Wilson 1967) and/or (2) that the total amount of niche space should increase with species richness (Tilman et al. 1997; Weiher et al. 1998). An open question for niche-based ecological theory is whether the amount of intra-specific variation compared with inter-specific variation actually varies with species richness as predicted by niche theory (Violle et al. 2012).

Consistent with niche theory, we showed that the ratio of intra- to inter-specific variation does decrease with increasing species richness across latitude and elevation. Decomposing the individual components of this ratio, we showed that inter-specific variation of SLA increased with species richness at a faster rate compared to intra-specific variation. This finding, while consistent with limiting similarity in tropical forest communities (e.g. Pianka 1966), may also suggest that other processes, such as developmental constraints, can limit intra-specific trait expression. Despite the use of functional traits to define species' niches, there is still a large gap in our understanding of how traits relate to fitness, as well as to the evolutionary mechanisms that drive niche differentiation (Sterck et al. 2011).

### Conclusions

We provide an investigation into the predominant patterns of trait variation across elevational gradients using mountains at three widely separated latitudes in the New World. This study combines measures of both intra- and inter-specific trait variation observed within each forest plot across multiple elevational gradients. Although intra-specific trait variation is thought to promote species diversity and improve detection of abiotic filtering and limiting similarity (Jung et al. 2010) and, as such, has appeared at the forefront of trait-based ecology (see Bolnick et al. 2011; Violle et al. 2012), there is a limited understanding of how both intra- and inter-specific variation change over latitudinal and elevational gradients. We demonstrate that patterns of

intra- and inter-specific trait variation at broad scales are consistent with the idea that local abiotic and biotic interactions influence diversity patterns across environmental gradients. While our findings support the use of a trait-based approach for understanding broad scale diversity gradients (see Roughgarden 1972; Violle & Jiang 2009; Violle et al. 2012), several key challenges remain for linking local ecological processes to broad environmental gradients.

First, our analyses include three elevational gradients that differ in a number of ways, including regional climate. Future studies are needed to compare elevational gradients with similar climatic regimes (such as in the moist tropics) in order to disentangle the effects of potentially confounding abiotic and biotic factors (Körner 2007; Malhi et al. 2010). Further, by only measuring SLA of woody species, our conclusions are limited to a single axis of plant variation in ecological strategies for one life form and we cannot infer how reproductive, regenerative (Grime 2006) or whole-plant strategies differ across broad spatial scales, life forms or even different taxa. In addition, testing for abiotic and biotic filters using a trait-based approach should be expanded to include experimental and demographic analyses (HilleRisLambers et al. 2012) to more strongly link traits to plant fitness. Finally, in order for intra-specific trait variation to be integrated into functional ecology, there is still a need to determine the magnitude and patterns of intra-specific variation within and across ecosystems. In summary, quantifying patterns of community assembly and trait variation across diverse environmental gradients will advance our understanding of the mechanisms that give rise to large-scale biogeographic gradients.

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## References

- Abramoff, M.D., Magelhaes, P.J. & Ram, S.J. 2004. Image Processing with ImageJ. *Biophotonics International* 11: 36–42.
- Baraloto, C. & Couteron, P. 2010. Fine-scale microhabitat heterogeneity in a French Guianan forest. *Biotropica* 42: 420–428.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26: 183–192.
- Bond, W.J. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society* 36: 227–249.
- Brown, J.H. 1975. Geographical ecology of desert rodents. In: Cody, M. & Diamond, J. (eds.) *Ecology and evolution of communities*, pp. 315–341. Belknap Press, Cambridge, MA, US.
- Bryant, J.A., Lamanna, C., Morlon, H., Kerkhoff, A.J., Enquist, B.J. & Green, J.L. 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11505–11511.
- Callaway, R.M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos* 82: 561–573.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional trait worldwide. *Australian Journal of Botany* 51: 335–380.
- Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L. & Pasteris, P. 2002. A knowledge-based approach to the statistical mapping of climate. *Climate Research* 22: 99–113.
- Damschen, E.I., Harrison, S. & Grace, J.B. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). *Ecology* 91: 3609–3619.
- Dobzhansky, T. 1950. Evolution in the tropics. *American Scientist* 38: 209–221.
- Fischer, A.G. 1960. Latitudinal variation in organic diversity. *Evolution* 14: 64–81.
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D. & Knapp, A. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53: 77–88.
- Gauch, H.G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge, MA, US.
- Gotelli, N.J. & Graves, G.R. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, DC, US.
- Gotsch, S.G., Powers, J.S. & Lerdau, M.T. 2010. Leaf traits and water relations of 12 evergreen species in Costa Rican wet and dry forests: patterns of intra-specific variation across forests and seasons. *Plant Ecology* 211: 133–146.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.
- Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.
- Harrison, S., Vellend, M. & Damschen, E.I. 2011. Structured beta diversity increases with climatic productivity in a classic dataset. *Ecosphere* 2: art11.
- HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. 2012. Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43: 227–248.
- Hoiss, B., Krauss, J., Potts, S.G., Roberts, S. & Steffan-Dewenter, I. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits, and diversity in bee communities. *Proceedings of the Royal Society of London, Biological Sciences* 279: 4447–4456.
- Holdridge, L.E., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. 1971. *Forest environments in tropical life zones: A pilot study*. Pergamon Press, Oxford, UK.
- House, J.I., Archer, S., Breshears, D.D., Scholes, R.J., Coughenour, M.B., Dodd, M.B., Gignoux, J., Hall, D.O., Hanan, N.P., Joffre, R., Le Roux, X., Ludwig, J.A., Menaut, J.-C., Montes, R., Parton, W.J., San José, J.J., Scanlan, J.C., Scurlock, J.M.O., Simioni, G. & Thorrold, B. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography* 30: 1763–1777.
- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81–101.
- Janzen, D.H. 1986. *Guanacaste National Park: tropical ecological and cultural restoration*. Editorial Universidad Estatal a Distancia, San José, CR.
- Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98: 1134–1140.
- Kluge, J. & Kessler, M. 2011. Influence of niche characteristics and forest type on fern species richness, abundance and plant size along an elevational gradient in Costa Rica. *Plant Ecology* 212: 1109–1121.
- Kooyman, R., Rossetto, M., Cornwell, W. & Westoby, M. 2011. Phylogenetic tests of community assembly across regional to continental scales in tropical and subtropical rain forests. *Global Ecology and Biogeography* 20: 707–716.
- Körner, C. 2007. The use of “altitude” in ecological research. *Trends in Ecology & Evolution* 22: 569–74.
- Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B. D., Harrison, S.P. & Myers, J.A. 2011. Disentangling

- the drivers of diversity along latitudinal and elevational gradients. *Science* 333: 1755–1758.
- Lomolino, M.V. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* 10: 3–13.
- MacArthur, R.H. 1972. *Geographical ecology: patterns in the distribution of species*. Princeton University Press, Princeton, NJ, US.
- MacArthur, R. & Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101: 377–385.
- MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Monographs in Population Biology. Princeton University Press, Princeton, NJ, US.
- Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. & Saatchi, S. 2010. Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Global Change Biology* 16: 3171–3175.
- McCain, C.M. & Grytnes, J. 2010. Elevational gradients in species richness. In: *Encyclopedia of life sciences*. John Wiley and Sons, Chichester, UK. doi: 10.1002/9780470015902.a0022548.
- McCarthy, M.C., Enquist, B.J. & Kerkhoff, A.J. 2007. Organ partitioning and distribution across the seed plants: assessing the relative importance of phylogeny and function. *International Journal of Plant Sciences* 168: 751–761.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.
- Pacala, S.W. & Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist* 143: 222–257.
- Pianka, E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100: 33–46.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Powers, J.S., Becknell, J.M., Irving, J. & Pérez-Aviles, D. 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *Forest Ecology and Management* 258: 959–970.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America* 94: 13730–13734.
- Ricklefs, R.E. 2009. Aspect diversity in moths revisited. *The American Naturalist* 173: 411–416.
- Roughgarden, J. 1972. Evolution of niche width. *The American Naturalist* 106: 683–718.
- Royer, D.L., Miller, I.M., Peppe, D.J. & Hickey, L.J. 2010. Leaf economic traits from fossils support a weedy habit for early angiosperms. *American Journal of Botany* 97: 438–45.
- Schemske, D.W. 2009. Biotic interactions and speciation in the tropics. In: Butlin, R.K., Bridle, J.R. & Schluter, D. (eds.) *Speciation and Patterns of Diversity*, pp. 219–239. Cambridge University Press, Cambridge, UK.
- Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution and Systematics* 40: 245–269.
- Shepherd, U.L. 1998. A comparison of species diversity and morphological diversity across the North American latitudinal gradient. *Journal of Biogeography* 25: 19–29.
- Shreve, F. 1915. *The vegetation of a desert mountain range as conditioned by climatic factors*. Carnegie Institution of Washington, Washington, DC, US.
- Spasojevic, M.J. & Suding, K.N. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* 100: 652–661.
- Stegen, J.C., Enquist, B.J. & Ferriere, R. 2009. Advancing the metabolic theory of biodiversity. *Ecology Letters* 12: 1001–1015.
- Stegen, J.C., Enquist, B.J. & Ferriere, R. 2012. Eco-Evolutionary community dynamics: covariation between diversity and invasibility across temperature gradients. *American Naturalist* 180: E110–E126.
- Sterck, F., Markesteijn, L., Schieving, F. & Poorter, L. 2011. Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy of Sciences of the United States of America* 108: 20627–20632.
- Stevens, R.D., Willig, M.R. & Strauss, R.E. 2006. Latitudinal gradients in the phenetic diversity of New World bat communities. *Oikos* 112: 41–50.
- Swenson, N.G. & Enquist, B.J. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94: 451–459.
- Swenson, N.G. & Weiser, M.D. 2010. Plant geography upon the basis of functional traits: an example from eastern North American trees. *Ecology* 91: 2234–2241.
- Swenson, N.G., Enquist, B.J., Pither, J., Thompson, J. & Zimmerman, J.K. 2006. The problem and promise of scale dependency in community phylogenetics. *Ecology* 87: 2418–2424.
- Swenson, N.G., Enquist, B.J., Pither, J., Kerkhoff, A.J., Boyle, B., Weiser, M.D., Elser, J.J., Fagan, W.F., Forero-Montaña, J., Fyllas, N., Kraft, N.J.B., Lake, J.K., Moles, A.T., Patiño, S., Phillips, O.L., Price, C.A., Reich, P.B., Quesada, C.A., Stegen, J.C., Valencia, R., Wright, I.J., Wright, S.J., Andelman, S., Jørgensen, P.M., Lacher, T.E. Jr, Monteagudo, A., Núñez-Vargas, M.P., Vasquez-Martínez, R. & Nolting, C.M. 2012. The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* 21: 798–808.
- Taylor, L.R. 1961. Aggregation, variance and the mean. *Nature* 189: 732–735.
- Tilman, D., Lehman, C.L. & Thomson, K.T. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America* 94: 1857–1861.

- Vázquez, D.P. & Stevens, R.D. 2004. The latitudinal gradient in niche breadth: concepts and evidence. *The American Naturalist* 164: E1–19.
- Violle, C. & Jiang, L. 2009. Towards a trait-based quantification of species niche. *Journal of Plant Ecology* 2: 87–93.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27: 244–252.
- von Humboldt, A. 1849. *Aspects of nature in different lands and different climates, with scientific elucidations*. Longman, Brown, Green and Longman, London, UK.
- Wang, Y.S., Chua, C.J., Maestre, F.T. & Wang, G. 2008. On the relevance of facilitation in alpine meadow communities: an experimental assessment with multiple species differing in their ecological optimum. *Acta Oecologica – International Journal of Ecology* 33: 108–113.
- Weiher, E. & Keddy, P.A. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74: 159–164.
- 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.
- Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentsen, S. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 366: 2403–2413.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279–338.
- Whittaker, R.H. & Niering, W.A. 1964. Vegetation of the Santa Catalina Mountains, Arizona. I. Ecological classification and distribution of species. *Journal of the Arizona Academy of Science* 3: 9–34.
- Wiens, J.J. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 366: 2336–2350.
- Willig, M.R., Kaufmann, D.M. & Stevens, R.D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annual Review of Ecology and Systematics* 34: 273–309.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Guillas, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I. & Westoby, M. 2005. Assessing the generality of global leaf trait relationships. *New Phytologist* 166: 485–496.

### Supporting Information

Additional supporting information may be found in the online version of this article:

**Figure S1.** Species richness as a function of elevation in Costa Rica (a), Arizona (b), and Oregon. (c) and across latitude