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# REVISITING DARWIN'S HYPOTHESIS: DOES GREATER INTRASPECIFIC VARIABILITY INCREASE SPECIES' ECOLOGICAL BREADTH?[1]

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- *Premise of the study:* Darwin first proposed that species with larger ecological breadth have greater phenotypic variation. We tested this hypothesis by comparing intraspecific variation in specific leaf area (SLA) to species' local elevational range and by assessing how external (abiotic) filters may influence observed differences in ecological breadth among species. Understanding the patterns of individual variation within and between populations will help evaluate differing hypotheses for structuring of communities and distribution of species.
- *Methods:* We selected 21 species with varying elevational ranges and compared the coefficient of variation of SLA for each species against its local elevational range. We examined the influence of external filters on local trait composition by determining if intraspecific changes in SLA with elevation have the same direction and similar rates of change as the change in community mean SLA value.
- *Key results:* In support of Darwin's hypothesis, we found a positive relationship between species' coefficient of variation for SLA with species' local elevational range. Intraspecific changes in SLA had the same sign, but generally lower magnitude than the community mean SLA.
- *Conclusions:* The results indicate that wide-ranging species are indeed characterized by greater intraspecific variation and that species' phenotypes shift along environmental gradients in the same direction as the community phenotypes. However, across species, the rate of intraspecific trait change, reflecting plastic and/or adaptive changes across populations, is limited and prevents species from adjusting to environmental gradients as quickly as interspecific changes resulting from community assembly.

**Key words:** community assembly; functional traits; intraspecific variation; species ecological breadth; specific leaf area.

For more than a century, ecologists have assumed that greater intraspecific variation reflects a greater ability of species to exist in a more diverse range of environments (Darwin, 1859). Since each environment presents a unique set of biotic and abiotic conditions, species adjust their form and function via phenotypic plasticity or natural selection to grow and reproduce under different environmental circumstances (Violle et al., 2007; Jung et al., 2010). Darwin first stated this idea in *The Origin of Species*:

> *…Plants which have very wide ranges generally present varieties; and this might have been expected, as they become exposed to diverse physical conditions, and as they come into competition… with different sets of organic beings. …The species which are most common… and the species which are most widely diffused within their own country… often give rise to varieties sufficiently well-marked to have been recorded in botanical works. …And this, perhaps, might have been anticipated; for, as varieties, in order to become in any degree permanent, necessarily have to struggle with the other inhabitants of the country, the species which are already dominant will be the most likely to yield offspring which, though in some slight degree modified, will still inherit those advantages that enabled their parents to become dominant over their compatriots.* (Darwin, 1859, pages 108-109)

Although Darwin recognized the fundamental importance of intraspecific variation in ecology, only recently have studies emphasized the considerable contribution of within-species' variation to community trait structure (de Bello et al., 2011; Albert et al., 2012). A better understanding of intraspecific variability may provide insight into the underlying processes that dictate species' ecological breadth (Ackerly and Cornwell, 2007) and community assembly (Jung et al., 2010; Violle et al., 2012).

Although intraspecific variation accounts for more than a quarter of community trait variance in both tropical and temperate systems (Albert et al., 2010a; Hulshof and Swenson, 2010; Jung et al., 2010; Messier et al., 2010), most studies have ignored the role of intraspecific trait variation in community assembly by using mean-species' trait values or data from global traits (Swenson and Enquist, 2007; Kraft et al., 2008; Freschet et al., 2011). This approach ignores variation among the most basic units of community assembly, the individual,

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which may overlook fundamental processes dictating community assembly and species' ecological breadth (Violle et al., 2012). In classical niche theory, intraspecific trait variation is thought to reflect niche breadth as the outcome of competitive ability (Macarthur and Levins, 1967; Roughgarden, 1974). Since functional traits influence plant fitness (Poorter, 1989; Reich et al., 1998; Wright et al., 2004), greater intraspecific functional variability may enable species to adjust to a wider range of competitive and abiotic conditions and therefore, have greater niche breadth.

The current view in trait-based plant ecology is that external filters (e.g., climate), and internal community filters (e.g., competition, biotic interactions, and microhabitat heterogeneity), are competing forces that influence community assembly (Keddy, 1992; Grime, 2006; Ackerly and Cornwell, 2007; Cavender-Bares et al., 2009; Violle et al., 2012). For a given community, if there is a mean optimal phenotype for fitness and/or growth rate (Norberg et al., 2001), then external filters promote convergence of traits around this local optimal phenotype (Violle et al., 2012). This idea follows from a central paradigm in ecology (Whittaker, 1972) and evolutionary biology (Levins and Morris, 1968) where observed shifts in phenotypes, species' abundances, and compositional changes across environmental gradients reflect differential sorting of phenotypes/species that maximize performance in different environments. Thus, a changing mean community phenotype can reflect the effects of external filtering along environmental gradients that select for differing phenotypes (Swenson and Enquist, 2007; Laughlin et al., 2011; Spasojevic and Suding, 2012; Violle et al., 2012).

Strong external filtering on species' traits limits the range of interspecific trait variation within a community (Keddy, 1992; Weiher and Keddy, 1999; Kattge et al., 2011); however, it remains poorly understood how individuals within a species respond to external filters. Since phenotypic variation and heritable differences cause individuals of the same species to differ morphologically and physiologically (Bolnick et al., 2003; Violle et al., 2007; Hulshof and Swenson, 2010), external filters may exclude certain individuals while including other individuals of the same species with appropriate phenotypes to establish under a community's external conditions. Thus, local filtering of intraspecific traits may lead to differential sorting of intraspecific phenotypes along environmental gradients. Cornwell and Ackerly (2009) demonstrated this phenomenon along a water availability gradient in costal California by showing that intraspecific traits covary in the same direction as community traits, but that intraspecific traits change at a slower rate. These findings support the idea that external filters select for an optimal phenotype in each community, which drives unidirectional trait shifts in both the community and individual species along environmental gradients. Few studies are available that address this similarity between intraspecific and community traits.

In the *Origin of Species*, Darwin (1859) argues that as competitively successful species in one community spread to new environments, the new populations experience unique selection pressures that lead to subtle but new trait differences across populations. If this process results in more competitive advantages across populations, then species will continue expanding and local selection will continue to generate more intraspecific trait variation. Intraspecific variation arises from both heritable differences and plasticity (Matesanz et al., 2012), and both may be important factors influencing niche breadth. This study does not separate the respective influence of plasticity and heritable variation, however, we take a purely macroecological approach to assess Darwin's prediction that species with greater total variation are also more widely distributed.

In this study, we measured intraspecific changes in a key functional trait, the ratio of leaf area and dry leaf mass (specific leaf area or SLA), within and across populations of 21 species along a subalpine elevational gradient in the Colorado Rockies, of the western USA. SLA is a central functional trait that underlies variation in plant growth (Evans, 1972; Poorter, 1989; Enquist et al., 2007) and is correlated with leaf life span and photosynthetic capacity (Wright et al., 2004). An important environmental factor along our study sites that may influence SLA is growing season length, which is shorter at high elevations due to later snowmelt (Appendix S1; see Supplemental Data with the online version of this article). With a shorter growing season, plants should have higher SLA (thin leaves) to reduce construction costs of building leaves and increase photosynthetic capacity to ensure positive carbon gain during the growing season (Kudo, 1996). Therefore, we predict that high-elevation plants should have higher SLA than low-elevation plants exposed to longer growing seasons and the need for longer-lasting, thick leaves. Additionally, species with greater intraspecific variation in SLA should be able to balance the tradeoff between maximizing photosynthetic capacity and maintaining an adequate leaf life span across a wider range of environmental conditions and therefore, have greater ecological breadth.

Due to the importance of SLA in plant fitness, previous studies have used SLA to quantify intraspecific variance (Albert et al., 2010b; Hulshof and Swenson, 2010) to address processes underlying community assembly (Jung et al., 2010; Spasojevic and Suding, 2012) and to quantify species' niche breadth (Ackerly and Cornwell, 2007; Violle and Jiang, 2009). While studies that measure intraspecific variance over environmental gradients normally contain a small proportion of the global SLA range, e.g., < 50% (Jung et al., 2010), the species in this study represent more than 75% of the global range in SLA (Wright et al., 2004). We selected elevation as the study's primary environmental gradient to maximize intraspecific and environmental variability.

This study tests three prominent hypotheses in trait-based community ecology. First, if external filters shift along an environmental gradient and select for different phenotypes/traits in separate communities, then intraspecific traits should change in the same direction as the community-weighted mean phenotype/trait (Cornwell and Ackerly, 2009). Specifically, intraspecific variation should allow individuals of a species to better match shifts in the local abiotic environment across a gradient. Second, if limited intraspecific phenotypic/trait variation confines species' distributions along environmental gradients, then intraspecific traits should change more slowly than the community mean trait along a gradient. Third, if intraspecific variation enables species to establish under differing internal and external filters, then species with greater intraspecific variability should have greater ecological breadth.

## MATERIALS AND METHODS

***Study site and species***—We collected data in subalpine meadows, dominated by dense perennials (*ca.* 150 individuals/ m$^2$), in Washington Gulch, a valley whose mouth lies at 2700 m a.s.l near the town of Crested Butte, Colorado, USA and that extends 12 km north-northwest to 3500 m a.s.l. at the base of Baldy Mountain. We chose six 50 × 50 m primary study sites located midslope in southeast-facing meadows at approximately even elevational intervals from

2710 m to 3380 m a.s.l. (Appendix 1) and measured 21 vascular plant species, which were herbaceous perennials except for *Potentilla fruticosa* L., a common subalpine shrub (Appendix 2). Approximately 100 vascular plant species occurred at one or more of the six primary sites. We selected study species to represent multiple elevational ranges and two seasonal flowering peaks. Study species included four early-season species that typically flower within one to three weeks after snowmelt and 17 peak-season species that begin flowering about four weeks after snowmelt. Because several study species occurred higher than 3380 m, we added supplemental sites at 3450 m, where three study species occurred, and at 3600 m, where one study species was found (Appendix 1). This ensured that we sampled the entire, local elevational range of each study species.

***Data collection—***We measured the abundance-weighted community SLA in summer 2010 and intraspecific SLA in summer 2011. To measure the abundance-weighted community SLA, we sampled one fully developed and sun-exposed leaf from every individual within a randomly selected 1.3 × 1.3 m plot at four (2710, 2820, 3160, and 3320 m) of the six 50 × 50 m primary sites during peak flowering at each site. To measure intraspecific trends, we sampled 20 flowering individuals of all study species present at a site by sampling each individual of each species nearest to a random point chosen by throwing a ruler. Since snowmelt date and therefore phenology vary with elevation, we sampled all plants in 2011 at the same phenological stage, flowering, rather than the same date. For example, early-season species' flower, and were therefore sampled, several weeks before species from the second flowering peak. Leaves were maintained at 5°C (no more than 6 h), scanned (including petiole) at 300 dpi to determine leaf area (mm$^2$) with ImageJ software (NIH, Bethesda, Maryland, USA), dried at 65°C for 72 hours, and then weighed (Cornelissen et al., 2003).

***Data Analysis—***To determine slope values, SLA was regressed against elevation for the community data and for all species that occurred at three or more sites. For community and intraspecific trends between SLA and elevation, we evaluated significance of linear regression with null models because species trends violated the homoscedasticity assumptions of parametric significance tests. All analyses were completed in R (R Development Core Team, 2011). Each null model consisted of 2000 randomized linear regressions where every elevation value of a species was assigned, without replacement, a randomly selected SLA value of that species. Slope values from the 2000 randomized linear regressions created a null distribution to which we compared the measured slope value for that species or community. We considered slope values significant if they were beyond the 2.5 or 97.5 percentiles of the corresponding null distribution.

Intraspecific slopes were compared to the community mean slope to determine if intraspecific slopes had the same directional trend, but lesser rates of change than the community. Since community data were collected during the second seasonal flowering peak, they did not incorporate the senescing early-season species, which were therefore excluded from the analysis with the community data. We used the 'SIGN.test' function from the 'BSDA' library in R (Arnholt, 2010) to determine if a greater number of species than expected by chance had the same direction of slope as the community. To determine if intraspecific slopes had lesser rates of change than the community, we $\log_{10}$ transformed the distribution of intraspecific slopes and compared it to the community slope using a one-tailed *t* test.

We measured growing-season soil and air temperatures (HOBO U12, Onset, Pocasset, Massachusetts, USA) in 2010 at four sites (2710, 2820, 3160, and 3320 m) to determine snowmelt date in 2011 and air temperatures 5 cm above the ground. At the same sites, weather stations at 3160 and 3320 m and ibutton temperature loggers (DS1921G, Maxim Integrated, San Jose, California, USA) at 2710 and 2820 m recorded summer air temperatures in 2011 at 1.3 m above the ground. We regressed daily air temperatures at 1100 h, a time when the sky is usually clear before frequent afternoon thunderstorms, for the first week after snowmelt against the elevation for four sites (2710, 2820, 3160, and 3320 m) to evaluate early-season growing temperatures. For peak season, we regressed daily growing temperatures at 1100 h one week prior to peak flowering (i.e., the average sampling date of peak-season species at a site).

To determine if species' local elevational range correlated with intraspecific SLA variability, we plotted the coefficient of variation (CV) of SLA for each species against its local elevational range, determined by subtracting the lowest from the highest sampling elevations of each species. We did not use other metrics of species' spatial distributions because this study accounts only for regional intraspecific trait variability. Since there is nothing to indicate that growing season affects the relationship between CV of SLA and ecological breadth, we included all study species in this analysis. We adjusted raw CV by recalculating CV from 40 (minimum sample size) randomly selected SLA values of each species because intraspecific CV of SLA was positively correlated to species' sample size ($R^2$ = 0.53, $P$ = 0.0001). We believe this to be the most appropriate analysis to address Darwin's prediction that trait variation arises across populations that experience unique selection pressures in new environments because it incorporates trait variation across each species' entire local elevational range while standardizing the effect of sample size on variation.

## RESULTS

***Specific Leaf Area (SLA)—***We measured SLA of 1908 leaves from four sites in 2010 and 1780 leaves from 21 species in 2011. Across all sampled leaves, SLA ranged between 1 and 68 mm$^2$/mg$^{-1}$. Within-site intraspecific variance also varied greatly among species and within species among sites. For example, *Claytonia lanceolata* Pursh had a variance of 11.955 at 3010 m and 206.699 at 3160 m, and *Hymenoxys hoopesii* (A. Gray) Bierner had consistently lower within-community variances with 4.193 at 3010 m and 10.322 at 3160 m (see Appendix S2).

***SLA along the elevational gradient—***Intraspecific SLA showed the same trend as the community, i.e., SLA increased with elevation. Intraspecific slope values from the second seasonal flowering peak ranged between 0.0037 and 0.0431 mm$^2$/mg$^{-1}$/m$^{-1}$, and 11 out of 14 slopes were significant (Fig. 1). These results showed that more species followed an increasing trend like the community than expected by chance (s = 14, $P$ = 0.0001, Fig. 2), and that the community slope was significantly greater than intraspecific slopes ($t$ = −5.268, df = 13, $P$ = 0.00008, Fig. 2).

Intraspecific SLA variability differed greatly among species, and species with greater variation in SLA had greater local range sizes. Sample size corrected CV of SLA for the 21 species ranged from 0.116 to 0.460, and was highly correlated to species' local range sizes ($F_{1,19}$ = 21.96, $R^2$ = 0.51, $P$ = 0.00017, Fig. 3).

***Early-season species—***SLA for all early-season species decreased with elevation, the opposite of the increasing trends for the community and later-season species (Fig. 1). Growing temperatures may provide insight into the reasons for this difference. Air temperatures for the first week after snowmelt varied little despite substantial elevational differences among sites (Appendix S1, $F_{1,26}$ =1.90, $R^2$ = 0.068, $P$ = 0.18; see Supplemental Data with the online version of this article), whereas air temperatures one week prior to the second flowering peak were lower at high elevations than low elevations (see Appendix S3; $F_{1,26}$ =19.71, $R^2$ = 0.43, $P$ = 0.00015).

## DISCUSSION

Since the early works of Darwin, individual variation has been a fundamental aspect of ecology and evolution. Utilizing a functional approach, we revisited Darwin's hypothesis that species with greater variation have greater ecological breadth. Our findings appear consistent with the expectation (Enquist et al., manuscript in review; Norberg et al., 2001) that there has been strong selection on individuals to adjust their phenotypes to better match an optimal phenotype within each community. Furthermore, since intraspecific traits change at a slower rate

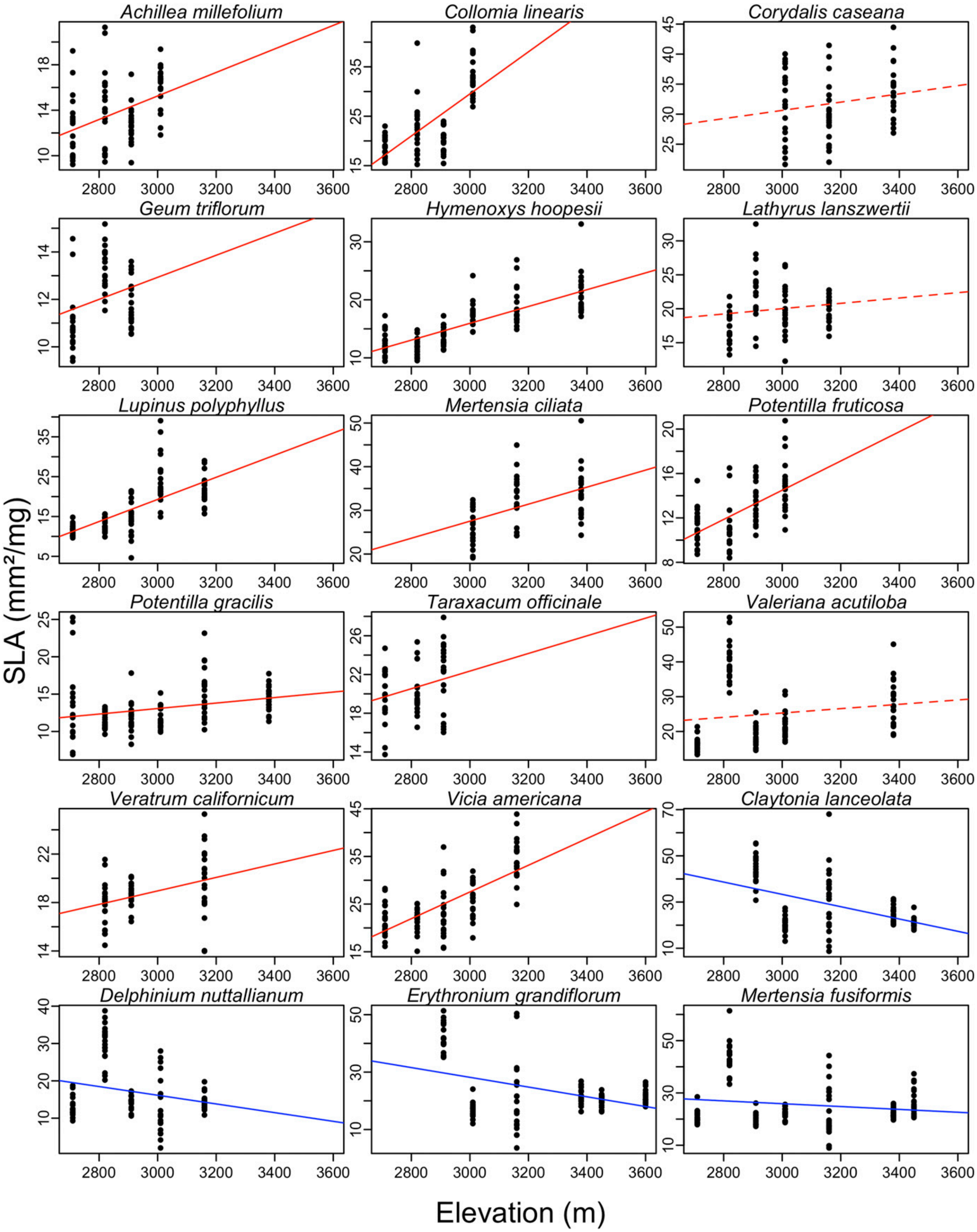

Fig. 1. Linear regressions for species that occurred at three or more sites. Significant trends as tested with null models have solid lines and nonsignificant trends have dashed lines. Species from the second seasonal flowering peak have red lines and early-season species have blue lines.

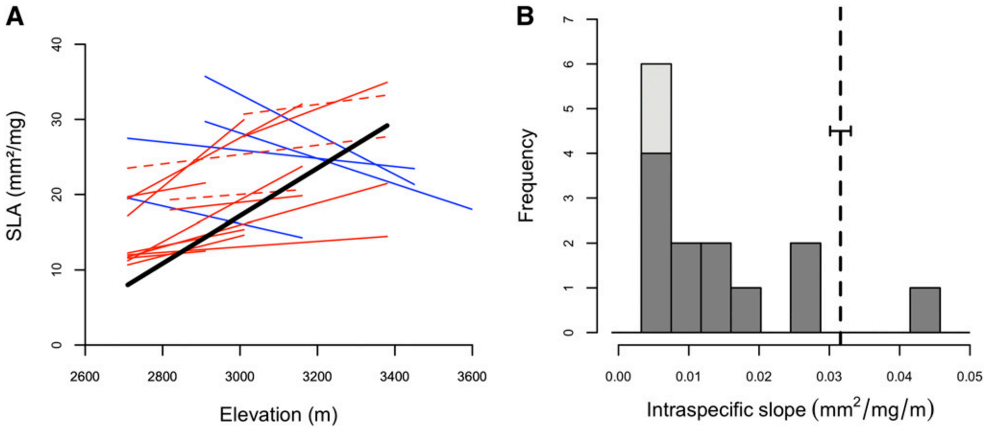

Fig. 2. (A) Trend lines for the community mean (black line) and individual species (red lines) during the second seasonal flowering peak and trend lines for early-season species (blue lines). Solid lines represent species with significant trends as tested with null models and nonsignificant trends have dashed lines. (B) Histogram of slopes of regressions between specific leaf area (SLA) and elevation (mm$^2$/mg/m) from Fig. 1 (excluding early-season species) and slope of the community mean SLA with elevation (dotted line). As early-season species had already begun senescing before the second flowering peak, they were excluded from analyses with community data that were collected during the second flowering peak. The horizontal error bars on the dotted line show the 95% confidence interval for the community mean slope. The dark columns represent species with significant slope values as determined by the null model analysis; species without significant slopes are light gray.

than the mean community trait along environmental gradients, we support the hypothesis that intraspecific trait variation limits species' distributions along environmental gradients. While this indicates that intraspecific trait variation should increase with ecological breadth, we further support this prediction by showing that species with higher variation in SLA have greater local range sizes.

Observed directional changes in trait variation ultimately reflect either local adaptation and/or phenotypic plasticity. While our data cannot differentiate between the two, our analyses nonetheless are consistent with several assumptions and predictions of trait-based ecology. For example, at the community and species-level scales, we observed a directional shift in mean trait values with elevation (Fig. 1). SLA increased with elevation for both individual species and the community from the second flowering peak. This may indicate that plants in higher elevation communities have greater photosynthetic capacities to ensure positive carbon gain over a shorter growing season (Kudo, 1996). This similarity between the community and intraspecific trends is consistent with the importance of external filters in limiting the range of intraspecific phenotypes capable of establishing in each community (Cornwell and Ackerly, 2009). Since SLA influences plant fitness (Reich et al., 1998; Wright et al., 2004), the observed shifts in SLA across the environmental gradient appear to indicate that variation in individual physiology and morphology may allow species to better respond to differing external filters along environmental gradients. These results are in concordance with Violle et al. (2012), who stated that filtering processes should function on the level of individuals instead of species, and therefore, only those individuals of a species with phenotypes matching the local community phenotypes should successfully establish under a community's external filters.

Similar to the results of Cornwell and Ackerly (2009), intraspecific slopes had a slower rate of change with elevation than the observed mean-weighted community slope (Fig. 2). These findings support our prediction that restricted phenotypic variation may limit a species' ability to establish under different external filters. Finite intraspecific variation, which reflects either the limits to local adaptation resulting from selection and/or phenotypic plasticity, confines intraspecific trait values (Hughes et al., 2008). However, community traits are influenced by interspecific turnover, in addition to intraspecific trait shifts (Garnier et al., 2004). Hence, greater species' turnover may enable communities to shift their traits to changing external filters more quickly than individual species across environmental gradients. Assuming community traits are well-adapted to local external filters and that the community mean is therefore representative of a local optimal phenotype, then the shallower slopes of intraspecific trait shifts may represent the failure of intraspecific traits to 'keep pace' with the changing optimal phenotypes across environmental gradients. Thus, species

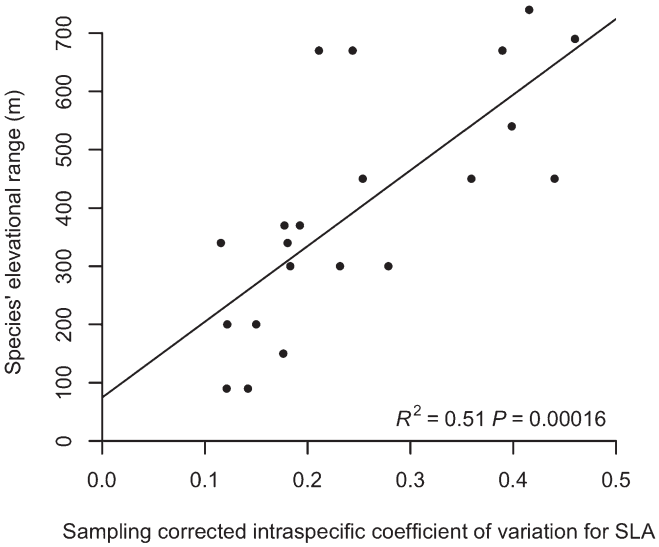

Fig. 3. Species' local elevational range vs. intraspecific coefficient of variation corrected for sample size by randomly sampling 40 SLA values for each species. All 21 study species, including early-season species, were used in this analysis.

with greater intraspecific variation may adjust to more external filters and therefore, have greater niche breadth.

All early-season species had negative relationships between elevation and SLA, which was opposite of the positive relationships of the species and community from the second flowering peak. As this study indicates, species respond to changing external and internal filters along environmental gradients. Elevational gradients serve as a proxy for other external factors that change with elevation (e.g., temperature and precipitation); however, the degree to which these climatic factors vary along the same gradient can differ seasonally. For example, there was no relationship between temperature and elevation immediately after snowmelt, but there was a prominent temperature change with elevation during the second seasonal flowering peak (see Appendix S3). Previous studies show SLA to be negatively correlated with temperature (Laughlin et al., 2011), which may have influenced the increasing trends of peak season species. However, the minimal temperature variation among communities during the early-season represents a less-pronounced temperature gradient than during the second flowering peak, indicating that additional factors may have influenced early-season species' trends.

We demonstrate that phenotypic variation may be important in influencing species' ecological breadth by showing that species with greater regional intraspecific variation in SLA have greater extent along environmental gradients (Fig. 3). By using local elevational range, which includes the effects of both internal and external filters, we show that greater intraspecific functional variation may allow species to adjust to a wider variety of biotic and abiotic conditions, and therefore have greater ecological breadth. These results demonstrate that patterns of individual variation within and between populations as well as between communities can help assess differing hypotheses for the structuring of communities and the distribution of species. While this study is unable to address the respective influences of heritable and plastic variation, our analyses support Darwin's species-level hypothesis that species with greater variation are also more widely distributed (Darwin, 1859).

## LITERATURE CITED

Ackerly, D. D., and W. K. Cornwell. 2007. A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters* 10: 135–145.

Albert, C. H., F. de Bello, I. Boulangeat, G. Pellet, S. Lavorel, and W. Thuiller. 2012. On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* 121: 116–126.

Albert, C. H., W. Thuiller, N. G. Yoccoz, R. Douzet, S. Aubert, and S. Lavorel. 2010a. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology* 24: 1192–1201.

Albert, C. H., W. Thuiller, N. G. Yoccoz, A. Soudant, F. Boucher, P. Saccone, and S. Lavorel. 2010b. Intraspecific functional variability: Extent, structure and sources of variation. *Journal of Ecology* 98: 604–613.

Arnholt, A. T. 2010. BSDA: Basic statistics and data analysis. R package version 1.0. Website: http://CRAN.R-project.org/package=BSDA [accessed 15 February 2012].

Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist* 161: 1–28.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.

Darwin, C. 1859. On the origin of species by means of natural selection. Murray, London, UK.

de Bello, F., S. Lavorel, C. H. Albert, W. Thuiller, K. Grigulis, J. Dolezal, S. Janecek, et al. 2011. Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution* 2: 163–174.

Enquist, B. J., A. J. Kerkhoff, S. C. Stark, N. G. Swenson, M. C. McCarthy, and C. A. Price. 2007. A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature* 449: 218–222.

Evans, G. C. 1972. The quantitative analysis of plant growth. University of California Press, Berkeley, California, USA.

Freschet, G. T., A. T. C. Dias, D. D. Ackerly, R. Aerts, P. M. van Bodegom, W. K. Cornwell, M. Dong, et al. 2011. Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. *Global Ecology and Biogeography* 20: 755–765.

Garnier, E., J. Cortez, G. Billes, M. L. Navas, C. Roumet, M. Debussche, G. Laurent, et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.

Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11: 609–623.

Hulshof, C. M., and N. G. Swenson. 2010. Variation in leaf functional trait values within and across individuals and species: An example from a Costa Rican dry forest. *Functional Ecology* 24: 217–223.

Jung, V., C. Violle, C. Mondy, L. Hoffmann, and S. Muller. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98: 1134–1140.

Kattge, J., S. Diaz, S. Lavorel, C. Prentice, P. Leadley, G. Bonisch, E. Garnier, et al. 2011. TRY—a global database of plant traits. *Global Change Biology* 17: 2905–2935.

Keddy, P. A. 1992. Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an amazonian forest. *Science* 322: 580–582.

Kudo, G. 1996. Intraspecific variation of leaf traits in several deciduous species in relation to length of growing season. *Ecoscience* 3: 483–489.

Laughlin, D. C., P. Z. Fule, D. W. Huffman, J. Crouse, and E. Laliberte. 2011. Climatic constraints on trait-based forest assembly. *Journal of Ecology* 99: 1489–1499.

Levins, R., and D. Morris. 1968. Evolution in changing environments: Some theoretical explorations. Princeton University Press, Princeton, New Jersey, USA.

MacArthur, R., and R. Levins. 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist* 101: 377–385.

Matesanz, S., T. Horgan-Kobelski, and S. E. Sultan. 2012. Phenotypic plasticity and population differentiation in an ongoing species invasion. *PLoS ONE* 7: e44955.

Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13: 838–848.

Norberg, J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proceedings of the National Academy of Sciences, USA* 98: 11376–11381.

Poorter, H. 1989. Interspecific variation in relative growth rate on ecological causes and physiological consequences. *In* H. Lambers, M.L. Cambridge, H. Konings, and T. L. Pons [eds.], Causes and consequences of variation in growth rate and productivity of higher plants, 45-68. SPB Academic Publishing, Amsterdam, Netherlands.

R DEVELOPMENT CORE TEAM. 2011. R: A language and environment for statistical computing, version 2.15.2. Website: http://www. R-project.org [accessed 15 February 2012].

REICH, P. B., M. B. WALTERS, D. S. ELLSWORTH, J. M. VOSE, J. C. VOLIN, C. GRESHAM, AND W. D. BOWMAN. 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: A test across biomes and functional groups. *Oecologia* 114: 471–482.

ROUGHGARDEN, J. 1974. Niche width: Biogeographic patterns among *Anolis* lizard populations. *American Naturalist* 108: 429–442.

SPASOJEVIC, M. J., AND K. N. SUDING. 2012. Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology* 100: 652–661.

SWENSON, N. G., AND B. J. ENQUIST. 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.

VIOLLE, C., B. J. ENQUIST, B. J. MCGILL, L. JIANG, C. H. ALBERT, C. HULSHOF, V. JUNG, ET AL. 2012. The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27: 244–252.

VIOLLE, C., AND L. JIANG. 2009. Towards a trait-based quantification of species niche. *Journal of Plant Ecology* 2: 87–93.

VIOLLE, C., M. L. NAVAS, D. VILE, E. KAZAKOU, C. FORTUNEL, I. HUMMEL, AND E. GARNIER. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

WEIHER, E., AND P. A. KEDDY. 1999. Assembly rules as general constraints on community composition. *In* E. Weiher, and P.A. Keddy [eds.], Ecological assembly rules: Perspectives, advances, retreats, 251-271. Cambridge University Press, Cambridge, UK.

WHITTAKER, R. H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.

WRIGHT, I. J., P. B. REICH, M. WESTOBY, D. D. ACKERLY, Z. BARUCH, F. BONGERS, J. CAVENDER-BARES, ET AL. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

APPENDIX 1. Geographical coordinates for the eight sites used in this study.

| Elevation (meters) | Geographical coordinates |
|---|---|
| 2710 | 38°52′55”N, 106°58′52”W |
| 2820 | 38°53′48”N, 106°58′43”W |
| 2910 | 38°55′40”N, 107°0’24”W |
| 3010 | 38°56′31”N, 107°1’30”W |
| 3160 | 38°57′39”N, 107°1’52”W |
| 3380 | 38°58′8”N, 107°2’28”W |
| 3450 | 38°58′23”N, 107°2’34”W |
| 3600 | 38°59′54”N, 107°4’40”W |

APPENDIX 2. Voucher information for all species in this study. Institutions where vouchers are deposited are in parentheses.

**Taxon**; Voucher (Herbarium).

***Achillea millefolium*** L.; Brian J. Enquist 833 (ARIZ388872). ***Claytonia lanceolata***; Brian J. Enquist 6040 (ARIZ405103). ***Collomia linearis*** Nutt.; Charles F. Williams 2010-0179 (RMBL9604). ***Corydalis caseana*** A. Gray; Brian J. Enquist 885 (ARIZ389477). ***Delphinium barbeyi*** (Huth) Huth; Brian J. Enquist 6066 (ARIZ405099). ***Delphinium nuttallianum*** Pritz.; Brian J. Enquist 712 (ARIZ404312). ***Eriogonum umbellatum*** Torr.; K Taylor 113 (RMBL3075). ***Erythronium grandiflorum*** Pursh; Brian J. Enquist 6140 (ARIZ 405570). ***Gayophytum racemosum*** Torr. & A. Gray; Brian J. Enquist 636 (ARIZ404886). ***Geum triflorum*** Pursh; Brian J. Enquist 853 (ARIZ388864). ***Hymenoxys hoopesii***; Charles F. Williams 2010-0281(RMBL9674). ***Lathyrus lanszwertii*** Kellogg; Charles F. Williams 2010-0149 (RMBL9577). ***Lupinus polyphyllus*** Lindl.; Brian J. Enquist 921 (ARIZ389853). ***Mertensia ciliata*** (James ex Torr.) G. Don; Brian J. Enquist 921 (ARIZ389853). ***Mertensia fusiformis*** Greene; Brian J. Enquist 6136 (ARIZ405579). ***Potentilla fruticosa***; Charles F. Williams 2010-0284 (RMBL 9677). ***Potentilla gracilis*** Douglas ex Hook.; Charles F. Williams 2010-0102 (RMBL9558). ***Taraxacum officinale*** F.H. Wiggers; Brian J. Enquist 826 (ARIZ389481). ***Valeriana acutiloba*** Rydb.; Charles F. Williams 2010-0102 (RMBL9558). ***Veratrum californicum*** Durand; John E. Williams 98 (RMBL2314). ***Vicia americana*** Muhl. ex Willd.; Brian J. Enquist 511 (ARIZ404323).