# Reports

# Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization

ALEX FAJARDO [iD][1,3] AND ANDREW SIEFERT[2]

[1]*Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Camino Baguales s/n, Coyhaique 5951601 Chile*
[2]*Department of Evolution and Ecology, University of California, Davis, California 95616 USA*

*Abstract.* Understanding patterns of functional trait variation across environmental gradients offers an opportunity to increase inference in the mechanistic causes of plant community assembly. The leaf economics spectrum (LES) predicts global tradeoffs in leaf traits and trait-environment relationships, but few studies have examined whether these predictions hold across different levels of organization, particularly within species. Here, we asked (1) whether the main assumptions of the LES (expected trait relationships and shifts in trait values across resource gradients) hold at the intraspecific level, and (2) how within-species trait correlations scale up to interspecific or among-community levels. We worked with leaf traits of saplings of woody species growing across light and soil N and P availability gradients in temperate rainforests of southern Chile. We found that ITV accounted for a large proportion of community-level variation in leaf traits (e.g., LMA and leaf P) and played an important role in driving community-level shifts in leaf traits across environmental gradients. Additionally, intraspecific leaf trait relationships were generally consistent with interspecific and community-level trait relationships and with LES predictions—e.g., a strong negative intraspecific LMA–leaf N correlation—although, most trait relationships varied significantly among species, suggesting idiosyncrasies in the LES at the intraspecific level.

*Key words: leaf area; leaf mass per area; leaf nitrogen concentration; Patagonia; plant community diversity and structure; temperate rainforest.*

## INTRODUCTION

In the last decade, trait-based approaches have rapidly gained prominence in plant ecology. In looking for mechanistic relationships between functional traits and community assembly, studies thus far have mostly focused on assessing mean trait values for species or populations, following the assumption that differences in functional trait values among species are greater than those within species (McGill et al. 2006). Plant species, however, can display high intraspecific variation in functional traits (ITV), reflecting heritable genetic variation and phenotypic plasticity, and this variation in trait expression influences plant growth responses to abiotic filters and biotic interactions (Violle et al. 2012, Siefert et al. 2015). The community-level trait response to abiotic and biotic factors is driven by a combination of both species turnover and ITV. Partitioning the relative contributions of species turnover and ITV to community trait patterns is essential for understanding how communities react to environmental changes.

Central to the trait-based approach, myriad studies have examined on plant functional trait relationships that constitute coordinated spectra related to variation in plant functional strategies. One example is the leaf economics spectrum (LES), which describes tradeoff in a suite of leaf traits related to plant carbon balance across species and resource availability gradients (Wright et al. 2004). LES theory holds that natural selection force all plants to fall along a universal axis running from "slow" to "fast" resource uptake and use strategies, further predicting how leaf traits should vary across environmental gradients and how leaf traits should co-vary with each other. The LES has been of great importance in guiding a better understanding of the roles of plants in global carbon cycling, particularly in the face of climate change. Most LES research has focused on interspecific trait variation and correlations, under the assumption that trait relationships within species mirror those found among species (Vasseur et al. 2012), and that within-species variation does not alter the basic relationships of the LES (Wright et al. 2004). However, leaf traits that comprise the LES, such as leaf mass per area (LMA) and leaf nitrogen (N) concentration, have been shown to vary considerably at the within-species level (Siefert et al. 2015). While the LES provides a general framework for trait-trait coordination across wide environmental gradients, we know little about the degree to which the leaf trait relationships predicted by the LES hold at the intraspecific level (Niinemets 2015). On the one hand, if the selection pressures that drive the LES are universal and apply at the intraspecific as well as interspecific level, the key trait relationships of

the LES should be consistent across levels of organization. On the other hand, if trait variation within species is shaped by unique selection pressures and phenotypic plasticity, trait relationships within species may be decoupled from the LES.

Several recent studies have examined whether interspecific trait relationships that form the LES also hold between populations or individuals of the same species (Vasseur et al. 2012, Wright and Sutton-Grier 2012, Niinemets 2015). For example, Niinemets (2015) studied whether there was a within-species leaf economics spectrum, using *Quercus ilex*, a widely distributed species in the Mediterranean basin that exhibits substantial ITV in leaf traits across its range, as a model species. Although he found a general agreement between interspecific and intraspecific trait relationships (a species economics spectrum within the general spectrum), there was still high variation in the global patterns at the low-return end of the economics spectrum at which *Q. ilex* is located. In contrast, Wright and Sutton-Grier (2012), working with multiple species but at a finer spatial scale, found little support for a correspondence between global-scale interspecific LES trait relationships and local within-community intraspecific trait relationships. These studies evince that species-level difference in leaf traits may affect our ability to observe the "universal" correlations expected by the LES.

The leaf economics spectrum (LES) is a core concept in the quest for a general and mechanistic understanding of plant function and community assembly worldwide. Despite increasing recognition of the importance of ITV in plant communities, integration of ITV into the LES is incomplete. LES theory makes predictions about (1) how leaf traits vary across environmental gradients, and (2) how leaf traits co-vary with each other. Here, we are testing whether ITV patterns fit both sets of predictions, and what are the consequences at the community level. Thus, we asked whether patterns of intraspecific leaf trait variation of tree saplings in temperate rain forests fit key predictions of the LES, i.e., how within-species trait correlations scale up to interspecific or among-community correlations. For this, we first estimated the relative contributions of ITV and species turnover to shifts in community mean leaf trait values across environmental gradients, and asked (1) are intraspecific trait responses to the environment consistent among species? (2) What is the relative contribution of ITV vs. species turnover to shifts in community-weighted mean functional traits (CWMs)? Secondly, we assessed whether trait relationships predicted by the LES hold across levels of organization, i.e., intra-, interspecific and community. With this we were interested in knowing whether intraspecific leaf trait correlations are consistent among species and with interspecific correlations. In particular, we asked (3) Are intraspecific trait relationships consistent across species? (4) Are trait relationships consistent in direction and strength at the intraspecific, interspecific, and among-community levels? To address these questions, we focused on leaf traits (leaf mass per area [LMA], leaf area [LA], leaf nitrogen [LN] and phosphate [LP] concentrations) of saplings of woody species belonging to the temperate rainforest of southern Chile. We concentrated on three environmental gradients that are important drivers of community assembly in temperate rain forests: light, soil N and P availability.

## Methods

### Research site descriptions

In the temperate rainforest of southern Chile, we selected four second-growth forests for our study: (1) Exploradores (EXP, 46°29′ S, 73°12′ W, 75 m above sea level), where the forest is on moraine deposits of glacial erosion originating from the Exploradores Glacier; (2) Aiken Private Park (AIK, 45°27′ S, 72°45′ W, 40 m a.s.l); (3) Queulat National Park (QUE, 44°28′ S, 72°33′ W, 57 m a.s.l), where the forest is on landslide deposits; and (4) Katalapi Private Park (KAT, 41°31′ S, 72°45′ W, 59 m a.s.l), near the Cordillera de Quillaipe (Andes' foothills). In the Exploradores, Aiken and Queulat sites, the soil is a typical Andisol, with acid pH and low N and P availability (A. Fajardo, *unpublished data*). The soil in Katalapi is of sandy-loam texture with low P and N concentrations. All the sites were either remote in location or under conservation (National or privates reserves) and thus had a minimal degree of recent human disturbance and were similar in tree species composition. Common, dominant species in this type of forests are *Drimys winteri* (Winteraceae), evergreen *Nothofagus* spp. (Nothofagaceae), *Luma apiculata* and *Amomyrtus luma* (Myrtaceae), *Laureliopsis philippiana* (Atherospermataceae), *Embothrium coccineum* and *Lomatia ferruginea* (Proteaceae), *Caldcluvia paniculata* and *Weinmannia trichosperma* (Cunnoniaceae), and *Podocarpus nubigenus* (Podocarpaceae).

### Sampling, tissue collection and processing

Sampling was conducted in February and March 2014 and 2015. At each site, we detoured from hiking trails and established a first sampling point at least 10 m away from the trail. Then a list of 10–15 sampling point coordinates was created using a random walk design with a random start point, where bearing directions (constrained to 180°) and distances (constrained from 10 to 30 m) were randomly generated using a spread sheet program. In this way we took advantage of natural variation in light and soil nutrient availability, and we were able to cover a significant range of environments, including deep shade understories and large canopy gaps. On average, we established 60 sampling points per site (55–66 plots). At each sampling point, we set a 2 m² circular plot and counted all saplings contained in the plot. Saplings were considered all woody plants with a height of 30–100 cm. We identified all species within the plot and estimated their percent cover (by two observers) as follows: species cover class 1, <1% of the plot area; class 2, 1–5%; class 3, >5–15%; class 4, >15–25%; class 5, >25–50%; class 6, >50–75%; and class 6, >75% of the plot area.

To measure species' leaf traits, we collected leaves from the upper portion (no self-shaded leaves) of one or two sapling individuals of each species, restricting the tissue collection to foliage without browsing or other damage. We did not fully follow the sampling protocol recommended by Pérez-Harguindeguy et al. (2013) for measurement of plant functional traits, because we intentionally considered leaves

*Reports*

of saplings, in some occasions under shade. Leaves of each species were placed in plastic bags, labeled, and stored in a cooler for transportation. In the laboratory, leaves from a given species and plot were pooled, laid flat and photographed with a reference square of known area using a Nikon Coolpix 5000 digital camera (Nikon Corporation, Tokyo, Japan), and the total projected leaf area was calculated using SIGMAPROC image-processing software (Systat Software Inc., Richmond, California, USA). Leaf area was computed as the total foliar surface of a given species and plot divided by the number of leaves. All leaves were then dried in a forced-air stove (Memmert GmbH, Schwabach, Germany) at 70°C for 72 h and subsequently weighed. We computed leaf mass per area (LMA, $g/m^2$) as the oven-dried leaf mass divided by total foliar surface area. Leaf N concentrations were determined by placing 200 mg of dry, ground tissue samples in a combustion analyzer (LECO TruSpec® Micro CHN, Centro de Investigación en Ecosistemas de la Patagonia, Coyhaique, Chile). Leaf P was extracted from the tissue by combining 20 mg of dry leaf material in 1 mL of 2% v/v acetic acid, and digesting this mixture for 30 min before centrifuging it at $4,300 \times g$ (Fredeen et al. 1989). Leaf P concentrations were then determined following Murphy and Riley's procedure (1962). We were able to determine leaf N and P concentrations for Exploradores, Aiken and Katalapi sites only. Concentrations of N and P were expressed on a leaf dry mass (mg/g).

### Light and soil nutrient availability

To characterize the light environment of each sampling point, we took digital hemispherical photographs of the canopy from a height of ~50 cm above the center of each plot. We used a 7-mm Nikon f 7.4 fisheye lens (orthographic projection of 180° angle of view), mounted on a Nikon Coolpix 5000 digital camera (Nikon Corporation). Photographs were taken under cloudy sky conditions or late in the day to avoid direct exposure to sun. Photographs were also under-exposed by two stops to increase contrast between the sky and foliage. From these digital photographs we computed the Gap Light Index (GLI, Canham 1988), which is defined as the percentage of photosynthetically active radiation reaching the point where the photograph is taken. The GLI was computed for each plot using the Gap Light Analyzer (GLA ver. 2) software (Frazer et al. 2000).

We assessed the relative availability of soil inorganic N and P in all sites except Queulat as the relative availability of ammonium ($NH_4^+$), nitrate ($NO_3^-$) and phosphate ($PO_4^-$) ions adsorbed to mixed bed ionic resin capsules. In the center of each 2 $m^2$ plot, we placed a polyester resin capsule containing 1 g dry weight of mixed bed ionic resins (PST1 capsule; Unibest, Bozeman, Montana, USA). Capsules were inserted at a 45° angle, with a final depth of 5 cm below the soil surface, which in all stand types was the upper mineral soil horizon. Capsules were tethered to a reference plastic stake using nylon fishing line in order to facilitate retrieval. Capsules were placed in the soil in March 2014 and removed in March 2015 in all sites. Ions were extracted from resins using three consecutive rinsing of 10 mL 1 mol/L KCl (30 mL total). The concentrations of $NH_4^+$, $NO_3^-$ and $PO_4^-$ from these extracts were measured using standard colorimetric techniques on an auto-analyzer (Instituto de Investigaciones Agropecuarias, Santiago, Chile). We calculated soil N availability as the sum of $NH_4^+$ and $NO_3$ concentrations in each plot.

### Data analysis

Trait values, GLI and soil N availability concentrations were log-transformed in all analyses.

*Leaf ITV-environment relationships and variance partitioning.*—To test whether ITV-environment relationships were consistent among species, for each trait-environment combination we fit a linear mixed model with the trait as the response variable, the environmental variable as a fixed effect, site as a random effect, and a random intercept and slope of the environmental effect within species. We tested significance of fixed environmental effects and random among-species variation in the slopes of environmental effects using likelihood ratio tests.

To quantify the relative contributions of species turnover and ITV to community-level responses of leaf traits to light and soil N availability, we partitioned the among-plot variation in leaf trait values explained by GLI and soil N into species turnover and ITV components following the approach of Lepš et al. (2011). Briefly, we calculated plot-weighted mean (CWM) leaf trait values for all sites as the abundance-weighted average of species mean trait values, using either species trait values measured within a particular plot ("specific" CWMs) or averaged across all plots in which a species was found ("fixed" CWMs). Among-plot variation in specific CWMs reflects the effects of both species turnover and ITV, whereas variation in fixed CWMs reflects only species turnover effects. For each plot, we calculated the "intraspecific CWM", representing the effect of intraspecific trait variability, as the difference between the specific and fixed CWMs. We then ran separate linear models with specific, fixed, or intraspecific CWMs as the response variable and either GLI or soil N as the predictor and extracted the sum of squares (SS) explained by GLI or soil N from each model ($SS_{specific}$, $SS_{fixed}$, and $SS_{intra}$, respectively). $SS_{specific}$ represents the total among-plot variation in leaf trait explained by GLI or soil N, and $SS_{fixed}$ and $SS_{intra}$ represent the contributions of species turnover and ITV, respectively. Finally, we calculated the covariation component ($SS_{cov}$) as the difference between $SS_{specific}$ and $SS_{fixed}$ plus $SS_{intra}$. Positive covariation indicates that species turnover and intraspecific variation are responding to the same environmental factors, whereas negative covariance indicates opposing effects of turnover and ITV. The trait variance partitioning analysis was conducted using the "cati" package (Taudiere and Violle 2016) in R version 3.3.0 (R Development Core Team 2016).

*Leaf trait relationships.*—To assess whether the leaf economics spectrum held across levels of organization, we quantified bivariate leaf trait relationships at intraspecific, interspecific, and community levels using standardized major axis (SMA) regression. We quantified trait relationships at the intraspecific level by fitting SMA regressions for each species using plot-specific species mean trait values. We

obtained adjusted *P*-values for individual species' intraspecific slopes using the false discovery rate procedure (Benjamini and Hochberg 1995). For each bivariate trait relationship, we estimated an overall mean intraspecific slope and tested whether slopes differed among species by conducting a random effects inverse variance-weighted meta-analysis of intraspecific slopes (Viechtbauer 2010). This method summarizes intraspecific slopes across species by using the inverse variances of the individual species' slopes as weights. We assessed interspecific and community-level trait relationships by fitting SMA regressions using study-wide species mean trait values and CWM trait values, respectively.

<center>RESULTS</center>

<center>*Leaf trait responses to environmental gradients*</center>

Across all species and sites, leaf area was negatively correlated with light availability ($P = 0.008$), whereas LMA was positively correlated with light availability ($P < 0.001$). Leaf N was positively correlated with soil N availability ($P < 0.001$); and leaf P was positively correlated with soil N ($P < 0.001$) and P availability ($P = 0.019$; Appendix S1: Table S1). Slopes of trait-environment relationships did not vary significantly among species, except in the cases of leaf area–light availability ($P < 0.001$) and leaf N–soil P availability ($P = 0.04$), indicating that intraspecific trait responses to the environment were relatively consistent among species.

<center>*Relative contribution of species turnover and intraspecific variation*</center>

The relative contributions of species turnover and ITV to shifts in community mean trait values in temperate rainforests differed according to the leaf trait and environmental factor (light or soil N availability). In terms of total among-plot trait variance, we found that the importance of ITV was higher than species turnover for LMA (48.53% of total variance) and leaf P concentrations (72.78%, Fig. 1; Appendix S1: Table S2), whereas species turnover showed higher variation than ITV in leaf area (67.01% of total variance) and leaf N concentrations (58.58%).

Across all plots, we found considerable variation in the relative extent of ITV among traits and environmental gradients. In general, leaf area and LMA tended to respond more strongly to the light availability gradient than to the soil nutrient gradients. Leaf area variation across the light availability gradient was almost exclusively due to species turnover (16.2% of explained variation, Fig. 1; Appendix S1: Fig. S1). Intraspecific responses of leaf area to light were rather weak (0.4%). There was also a weak positive covariation between species turnover and ITV (5.08% explained variation), indicating that both intraspecific and species turnover are responding similarly to light availability (i.e., plots dominated by species with large mean leaf area also contained individuals with large leaf area for their species). In contrast, the community-level response of LMA to light was primarily driven by ITV (26.7%), whereas the contribution of species turnover was relatively weak (8.96%). There

was also a strong positive covariation value between ITV and species turnover (30.97%). Leaf N and P concentrations did not respond significantly to light availability, but where significantly correlated with soil N and P availabilities, respectively (Fig. 1). The response of leaf N concentrations to soil N availability was mostly due to ITV (8.84% explained variation) and covariation between ITV and species turnover (9.58%), while species turnover per se made a minor contribution (2.53%). The response of leaf P concentrations to soil P availability was also mostly due to ITV (12.09% explained variation) and covariation between ITV and species turnover (7.02%), with species turnover having a low contribution (1.45%, Fig. 1; Appendix S1: Fig. S1).

<center>*Leaf trait relationships across levels of organization*</center>

Slopes of bivariate trait relationships were consistent in direction at the intraspecific, interspecific, and community-levels, indicating that the leaf economic spectrum generally held across levels of organization (Appendix S1: Table S2, Fig. S2). While the direction of the trait bivariate relationships was consistent across levels, the strength of leaf trait relationships (steepness of slopes) was generally greatest at the community level and weakest at the intraspecific level (Fig. 2). Nonetheless, we found a strong negative intraspecific correlation (slope significantly different from zero) between leaf N and LMA ($b = -0.30$, $P < 0.001$, Fig. 2; Appendix S1: Table S2), in accordance with the LES. Although marginal, we also found a negative intraspecific relationship between leaf area and LMA ($b = -0.24$, $P = 0.07$, Table 1, Fig. 2). Although the relationship between leaf area and leaf N concentration was positive and strong across species and communities, it was not significant at the intraspecific level; a similar result was found for the leaf area–leaf P concentration relationship. The relationship between leaf N and P concentrations was also positive and significant at all organization levels, including within species, consistent with the LES.

Slopes of intraspecific trait-trait relationships were generally consistent among species for LMA–leaf N (test of null hypothesis that all species have same slope, $P = 0.55$) and relatively consistent for leaf N–leaf P ($P = 0.10$). For the remaining bivariate trait relationships, the strength and even direction of intraspecific slopes varied strongly among species ($P < 0.001$), contributing to the non-significant overall intraspecific relationships for these traits when aggregated across species.

<center>DISCUSSION</center>

<center>*Trait variance partitioning*</center>

We found that ITV accounted for a large proportion of community-level variation in leaf traits and played an important role in driving community-level shifts in leaf traits across environmental gradients predicted by the LES (Fig. 1). In particular, shifts in community mean LMA and leaf N and P concentrations along resource availability gradients were primarily driven by ITV. These results are consistent with previous studies demonstrating the large role of
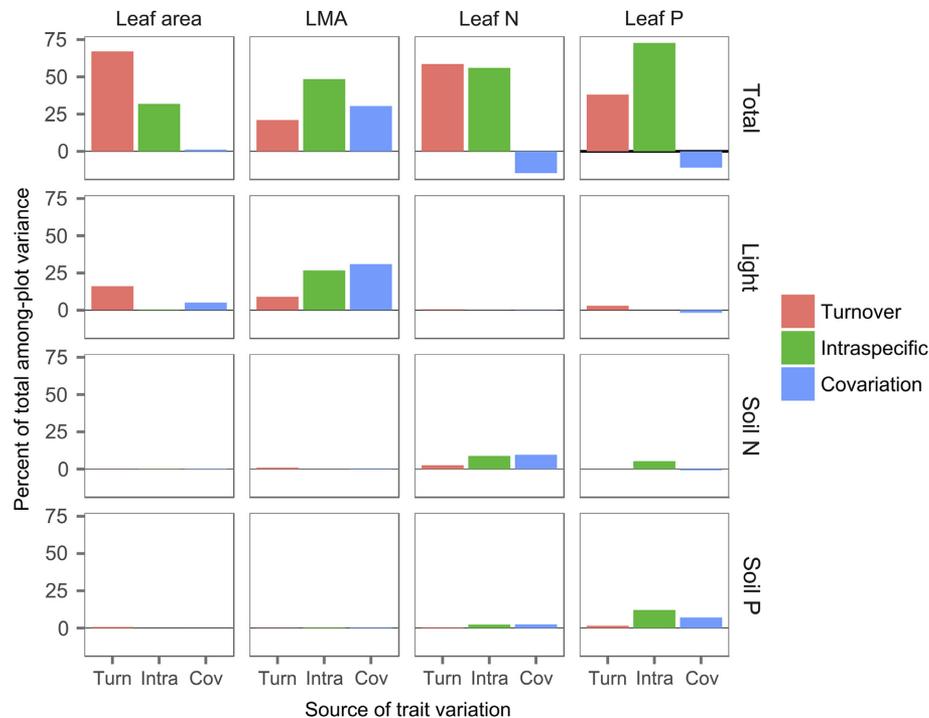
FIG. 1. Variance partitioning of community trait responses to environmental gradients in temperate rainforest communities in southern Chile. The total among-plot variance in leaf trait values explained by gap light index (gli), soil nitrogen, and phosphate availability was partitioned into species turnover, intraspecific trait variation (ITV), and covariation components. Variance partitioning was conducted for four leaf traits: leaf area, leaf mass per area (LMA), leaf nitrogen (leaf N), and phosphate (leaf P) concentrations.
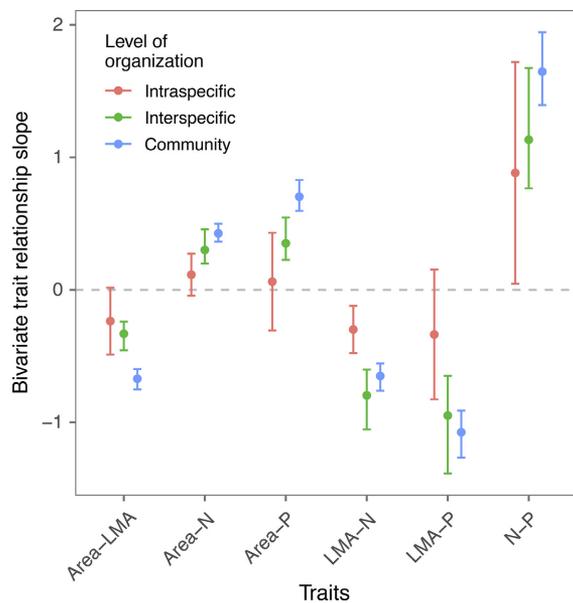


FIG. 2. Leaf trait–trait relationships' slopes at different levels of organization for saplings of woody species in temperate rainforests in southern Chile. The levels of organization are within–species (intraspecific), among–species (interspecific) and among–communities (community). The leaf traits are leaf area (Area), leaf mass per area (LMA), leaf nitrogen (N) and phosphate (P) concentrations.

ITV at the community level (Albert et al. 2010, Violle et al. 2012, Siefert et al. 2015), particularly for trait related to the leaf economics spectrum. LMA in particular has

continuously been found to be a leaf functional trait with relatively high ITV (Fajardo and Piper 2011, Siefert et al. 2015), even at the within-community level. These results highlight the need for ecologists to include ITV in their approaches to plant community ecology, especially when dealing with leaf economics traits. The identification of traits that consistently have large ITV (e.g., LMA) and general trends in how ITV varies among species are important steps toward simplifying the inclusion of ITV in community ecology studies.

### The LES at different organization levels

Most trait relationships varied significantly among species, suggesting idiosyncrasies in the LES at the intraspecific level. Why were the strong bivariate trait correlations found across species and large spatial scales not found at the intraspecific level? We propose several potential explanations. First, the LES is built on interspecific trait correlations among a large number of species, where the general tradeoff trends found are made up by extreme examples with a high variation of the values of one trait given another trait (Grubb 2016). Studies conducted within narrower subsets of the functional space within the global spectrum of plant form and function (e.g., within species) may not capture such strong trait combination trends. Consequently, our data set likely included just a narrow range of trait values when compared to global trait collections. Second, the slopes of trait relationships varied strongly among species for some trait combinations (Appendix S1: Fig. S2), leading to weak overall intraspecific trends when aggregated across

species. Variation in trait relationships could result from many factors, including differing levels of genetic or plastic variability or differing trait responses to environmental gradients and other selective agents among species (Violle et al. 2012). Moreover, multivariate trait coordination itself may be under selection and subject to genetic constraints, with the result that bivariate trait correlations are influenced by a species' unique evolutionary history. Our results suggest that most species do not deviate strongly from the trait relationships expected by the LES, indicating constraints on trait values at the intraspecific level, but there is still room for considerable idiosyncrasy in trait relationships across species.

One interesting exception and novel result of our study was that the negative leaf area–LMA and LMA–leaf N relationships were found across all organizational levels, including the intraspecific level. This result is interesting given that we worked with saplings, with many of the individuals under limited light or soil nutrient conditions; functional trait protocols (Pérez-Harguindeguy et al. 2013) recommend sampling individuals with leaves fully exposed to light in order to capture optimal performance. In our study, the negative leaf area–LMA and LMA–leaf N relationships emerged as a strong trend not only at the intraspecific level but also in early stages of plant development. This result has important consequences for plant resource economics across ontogeny and for trait predictions across broad environmental gradients and organizational levels. The incorporation of functional traits of the regeneration phases of plant communities has been a neglected aspect in trait-based ecology in general and the LES in particular. Incorporation of trait-trait and trait-environment relationships during the regeneration stage would enhance the utility of models of species' abundances, distributions and responses to environmental change (Larson and Funk 2016).

From a physiological perspective, we suggest that a negative LMA–leaf N relationship at the intraspecific level may be the result of a negative LMA–light availability relationship. For a given leaf N concentration, individuals growing under limited light conditions have lower LMA than individuals growing in full-light conditions. Thus, individuals with higher LMA found at full-light conditions will have relatively less N than conspecifics growing under shade with lower LMA. This pattern, which is contrary to what is commonly found at the interspecific level in tropical and northern hemisphere temperate forests (Walters and Reich 1999, Poorter et al. 2008), was also found across species in the temperate rainforest of southern Chile (Fajardo and Siefert 2016).

In conclusion, although not all trait combinations predicted by the LES and previously demonstrated at the interspecific level were mirrored within species, the LMA–leaf N relationship did hold at the intraspecific level and also when saplings were considered. These results suggest that some predictions of the leaf economics spectrum hold across levels of biological organization and plant developmental stages.

### Literature Cited

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

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B 57:289–300.

Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. Ecology 69:1634–1638.

Fajardo, A., and F. I. Piper. 2011. Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in southern Chile. New Phytologist 189:259–271.

Fajardo, A., and A. Siefert. 2016. Temperate rain forest species partition fine-scale gradients in light availability based on their leaf mass per area (LMA). Annals of Botany 118:1307–1315.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 2000. Gap Light Analyzer (GLA), version 2.0: image processing software to analyze true-colour, hemispherical canopy photographs. Bulletin of the Ecological Society of America 81:191–197.

Fredeen, A. L., I. M. Rao, and N. Terry. 1989. Influence of phosphorus nutrition on growth and carbon partitioning in *Glycine max*. Plant Physiology 89:225–230.

Grubb, P. J. 2016. Trade-offs in interspecific comparisons in plant ecology and how plants overcome proposed constraints. Plant Ecology and Diversity 9:3–33.

Larson, J. E., and J. L. Funk. 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. Journal of Ecology 104:1284–1298.

Lepš, J., F. De Bello, P. Šmilauer, and J. Doležal. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. Ecography 34:856–863.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31–36.

Niinemets, Ü. 2015. Is there a species spectrum within the worldwide leaf economics spectrum? Major variations in leaf functional traits in the Mediterranean sclerophyll *Quercus ilex*. New Phytologist 205:79–96.

Pérez-Harguindeguy, N., et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61:167–234.

Poorter, L., et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. Ecology 89:1908–1920.

R Development Core Team. 2016. R: a language and environment for statistical computing. Version, 3.3.0. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Siefert, A., et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters 18:1406–1419.

Taudiere, A., and C. Violle. 2016. cati: an R package using functional traits to detect and quantify multi-level community assembly processes. Ecography 39:699–708.

Vasseur, F., C. Violle, B. J. Enquist, C. Granier, and D. Vile. 2012. A common genetic basis to the origin of the leaf economics

*Reports*

spectrum and metabolic scaling allometry. Ecology Letters 15:1149–1157.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36:1–48.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology and Evolution 27:244–252.

Walters, M. B., and P. B. Reich. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: Do winter deciduous and broad-leaved evergreen species differ? New Phytologist 143:143–154.

Wright, J. P., and A. Sutton-Grier. 2012. Does the leaf economic spectrum hold within local species pools across varying environmental conditions? Functional Ecology 26:1390–1398.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

## SUPPORTING INFORMATION

*Reports*