

## Research

### The interplay among intraspecific leaf trait variation, niche breadth and species abundance along light and soil nutrient gradients

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It is assumed that widespread, generalist species have high phenotypic variation, but we know little about how intraspecific trait variation (ITV) relates to species abundance and niche breadth. In the temperate rainforest of southern Chile, we hypothesized that species with wide niche breadth would exhibit 1) high among-plot ITV, 2) a strong relationship between trait values and the environment, and 3) a close fit between traits and local environment trait optima. We measured leaf functional traits (leaf area, LMA, leaf N and P concentrations) of saplings in woody species, and compared the relative abundance of each species with its niche breadth, measured as the range of light, soil N and P availability. We used the slope of the linear regression of species' trait–environment relationships to assess the strength and direction of these relationships, and measured the degree to which species' trait values track the environmental optimum across plots. In some cases, species having wide niche breadth had high ITV in leaf N and also matched traits (LMA and leaf P) to local optima along the light gradient; they also had high ITV in general and matched leaf P to local optima along the soil P gradient. The relationship between species with wide niche breadth and the strength of intraspecific trait–environment relationships was generally weak and varied depending on the niche dimension and trait in question. Species varied considerably in the strength of trait–environment relationships and total magnitude of ITV, and this variation was not generally strongly related to species abundances or niche breadth patterns. In conclusion, trait variation at the community level is not driven by a few abundant, widely distributed species, but depends on the aggregate trait responses of both abundant and rare species. This makes it difficult to scale individual species trait responses up to the community level.

Keywords: community weighted mean trait value, temperate rainforests, trait–environment relationships, Patagonia

## Introduction

Variation in community-weighted trait means along environmental gradients is the result of species turnover and intraspecific trait variation (ITV). A number of studies have demonstrated that ITV is an ecologically important source of trait variation in plant communities, and that incorporating ITV in trait-based research can improve our understanding of plant community assembly (Albert et al. 2010, Violle et al. 2012, Siefert et al. 2015, Funk et al. 2017). ITV will most likely have a strong influence on community-level functional responses to the environment if intraspecific trait responses are 1) consistent in direction among species, and/or 2) strongest in the dominant (i.e. abundant and widely distributed) species within a community (Cornwell and Ackerly 2009, Funk et al. 2017). Previous studies have found that the magnitude of ITV and the strength and sometimes direction of trait–environment relationships can vary strongly among species (Albert et al. 2010, Kichenin et al. 2013), but whether and how patterns of individual species' ITV relate to species abundances and distributions along environmental gradients remains poorly understood.

It seems intuitive to think that species' niche breadth correlates positively with ITV (Darwin 1859, Burns 2004, Violle and Jiang 2009, Sides et al. 2014); that is, a greater intraspecific variation will translate into a greater ability of species to prevail in a wider range of environments. If high ITV allows generalist species to match their traits to different local environmental conditions and thus achieve a good fit of their traits to the environment (Pohlman et al. 2005, Muscarella and Uriarte 2016), the extent of ITV and the strength of trait–environment correlations within species should be positively related to species' niche breadth and potentially to regional species abundance. Despite the appealing simplicity of this notion, the studies that have tested whether ITV is positively related to niche breadth have not been conclusive. In a study of 12 salt marsh grass species, Richards et al. (2005) found a weak positive relationship between species' phenotypic variation and niche breadth along a composite environmental axis. Sides et al. (2014) did find a positive relationship between specific leaf area (SLA) intraspecific variation of 21 species with species' local elevational ranges. Additional indirect evidence for a positive relationship between ITV and niche breadth comes from studies showing high plasticity in widely distributed invasive species (Richards et al. 2006, Funk et al. 2008), a tight relationship between ITV and habitat suitability in alpine flora (Thuiller et al. 2010), and in competitively dominant compared to subordinate species (Ashton et al. 2010, Grassein et al. 2010).

Another aspect involving ITV that is still poorly understood is the relationship between ITV and species abundance. Again, studies that have examined this relationship have produced inconsistent results. For instance, in an experiment with alpine forbs, Ashton et al. (2010) found that competitively dominant, abundant species had high plasticity (high ITV) in resource acquisition, which they termed dominant plasticity, whereas competitively inferior, rare

species were not highly plastic. Similarly, Lajoie and Vellend (2015) found that ITV in SLA of understory herbaceous species was high in dominant species and low in rare species. However, Umaña et al. (2015), working with tree seedlings in tropical forest communities, found that in homogeneous environments abundant species exhibited low ITV, which they attributed to convergence of traits on the optimum value in the given environment, while rare species exhibited high ITV because they had trait values not attuned to the environment. When comparing, experimentally, pairs of widespread and narrowly distributed *Acacia* species in eastern Australia, Pohlman et al. (2005) found that the relationship between species range distributions and trait variation was both context- and taxon-specific. The generality of the relationship between ITV, local abundance and ecological niche breadth therefore remains unclear and may depend on the spatial scale and environmental gradient in question. Overall, understanding relationships between species' abundance, niche breadth and ITV could have important consequences for predicting community responses to local or global environmental changes and hence give valuable insights into the mechanisms that control local functional diversity.

In this study, we explored the relationships between relative abundance, niche breadth and ITV of saplings belonging to woody species in the temperate rainforest of southern Chile. In particular, our expectations were that species with high abundance and wide niche breadth would have 1) high among-site ITV (in accordance with Burns 2004, Pohlman et al. 2005, Ashton et al. 2010, Sides et al. 2014, Lajoie and Vellend 2015), 2) strong relationships between trait values and the environment, and 3) a close fit between traits and local environment trait optima, represented by the community-weighted mean (CWM) trait values – plot-level trait values weighted by species abundance. The CWM–optimality hypothesis predicts that fitness is highest in locations where species' trait values match the local CWM values of such traits (Laughlin et al. 2011, Shipley et al. 2011, Muscarella and Uriarte 2016). If this is the case, and if species' ITV is adaptive, variation in species' trait values among sites should 'track' variation in CWM values, allowing species to maximize their fitness by having trait values close to the local optima. To test these hypotheses, we examined species' niche breadth along three environmental gradients that are important drivers of community assembly in temperate rainforests: light, soil N and soil P availability. The partitioning of light and soil nutrient availability gradients encountered in the early phases of a plant's life cycle is known to play a central role in coexistence of woody species (Grubb 1977, Poorter 2007, Fajardo and Siefert 2016). To relate patterns of ITV to species' niche breadth along these gradients, we focused on four leaf traits – leaf area ( $\text{cm}^2$ ), leaf mass per area (LMA,  $\text{g m}^{-2}$ ), leaf nitrogen (N) and phosphorus (P,  $\text{mg g}^{-1}$ ) concentrations. These traits are intimately related to light and soil nutrient availability – and therefore carbon investment and ultimately carbon economy (Wright et al. 2004, Fajardo and Siefert 2018) – corresponding to different plant strategies of resource acquisition and utilization (Poorter et al.

2009). Thus, trait–environment relationships can be interpreted in terms of physiological tradeoffs related to resource availability.

## Methods

### Research site descriptions

Temperate rainforests in southern Chile are characterized by a cold-temperate and super-humid climate, with mean annual temperature of  $\sim 10^{\circ}\text{C}$  and annual precipitation of 2500 mm or more, regularly distributed throughout the year (Luebert and Plissock 2006). Commonly, these forests are dominated by shade-intolerant *Nothofagus* species, which maintain dominance by following either large-scale disturbance (e.g. mass movements by earthquakes, volcanism and windblows) or gap-phase (i.e. tree fall canopy gaps) dynamics (Veblen 1985). Other less shade-intolerant species dominate the understory and if there are no major disturbances can reach with time the overstory. These late-successional species include: *Drimys winteri* (Winteraceae), *Luma apiculata* and *Amomyrtus luma* (Myrtaceae), *Laureliopsis philippiana* (Atherospermataceae), *Embothrium coccineum* and *Lomatia ferruginea* (Proteaceae), *Caldecluvia paniculata* and *Weinmannia trichosperma* (Cunnoniaceae), and *Podocarpus nubigenus* (Podocarpaceae). We selected four second-growth, temperate rainforests for our study (Fig. 1) (Fajardo and Siefert 2016, 2018). The first site was Exploradores (EXP,  $46^{\circ}29'S$ ,  $73^{\circ}12'W$ , 75 m above sea level), where the forest is on moraine deposits of glacial erosion originating from the Exploradores Glacier (Aniya et al. 2011). The second site was located in the Aiken Private Park (AIK,  $45^{\circ}27'S$ ,  $72^{\circ}45'W$ , 40 m a.s.l.). The third site was located in the Queulat National Park (QUE,  $44^{\circ}28'S$ ,  $72^{\circ}33'W$ , 57 m a.s.l.), where the forest is on landslide deposits. Finally, our fourth site was located in the Katalapi Private Park (KAT,  $41^{\circ}31'S$ ,  $72^{\circ}45'W$ , 59 m a.s.l.), near the Cordillera de Quillaiepe (Andes' foothills). In the Exploradores, Aiken and Queulat sites, the soil is a typical Andisol, with acid pH and low N and P availability (Supplementary material Appendix 1 Table A1). The soil in Katalapi is of sandy-loam texture with low P and N concentrations. These sites were either remote in location or under conservation (national or private reserves) and thus had a minimal degree of recent human disturbance and were similar in tree species composition.

### 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 60 sampling point coordinates was created using a random walk design with a random start point, where bearing directions (constrained to  $180^{\circ}$ ) and distances (constrained from 10 to 30 m) were randomly generated

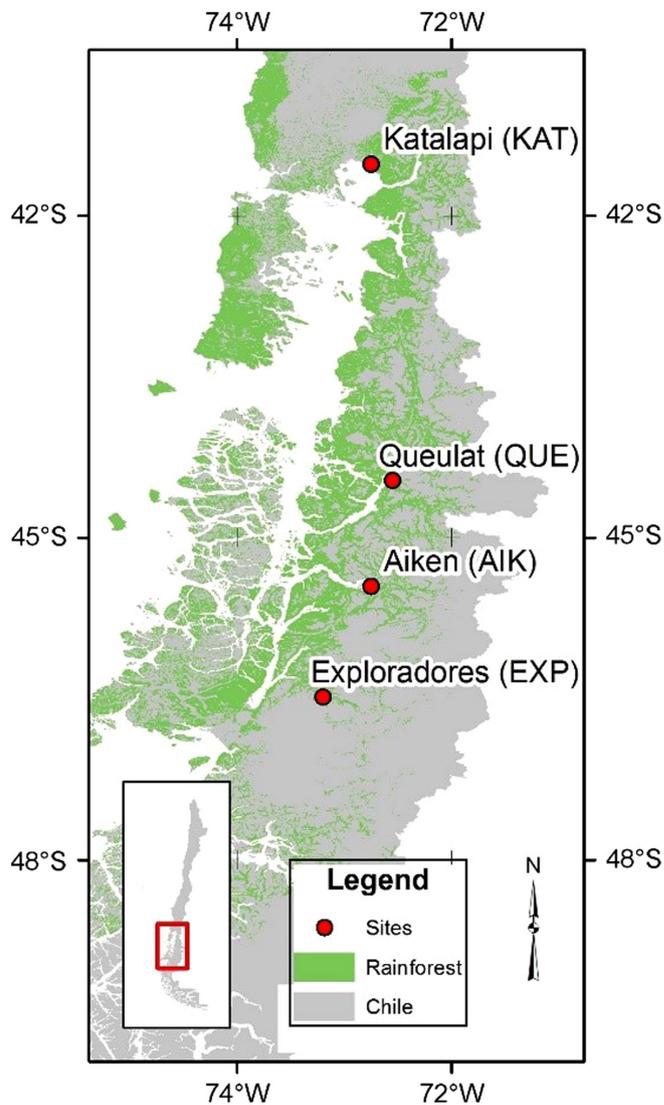


Figure 1. Map of southern Chile showing the locations where the study was conducted.

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  $2\text{-m}^2$  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 at each plot, restricting the tissue collection to foliage without browsing or other damage.

We departed from the sampling protocol recommended by Pérez-Harguindeguy et al. (2013) for measurement of plant functional traits, because in many cases we intentionally considered leaves of saplings under shade. Leaves of each species were placed in plastic bags, where they were slightly sprayed with water, 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 digital camera, and the total projected leaf area was calculated using SIGMAPROC image-processing software. Leaf area was computed as the total foliar surface (including petioles) of a given species and plot divided by the number of leaves. All leaves were then dried in a forced-air stove at 70°C for 72 h and subsequently weighed. We computed leaf mass per area (LMA,  $\text{g m}^{-2}$ ) 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. We were able to determine leaf N and P concentrations for Exploradores, Aiken and Katalapi sites only. For leaf P concentration determination, P was extracted from leaves by combining 20 mg of dry leaf material in 1 ml of 2% acetic acid, and digesting this mixture for 30 min before centrifuging it at 6000 rpm (Fredeen et al. 1989). Then, final leaf P concentrations were determined following Murphy and Riley's procedure (1962), which, briefly, consists of the formation of an antimony–phosphomolybdate complex and its subsequent reduction to phosphomolybdenum blue, a bluish–purple colour complex. The absorbance of this complex is read at 880 nm and converted into a phosphate concentration using a calibration curve of potassium dihydrogen phosphate. Concentrations of N and P were expressed per unit leaf dry mass ( $\text{mg g}^{-1}$ ).

### 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 centre of each plot. We used a 7-mm fisheye lens (orthographic projection of 180° angle of view), mounted on a digital camera. Photographs were taken under cloudy sky conditions or late in the day to avoid direct exposure to sun. Photographs were also underexposed by two stops (either by increasing the diaphragm aperture or by decreasing shoot speed two times) 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 ( $\text{NH}_4^+$ ), nitrate ( $\text{NO}_3^-$ ) and phosphate ( $\text{PO}_4^-$ ) ions adsorbed to mixed bed ionic resin capsules. In the centre of each 2-m<sup>2</sup> plot, we placed a polyester resin capsule

containing 1 g dry weight of mixed bed ionic resins (PST1 capsule). Resin capsules were inserted at a 45° angle, with a final depth of 10 cm beneath the surface of the humus. They were tethered to a reference stake using nylon fishing line in order to facilitate retrieval. Resin 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 rinsings of 10 ml 1 M KCl (30 ml total) (Gundale et al. 2011). The concentrations of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{PO}_4^-$  from these extracts were measured using standard colorimetric techniques on an auto-analyzer. We calculated soil N availability as the sum of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations in each plot. We preferred to use resin capsules instead of traditional soil samples, because resin adsorption of N and P compounds represent the accumulation (one year) of bioavailable substrates for both plants and microbes, as the resins take up and hold onto ions for long periods of time while minimizing their further transformations (Binkley and Matson 1983, Friedel et al. 2000).

### Data analysis

Given that all sites were similar in terms of climate and species composition, we pooled data from all four sites to use in the analysis. We conducted variance partitioning analysis using random-effects models to examine the distribution of variance in environmental variables within and among sites. We found that 88% of variance in GLI, 81% of variance in soil N and 62% of variance in soil P occurred within sites (i.e. among plots), supporting our decision to pool sites. Trait values, GLI, soil N and P availability concentrations were log-transformed (natural log) in all analyses. Analyses were conducted in R ver. 3.3.0 (<[www.r-project.org](http://www.r-project.org)>).

We calculated the relative abundance of each species as the sum of its cover in all plots divided by the total cover of all species. We calculated species' niche breadths with respect to light and soil nutrient availability gradients as the range of GLI, soil N and P values, respectively, of plots in which a given species occurred, divided by the total range of values across all sites. To quantify ITV, we calculated the among-plot coefficient of variation (CV) in species' values of each trait.

To test our first hypothesis, i.e. species with high abundance and wide niche breadth will have a high among-site ITV, we made comparisons of niche breadth and ITV for species using a nested niche approach. One problem that may occur when comparing niche breadth and ITV for species with very different abundances across environmental gradients is that contrasting-abundance species may not be sampled from the same range of environments; i.e. comparing common species from a large number of plots and hence a wide range of environments, and rare species from fewer plots and hence fewer environments. In order to avoid this potential sampling artifact, we identified all pairs of species with nested niches along each gradient, i.e. the range of narrow-niche species is completely within the range of the wide-niche species. For each species pair, we calculated the difference in niche breadth and the difference in ITV,

measured as the among-plot trait variance. In measuring ITV, we only included plots within the range of the narrow-niche species to ensure that ITV is compared across a common range of environments. We tested the relationship between the difference in niche breadth and the difference in ITV across species pairs using a permutation test to account for non-independence in the data (each species could appear in multiple pairs). A positive relationship indicates that species with wider niche breadth have larger ITV across a common range of environments, thus giving support to our hypothesis.

To test our second hypothesis that there is a strong relationship between trait values and the environment in species with wide niche breadths, we measured the strength and direction of species' trait–environment relationships for each trait–environment combination as the slope of the linear regression of species' trait values on environmental values across plots. We expected that species with wider niche breadths would have stronger relationships between trait values and the environment (i.e. slopes of trait–environment relationships farther from zero). Because of large differences in sample size among species, we used rarefaction to obtain comparable estimates of ITV and trait–environment slopes among species. For species that occurred in 10 or more plots (six or more plots for analysis of leaf N and P, due to lower sample sizes), we randomly selected without replacement 10 plots and calculated the trait variance and slopes of trait–environment relationships using those plots. We repeated the procedure 999 times to calculate mean values and 95% confidence intervals for the variables of interest. By using the slope we are measuring the amount of trait change (ITV) per unit change in the environment. It therefore tests whether generalist species have a greater trait change over a common environmental gradient.

To quantify the fit between species' trait values and local environmental optima, we calculated  $\Delta\text{CWM}_{\text{tip}}$  as the absolute difference between the value of trait  $t$  of species  $i$  in plot  $p$  and the CWM value of trait  $t$  in plot  $p$ . The CWM corresponds to the plot-level trait values weighted by species abundance. To avoid circularity, when calculating  $\Delta\text{CWM}_{\text{tip}}$  values for each species, we excluded that species trait values in the CWM calculations (Muscarella and Uriarte 2016). We averaged  $\Delta\text{CWM}_{\text{tip}}$  values across plots to obtain a mean  $\Delta\text{CWM}$  for each species and trait. A low value of  $\Delta\text{CWM}$  indicates a close fit between species' trait values and local optima, and high values indicate a poor fit. We assessed whether species tracked environmental optima better or worse than expected by chance (i.e. if species' traits varied randomly among sites) using a null model in which we randomized species' trait values among sites and calculated the degree of trait fitting using the randomized data ( $\Delta\text{CWM}_{\text{null}}$ ). We repeated the randomization 999 times and calculated the degree of trait–CWM matching each time to obtain a distribution of  $\Delta\text{CWM}_{\text{null}}$  values. We assessed the degree of trait tracking (trait.track) as the difference

between the observed average  $\Delta\text{CWM}$  and the mean of the null distribution of  $\Delta\text{CWM}_{\text{null}}$  values for each species and trait. A negative value of trait.track indicates that the species tracks the local trait optimum more closely than expected by chance across sites.

We assessed whether species' relative abundance and niche breadth were related to ITV, slopes of trait–environment relationships, and degree of trait tracking using linear regressions. For each relationship, we fitted a simple linear model and a quadratic model and compared goodness of fit using a likelihood-ratio test.

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.tr3dq8c>> (Fajardo and Siefert 2019).

## Results

### Hypothesis 1. Species with high abundance and wide niche breadth have high among-plot ITV

In the four temperate rainforest sites, we found a total of 36 woody species, of which 30 occurred in at least 10 plots (Supplementary material Appendix 1 Table A1). In general, we found positive and significant relationships between species abundance and niche breadth along the gradients of light (quadratic model:  $R^2=0.48$ ,  $p<0.001$ ), soil N (quadratic model:  $R^2=0.33$ ,  $p=0.001$ ), and P (quadratic model:  $R^2=0.55$ ,  $p<0.001$ ) availability indicating that more abundant species occurred in a wider range of resource environments (Fig. 2).

We found mixed support for our hypothesis that species with wide niche breadth should have high among-plot ITV. When comparing the extent of among-plot ITV across a common set of environments of species pairs with nested environmental ranges, we found significant positive relationships between ITV and niche breadth for three of the twelve trait–environment combinations (four traits  $\times$  three environmental gradients) that we examined. Specifically, species with wider niche breadth along the light availability gradient had significantly higher ITV in leaf N ( $R^2=0.28$ ,  $p=0.005$ ), and species with wider niche breadth along the soil P gradient had greater ITV in leaf N ( $R^2=0.24$ ,  $p=0.025$ ) and leaf P ( $R^2=0.15$ ,  $p=0.073$ ) concentrations, compared to narrower niche species. In contrast, we found a negative relationship between ITV and niche breadth for one trait–gradient combination. Specifically, species with narrower niche breadth along the light availability gradient had marginally higher ITV in leaf area ( $R^2=0.15$ ,  $p=0.073$ ) compared to species with wider niches, contrary to our initial hypothesis. We did not find a significant difference in ITV of any trait between species with wider vs. narrower niche breadths along the soil N gradient (Fig. 3).

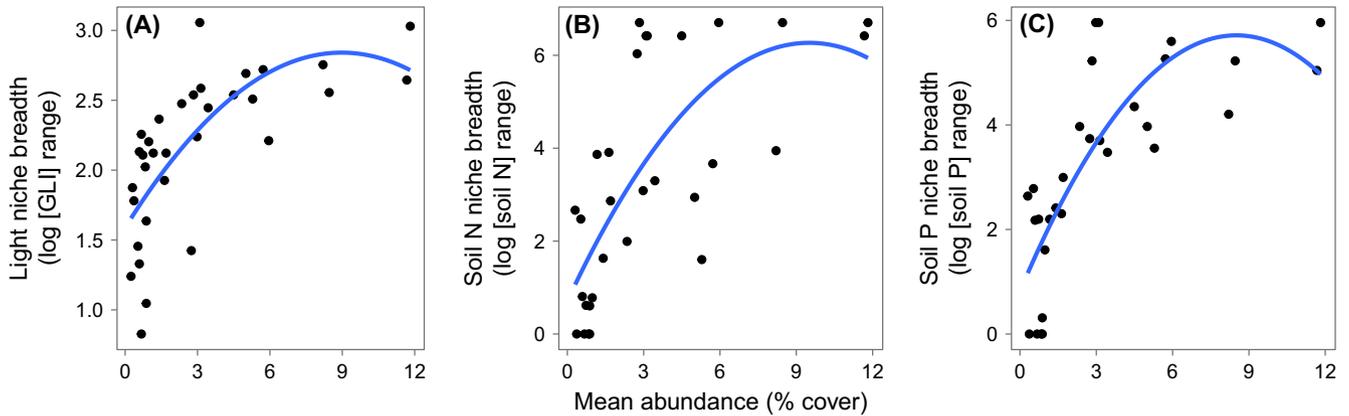


Figure 2. Relationship between relative abundance and niche breadth of temperate rainforest tree species in southern Chile. Relative niche breadth along light (GLI) (A), soil nitrogen (N) (B), and phosphorus (P) availability (C) gradients is expressed as the range of environmental values of plots in which a species occurred, divided by the total range of values measured across all plots. Regression lines are shown for significant ( $p < 0.05$ ) quadratic relationships (best model determined by likelihood ratio test).

### Hypothesis 2. Species with wide niche breadth have strong trait–environment relationships

Relationships between species' niche breadth and the strength of their trait–environment relationships depended on the trait and environmental gradient in question (Fig. 4), but overall the results did not support our hypothesis that species with wide niche breadth should have strong trait responses to the environment. Contrary to our hypothesis, species with wider niche breadth had significantly weaker trait responses to the environment (measured as absolute value of slope of trait–environment relationship) for four of the twelve trait–environment combinations we tested. For example, niche breadth along the light availability gradient was highest in species that had weak responses (slopes near zero) of leaf area to GLI ( $R^2 = 0.11$ ,  $p = 0.07$ ) and moderately strong responses of LMA to GLI (quadratic relationship,  $R^2 = 0.25$ ,  $p = 0.02$ ). Along the soil N availability gradient, species with the widest niche breadth tended to have weak responses of leaf area (linear relationship,  $R^2 = 0.34$ ,  $p = 0.002$ ), LMA (quadratic relationship,  $R^2 = 0.50$ ,  $p = 0.001$ ), and leaf N (linear relationship,  $R^2 = 0.23$ ,  $p = 0.058$ ) concentrations to soil N availability. Finally, along the soil P availability gradient, species with the widest niche breadth again tended to have weak responses of LMA (linear relationship,  $R^2 = 0.31$ ,  $p = 0.007$ ) and leaf N (linear relationship,  $R^2 = 0.47$ ,  $p = 0.003$ , Fig. 4) concentrations to soil P availability.

### Hypothesis 3. Species with wide niche breadth adjust traits to match local trait optima

We found limited support for our hypothesis that species with wide niche breadth are especially good to adjusting their traits to match local trait optima (represented here by community-weighted mean trait values, CWM's). Overall, many species showed evidence of tracking local trait optima, indicated by a closer fit between species' plot-specific trait values and CWM's than expected by chance

(negative trait.track values; Fig. 5). However, the degree of trait tracking was significantly related to niche breadth for only three of the twelve trait–environment combinations we tested. Specifically, niche breadth along the light availability gradient was significantly correlated with species' ability to track local optima of LMA ( $R^2 = 0.099$ ,  $p = 0.044$ ) and leaf P ( $R^2 = 0.266$ ,  $p = 0.017$ ). This means that species with wider niche breadth across the light gradient tended to have a closer fit of their LMA and leaf P concentration values to local environmental optima (relative to the null expectation) than species with narrower niche breadths. Similarly, species with wider niche breadth along the soil P gradient were significantly better at tracking local optimum leaf P ( $R^2 = 0.419$ ,  $p = 0.002$ ; Fig. 5) compared to species with narrower niche breadth.

## Discussion

### Hypothesis 1. Species with wide niche breadth will have a high among-plot ITV

In temperate rainforests of southern Chile, where as many as 25 woody species per hectare can co-occur within forest communities, species can be found in a variety of local environmental conditions, from deep shade to tree-fall canopy gaps (Veblen 1985, Lusk 2002, Fajardo and Siefert 2016, 2018), and from spots with poor to rich nutrient availability. Given these apparent strong environmental gradients, we expected that species achieving high local abundance would be those that could tolerate a wide range of environments by adjusting their trait values to local conditions (Darwin 1859, Sides et al. 2014). Working with saplings of woody species in four temperate rainforest sites, we found that species abundance was positively related to niche breadth along gradients of light and soil nutrient availability. Moreover, species with wide niche breadth tended to have high ITV in leaf traits for some trait–gradient combinations. Specifically, species that

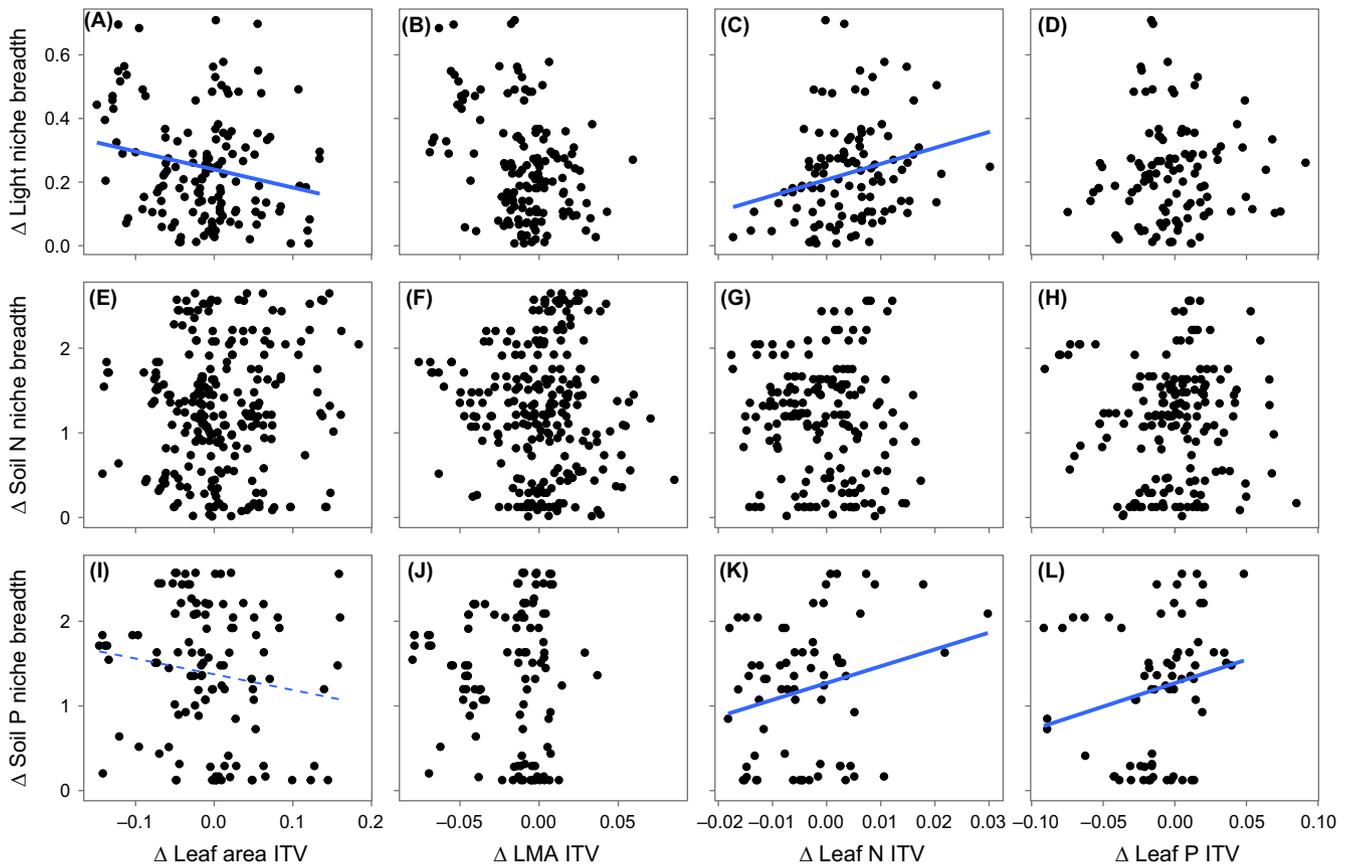


Figure 3. Relationship between mean leaf trait values and niche breadth along light (A–D), N (E–H), and P availability (I–L) gradients of temperate rainforest tree species in southern Chile. Niche breadth along light, soil N and P availability gradients is expressed as the range of environmental values of plots in which a species occurred, divided by the total range of values measured across all plots. Regression lines are shown for significant ( $p < 0.05$ , solid lines) and marginally significant ( $p < 0.1$ , dashed lines) linear or quadratic relationships (best model determined by likelihood ratio test).

occurred across a wide range of light environments had high ITV in leaf N concentration, and species broadly distributed along the soil P availability gradient had high ITV in leaf N and P. Importantly, we found these positive relationships between niche breadth and ITV by comparing species' ITV measured across a common set of environments. Research conducted in these southern hemisphere cool temperate rainforests thus far (Lusk 2002, Fajardo and Siefert 2016, Peltzer and Wardle 2016) has commonly focused on light availability as the limiting factor, especially, for regeneration, but here we show that soil N and P availability had a strong positive relationship with leaf trait variation, indicating that multiple environmental filters drive regeneration dynamics (see also Lusk and Laughlin 2017, Fajardo and Siefert 2018). Although some studies have found that N is the most limiting nutrient in soils of temperate rainforests in southern Chile (Huygens et al. 2008), the volcanic origin of these soils makes them very poor in available P for plants (large amount of allophane and sesquioxide in the soil, which have a high phosphate-fixing capacity, making P not readily available for plants) (Fajardo and Piper 2015). Our finding of a positive relationship between species' niche breadth along the soil P gradient and ITV in leaf N and P suggests that plasticity in

leaf nutrient concentrations may allow generalist species to succeed in sites with varying degrees of P limitation.

Previous studies have also found support for a positive relationship between ITV and species niche breadth (Pohlman et al. 2005, Griffith and Sultan 2012, Canessa et al. 2018). Using congeneric species in a field common garden experiment, Griffith and Sultan (2012) found that the generalist species *Polygonum persicaria* showed greater adaptive plasticity for leaf area than the specialist *P. hydropiper*. Similarly, Pohlman et al. (2005), working with several species of *Acacia* that differ in their geographic range size, found greater plasticity of some leaf traits in widespread species than in narrowly distributed species. Studies considering widely-distributed invasive species have also found a positive relationship between ITV and niche breadth (Richards et al. 2006, Funk et al. 2008, Sides et al. 2014). These results are in line with the idea that high phenotypic plasticity (high ITV) enhances niche breadth because plastic responses allow organisms to express advantageous phenotypes in a broad range of environments (Sultan 2001, Richards et al. 2005, Sides et al. 2014). Accordingly, our results suggest that species having wide niche breadth had high ITV in leaf N and also matched traits (LMA and leaf P) to local optima along

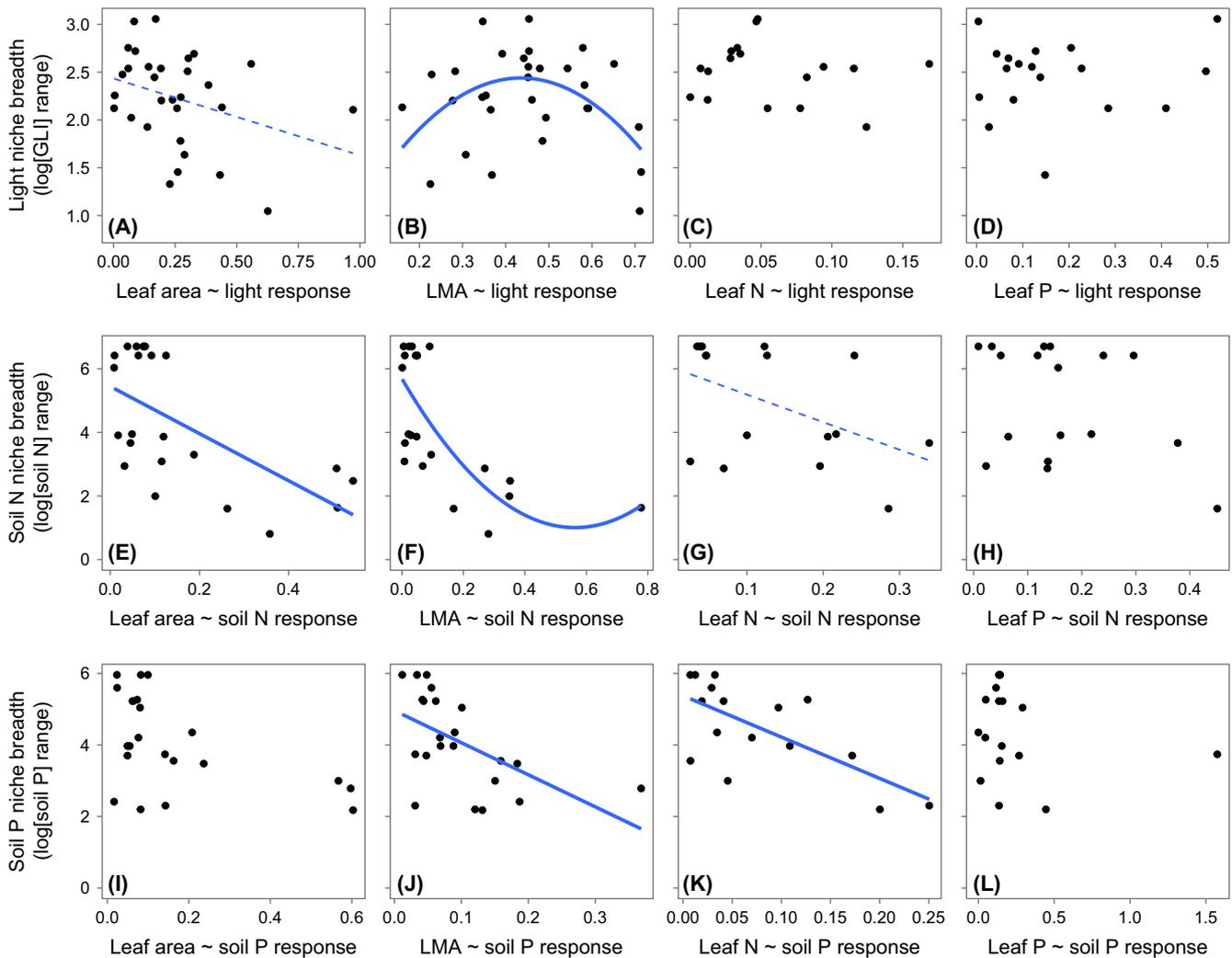


Figure 4. Relationship between the strength of leaf trait responses to environmental gradients (measured as the slope of linear regression of log-transformed trait values on log-transformed environmental values across sites) and niche breadth of temperate rainforest tree species in southern Chile. Trait-environment relationships were assessed for three leaf traits: leaf area (A, E and I), leaf mass per area (LMA, B, F and J), leaf N (C, G and K), and leaf P concentrations (D, H and L); and three environmental gradients: light, measured as gap light index (GLI, A–D), soil N (E–H), and soil P availability (I–L). Niche breadth is expressed as the range of environmental values of plots in which a species occurred, divided by the total range of values measured across all plots. Regression lines are shown for significant ( $p < 0.05$ , solid lines) and marginally significant ( $p < 0.1$ , dashed lines) linear or quadratic relationships (best model determined by likelihood ratio test).

the light gradient; they also had high ITV in general and matched leaf P to local optima along the soil P gradient. Because our study was observational, we cannot conclude to what extent the measured ITV represents genetic variation or phenotypic plasticity, but given the fine spatial scale of the variation in light and soil P, it is likely that plasticity played an important role.

**Hypothesis 2. Species with wide niche breadth will exhibit a strong relationship between trait values and the environment**

Our results did not support the hypothesis that species with wide niche breadths (generalists) exhibit stronger shifts in trait values in response to variation in the environment than

species with narrow niche breadths (specialists). We actually found the opposite for several trait–environment combinations. These results suggest that specialist species had stronger shifts in trait values – measured as the slope of intraspecific trait–environment relationships – in response to a given range of environmental conditions. There are several possible explanations for this result. First, it is possible that ITV was not adaptive for some trait–environment combinations, and that species were able to maintain high fitness across a range of environments by maintaining constant trait values. For example, our finding that species with wide niche breadth across the soil N gradient had weak responses of leaf area and LMA to soil N variation suggests that species succeeded across a range of soil N environments by maintaining consistent leaf morphology. In this scenario, the strong

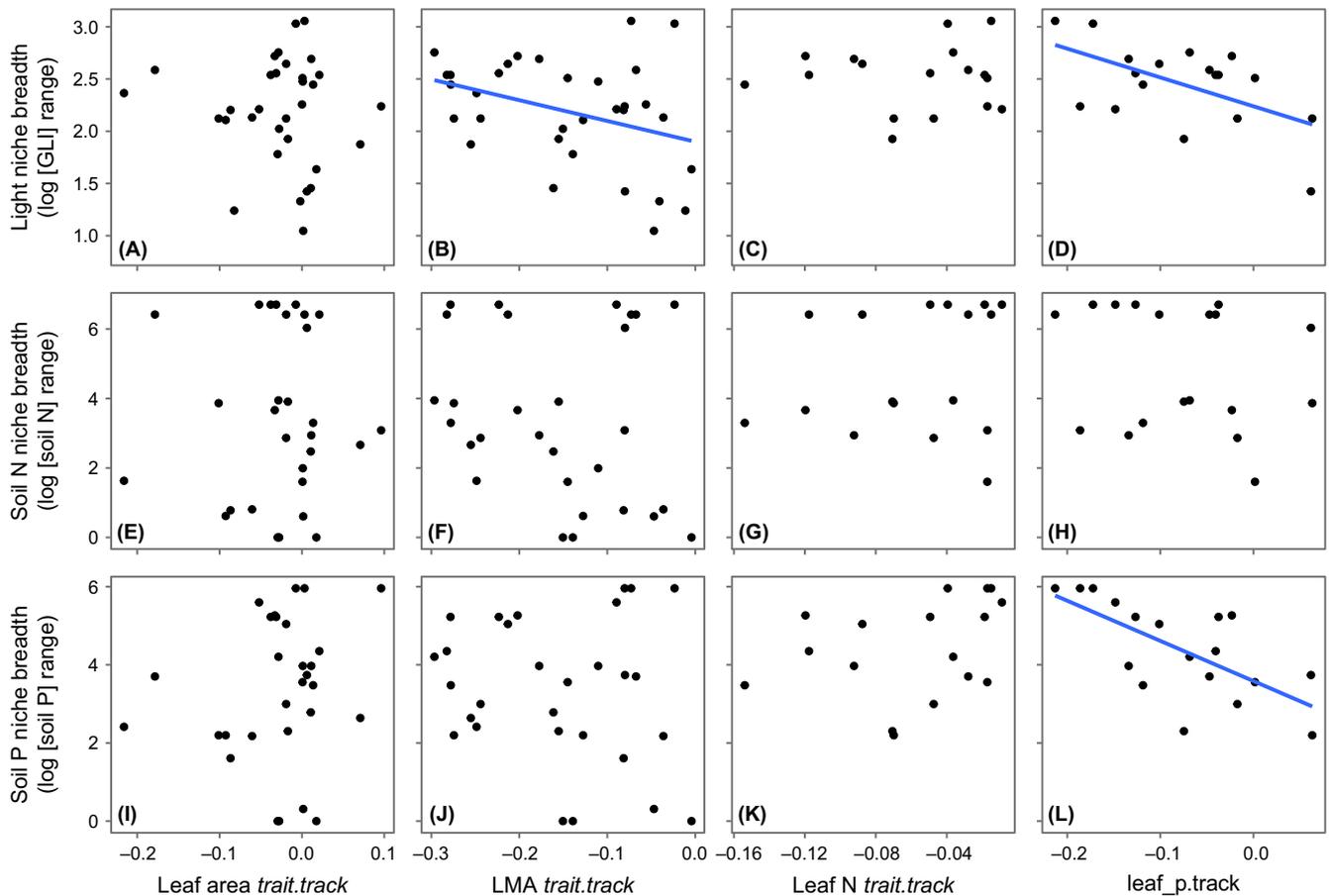


Figure 5. Relationship between degree of trait tracking of local environmental optima (trait.track) and niche breadth of temperate rainforest tree species in southern Chile. A negative trait.track value indicates that a species' trait values are on average closer to the local trait optima (defined as community-weighted mean trait values, CWM) than expected given a null model in which trait values vary randomly among plots. Niche breadth along light (A–D), soil N (E–H) and soil P availability (I–L) gradients is expressed as the range of environmental values of plots in which a species occurred, divided by the total range of values measured across all plots. Regression lines are shown for marginally significant ( $p < 0.1$ , dashed lines) linear or quadratic relationships (best model determined by likelihood ratio test).

trait–environment relationships of species with narrow niche breadth could represent passive responses to the stress of growing outside their preferred environmental ranges, rather than adaptive plastic responses (Ghalambor et al. 2007). Second, it is possible that the capacity to reach high ITV was adaptive, but that adaptive shifts in trait values along environmental gradients were not well-described by linear relationships. Finally, because we only measured trait values in sites in which species naturally occurred, species with wider niches were necessarily measured across a wider range of environments. If species have limited trait variability in response to the environment (i.e. trait responses to environment flatten out toward extreme ends of the environmental gradient), the slopes of trait–environment relationships (change in trait values divided by change in environmental values) will necessarily be shallower for species with wide niches.

### Hypothesis 3. Species with wide niche breadth will exhibit a strong relationship between leaf traits and CWM trait values

We found some support for this hypothesis. Specifically, woody species with wide niche breadths along the light gradient had closer tracking of LMA and leaf P concentrations to CWM trait values than did more specialized species. Similarly, species with wide niche breadth along the soil P gradient closely tracked CWM leaf P values. For other trait–environment combinations, we did not find significant relationships between niche breadth and the degree of trait tracking, but most species did track CWM trait values more closely than expected by chance, regardless of niche breadth. These results suggest that woody species are able to adjust their trait values to local conditions, and that for some traits

and environmental gradients, generalist species can do so more effectively than specialists. High phenotypic plasticity (high ITV) in this case enhances niche breadth because plastic responses allow organisms to express advantageous phenotypes in a broad range of environments (Sultan 2001, Richards et al. 2005).

### Limitations and future directions

This study was observational and therefore could only measure traits of species in the environments in which they were found. As with previous observational studies examining the relationship between ITV and niche breadth, this makes it difficult to infer the direction of causality. It is difficult to know whether high ITV allowed species to be successful in a range of environments and thus have wide niche breadth, or if growing in a wide range of environments caused species to express a wide range of trait values and thus have high ITV. We attempted to overcome this limitation by 1) comparing ITV measured across a common set of environments for species with nested niche breadth, and 2) comparing slopes of trait–environment relationships, which measure the amount of trait change per unit environmental change. While these comparisons offer stronger support for the hypothesis that high ITV allows species to have wide niche breadth than previous observational studies, experimental approaches are needed to further clarify the causal relationships between ITV and niche breadth. For example, reciprocal transplant or growth chamber experiments that measure variation in functional traits and performance of species across a common set of environmental conditions could demonstrate that ITV allows generalist species to maintain high relative fitness across a range of environments. Finally, with this observational study we were not in a position to distinguish between heritable genetic variation and phenotypic plasticity as the causes of ITV.

### Conclusions

Here, using saplings of woody species – an important life stage in responding to fine-scale resource limitation – in temperate rainforest communities, we found some evidence supporting the longstanding assumption that species with wide niche breadth have high ITV. Specifically, our results suggest that species achieved wide niche breadth along light and soil P availability gradients by having high ITV in leaf nutrient concentrations and by matching traits to local optima. In contrast, species achieved wide niche breadth along soil nutrient (N and P) gradients by maintaining consistent leaf morphology (leaf area and LMA). A significant coupling between leaf and soil nutrient concentrations is rather expected, however, the fact that leaf morphological traits respond differently to the light gradient signifies that there is no single morphological leaf trait as an optimal solution for light availability. Combined, our results show that the relationship between ITV, species abundance and niche breadth is idiosyncratic; trait variation at the community level is not driven by a few

abundant, widely distributed species, but depends on the aggregate trait responses of both abundant and rare species. This makes it difficult to scale individual species trait responses up to the community level.

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Supplementary material (available online as Appendix oik-05849 at <[www.oikosjournal.org/appendix/oik-05849](http://www.oikosjournal.org/appendix/oik-05849)>). Appendix 1.