

Does environmental heterogeneity drive functional trait variation? A test in montane and alpine meadows

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While community-weighted means of plant traits have been linked to mean environmental conditions at large scales, the drivers of trait variation within communities are not well understood. Local environmental heterogeneity (such as microclimate variability), in addition to mean environmental conditions, may decrease the strength of environmental filtering and explain why communities support different amounts of trait variation. Here, we assess two hypotheses: first, that more heterogeneous local environments and second, that less extreme environments, should support a broader range of plant strategies and thus higher trait variation. We quantified drivers of trait variation across a range of environmental conditions and spatial scales ranging from sub-meter to tens of kilometers in montane and alpine plant communities. We found that, within communities, both environmental heterogeneity and environmental means are drivers of trait variation. However, the importance of each environmental factor varied depending on the trait. Our results indicate that larger-scale trait–climate linkages that hold across communities also apply at small spatial scales, suggesting that microclimate variation within communities is a key driver of community functional diversity. Microclimatic variation provides a potential mechanism for helping to maintain diversity in local communities and also suggests that small-scale environmental heterogeneity should be measured as a better predictor of functional diversity.

What are the central drivers of functional diversity in ecological communities? This long-standing question (Schimper and Fisher 1903, Westoby and Wright 2006) is often addressed by studying functional composition across broad environmental gradients and comparing observed diversity to a null model of randomly assembled communities (Keddy 1992, Weiher and Keddy 1995, Weiher et al. 1998, Cornwell et al. 2006, Kraft et al. 2015). Often, focus is placed on determining whether local community diversity is shaped by abiotic factors through environmental filtering (Ackerly 2003, Swenson and Enquist 2007). While many studies have demonstrated that communities have differing amounts of trait variation (Kraft et al. 2008, Cornwell and Ackerly 2009, Messier et al. 2010, Baraloto and Couteron 2010, Lamanna et al. 2014), quantitative predictors of this variation are still needed. To assess the relative strength of abiotic drivers on local community functional composition, tests of ecological theory require rigorous analyses of the relationship between community trait variation and local environmental conditions (McGill et al. 2006). More detailed measurements of how environmental means and environmental heterogeneity vary at both large and small spatial scales may provide a key to understanding the strength of environmental filters. Such scale-dependent measures may also help explain trait variation within and

across communities (Weiher and Keddy 1995, Swenson and Enquist 2007, 2009, Kraft et al. 2008).

Most studies of trait–climate linkages focus on assessing mean environmental conditions within communities (Kraft et al. 2015). At a local scale, trait-based ecology has largely treated observed community trait variation as reflecting internal niche partitioning driven by species interactions (Keddy 1990, Weiher and Keddy 1995, Wright et al. 2001). However, environmental filtering has also been shown to operate within communities (Adler et al. 2013). Thus, the environmental mean hypothesis states that the mean climatic conditions over a given area filter for a set of traits that optimizing growth and reproduction.

In contrast to the environmental mean hypothesis, two established ecological relationships support the role of local abiotic variance or heterogeneity as a key driver of functional diversity. First, several studies have demonstrated that small-scale environmental heterogeneity can affect the ability of different plant species to persist within communities (Palmer and Dixon 1990, Chesson 2000a, Baraloto and Couteron 2010, Scherrer and Körner 2011). We call this the ‘environmental mean’ hypothesis. Indeed, many studies have linked variation in species richness to environmental heterogeneity (Palmer and Dixon 1990, Dufour et al. 2006, Opedal et al. 2015, reviewed by Stein et al. 2014). Second, regional

variation in plant functional traits is linked to heterogeneity in climate (Diaz et al. 1998, Swenson et al. 2012, Šímová et al. 2014). However, it is still not clear whether this link between functional traits and climate extends to the microclimate scale and drives within-community functional composition. To our knowledge, only one other study (Price et al. 2017) has addressed this question directly. They find support for the role of soil depth and moisture heterogeneity in driving several functional traits. Other studies of microclimate effects on trait variation are limited in scope. These studies have generally examined the effect of microclimate variability created by nurse plants (García-Cervigón et al. 2015, Schöb et al. 2012) or measured traits of focal species rather than entire communities (Opedal et al. 2015).

Environmental filtering is a central concept in understanding the drivers of community-scale functional diversity. Niche theory states that species have different environmental requirements, and so vary in their performance along environmental gradients based on their ecological strategies (Grime 1977, Weiher et al. 1998, McGill et al. 2006, Violle and Jiang 2009). At the extreme edges of a species' environmental niche, individuals will have difficulty surviving or reproducing, and beyond this range of suitable conditions environmental filtering will remove species with unsuitable phenotypes from the community (Pulliam 1988, Angert 2009; see also Janzen 1985).

While most studies on the link between functional traits and climate focus on large-scale relationships, the success

of individuals depends on the conditions they experience directly rather than mean site conditions (Diaz et al. 1998, Kraft et al. 2008). Therefore, sites with a wide range of microclimates or resources – in effect, several distinct environmental filters, perhaps themselves created by biotic interactions with individuals of the same or other species – should support a wider distribution of ecological strategies and more variation in functional traits (Tilman 1994, Grime 2006, HilleRisLambers et al. 2012, Adler et al. 2013, Laughlin and Joshi 2015, Kraft et al. 2015, Price et al. 2017).

From the perspective of coexistence theory, increased environmental heterogeneity provides more opportunities for niche partitioning and should be reflected by higher functional diversity and ultimately higher species richness (Chesson and Warner 1981, Tilman 1982, Kohn and Walsh 1994, Chesson 2000a, b, Amarasekare 2003). While there are few trait-based tests of the role of environmental heterogeneity, ecology theory has increasingly discussed its importance in community assembly (Palmer and Dixon 1990, Kraft et al. 2015, Grime 2006).

Trait variation within a given area could be driven by environmental heterogeneity or by environmental means through a variety of processes (Fig. 1). First, local trait variation could be driven by local environmental variation. We call this the 'environmental heterogeneity hypothesis'. For example, a positive relationship between environmental variability and trait variation across communities can occur when all communities share a common trait-environment

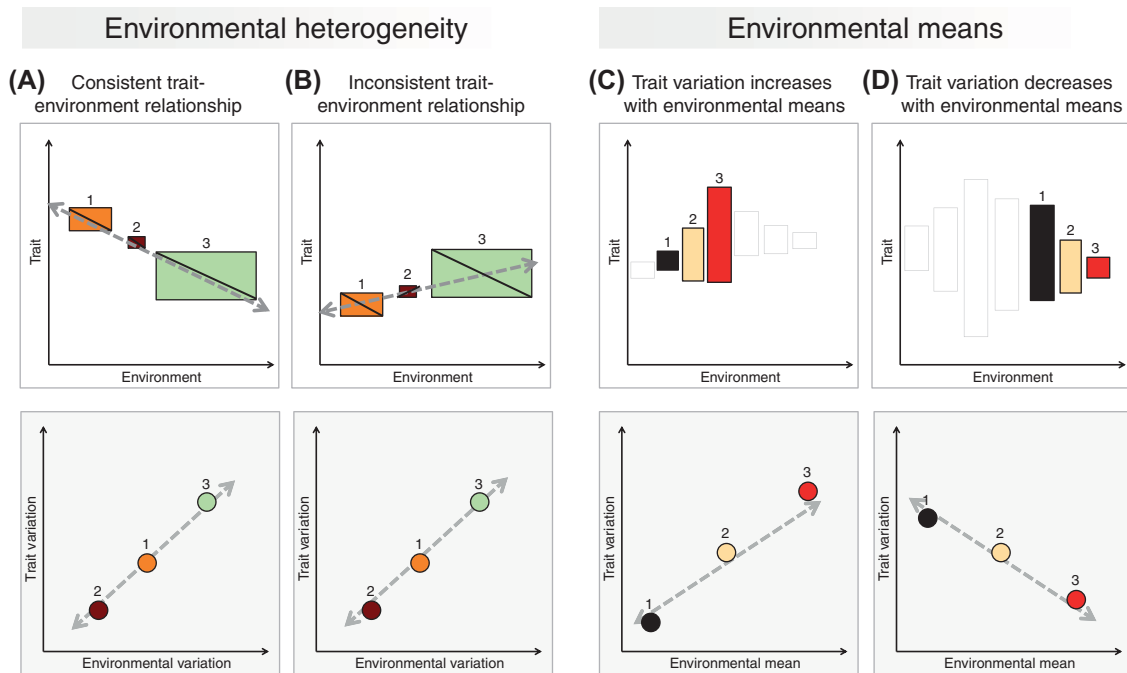


Figure 1. Two hypotheses for the drivers of trait variation based on environmental means and heterogeneity. These hypotheses are illustrated for three test communities with either a positive or negative trait–environment relationship between communities (gray line) or within communities (black line), although relationships between environmental heterogeneity and trait variation could occur even without a consistent link between trait values and environmental values. In the environmental heterogeneity hypothesis, (A) Local and global trait–environment relationships can produce between-community correlation between trait variation and environmental heterogeneity. (B) However, even without consistent trait–environment relationships across communities, trait variation can still be correlated with environmental heterogeneity. In the environmental extremes hypothesis, (C, D) communities can vary in their trait distributions (vertical bars). Those with more extreme environments have stronger environmental filtering and reduced trait variation. Local-scale measurement of traits over partial gradients (colored bars) should demonstrate that communities with more extreme environmental means have less trait variation. Unimodal relationships are also possible if a complete gradient is studied (white bars).

relationship (Fig. 1A). In this case, broader ranges of environmental heterogeneity yield equivalently broad ranges of trait variation. However, a similar across-community pattern can also arise even with between-community differences in trait–environment relationships (Fig. 1B). Even if there is no trait–environment relationship within or among communities, higher environmental heterogeneity could still yield higher trait variation. That is, there may be a relationship between trait and environment variances even without a covariance between the trait and environment. Thus, any environmental filtering scenario in which higher environmental variance yields higher trait variance will be sufficient to support this hypothesis.

Second, trait variation could be driven by environmental means – the ‘environmental means hypothesis’ (Fig. 1C–D). Different ecological strategies are more viable under different large-scale climatic regimes. At either biological extreme of a climate gradient, environmental filtering should reduce species richness and thus trait variation as increasingly large numbers of strategies become nonviable (von Humboldt and Bonpland 1807). For example, many species can tolerate warm conditions, but few species can tolerate very cold or very hot conditions. Generally, the strength of environmental filtering is understood to reflect environmental harshness (Terborgh 1973, Weiher et al. 1998, Boucher et al. 2013). Few studies can capture a full biological gradient, and instead measure only a smaller fraction of the gradient. Over such scales this curvilinear relationship becomes approximately linear, yielding either a positive or negative relationship between environmental means and trait variation.

The environmental mean and heterogeneity hypotheses are not mutually exclusive and may both play ecologically relevant roles in determining trait variation. Additionally, these hypotheses may be easily confounded because distributions with higher means often also have higher variances because of proportional rescaling. To avoid this scaling issue, it is necessary to assess covariation or co-linearity between environmental metrics and to use scale-independent measures of variation. We are unaware of any trait-based tests that contrast the predictions made by the environmental variation and environmental means hypotheses.

Here, we examine the relationship between variation in several traits and both environmental means and environmental heterogeneity (temperature and soil moisture axes) using plant communities spanning a > 700 m elevation gradient in the Colorado Rocky Mountains. Sites included 25 spatially nested montane, subalpine, and alpine transects. We simultaneously test the role of local environmental means and environmental heterogeneity in driving functional trait variation within communities.

Material and methods

Study sites

Five study sites were in montane, subalpine, and alpine meadows in the Gunnison Valley, Colorado. Site elevation ranged from 2820 to 3537 m a.s.l. Growing season for these sites spans approximately June–August with snow cover

typically from November to May. While some forested areas also occur at these elevations, study sites were located within large open areas dominated by herbaceous vegetation including grasses, rushes, forbs, and in some cases, small shrubs.

Within each of these five study sites, we assessed small-scale community functional composition and microclimate variation by delineating five transect lines spaced 10 m apart parallel to the downslope gradient. Each 10 m transect was then characterized at nine logarithmically spaced sampling locations perpendicular to the downslope gradient (Fig. 2). The overall effect was to create a grid pattern that enabled us to assess variation in traits and environment at a range of spatial scales, while still working within the same overall site type.

Environmental measurements

In June and July of 2015, we placed one iButton ThermoChron datalogger at each sampling location ($n = 225$ in 25 transects at five sites). Each logger recorded temperature every 30 min for 22–60 days, depending on site accessibility given snowmelt dates. Measurement at all sites overlapped between 14 July and 3 August, with measurement at lower elevation sites beginning and ending earlier than measurement at higher elevation sites. We removed all iButtons from their sites by 7 August. Each iButton was suspended 1–2 cm above the ground on a galvanized steel nail and covered by a radiation shield made from white duct tape. Prior to this study, we tested several radiation shield designs and found that this design minimized thermal buffering (Supplemental material Appendix 1 Fig. A1).

We measured soil moisture at each sampling location next to the iButton using a time-domain reflectance moisture probe. Measurements were standardized at 10 cm depth and conducted on days with no rain in the previous 12 h. Moisture was measured at each sampling location ($n = 225$) approximately once per week in July and early August ($n = 3$ at higher elevation sites, $n = 4$ at lower elevation sites).

Functional trait measurements

Close to the date of peak biomass for each site, we measured traits of the five plants (or for clonal species, ramets) with leaves whose vertically projected distance to the datalogger was smallest, resulting in a spatially-explicit sample of the plants in each transect. Because we were interested in estimating community-wide trait distributions, we used this taxon-free sampling approach (Paine et al. 2015). This approach also accounts for both inter- and intra-specific variation in traits at the local scale, rather than averaging species means (Price et al. 2017). We selected plant height, leaf area, specific leaf area (SLA) and leaf dry matter content (LDMC) as relevant traits because they are commonly thought to be linked to major ecological strategy axes (Diaz et al. 1998, Westoby 1998). For each plant, we measured the height of the highest leaf (i.e. not including flowering stalks) and collected two leaves. We stored collected leaves in a cooler with ice packs and a damp paper towel until making measurements no more than six hours later. In the lab, we measured leaf area, wet weight and dry weight to calculate SLA and LDMC (Pérez-Harguindeguy et al. 2013). Dry weight was measured after a minimum of 48 h in a drying

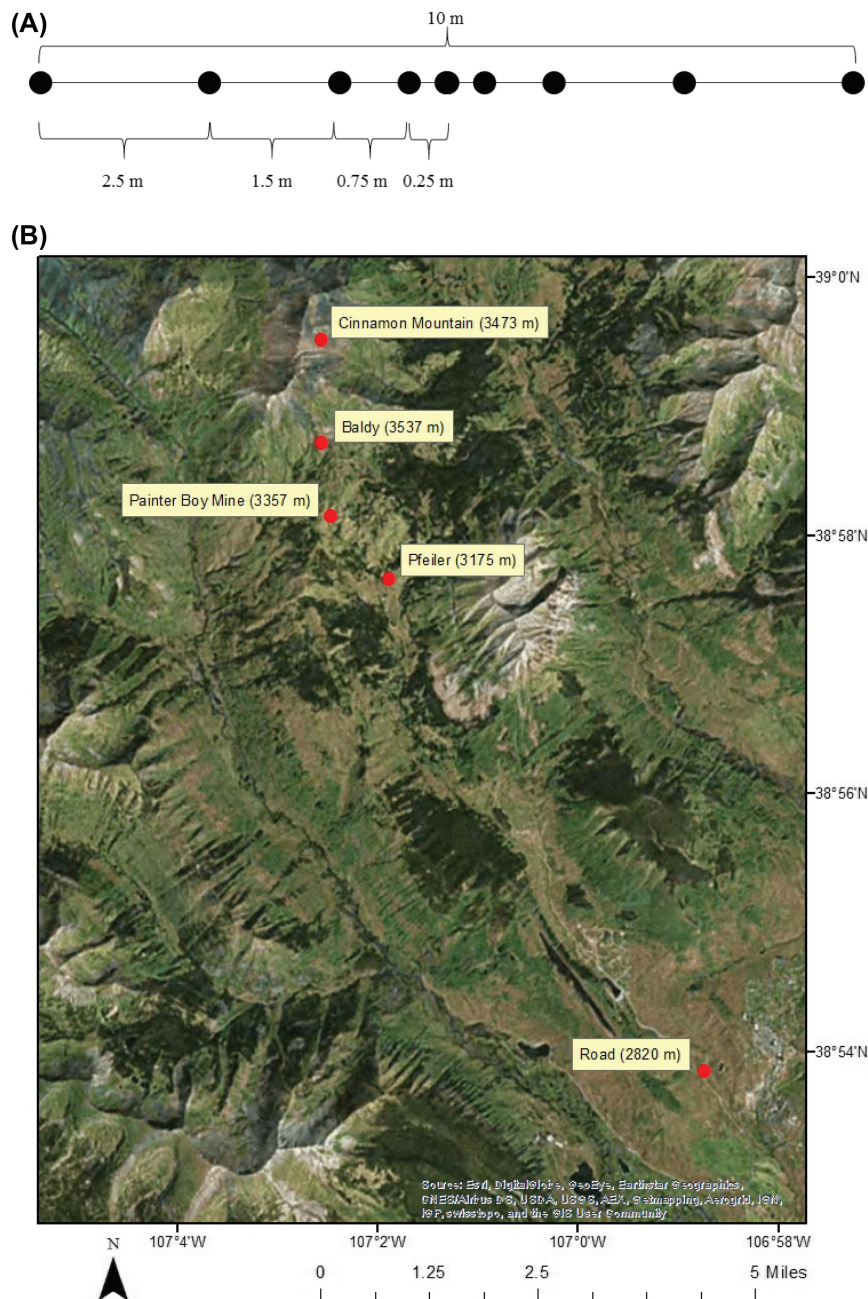


Figure 2. Five communities were sampled using logarithmically-spaced transects (A) spaced 10 m apart at each of five sites (B).

oven at 65°C. Leaf area was calculated by digitally scanning each leaf individually and then analyzing the images using an ImageJ program (available at <www.github.com/bblonder/leafarea/>). SLA was calculated as the ratio of leaf area to dry leaf mass. LDMC was calculated as 100 times the ratio of leaf dry mass to leaf wet mass.

Statistical analysis

Before conducting analyses, we removed high LDMC and SLA values (LDMC > 50 g dry / 100 g wet; SLA > 470 cm² g⁻¹) for a subset of leaves too small to accurately measure dry weights with our balance (precision ± 0.01 g). Upper cut-off values were chosen based on the 97.5 quantile reported in the dataset of Kattge et al. 2011. For linear models, we

used multiple imputation by chained equations (R package ‘mice’) to impute missing values using measured values of all other traits (213 LDMC values, 322 SLA values). We selected a single random imputation of the dataset to conduct linear models. This imputation method can yield an unbiased estimate of the true parameters, improving model outputs over missing data (Horton and Kleinman 2007, van Buuren and Groothuis-Oudshoorn 2011). To test the effects of imputed values on model results, we also ran models with incomplete cases omitted. This resulted in largely the same model outcomes (Supplemental material Appendix 1 Fig. A2).

For each transect (n = 25, nested within five sites), we calculated the standard deviation in trait values across measures of the mean and spatial heterogeneity in microclimate.

Mean temperature and moisture were calculated as the average value of available measurements from all sampling points and times. For spatial heterogeneity in temperature, we determined the 95th percentile temperature on each day for each sampling location ($n = 225$). We then calculated the coefficient of variation (CV) for these temperatures among the nine sampling locations in each transect on each day. Finally, we calculated the average CV across all measured days for each transect ($n = 25$). This approach allowed comparison of spatial heterogeneity in the highest daily temperatures for each transect across all sites. For spatial heterogeneity in moisture, we calculated the CV in soil moisture across the nine sampling locations in each transect for each sampling date. We then calculated the average CV across all sampling dates for each transect ($n = 25$). This approach mirrored calculation of spatial heterogeneity in temperature but used the single measurement available for each sampled date rather than a daily peak.

All measures of abiotic mean and heterogeneity were log-transformed to improve normality. Trait values were approximately normally distributed and were not transformed. We then rescaled environmental variables and traits to zero mean and unit variance to improve comparability.

To test the two main predictions, we built a linear mixed model for each trait. We then created a model with trait standard deviation as a dependent variable, fixed effects for temperature heterogeneity, soil moisture heterogeneity, temperature mean, and soil moisture mean, and with a random intercept for site to account for the nesting of transects within sites. Finally, we calculated bootstrapped confidence intervals for each fixed effect. When these intervals did not overlap zero, we assumed the predictor had a significant effect in the model.

While we primarily examined individual traits, we also assessed all traits together using a mixed model with response variable as convex hull volume, a multidimensional functional diversity metric (Cornwell et al. 2006). Results for this analysis are reported in the supplementary material (Supplementary material Appendix 1 Fig. A3).

To determine the explanatory value of these models, we used the R package ‘MuMIn’ to calculate marginal and conditional r^2 -values (Nakagawa and Schielzeth 2013, Johnson 2014). We also calculated a metric of variable importance as the deviance (changes in negative log-likelihoods) between full models and those omitting the variable of interest. To check for multicollinearity of predictors, we calculated variance inflation factors (Frank 2011). To examine the spatial structure and autocorrelation of the data, we calculated semi-variograms (Supplementary material Appendix 1 Fig. A4) and conducted a variance partitioning analysis using the R package ‘varComp’ on a hierarchical mixed model for each trait (package ‘lme4’) (Supplementary material Appendix 1 Fig. A5).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.772h7>> (Stark et al. 2017).

Results

Trait and environment patterns

Across the elevation gradient there was wide variation in the means and standard deviations of environmental conditions and plant traits (Table 1). Transect mean temperature ranged from 9.3 to 14.4°C, while standard deviation in temperature

Table 1. Summary of environmental conditions and plant traits across sites.

Site	Elevation (m)	Transect	Temperature (°C)		Moisture (%)		Height (cm)		LDMC (g/100g)		SLA (cm ² g ⁻¹)		Leaf area (cm ²)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Road	2820	A	14.3	4.1	11.8	2.9	22.0	13.0	28.1	10.4	188.6	77.9	9.5	14.0
		B	14.0	3.7	12.6	3.0	24.2	13.8	29.3	9.7	176.0	62.1	8.9	8.9
		C	13.8	3.0	13.4	3.5	25.3	17.5	31.2	9.2	193.6	85.1	9.1	8.7
		D	14.4	3.9	12.0	3.4	28.8	17.5	28.1	10.8	214.5	76.7	9.2	10.3
		E	13.3	3.9	20.5	4.4	20.5	16.1	30.2	9.4	210.3	78.0	15.2	17.6
Pfeiler	3175	A	12.5	3.2	21.4	3.1	33.7	16.0	28.1	6.9	248.8	60.9	9.0	6.3
		B	11.5	2.6	23.2	3.5	49.4	29.7	27.2	7.7	220.9	73.7	31.8	55.9
		C	10.4	2.6	28.7	4.5	96.8	46.3	15.6	3.8	284.4	92.4	94.8	121.6
		D	11.2	2.4	26.3	4.8	67.9	25.1	22.7	6.8	253.3	85.9	37.8	48.9
		E	10.9	1.8	25.7	4.6	76.0	25.2	22.8	6.0	261.5	78.8	50.3	55.3
Painter Boy	3357	A	12.4	1.8	14.8	4.2	7.7	4.4	28.8	11.7	282.7	85.7	3.5	4.6
		B	11.9	2.4	17.5	4.4	17.1	13.6	30.1	11.0	192.7	76.7	9.5	8.7
		C	9.3	5.0	25.5	5.9	75.4	51.1	19.1	7.2	275.1	85.0	38.6	50.1
		D	9.8	2.3	23.7	4.4	52.3	38.9	17.8	6.4	265.0	90.1	63.4	85.3
		E	10.2	3.6	21.2	4.2	53.5	33.8	20.1	6.4	260.5	76.0	55.6	74.1
Cinnamon	3473	A	10.6	2.1	17.5	6.6	11.2	5.8	33.7	11.7	257.4	97.0	3.2	4.9
		B	11.1	2.3	19.4	4.7	8.6	4.7	31.9	10.8	252.5	102.8	2.4	3.8
		C	11.2	3.1	20.3	6.7	10.8	5.1	30.8	10.9	241.2	109.4	4.0	8.1
		D	11.4	2.2	24.4	4.8	9.9	6.7	32.5	11.7	264.8	95.9	3.0	4.3
		E	10.8	2.0	23.2	4.6	9.7	5.0	29.4	11.2	250.6	93.5	3.6	3.6
Baldy	3537	A	11.1	1.4	10.1	2.8	4.2	2.5	30.8	9.9	199.4	68.7	2.4	2.0
		B	11.0	2.0	11.5	2.1	5.6	4.2	29.3	10.4	196.2	72.1	2.6	2.6
		C	10.9	1.7	8.9	1.1	6.2	7.4	29.4	7.7	181.7	68.1	3.9	4.5
		D	11.3	1.9	9.0	1.9	6.4	6.1	32.5	10.0	178.8	62.9	2.8	3.1
		E	11.5	2.4	11.1	2.2	7.9	7.3	30.5	8.3	194.3	76.0	3.4	4.9

ranged from 1.7 to 5.0°C. Mean moisture ranged from 8.9 to 25.7%, while standard deviation in moisture ranged from 1.1 to 6.7% (Fig. 3). Transects contained 8–19 sampled species (see Supplementary material Appendix 1 Table A1 for full species list by transect).

Semivariograms also indicated that most spatial variation in traits occurred at or below spatial scales characteristic of individual transects (Supplementary material Appendix 1 Fig. A4). Variance partitioning analysis indicated that most trait variation occurred either between or within individual

sampling locations, rather than at the transect or site scale (Supplementary material Appendix 1 Fig. A5). Indeed, for most traits, small scale variation (within sampling points) accounted for > 50% of the observed trait variation.

Effects of environmental means and variation

Trait variability in all traits except SLA was predicted by transect mean environmental conditions (mean temperature), while variability in two traits (height and LDMC)

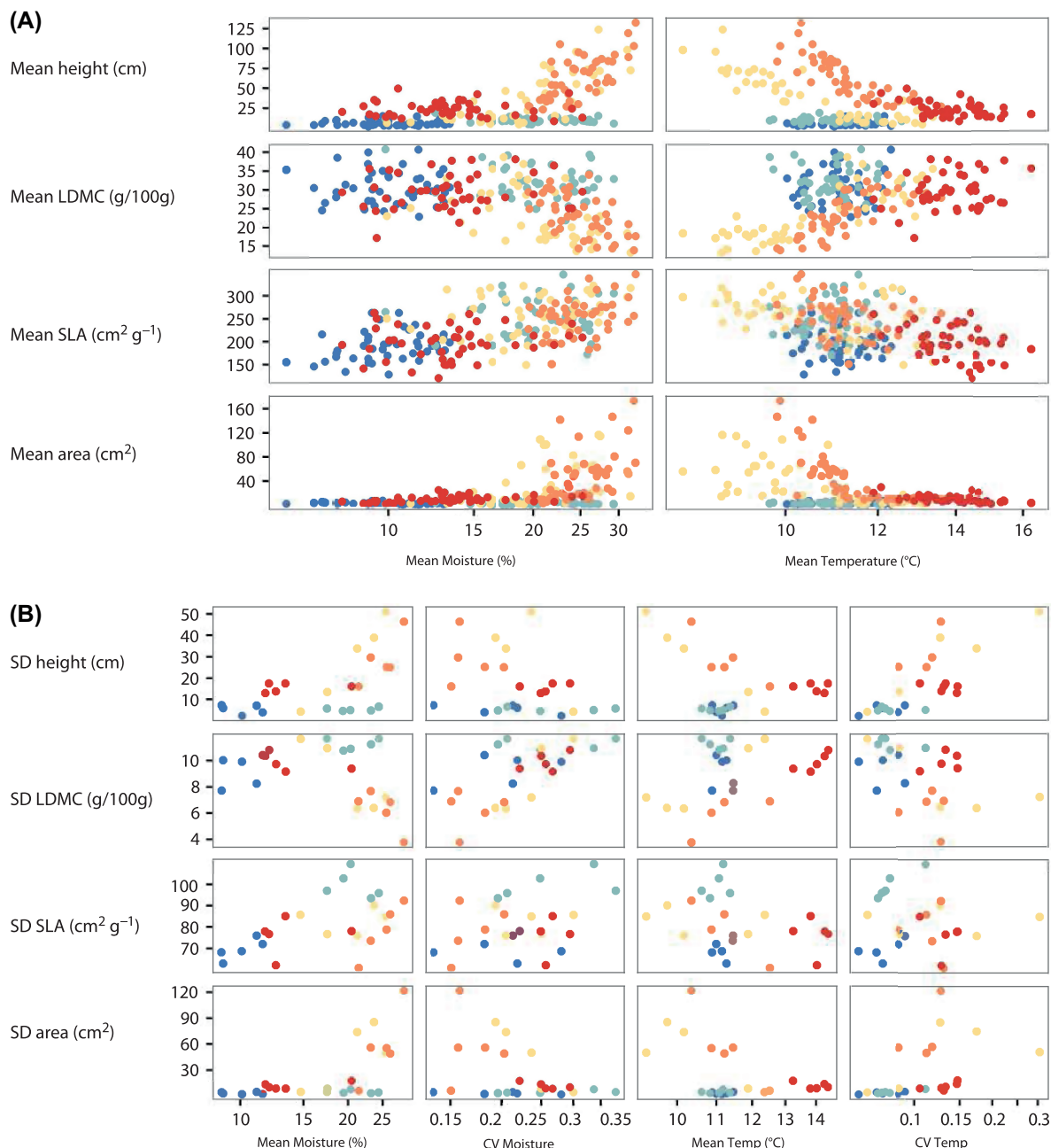


Figure 3. Observed relationships between trait and environmental values. (A) Relationships between mean trait values and mean environmental values at each sampling site ($n = 225$). (B) Relationships between trait standard deviations in each transect ($n = 25$) and environmental means and heterogeneity. X-axes are presented with a visual log transformation. All environmental variables were log transformed to improve normality in linear modelling. Dark blue circles-3537 m; light blue-3473 m; yellow-3357 m; orange-3175 m; red-2820 m.

was predicted by within-transect environmental variability (Fig. 4). These results were not due to predictor collinearity as variance inflation factors were <2.5 for all models. Standard deviation in height was best predicted by both environmental means and heterogeneity (mean temperature 95% CI [-1.120, -0.482] SD from mean, temperature CV 95% CI [0.108, 0.490] SD from mean). Standard deviation in LDMC was also predicted by both environmental means and heterogeneity (moisture CV 95% CI [0.002, 0.486] SD from mean, mean temperature 95% CI[0.185, 1.031] SD from mean). Standard deviation in leaf area was predicted by mean temperature (95% CI [-1.382, -0.283] SD from mean). However, no environmental variables significantly predicted functional richness distributions (Supplementary material Appendix 1 Fig. A3).

Fixed effects within these models explained 23–47% of the variation (marginal r^2), while the full models explained 60–95% of the variation (conditional r^2 ; Table 2). Individual significant environmental predictor variables explained 4–17% of the variation using a deviance statistic, with mean temperature or mean moisture explaining more variation across models (see Supplementary material Appendix 1 Table A2 for full results).

Discussion

Our results showed that both environmental heterogeneity and environmental means are drivers of trait variation within communities. However, the importance of each environmental factor varied depending on the trait of interest. Therefore, both hypotheses (Fig. 1) received partial support. The local-scale relationships investigated here provide a more direct explanation for the established links between heterogeneity and species richness (Stein et al. 2014) and

Table 2. Explanatory power of linear mixed models, based on Nakagawa and Schielzeth 2013 and Johnson 2014. Marginal r^2 represents the fraction of variance explained by fixed effects; conditional r^2 represents the fraction of variance explained by the full model.

Modeled trait	Marginal r^2	Conditional r^2
Height	0.47	0.95
SLA	0.23	0.60
LDMC	0.42	0.87
Leaf area	0.44	0.86

between richness and functional diversity (Petchey and Gaston 2002), since the conditions supporting ecological strategies (traits) of more species also occur in heterogeneous environments. Here, trait values and environmental conditions were related even within small (10 m long) transects, leading to relationships between trait values, within-community heterogeneity, and local mean environmental conditions. While relationships between trait variation and environmental means have been documented in many other studies (Diaz et al. 1998, Swenson et al. 2012, Šimová et al. 2014), to the best of our knowledge this study is the first to show that there is a sizeable effect of small-scale local heterogeneity in temperature and soil moisture on community-level trait variation. These results complement recent documentation of the role of soil depth and moisture heterogeneity in driving functional diversity (Price et al. 2017) and demonstrate the value of examining effects of heterogeneity and mean conditions simultaneously within communities. However, our results also contrast with several studies that have proposed or found negative or neutral relationships between local heterogeneity and species diversity when mediated by species interactions or disturbance regimes (Baer et al. 2004, Tamme et al. 2010, Bartels and Chen 2010).

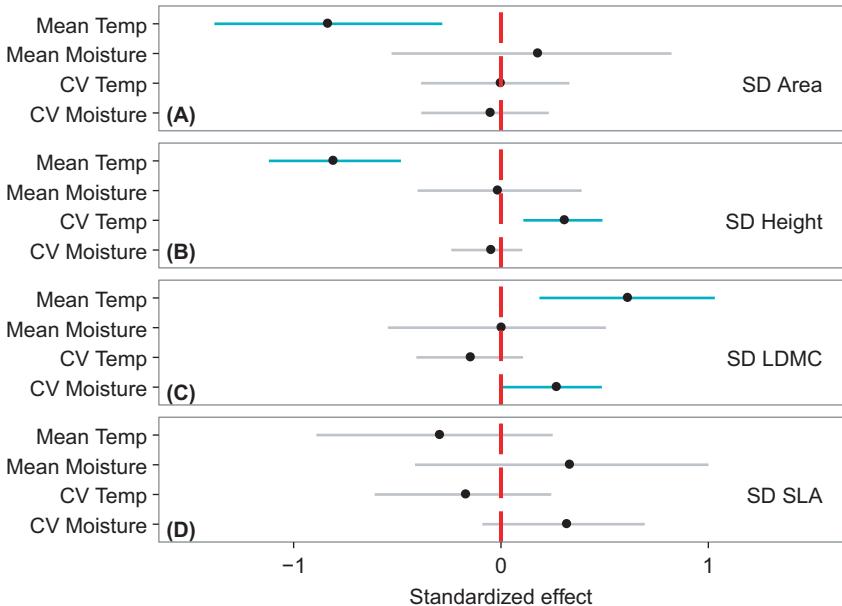


Figure 4. Effect of environmental means and variation on standard deviation of (A) leaf area, (B) height, (C) leaf dry matter content (LDMC), and (D) specific leaf area (SLA). See Methods for details of data transformations and linear mixed models. Horizontal bars show bootstrap 95% confidence intervals from a linear mixed model with all environmental variables for each trait. Bars colored blue have confidence intervals that do not overlap zero. Center points show parameter estimates.

A range of mechanisms could generate the observed relationships between trait variability and environmental conditions (Fig. 3, 4). The relationship between height and temperature heterogeneity is consistent with variation in thermal environments expected due to increased boundary layer thermal conductance and reduced longwave heating for taller plants (Monteith and Unsworth 2007). The relationship between moisture heterogeneity and LDMC variation is consistent with the importance of water availability for determining water allocation within plant tissues (Lambers et al. 2008). Mean temperature was negatively related to variation in both height and leaf area but positively related to variation in LDMC. This result may reflect trait-specific responses to environmental gradients, where either high or low values of an environmental variable can be more limiting depending on the trait of interest. For example, the negative relationship between leaf area variation and mean temperature is consistent with a reduced range of possible energy balance strategies in cold environments (Nicotra et al. 2011), while the positive relationship between LDMC variation and mean temperature is consistent with a reduced range of possible carbon allocation strategies in warm environments (Wilson et al. 1999).

The climate variables we explored had a large role in explaining trait variation. Marginal r^2 -values ranged from 0.23 to 0.47 for the linear mixed models. These values are high given that other conditions such as soil nutrient load (Wright et al. 2001, Lavorel and Garnier 2002), soil depth (Price et al. 2017), and light availability (Poorter 1999) may also play a large role in determining plant trait values. While we did not measure these variables in the current study, their heterogeneity may also contribute to and drive trait variation across scales, and be determined by both external climatic conditions and biotic interactions, e.g. shading of one individual by another.

Non-environmental processes also may have strong effects on trait variation at the local scale. Many previous studies have focused on internal niche partitioning driven by species interactions (Keddy 1990, Weiher and Keddy 1995, Wright et al. 2001). In addition, dispersal limitation or mass effects from nearby communities (Leibold et al. 2004, Ozinga et al. 2005) may lead to changes in trait variance without any direct effect from small-scale environmental conditions (Enquist et al. 2015). Such effects are widely thought to be important in determining local richness patterns (Hurt and Pacala 1995, Hubbell 2001) and should also be relevant for trait distributions (but see Spasojevic and Suding 2012).

The increased role of environmental heterogeneity we propose here does not necessarily imply that abiotic factors are more important than biotic factors in community assembly. Rather, it suggests that two of the major components of community assembly – environmental filtering and biotic interactions – are closely linked and possibly not separable. This conclusion seemingly contrasts with conceptual frameworks (HilleRisLambers et al. 2012, Kraft et al. 2015) in which assembly is seen as a sequential process of filtering followed by interactions. At sufficiently fine spatial scales, these two processes may become functionally equivalent. For example, individual plants can shade out other plants – a competitive interaction – but do so by

filtering based on light resource requirements (e.g. Fajardo and Siefert 2016). Thus, it may not always be possible to tease apart environmental filtering and biotic interactions in community assembly, particularly at scales where individuals can interact with multiple biotic and abiotic conditions (Tamm et al. 2010).

The results of this study and several others (Swenson and Enquist 2009, Baraloto and Coutron 2010, Scherrer and Körner 2011) do point to the need to measure environmental conditions at scales relevant to physiological and ecological processes. While detailed measurements are inherently more challenging to conduct, new remote sensing technologies including infrared cameras (Costa et al. 2013, Faye et al. 2015) and hyperspectral imaging (Asner et al. 2015) can make measurements of microclimate and trait variation more tractable. Determining the appropriate spatial scales at which to conduct these analyses remains an open question. Our variance partitioning and spatial variogram analyses showed that in the communities studied here, high levels of variation in both traits and climate occurred at the < 20 cm scale (Supplementary material Appendix 1 Fig. A4–A5). We note that at these small scales, organisms can alter their surrounding environmental conditions – for example, a plant with larger leaves reducing temperatures through shading. Therefore, while this study investigates empirical predictors of community functional trait distributions, feedback from organisms makes it difficult to tease apart cause and effect.

Broadly, this study shows the importance of small-scale environmental conditions (both means and heterogeneity) in driving community trait variation. Our results indicate that within-community functional trait variation can be a large component of the observed trait variation ($\sim 50\%$) and can be driven in part by local abiotic factors including environmental variability. Thus, the presumed matching between phenotypes and the abiotic environment (Norberg et al. 2001, Enquist et al. 2015) may happen at much finer spatial scales than previously assumed. Intriguingly, our results also suggest that observed measures of community trait variance may be a good proxy for the degree of local abiotic heterogeneity. Understanding local linkages between environmental conditions, physiological tolerances and species interactions may ultimately prove important for managing functional diversity and ecosystem processes in applied contexts (Lavorel and Garnier 2002, Laughlin 2014). For example, increased heterogeneity could help to buffer communities against changes in mean environmental conditions (Fridley et al. 2011, Scherrer and Körner 2011). The mechanisms linking these variables should be relevant at both local and regional scales, suggesting that local-scale environmental heterogeneity as well as environmental means are key drivers of functional diversity globally.

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Supplementary material (Appendix oik-04311 at <www.oikosjournal.org/appendix/oik-04311>). Appendix 1.