



Research

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Do community-weighted mean functional traits reflect optimal strategies?

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The notion that relationships between community-weighted mean (CWM) traits (i.e. plot-level trait values weighted by species abundances) and environmental conditions reflect selection towards locally optimal phenotypes is challenged by the large amount of interspecific trait variation typically found within ecological communities. Reconciling these contrasting patterns is a key to advancing predictive theories of functional community ecology. We combined data on geographical distributions and three traits (wood density, leaf mass per area and maximum height) of 173 tree species in Puerto Rico. We tested the hypothesis that species are more likely to occur where their trait values are more similar to the local CWM trait values (the ‘CWM-optimality’ hypothesis) by comparing species occurrence patterns (as a proxy for fitness) with the functional composition of forest plots across a precipitation gradient. While 70% of the species supported CWM-optimality for at least one trait, nearly 25% significantly opposed it for at least one trait, thereby contributing to local functional diversity. The majority (85%) of species that opposed CWM-optimality did so only for one trait and few species opposed CWM-optimality in multivariate trait space. Our study suggests that constraints to local functional variation act more strongly on multivariate phenotypes than on univariate traits.

1. Background

Determining how functional traits respond to environmental conditions to mediate species distributions and patterns of community diversity is a central question in ecology [1–3]. These links are critical for understanding ecosystem functioning and community-level responses to environmental change. However, two prominent and contrasting patterns pose serious challenges for our understanding of trait–environment relationships: strong community-level trait–environment relationships and high amounts of local trait variation [1,4].

On one hand, a number of studies have demonstrated systematic variation of community-weighted mean (CWM) trait values (i.e. plot-level trait values weighted by species abundance) along abiotic gradients (e.g. [5–7]). When these patterns are consistent with known physiological mechanisms (e.g. dominance of traits associated with drought tolerance in arid sites), they imply environmentally mediated fitness differences among species with different functional strategies (‘environmental filtering’). For instance, CWM values of tree wood density (WD; g cm^{-3}) and leaf mass per area ($\text{LMA} = 1/\text{specific leaf area (SLA)}$; g m^{-2}) generally decline with increasing precipitation [5,8]. Because these traits correspond to resource acquisition and utilization strategies [9,10], these trait–environment relationships can be interpreted in terms of physiological trade-offs related to resource availability (i.e. drought resistance and resource conservation in dry conditions versus rapid growth and resource acquisition when water is abundant). Highlighting this concept, several trait-based models of plant community assembly are built on the assumption that CWM trait values reflect the locally ‘optimal’ trait strategy given the regional species pool and environmental conditions of a site (figure 1a; e.g. [11–14] but see [4] for an approach based on intraspecific trait variation). In other words, species with trait values nearest to the CWM values in a particular location are predicted have relatively high fitness, because they presumably occur at relatively high abundance and thus contribute most strongly to

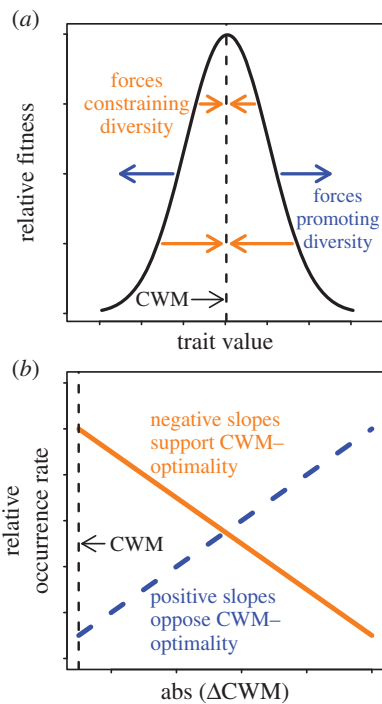


Figure 1. (a) Variation of CWM traits suggests selection towards a locally optimal trait value (inward-pointing arrows). However, local functional diversity implies opposing mechanisms that promote local functional diversity (outward-pointing arrows). We used ENMs to test the hypothesis that species would be less likely to occur in areas where their trait values are more distant from the local CWM values (the ‘CWM-optimality hypothesis’). See online version for colour legend. For each species and trait, we calculated ΔCWM as the absolute difference between the species-mean trait value and the CWM value at each study plot. (b) Summarized predictions of the CWM-optimality hypothesis. (Online version in colour.)

the CWM [14]. This ‘CWM-optimality’ hypothesis thus emphasizes processes that constrain local functional diversity (e.g. environmental filtering) and is consistent with (beta) niche partitioning along resource gradients as a primary driver of species distributions and community diversity patterns [15].

On the other hand, a high proportion of functional diversity is typically reported within local communities and among sites with similar abiotic conditions, e.g. [5,16,17]. For instance, de Bello *et al.* [16] found that within-site variation of SLA accounted for approximately 90% of the total observed variation across regional climatic gradients. At a larger scale, more than one-third of the total global variation in SLA occurs within areas of similar abiotic conditions, as opposed to among sites that vary with respect to climate variables [5]. Together, shifts of CWM trait values along abiotic gradients and the substantial proportion of local trait variation represent a major challenge for prediction in community ecology (and for the CWM-optimality hypothesis in particular), because they imply the combined action of mechanisms that constrain and maintain local functional diversity [18–20]. Reconciling these contrasting patterns is a key to advancing a predictive theory of functional community ecology.

Several mechanisms that may promote or maintain local functional diversity are at least partly consistent with the CWM-optimality hypothesis. For instance, species with trait values that diverge from the local CWM on one trait axis may persist locally if environmental constraints act more strongly on multivariate phenotypes than individual traits [3,21,22]. In fact, Shipley *et al.*’s [11,23] maximum entropy model of

community assembly suggests that the ‘optimal’ local trait strategy should be best reflected by the full vector of CWM values, not necessarily the CWM value of any single trait. Additionally, disequilibrium dynamics (e.g. source–sink populations) could lead to the local occurrence of functional types with inferior fitness [24]. Other mechanisms that could contribute to the maintenance of local functional diversity are, however, not entirely consistent with the CWM-optimality hypothesis. For example, relatively fine-scale spatial or temporal resource heterogeneity could promote local (alpha) niche partitioning in the context of regional (beta) niche partitioning. In general, a better understanding of occurrence patterns and functional characteristics shared by species that support and oppose the CWM-optimality hypothesis could give valuable insight into the mechanisms that promote local functional diversity.

A strict test of the CWM-optimality hypothesis requires data on variation of fitness and functional traits of numerous species in local communities across environmental gradients. Combined with information on functional traits, however, ecological niche models (ENMs) that characterize species occurrence patterns across environmental gradients represent an unexploited opportunity to examine whether the core prediction of the CWM-optimality hypothesis (fitness is highest in locations where a species trait value matches the local CWM) holds true for patterns of species occurrence. Although occurrence patterns may not directly reflect fitness (*also see* §4), ENMs enable us to examine how species’ predicted potential distributions (given the abiotic conditions of a site) relates to the functional composition of local communities.

We combined data on geographical distributions and three key functional traits (WD, LMA) and maximum height) for 173 tree species in Puerto Rico. We compared predicted occurrence patterns with the functional composition of forest plots across a precipitation gradient to address the following questions:

- (1) *Are species more likely to occur in areas where their trait values are more similar to the local CWM?* If CWM trait values reflect optimal functional strategies given local abiotic conditions, we expect negative relationships between the probability of occurrence and the difference between a species trait value and the local CWM value. Positive relationships between occurrence probability and the difference between a species trait value and the local CWM would oppose the CWM-optimality hypothesis and reflect successful alternative strategies.
- (2) *To what extent do species support or oppose the CWM-optimality hypothesis on single versus multiple univariate trait axes, and in multivariate trait space?* If environmental constraints on fitness act more strongly on multivariate phenotypes than on individual traits [3,20,25], we expect species that oppose the CWM-optimality hypothesis will be most likely do so for only a single univariate trait axis. Similarly, we expect stronger support for CWM-optimality in the context of multivariate trait space than for univariate trait axes, and few species to oppose CWM-optimality in multivariate trait space. In parallel, we expect that species will likely support the CWM-optimality hypothesis for multiple univariate trait axes and in multivariate trait space.
- (3) *Do the groups of species that support and oppose the CWM-optimality hypothesis share particular trait values or occurrence patterns?* We predict that the strongest support and opposition for the CWM-optimality hypothesis will

be evident among species that typically occur in locations subject to strong stabilizing selection for particular trait axes (e.g. drought exerts stabilizing selection for high WD and LMA, and sets a physiological limit to $H_{\max}$ [26]). Consequently, we expect that species with trait values closely matching the CWM values in dry locations will most strongly support the CWM-optimality hypothesis, whereas species with divergent trait values in these locations will provide the strongest opposition.

2. Material and methods

(a) Study system and tree census plots

We established 12, 0.25 ha (50×50 m) plots in four protected forests of Puerto Rico that occur across a precipitation gradient ranging from ca 800 to 2200 mm yr⁻¹ (electronic supplementary material, table S1). All plots are located on limestone-derived soils, which constitute about one-third of Puerto Rico's land area [27]. Plots were located randomly in mature stands that lacked signs of human land-use and recent natural disturbance. In each plot, we identified all woody stems (excluding lianas) of 1 cm or more diameter at 1.3 m above the ground (diameter at breast height, DBH), measured their DBH and estimated their height to the nearest 0.5 m.

(b) Functional traits

We collected trait data from 1 to 32 (mean = 9) individuals of 173 species from each forest where individuals were available. Electronic supplementary material, appendix S1 provides details on trait measurements. Briefly, WD (g cm⁻³) is related to a growth/mortality trade-off; low WD confers rapid growth, high hydraulic conductance and low investment in structural materials [8], whereas high WD is associated with resistance to drought-induced cavitation and low mortality [10,28]. LMA (g cm⁻²) is positively related to leaf lifespan and, more generally, to variation in life-history strategies ranging from fast growth and high mortality by rapid photosynthetic return on carbon investment (low LMA) to slow growth and low mortality by retaining nutrients for a longer time (high LMA) [5]. *Maximum height* ($H_{\max}$; m) is associated with competitive ability in light-limited environments [29] but can be constrained by water availability [26]. Prior to analysis, we log-transformed LMA and $H_{\max}$ values to correct for skewness. Here, we use species-mean trait values because the diversity and spatial extent of our study area precluded thorough measurement of intra-specific variation (see §4). Our trait dataset represents 83% of the observed species (accounting for 98% of the total basal area).

(c) Ecological niche models

We used Maxent v. 3.3.3 k [30] to quantify the statistical relationships between predictor variables at locations where each species was observed versus 'background' locations in the study region. Full details on methods of ENM construction (including data processing and model evaluation) are provided in the electronic supplementary material, appendix S2. Briefly, we compiled georeferenced occurrence records from online databases, several herbaria and georeferenced observations from other studies (e.g. [31]). The full dataset contains 17 479 records, with 11–192 (mean = 54) observations for each focal species. Note that observations from the plots used to calculate CWM values for this study were not included in the occurrence dataset. We used one edaphic and four climatic variables known to influence tree growth and mortality as predictor variables: soil parent material [32], logarithm of mean annual precipitation (mm yr⁻¹), coefficient of variation of monthly precipitation (unitless), the average temperature of coldest month (°C) and mean daily temperature range (°C) [33].

Maxent generates a gridded surface of values proportional to the expected number of occurrences per unit area for each species

(i.e. the 'relative occurrence rate', ROR) [34]. To facilitate comparison across species, we rescaled ROR values within species to range from 0 to 1 across the study extent. To balance model fit and predictive ability, we conducted species-specific tuning using the R package ENMeval [35]. We measured performance of ENMs using test AUC values and the test point omission rate based on the minimum training presence value (OR_{MTP}) [36].

(d) Statistical analyses

To evaluate the relationship between ROR (output of ENMs) and distance from the local CWM for each trait, we calculated the CWM values for each trait t and each plot p as: $CWM_{tp} = \sum_{i=1}^S a_{ip} \times t_i$, where a_{ip} is the relative basal area of species i in plot p and t_i is the mean trait value of species i . We then calculated ΔCWM_{tip} as the absolute difference between the species-mean value of trait t for species i (t_i) and the CWM value of trait t for plot p (CWM_{tp}). To facilitate comparison across traits, we scaled the trait values prior to analysis by subtracting the mean and dividing by the standard deviation of each trait, across species. If CWM trait values simply reflect the trait values of dominant species, our hypothesis may be trivial (i.e. species are most likely to occur where they are most abundant). To avoid this possibility, when calculating ΔCWM_{tip} values for each focal species, we excluded the focal species from the CWM calculations. In other words, we calculated the distance in trait space between each focal species and the CWM value based on *all other species* in each plot. Our results, however, were nearly identical if focal species were included in these calculations (electronic supplementary material, appendix S3). Values of ΔCWM increase from zero as t_i becomes more different from the local CWM value. To quantify ΔCWM in multivariate trait space, we measured the Euclidean distance between the vector of scaled trait values for each species and the multivariate centroid of each plot. Separately for each species, we used regression to relate ΔCWM values (separately for each trait and the multivariate metric) with ROR values at each plot. We refer to species with significantly negative [or positive] slopes as those that support [or oppose] the CWM-optimality hypothesis (figure 1b).

To address *Question 1* (below), we used a randomization procedure to determine whether the number of species with significant slopes (positive and negative) for the relationship between ΔCWM and ROR was greater than expected by chance. Specifically, we shuffled ROR values among plots and within species 999 times. During each iteration, we counted the number of statistically significant ($p < 0.05$) slopes across species. We then compared the observed number of significant slopes to the 2.5 and 97.5% quantiles of these distributions. This approach maintains species traits values, CWMs, and the observed distribution of RORs within species. We addressed *Question 2* by counting the number of univariate trait axes for which individual species showed significant support or opposition to the CWM-optimality hypothesis. Note that a single species could exhibit negative *and* positive slopes for different trait axes.

To determine how species trait values are related to the conditions where they most often occur, we extracted values of the four climate variables included in the ENMs from the grid cell(s) with maximum values of ROR for each species. These values correspond to measures of niche position with respect to climate gradients and below we refer to them as the conditions at maximum ROR (or, ROR_{max}). Here we focus on occurrence patterns with respect to mean annual precipitation based on our *a priori* expectations about relationships between the functional traits under consideration and water availability (see §§1 and 2). We used linear regression to evaluate whether species-mean trait values were related to their value of mean annual precipitation at ROR_{max}.

We also used a randomization procedure to determine whether certain trait values or occurrence patterns are shared within the

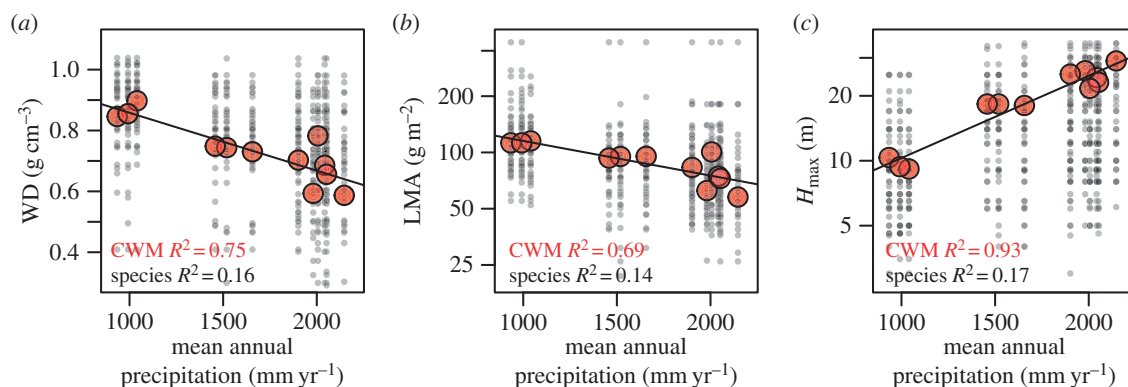


Figure 2. Variation in (a) WD, (b) LMA, (c) and $H_{\max}$ along a gradient of mean annual precipitation for 12 forest plots. Large circles represent CWM trait values, smaller points represent trait values of species that occurred in each plot. Trend lines and R^2 -values correspond to regressions of CWM values and mean annual precipitation. (Online version in colour.)

groups of species that significantly supported and opposed the CWM-optimality hypothesis (Question 3). For this, we calculated the mean trait value and precipitation at $ROR_{\max}$ for 9999 randomly selected assemblages comprising the same number of species in each of these groups, for each trait. We compared observed mean values for each group with the 95%- and 90%-quantiles of these distributions to determine whether the species that supported and opposed the CWM-optimality hypothesis (i) have relatively high or low trait values and (ii) tend to occur in relatively dry or wet locations. All analyses were conducted in R v. 3.1.3 [37].

3. Results

For all three traits, CWM values varied strongly with respect to mean annual precipitation (figure 2). Specifically, WD and LMA declined, and $H_{\max}$ increased, with increasing precipitation (R^2 -values were all greater than or equal to 0.69). At the same time, species-mean trait values showed a high degree of within-plot variability (figure 2). Across species, ENMs had moderate to good prediction accuracy (mean test AUC = 0.74) and low values of OR_{MTP} , indicating that models were generally not overfit (mean OR_{MTP} = 0.06; electronic supplementary material, appendix S2). Species-mean trait values were correlated with their values of precipitation at $ROR_{\max}$ in ways that mirrored shifts in CWM traits across the precipitation gradient. Specifically, species that tend to occur in relatively wet areas had relatively low WD (R^2 = 0.24) and LMA (R^2 = 0.23), and higher $H_{\max}$ (R^2 = 0.23). All pairwise comparisons of species-mean trait values were significantly correlated (Pearson's r for WD–LMA = 0.56; WD– $H_{\max}$ = –0.44; LMA– $H_{\max}$ = –0.21), as were CWM trait values (Pearson's r for WD–LMA = 0.97; WD– $H_{\max}$ = –0.92; LMA– $H_{\max}$ = –0.86).

(a) Question 1. Are species more likely to occur in areas where their trait values are more similar to the local community-weighted mean?

Figure 3a–d shows histograms of species-specific regression slopes between ΔCWM and ROR. The proportions of the 173 focal species with statistically significant slopes (i.e. p < 0.05) were 51% for WD, 48% for LMA, 61% for $H_{\max}$ and 57% for the multivariate trait metric. These values were far higher than the random expectation of 8% for each trait. Across species, the mean R^2 of the regression models between ΔCWM and ROR was 0.36 for WD, 0.31 for LMA, 0.46 for $H_{\max}$ and 0.40 for the multivariate trait metric.

In support of the CWM-optimality hypothesis, there were more species with significantly negative slopes than randomly expected for all three univariate traits and the multivariate trait metric (expected 97.5% quantile = 5%; observed for WD = 43%, LMA = 39%, $H_{\max}$ = 48%, multivariate = 51%). When considering only the statistically significant slopes, more than 79% were negative for each individual trait and 89% were negative for the multivariate metric. To a lesser degree (and contrary to the CWM-optimality hypothesis), there were also more species with significantly positive slopes with respect to univariate and multivariate trait axes than the 5% based on random expectation (WD = 8%, LMA = 9%, $H_{\max}$ = 13%, multivariate trait = 6%).

(b) Question 2. To what extent do species support or oppose the community-weighted mean-optimality hypothesis on single, multiple and multivariate trait axes?

Figure 4 shows the proportions of study species that significantly supported [or opposed] the CWM-optimality hypothesis for different numbers of trait axes. In total, 70% of the study species supported CWM-optimality for at least one univariate trait axis. Similar proportions of species supported CWM-optimality along one (28%) and two (25%) trait axes, and somewhat fewer species (17%) did so for all three traits. The proportion of species showing significant support for CWM-optimality in multivariate trait space (51%) was higher than the proportion for any one of the univariate traits. By contrast, 25% of the study species significantly opposed CWM-optimality for at least one univariate trait axis, and the majority (84%) of these did so only for a single trait. Moreover, most species (69%) that opposed the CWM-optimality hypothesis on one trait axis also showed significant support for CWM-optimality with respect to at least one other trait (electronic supplementary material, appendix S4). Only 6% of species (one more than the random expectation) significantly opposed CWM-optimality when considering multivariate trait space.

(c) Question 3. Do the groups of species that support and oppose the community-weighted mean-optimality hypothesis share particular trait values or occurrence patterns?

We predicted that the strongest evidence both for and against the CWM-optimality hypothesis would be among species

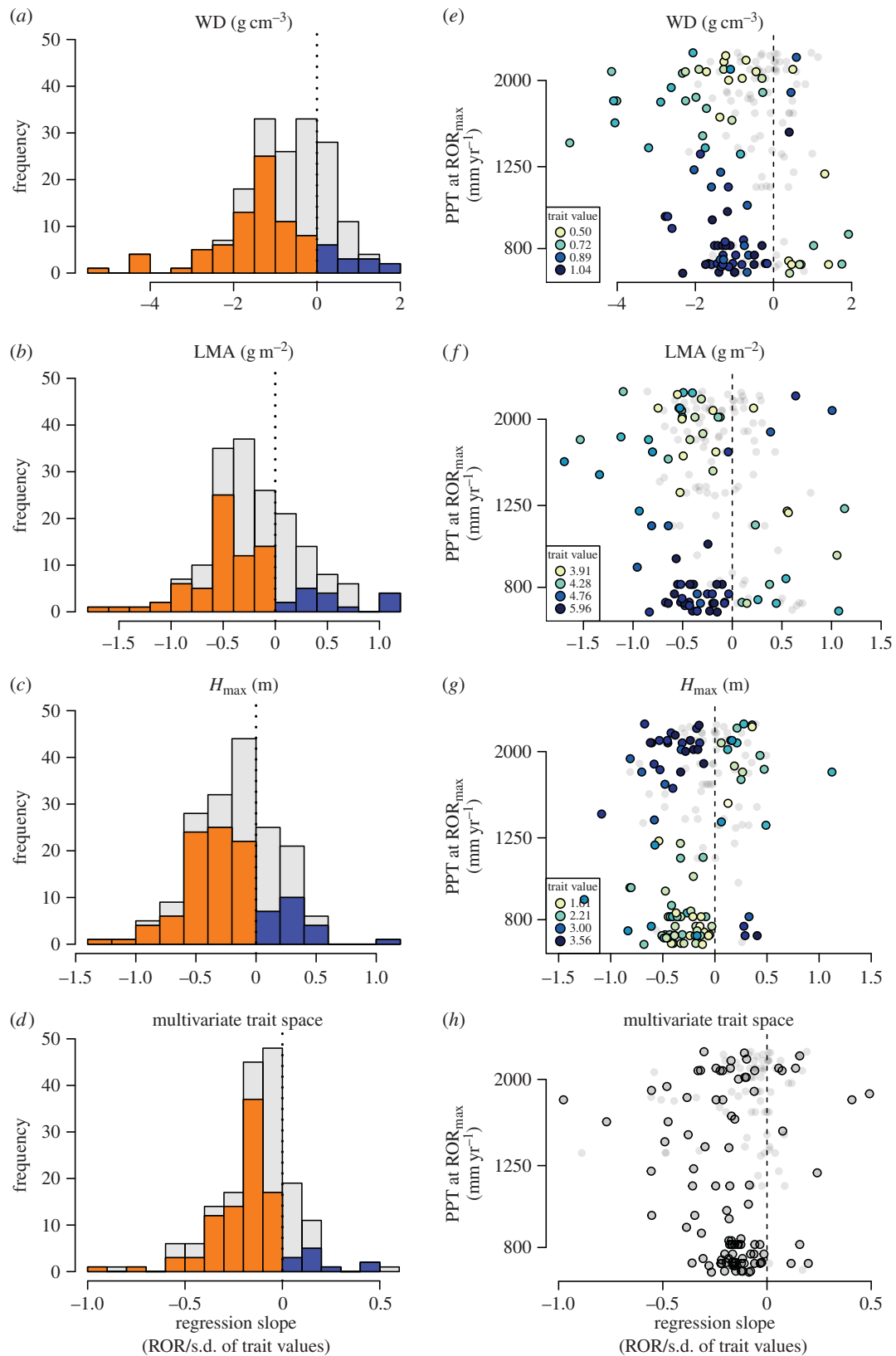


Figure 3. Panels (a–d) show histograms of species-specific slopes for the regression between ΔCWM values and ROR. Light grey bars show slopes for all species; statistically significant slopes (i.e. $p < 0.05$) are darkened (negative and positive slopes are orange and blue in the online version of the figure, respectively). Panels (e–h) show species-specific slope values (as in a–d) plotted against their value of precipitation at ROR_{max}. In (e–g), point colours represent species trait values (see legends) and species with non-significant slopes are grey without black circles. In (h), species with significant slopes are shown with black circles. Units of slope values are ROR divided by 1 s.d. of the relevant trait. (Online version in colour.)

that typically occur in locations facing strong stabilizing selection for particular traits. Consistent with this prediction, species that supported CWM-optimality for the univariate traits and the multivariate trait metric had, on average,

relatively high WD and LMA, low H_{max} (i.e. short stature) and predominantly occurred in dry areas (figure 3e–h; electronic supplementary material, appendix S5). Species that opposed the CWM-optimality hypothesis for WD and LMA

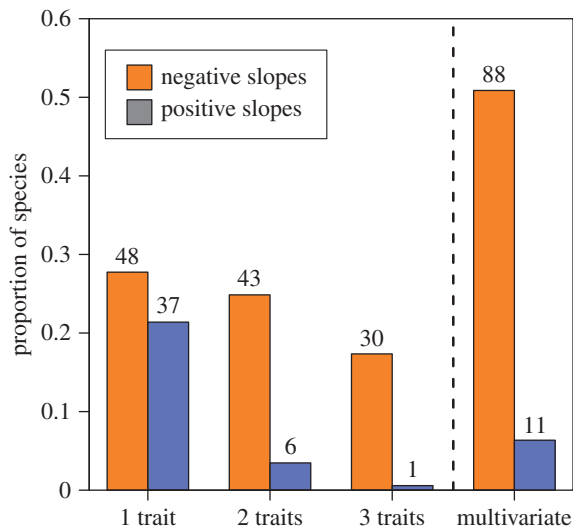


Figure 4. Barplot with the proportion (and number) of study species ($N = 173$) with significantly negative and positive regression slopes between ΔCWM and ROR for different numbers of univariate trait axes, and in multivariate trait space. Because some species exhibited both positive and negative slopes for different trait axes, the sum of the numbers of species shown is greater than the total number of study species. (Online version in colour.)

had relatively low values, on average, for these traits and tended to occur in relatively dry areas. Species that opposed CWM-optimality with respect to $H_{\max}$, however, tended to be short statured and to occur in relatively wet forests. Species that opposed CWM-optimality in multivariate trait space had, on average, relatively low values of LMA but were not associated with particularly high or low values of WD, $H_{\max}$ or precipitation at $\text{ROR}_{\max}$.

4. Discussion

Overall, our results provide mixed evidence for the CWM-optimality hypothesis, suggesting both broad-scale environmental filtering and fine-scale niche partitioning as important drivers of functional diversity across environmental gradients. Below, we evaluate evidence for the CWM-optimality hypothesis and highlight insight gained to the mechanisms that promote local functional diversity in this system. We then discuss the implications for our finding that constraints to local functional variation appear to act more strongly on multivariate phenotypes than univariate trait axes.

(a) Evaluating the community-weighted mean-optimality hypothesis

A prerequisite for the CWM-optimality hypothesis is that CWM trait values vary with respect to environmental gradients. Indeed, we observed clear shifts of CWM traits that are consistent with physiological trade-offs mediated by water availability and competition for light [9,10,29]. These trends imply different mechanisms of selection (e.g. environmental filtering, competitive dominance hierarchies) that constrain local trait diversity at different ends of the precipitation gradient. Specifically, hydraulic safety appears to be particularly important in dry forests, especially those on limestone soils with low water-holding capacity [38]. Short stature in

these forests is likely the result of hydraulic limitation [26]. In wetter sites, a decline in hydraulic limitation is coupled with an increased competitive advantage in terms of carbon gain for rapid growth and tall stature [29].

Also consistent with the CWM-optimality hypothesis, RORs were negatively related to ΔCWM values for more species than randomly expected, for all three univariate traits. In general, these results provide additional support to the role of physiological constraints mentioned above that appear to underlie broad-scale environmental filtering. In our study in particular, the majority of species supporting the CWM-optimality hypothesis tended to occur in dry locations and have relatively high values of WD and LMA. These species make large investments in wood and leaf construction, which could limit their distributions to areas where those costly strategies are most advantageous.

Our results are consistent with another recent study (involving tree seedlings in China and Puerto Rico) that examined the relationship between local abundance and the deviation of species trait values from the local CWM [24]. In that study, abundance was higher for species whose trait values were closer to the local CWM for a majority of univariate traits studied. Notably, however, the relationship between abundance and deviation from the CWM was only significant for one trait at the Puerto Rico site, potentially reflecting site or regional differences in the degree to which univariate CWM values reflect optimal phenotypes. This difference might suggest that different traits (or multivariate phenotypes) exert a particularly strong influence on local abundance in some sites.

Here, we focused on the absolute value of the difference between species trait values and CWM values, because it provides a relatively straightforward answer to our central question. However, future work examining the signed value of this difference might provide additional insight. For instance, significant slopes between fitness (or some fitness proxy) and the signed value of ΔCWM might help to disentangle the effects of directional versus stabilizing selection.

Additional evidence in support of the CWM-optimality hypothesis comes from our observations that species-mean trait values were correlated with values of precipitation at $\text{ROR}_{\max}$ (i.e. the level of precipitation where a species is most likely to occur). Generally, these results offer additional support for broad-scale environmental filtering (driven by precipitation) as an important mechanism in determining species geographical distributions and constraining local functional diversity. On the other hand, the fairly low proportion of explained variance in these relationships (less than 25%) indicates a substantial amount of functional variation among species for which similar abiotic conditions represent highly suitable habitat. One probable explanation for these results is that while highly aggregated climatic variables capture coarse trends in community functional composition, some combination of fine-scale habitat heterogeneity, temporal niche partitioning and recruitment limitation is critical for the maintenance of local diversity. Regions of karst topography, including our study system, are noted for particularly high levels of microhabitat heterogeneity [27]. Environmental conditions including soil depth, chemistry, water-holding capacity and exposure to sun and wind vary dramatically at fine scales, thus providing the potential for fine-scale niche partitioning as an important mechanism for the maintenance of local functional diversity. Temporal variability in the system could also promote local

functional variation [39]. For instance, if dry and wet years favour species with different trait values, species with ‘sub-optimal’ traits could persist during ‘off’ years because of temporal variation [22]. Finally, recruitment limitation (e.g. dispersal limitation) of competitively dominant species can facilitate coexistence of inferior competitors [40]. Future work aimed at directly linking functional traits to mechanisms of species coexistence, therefore, will benefit by incorporating data on fine-scale environmental heterogeneity [18] and temporal variation in resource availability and demographic performance.

Contrary to the CWM-optimality hypothesis, more species than expected also had significantly positive relationships between ROR and ΔCWM , reflecting the success of alternative functional strategies and the high-dimensional nature of species coexistence [17,25,41,42]. For instance, several species with low WD that are particularly abundant in dry forests of our study system (e.g. *Bursera simarubra*, *Pisonia albida*) appear to cope with limited water availability via rapid water uptake, water storage in the stem, and a deciduous habit to reduce transpirational water loss [43]. In fact, most species that deviated from the CWM-optimality expectations with respect to WD and LMA have relatively low trait values and tend to occur in dry locations. By allocating relatively few resources to stem and leaf construction, it is possible that these ‘renegade’ dry forest species free up resources to devote towards construction of other materials (e.g. taproots or reproductive output) that promote their ability to tolerate drought conditions. By contrast, the majority of ‘renegade’ species with respect to H_{max} tend to be relatively short statured shrubs and trees that occur most commonly in wetter forests. These species are understory and gap specialists that are capable of either regeneration in low light conditions or rapid reproduction in ephemeral, high-resource conditions typical of forest gaps. In general, we found strong evidence that the traits examined here are linked to fitness differences along the precipitation gradient. However, a high degree of local functional variation also suggests that these trait axes reflect important niche differences essential for maintaining local biodiversity.

We reiterate that while correlative ENMs are useful tools for predicting species’ potential occurrence patterns, they do not necessarily correspond to local abundance [44–46] or demographic performance [47]. Future studies that incorporate experimental manipulations (where possible) and dynamic demographic data are essential to identify the ultimate fitness consequences of functional variation as well as the particular mechanisms underlying trait-mediated niche partitioning [3,18,25,48,49]. Another limitation of our study is that species-mean trait values obscure the contribution (and consequences) of intraspecific variation to functional diversity patterns [3,4,50]. However, we do not expect intraspecific trait variation to change the overall conclusions reached here for two main reasons. First, a high degree of species turnover across our plots suggests that intraspecific trait variation accounts for a relatively minor proportion of total trait variation in this study. Second, we expect trends in intraspecific trait variation to mirror trends in interspecific variation. This would reduce the range of ΔCWM values observed but should not change the overall results. Nonetheless, work incorporating intraspecific trait variation will continue to yield valuable insights to understanding fitness consequences of trait–environment relationships [3,4,50].

(b) Trait correlations, trade-offs and the multidimensional phenotype

As we predicted, most species that supported the CWM-optimality hypothesis did so on multiple univariate trait axes, and there was substantial support for CWM-optimality when considering multivariate trait space. By contrast, most species that exhibited a ‘renegade’ strategy did so for only one univariate trait axis and the majority of these species supported CWM-optimality for at least one other trait axis (electronic supplementary material, appendix S4). Moreover, only one more species than randomly expected deviated from CWM-optimality expectations when considering multivariate trait space. This result is particularly striking given that our measure of multivariate trait space is based on only three moderately correlated traits. While we currently lack data to examine them here, below-ground traits are undoubtedly important for describing hydrological strategies in this system [51] and would provide valuable additional insight to the diversity of successful strategies.

Together, our results suggest that species with ‘alternative strategies’ on one trait axis are more strongly constrained when considering the multivariate phenotype. This has particular relevance for methods designed to predict species abundances based on functional traits (e.g. CATS; [11,13]). Specifically, our study supports the idea that functional strategies are more strongly constrained in multivariate trait space than with respect to univariate trait axes [3,21,52]. While our results therefore support the use of multiple CWM trait values as the optimal multidimensional phenotype, future work should strive to directly link fitness components (e.g. survival, growth and reproduction) to trait–environment interactions.

One of our central arguments is that resolving the contrasting patterns of trait–environment relationships and high local trait variation is critical for developing predictive models in community ecology. This is especially important because local functional diversity, in addition to the functional composition of dominant species, may be crucial in terms of community- and ecosystem-level responses to environmental change [53]. An analogous pair of contrasting patterns found in evolutionary biology is the prevalence of genetic variation in the midst of strong stabilizing and directional selection (which is expected to deplete genetic diversity) [54]. In their review, Walsh & Blows [54] argued that the apparent contradiction has emerged, at least in part, through the examination of individuals traits that may only be relatively weakly correlated with actual fitness. By contrast, multivariate combinations of traits (that reflect various components of fitness) may be more tightly correlated with total fitness and thus more likely to be constrained by selective pressure [3]. Fluctuating environmental conditions may also contribute to local genetic diversity analogously to the ways that temporal and fine-scale spatial environmental heterogeneity could promote functional diversity of ecological communities [55]. Ultimately, we envision continued progress on these questions through synthesis of related questions in community ecology and population genetics (e.g. [3,56]).

5. Conclusion

The infusion of a functional perspective into community ecology is providing valuable insight into both the physiological mechanisms underpinning species’ broad-scale geographical distributions and patterns of local diversity [57]. However,

continuing to advance our understanding of the factors governing local functional diversity requires a stronger integration of local processes and community context with species population dynamics and geographical distributions [58]. Further development of a functional perspective in community ecology will help fill these gaps by providing mechanistic links between abiotic gradients and diversity patterns.

Data accessibility. Data associated with this publication are available from Dryad: <http://dx.doi.org/10.5061/dryad.34kt1>.

Authors' contributions. Both authors conceived the conceptual framework; R.M. collected data, designed and conducted analyses; M.U. oversaw analyses; both authors wrote the manuscript.

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