TITLE

When traits vary across species but performance doesn't: One solution to the paradox

AUTHORS

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ABSTRACT

Variation in plant traits related to size and architecture, water relations, and resource uptake reflect important dimensions of plant function that may explain how different species are adapted to their local environments. Within a local community, variation in many of these traits may promote coexistence of competing species through niche partitioning. If differences in traits are associated with differences in performance, and there is substantial trait variation within local communities, we might expect competitive asymmetries that would lead to competitive exclusion. Alternatively, if combinations of trait differences converge on similar performance trait differences associated with niche partitioning may lead to phenotypically diverse species that exhibit similar performance. Here we develop a model showing that when the major axes of trait covariation do not align with the axis of performance variation, species that differ in structural traits, i.e., species having ‘alternative designs,’ may achieve similar performance. We apply this model to data from commonly co-occurring *Protea* species in the Cape Floristic Region, South Africa and demonstrate that despite large differences in traits that are related to performance, trait covariation leads to minimal performance differences among species.

KEYWORDS

Intraspecific trait variation, trait covariation, alternative designs, plant functional traits

INTRODUCTION

Hutchinson noted in his seminal paper – *"An Homage to Santa Rosalia"* – that there seem to be more species on the planet than niches to hold them (Hutchinson 1959). Since then, many investigators have sought to identify niche axes along which species differ that might allow species to coexist, often using traits to understand the functional link between an organism's phenotype and its fitness in a given environment (Schoener 1968; Brown and Lieberman 1973; Cody 1986; Gillespie 2004; Treurnicht et al. 2020). In contrast, a few authors have instead proposed that trait differences among species do not lead to competitive differences among them (Hubbell 2001).

Global surveys of trait variation in land plants reveal large differences (Reich et al. 1997; Wright et al. 2004; Díaz et al. 2016), and studies of trait differences among species within diverse clades such as *Helianthus* demonstrate that the magnitude of interspecific trait variation can rival that seen in global surveys (Mason and Donovan 2015). Even within local plant communities and assemblages the trait variation observed among co-occurring species can span orders of magnitude (Wright et al. 2004; Baraloto et al. 2010; Aiello-Lammens et al. 2017) and can be greater than expected given regional species pools (Swenson et al. 2012). As these examples suggest, it is common to find substantial trait variation at almost any scale, even among individuals within a species growing at a single site (Messier et al. 2010; Umaña and Swenson 2019; Nolting et al. 2021; Taseski et al. 2021). In contrast, substantial performance differences are less commonly documented, especially among co-occurring species (Becker et al. 1999; Worthy et al. 2020; Nolting et al. 2021). Why do we fail to see large differences in performance when we see large differences in individual structural traits that are related to performance?

Twenty years ago Marks and Lechowicz (2006) hinted at a solution to this paradox. They showed that selection on multivariate trait combinations within a single environment can

produce many different functional forms ("alternative designs") with roughly equivalent performance. This result suggests that while individual ***trait*** differences among species may reflect differential resource use (and niche partitioning), ***performance*** differences among species within a community are likely to be minimal, a conclusion consistent with the expectation from coexistence theory (Chesson 2000; Clark et al. 2007), whereby coexisting species should be roughly equivalent in performance if stabilizing differences are not pronounced. Marks and Lechowicz (2006) argue that while trait variation in natural communities is often assumed to reflect species' optimization to microenvironments, it could be that "…aside from major environmental heterogeneity, alternative designs are a major, if not the main, cause of functional diversity in nature" (Marks and Lechowicz 2006, p. 62). In spite of their provocative suggestion, few studies have investigated this outcome in empirical systems and the way in which trait covariation can lead to alternative designs has not been described.

Here we use an extensive collection of structural and physiological performance traits measured on individual plants to demonstrate that multivariate combinations of structural traits differ markedly among species but lead to similar physiological performance among co-occurring *Protea s*pecies sampled from natural communities in the Cape Floristic Region, South Africa (data originally published in Nolting et al. 2021). We develop a simple model to explain these results, and we conclude that the presence of persistent 'alternative designs' (i.e., large variation among species in individual structural traits that converge on similar performance, (Marks and Lechowicz 2006; Marks 2007)) within natural communities could be the result of selection that minimizes performance differences among species. This outcome may be prevalent in natural plant and animal communities, and has important implications for understanding the ecological and evolutionary mechanisms contributing to persistence of species-diverse assemblages world-wide.

MATERIALS AND METHODS

EMPIRICAL DATA COLLECTION

We use data from (Nolting et al. 2021) to explore the relationship between structural trait variation and physiological performance. Specifically, we demonstrate that (1) traits predict physiological performance relatively well, and (2) species differ markedly in their traits, but do not substantially differ in their physiological performance.

Study Site and Species

Nolting et al. (2021) investigated multivariate trait-performance relationships for five *Protea* species sampled across three sites in the Cape Floristic Region, South Africa. The Cape Floristic Region (CFR) is the smallest of the world's six floral kingdoms (area ~90,000 km^2), but it hosts over 9,000 plant species (Linder 2003; Peter Linder 2005) making it the most diverse of the five Mediterranean regions (Cowling et al. 1996). Like other Mediterranean biomes, the CFR is characterized by warm, dry summers and cool, wet winters (Cowling et al. 1996), but there is also a west-east seasonality gradient with winter rainfall in the west and relatively constant, low rainfall in the east. *Protea* species primarily occur in fynbos habitat, which is characterized as a shrubland with nutrient-poor soils (Allsopp, N. Colville, J.F. Verboom, G.A. 2014) and natural, recurring fires that sweep through sites on average every 10-12 years (Van Wilgen et al. 2010).

The genus *Protea* L. (Proteaceae) represents a morphologically diverse (~112 species in Africa, with ~60% endemic to the Cape Floristic Region; (Schnitzler et al. 2011)), iconic, and locally abundant plant genus that typifies many fynbos communities. *Protea* exhibit a diversity of form and function with respect to growth form (e.g., low growing, prostrate shrubs to upright shrubby trees), response to fire (e.g., reseeding species that die with fire but release all of their

seeds during the fire event from persistent infructescences versus resprouting species that regrow after fire in addition to releasing seeds), and vegetative traits associated with carbon and water use strategies (e.g., leaf size and shape variation). Previous studies on *Protea* have demonstrated that variation in structural traits (e.g., leaf mass per area and wood density) and physiological traits (e.g., photosynthetic rates and stem hydraulic conductance) are associated with fitness differences (Carlson et al. 2011; Prunier et al. 2012; Nolting et al. 2021). Further, variation in these traits is associated with variation in the abiotic environment, such as precipitation and temperature gradients across the CFR (Carlson et al. 2011; Mitchell et al. 2015).

Trait Collection

The samples included in Nolting et al. (2021) occur at three sites and include 11-20 individuals of each species per site (a total of 8 populations and 132 individuals). On each individual plant sampled, Nolting et al. (2021) recorded measures of plant size (e.g., height and canopy area) and reproductive effort measured as the total number of inflorescences and infructescences retained on a plant. The *Protea* species included in the study either regenerate from seed or resprout after fire, meaning that adults (a) are all roughly the same age within a stand as they either recruit as seedlings together post-fire or regrow from persistent stems, and (b) all retain their infructescences until these 'seedheads' split and release seeds during a fire. These characteristics make it possible to record reproductive effort for individuals (e.g., inflorescences plus infructescences) which has been shown to covary with seed production (Carlson and Holsinger 2013), representing a proxy for fitness (Nolting et al. 2021).

On each individual, Nolting et al. (2021) also measured area-based, light-saturated photosynthetic rates (A_{area}), stomatal conductance (g_s), and instantaneous water-use efficiency (WUE_{Instan}) in the field. They collected branches to measure sapwood-specific hydraulic

conductivity (K_s) following Espino and Schenk (2011), and quantified the Huber value of each stem (the sapwood cross-sectional area of a stem relative to the total one-sided leaf area per area, (Mencuccini and Bonosi 2001)) on which hydraulic measures were recorded, to calculate leaf-specific conductivity (LSC, sapwood-specific conductivity divided by total leaf area of the stem, Tyree and Zimmerman 2002) and leaf-specific photosynthetic rates (LSP, light-saturated photosynthetic rate per area divided by Huber value). From the stems and leaves on which physiological traits were measured, Nolting et al. (2021) measured a suite of structural traits (e.g., traits related to organ morphology and allocation): leaf area (LA, cm^2), leaf mass per area (LMA, g cm^{-2}), lamina density (LD, g cm^{-3}), leaf length-width ratio (LWR, unitless), stomatal pore length (SL, mm), stomatal pore density (SD, mm^{-2}), bark thickness (BT, mm), and wood density (WD, g cm^{-3}). These structural and physiological performance traits were chosen based on the large literature in plant functional ecology suggesting that they are key indices of carbon uptake and allocation and water-use strategies (see Nolting et al. 2021 for further discussion of functional significance of each trait, and of trait complexes). Further, Nolting et al. (2021) demonstrate that many of these structural and physiological performance traits are directly and/or indirectly associated with individual plant size and reproductive effort.

TRAIT DIFFERENCES DO NOT LEAD TO PERFORMANCE DIFFERENCES IN PROTEA

Nolting et al. (2021) showed that the measures of physiological performance we investigate below are associated with plant size and reproductive effort, which we take to be reasonable proxies for fitness. Thus, we focus on investigating the relationship between eight individual structural traits and six measures of physiological performance.

Structural Traits Predict Physiological Performance

We evaluated the relationship between structural traits and each of our physiological performance traits using Bayesian linear mixed effects models (one model for each of the six physiological performance traits) using the package 'brms' (Bürkner 2017, 2018, 2021) (version 2.16.3) in the R programing environment (R Core Team 2020; version 4.0.2). All performance and structural traits were standardized to a mean of zero and a unit standard deviation prior to analysis. Sample site, species identity, and the interaction between site and species were included as random effects. We used independent N(0,1) priors on the intercept and regression coefficients, and half Cauchy (0,5) priors on the variance parameters. We used four chains with a warm-up of 2000 iterations and a sampling of 2000 iterations for a total of 8000 samples from the posterior with delta = 0.999. All parameters had Rhat < 1.01, and no divergent transitions were reported. In Figure 1 we plot the predicted performance values versus the observed values, and report the mean Bayesian R^2 estimates (Gelman et al. 2017). Consistent with Nolting et al. (2021), we demonstrate that combinations of structural traits predict performance reasonably well (i.e., full model R^2 values range from 0.26 to 0.44; marginal R^2 values – fixed effects only – ranging from 0.19 to 0.36).

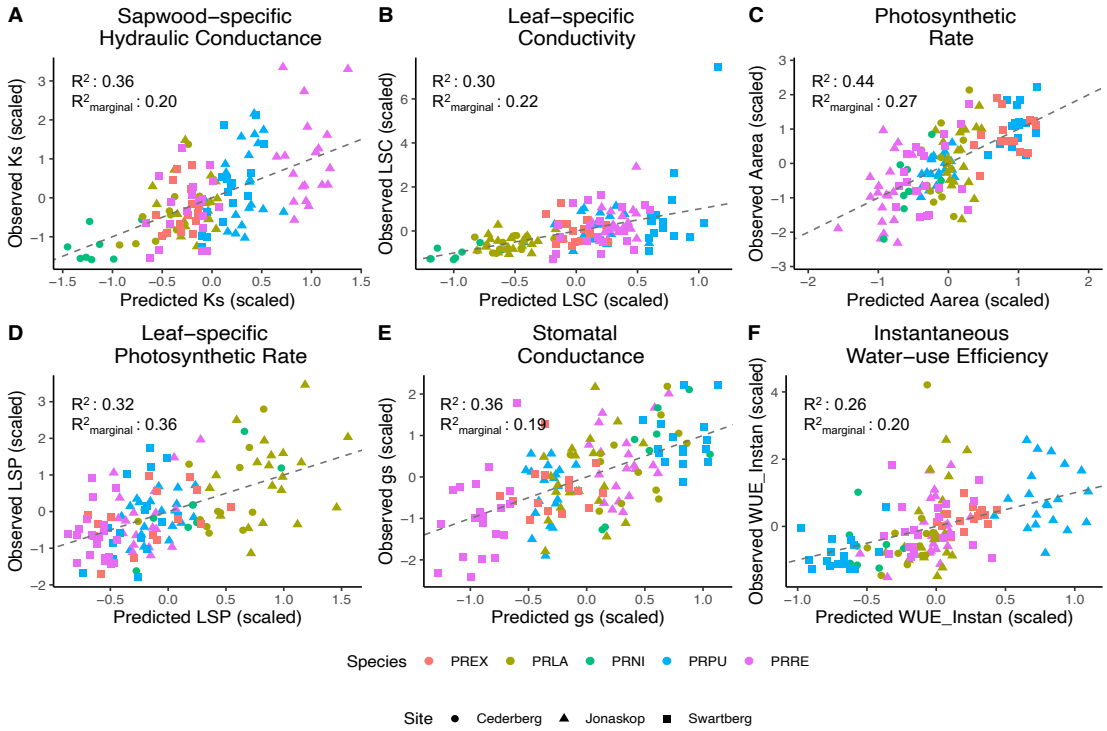

Figure 1: For each multiple regression modeling the relationship between the eight structural traits and each of the six performance traits, we plot the predicted performance values versus observed (with traits centered with a mean of zero and scaled to unit variance). (A) Ks: Stem-specific hydraulic conductance, (B) LSC: Leaf-specific conductivity, (C) Photosynthetic rate, (D) LSP: Leaf-specific photosynthetic rate, (E) Stomatal conductance, and (F) Instantaneous water-use efficiency. The dotted gray line reflects the 1:1 line. Colors represent different species and shapes represent different sites. We report the mean Bayesian R2 value for the fixed effects for each model.

Species Differ in Structural Traits but Not in Physiological Performance Traits

We evaluated the among species variation (relative to residual variation) in each of our structural and performance traits using a simple regression model with species as a random intercept. We fit these models in 'brms' as above, using the same priors, model specification, and sampling. As Nolting et al. (2021) discuss in more detail, the proportion of variation among

species in structural traits (Figure 2a) is much greater than that in physiological performance traits (Figure 2b). As individuals sampled were of similar size within each population, size-mediated trait differences are unlikely to contribute to the observed differences. In short, there are substantial differences among species in structural traits that are associated with performance, but there are only minimal differences among species in physiological performance traits.

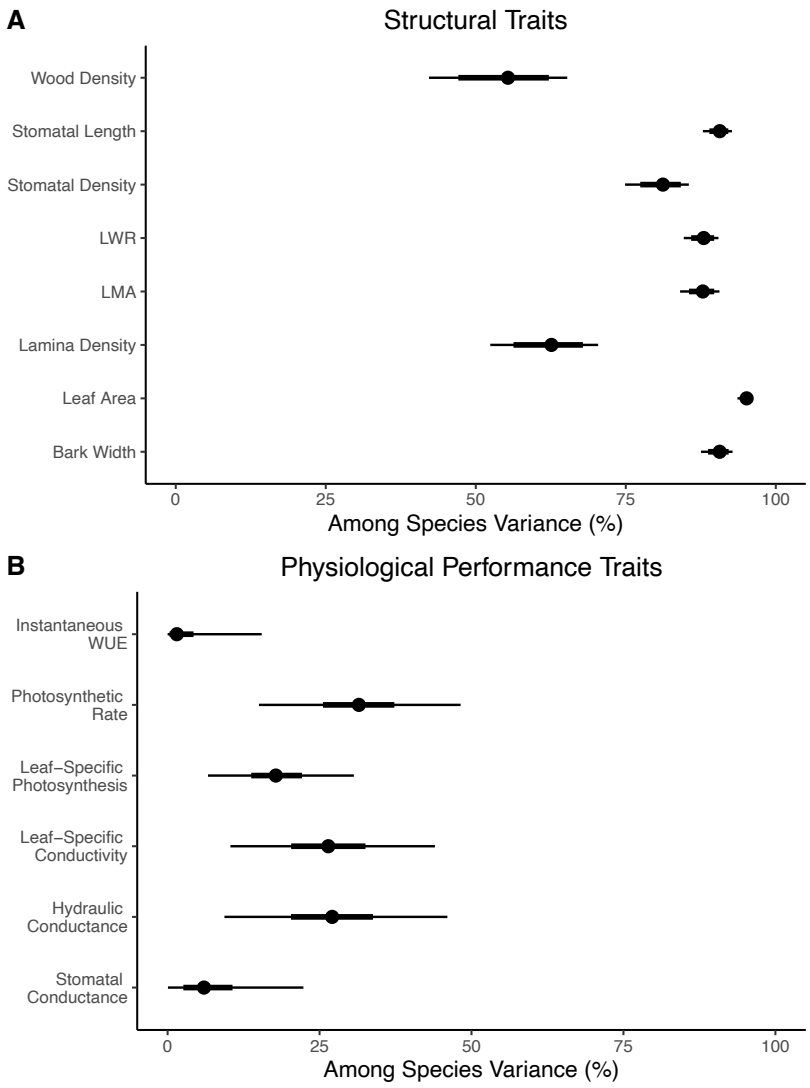

Figure 2: Among species variance partitioning for the eight structural traits (A) and the six performance traits (B). The gray histograms reflect the full posterior distribution, the black circles represent the mean of the posterior, the thick black lines reflect the 50 percent credible intervals, and the thin black line reflects the 95 percent credible intervals. Adapted from Nolting et al. 2021, with permission from *Annals of Botany*.

EXPLAINING THE PARADOX WITH A SIMPLE MODEL

Our intuition tells us that the variance in physiological performance is smaller than we might expect because many different combinations of traits, i.e., alternative designs, lead to similar performance. Here we develop that intuition further by investigating how the variance in performance is related to covariation among the traits that influence performance. We begin with a simple simulation to illustrate the phenomenon.

Simulating Variance in Performance in a Two-Trait Model

Assume that we have a single performance trait that is linearly predicted by two structural traits:

$$y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \varepsilon_i \ ,$$

where performance trait y and structural traits x_1 and x_2 are measured on all individuals, i, with ϵ_i as the residual error. β_1 and β_2 reflect the associations between traits x_1 and x_2 with y, and β_0 is the intercept. For simplicity, we will assume that x_1 and x_2 are centered and scaled to have a mean of zero and standard deviation of 1. Traits x_1 and x_2 are non-independent, and their correlation is given by ρ.

For the simulation, we assume $\rho = 0.8$, and we explore two scenarios: one in which the regression coefficients (β_1 and β_2) describing the relationship between our two traits and performance are both positive and of the same magnitude, and a second scenario in which the regression coefficients are of the same magnitude but opposite in sign:

Scenario 1: $\beta_1 = 0.5, \beta_2 = 0.5.$

Scenario 2: $\beta_1 = 0.5, \beta_2 = -0.5.$

We'll also assume $\beta_0 = 0$ (i.e., the expected intercept is zero) in our models under each scenario, which is a reasonable approximation if we've centered and scaled the response variable as well as the covariates. We display the outcomes under these two scenarios, by simulating trait data under each scenario for 1000 individuals, sampled from a multivariate normal distribution. The performance value, y_i, for each individual in each scenario was determined from the simulated trait data and the linear model described for each scenario, assuming a sampling variance of 0.05. Figure 3a (scenario 1) and 3b (scenario 2) reflect the outcome of a single realization of this process. We also report the variance in our performance trait across 1000 realizations for each scenario, and we summarize the distribution of reported variance across realizations in Figure 3c (scenario 1) and Figure 3d (scenario 2).

Figure 3a shows the distribution of simulated trait data from one realization in scenario 1 with the different color of each point corresponding to the performance predicted for that individual from the linear regression. In Figure 3c, we use the same simulated trait data but the colors correspond to the performance predicted under scenario 2. The magenta dashed line represents the regression vector associated with performance in each scenario, and the gray arrows are the principal components associated with the trait data.

It may not be surprising that in scenario 2, where there is a positive association of trait x_1 with performance and a negative association of trait x_2 with performance, there is less variation across the 1000 individuals in performance than in scenario 1 in which both traits have a positive association with performance. If we examine these figures a bit more carefully, we also notice that the regression vector is parallel to major axis of trait variation (PC1) in scenario 1 and orthogonal to it in scenario 2. This suggests that when many individual structural traits are

associated with a single performance trait, there might be little variation in the performance trait if the regression vector is orthogonal to the major axes of trait variation.

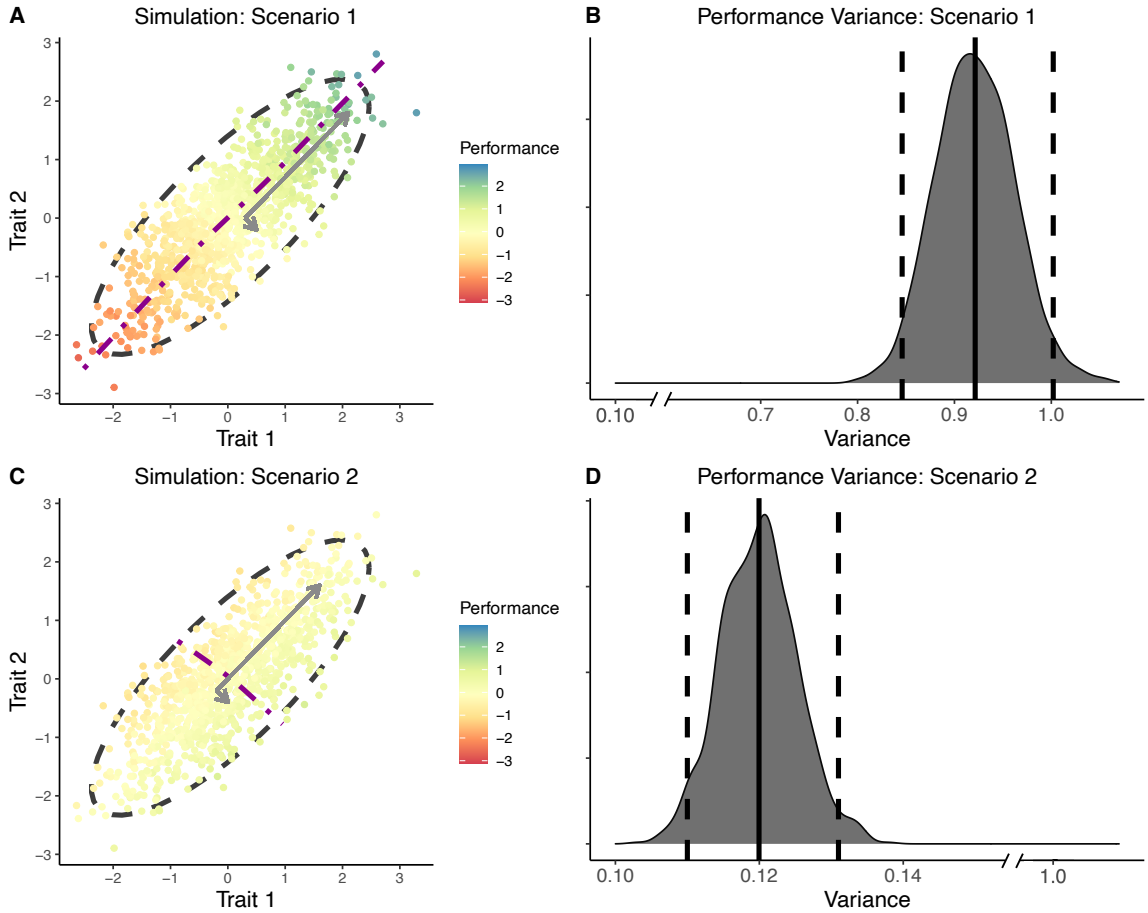

Figure 3: Simulating variation in performance with two traits under two different scenarios. In scenario one (A) both trait one and trait two are positively associated with performance (e.g., β_1 and $\beta_2 = 0.5$), and in scenario two (B) trait one is positively associated with performance and trait two is negatively associated with performance (e.g., $\beta_1 = 0.5$ and $\beta_2 = -0.5$). Trait data was simulated from a multivariate normal distribution with a correlation matrix described by rho = 0.8, and performance values were sampled under each scenario with this trait data and a sampling variance of 0.05. In (A) and (B) the gray arrows correspond to the principal components of the trait data, and the magenta line reflects the regression vector for each scenario. The black dashed ellipses reflect the 95% confidence limits. Panels (C) and (D) summarize the variation in the performance trait, y, across 1000 realizations under each scenario. In (C) and (D) the solid dashed lines represent the mean of the distribution, and the dashed black lines reflect the 95% confidence limits.

Developing a General Model

We specify the relationship between structural traits and performance traits using the multivariate version of our two-trait model:

$$
\begin{aligned}
y_i &= \beta_0 + \sum_{k=1}^{K} \beta_k x_{ik} + \varepsilon_i \\
&= \beta_0 + x_i^T \beta \qquad ,
\end{aligned}
$$

where y_i is the observed physiological performance of individual i, β_0 is the intercept, x_{ik} is the trait value for trait k in individual i, β_k is the regression coefficient for trait k, and ϵ_i is the residual error (with mean 0 and variance σ^2). x_i is the vector of traits in individual i and β_k $(k = 1, \ldots, K)$ is the regression vector. We assume that traits are drawn independently from a multivariate distribution with mean μ and covariance Σ_W. We will take expectations with respect to the distribution of x_{ik}.

The variance of y is

$$
\begin{aligned}
&Var(y_i) = E(y_i - \mu)^2 \\
&= E\left((\beta_0 + x_i^T \beta + \epsilon_i) - (\beta_0 + \mu^T \beta)\right)^2 \\
&= E(((x_i - \mu)^T \beta)^2 \; + \; x_i^T \beta \epsilon_i + \epsilon_i^2) \\
&= \beta^T \Sigma \beta + \sigma^2
\end{aligned}
$$

Using the spectral decomposition theorem (Szabo 2015) we can rewrite Σ as

$$
\Sigma = \lambda_1 u_1 u_1^T + \cdots + \lambda_K u_K u_K^T
$$

where the eigenvalues λ_i are numbered from the largest to the smallest, and the corresponding eigenvalues have unit length. This allows us to rewrite $Var(y_i)$ as

$$Var(y_i) = \beta^T(\lambda_1 u_1 u_1^T + \cdots + \lambda_K u_K u_K^T)\beta + \sigma^2$$

Suppose that the vector of regression coefficients is parallel with the *i*th principal component. It is, by definition, orthogonal to all of the remaining components, and $Var(y_i)$ reduces to

$$Var(y_i) = \lambda_i \beta^T u_i u_i^T \beta + \sigma^2$$

Thus if the regression vector is parallel to one of the minor axes of trait variation, the variation in performance will be much smaller than if it is parallel to one of the major axes of trait variation. More generally, if the regression vector is mostly orthogonal to the major axes of trait variation, there may be little variation in performance.

Applying these Insights with Protea

Recall that in the *Protea* example we observe (a) that combinations of structural trait values explain much of the variance in physiological performance traits (Figure 1), and (b) species differ markedly in structural traits but largely overlap with respect to physiological performance traits (Figure 2). Our simple, generalized model suggests that the vector of regression coefficients summarizing the trait-performance associations in four *Protea* models are not aligned with the major axes of structural trait variation. We explore this possibility here.

Using the princomp function in R (R Core Team 2020; version 4.0.2) we performed a principal components analysis on the centered and scaled structural trait data in our *Protea* dataset, yielding eight principal components. We evaluated the alignment of each of these PC axes with the vector of regression coefficients estimated from each multiple linear regression models (i.e., there is a regression vector for each of the six physiological performance traits in our dataset). As the generalized model presented above excludes any species or site distinctions, we re-ran the structural trait-performance multiple regressions as before, but excluded the site and species random effects.

We quantified the degree of alignment for each performance trait model by estimating the angle between the vector of regression coefficients for each response and each of the eight principal components summarizing the variation in structural traits (Figure 4). As we fit the multiple regression models using 'brms', we can present a posterior distribution for each of the angles, where an angle closer to 90 degrees reflects a case in which the PC axis is more orthogonal to the regression vector, and an angle closer to zero degrees indicates the PC axis and the regression vector are more parallel (Figure 4). While there is some heterogeneity in the degree of alignment of the PC axes with the regression vectors representing each physiological performance trait, it is striking that for each performance trait evaluated, the major axes of trait variation (i.e., PC axes 1 and 2) are generally the axes that are closest to orthogonal with the regression vector. Instead, the minor axes of trait variation (often the axes excluded from analyses that use dimension reduction to estimate functional associations from trait matrices and performance) are the axes most parallel with the regression vector.

We see little differentiation in performance in our data despite considerable trait differences because the axis along which trait differences are associated with differences in physiological performance is largely orthogonal to the axes that account for most structural trait variation. An important implication of this result is that reducing trait variation to the first few PCs

343 and attempting to associate those with functional differences may fail to find real associations of

344 traits with functional differences.

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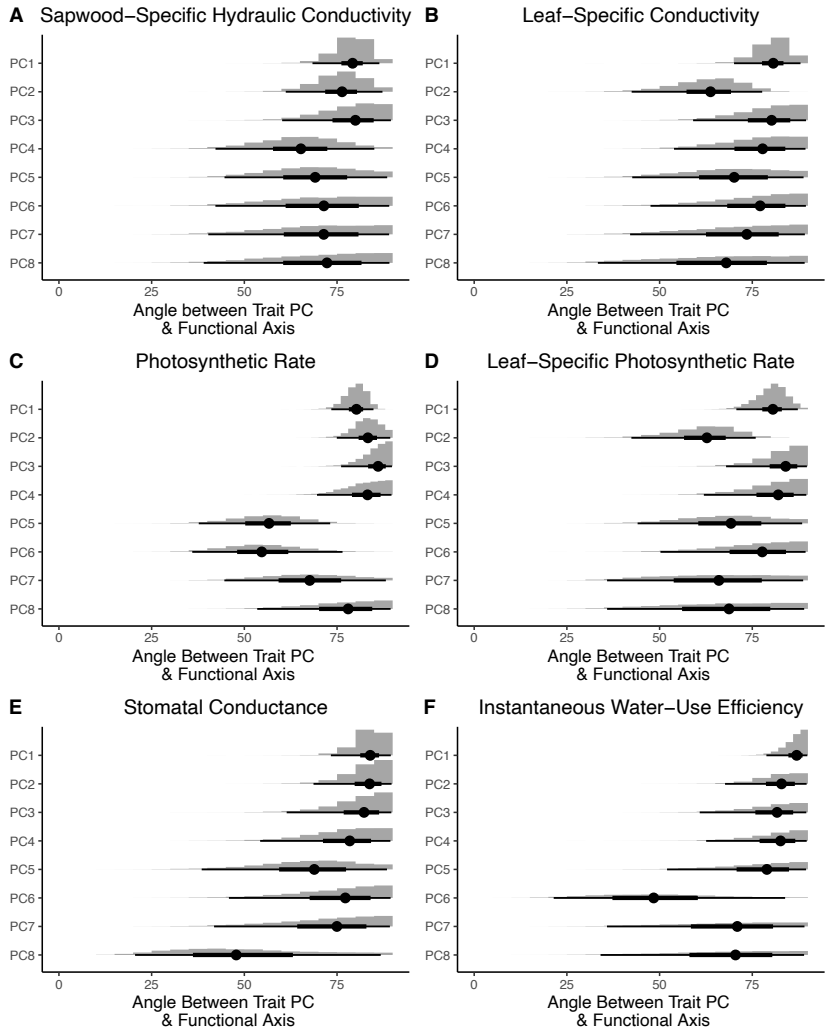

Figure 4: Alignment of each principal component with the regression vector describing the functional relationship between structural traits and each of six performance traits. (A) Sapwood-specific conductivity, (B) Leaf-specific conductivity, (C) Photosynthetic rate, (D) Leaf-specific photosynthetic rate, (E) Stomatal conductance, and (F) Instantaneous water-use efficiency. The horizontal axis is the angle (0-90°) between each of the eight principal components for the structural trait data and the regression vector associated with each physiological performance trait. Angles closer to 90° indicate that the functional axis (i.e., the vector of regression coefficients) and the PC axis are largely orthogonal (angles closer to 0° indicate they are more aligned). The gray histograms reflect the posterior distribution of angles, the black circles represent the mean of the posterior, the thick black lines reflect the 50 percent credible intervals, and the thin black line reflects the 95 percent credible intervals.

DISCUSSION

Given the well-established functional relationships between plant traits and aspects of plant performance, it may be surprising that the magnitude of species differences in performance is much less than might be expected given the often large differences among species in suites of structural traits. Here we unraveled this paradox using a recently published dataset of plant structural traits and physiological performance traits measured in several natural populations of *Protea* species from the Cape Floristic Region, South Africa (Nolting et al. 2021). We (a) demonstrated that combinations of structural traits predict variation in plant performance well (Figure 1), and (b) we showed that there are clear species differences in eight leaf and wood structural traits, but that there is extensive species overlap with respect to six physiological performance traits measured (Figure 2).

Using a linear regression to model the association between structural traits and physiological performance, we show that the misalignment between major axes of variation in structural traits and regression vectors leads to a smaller amount of performance variation than might be expected. This suggests that in future studies it will be important not only to evaluate axes of trait variation and covariation in commonly measured functional traits, but also to determine whether major axes of trait variation align with the axis associated with differences in performance.

Different Structural Trait Combinations Lead to Similar Performance within and across Species

Our model shows that very different trait combinations lead to similar measures of performance when the axis of performance variation does not align with the major axes of trait variation.

383 Depending on the focal study system and the scale of trait measurement, these 'alternative
384 designs' (Marks and Lechowicz 2006; Marks 2007) might not only exist across distantly related
385 taxa but might also exist *within* species that demonstrate significant trait variation.
386 To illustrate how combinations of structural traits can lead to similar performance both
387 within and across species in our dataset, we plot our sampled individuals in structural trait space
388 (Figure 5a,b,c: using the first two PC axes), but color the individuals based on their relative
389 performance values. Each panel in the top row of Figure 5 reflects the position of each
390 individual in the first two dimensions of structural trait space, i.e., the two most important axes of
391 structural trait variation. In each panel the points are in the same position, but their coloring
392 reflects the relative performance of each individual (using a subset of three physiological
393 performance traits). For example, in Figure 5A the ***position*** of each sampled individual is
394 determined by its position in the structural trait PCA, but the ***coloring*** of each individual is
395 based on the quintile of K_s (sapwood-specific hydraulic conductivity) into which it falls.
396 Confidence ellipses in this figure correspond to species groupings based on the first two PC
397 axes for structural traits. In the bottom panel of Figure 5 (Figure 5d,e,f), we color the points in
398 the same way but plot individuals in structural trait space using the PCs that are most aligned
399 with performance (i.e., the two PCs that were most parallel to the regression vector).
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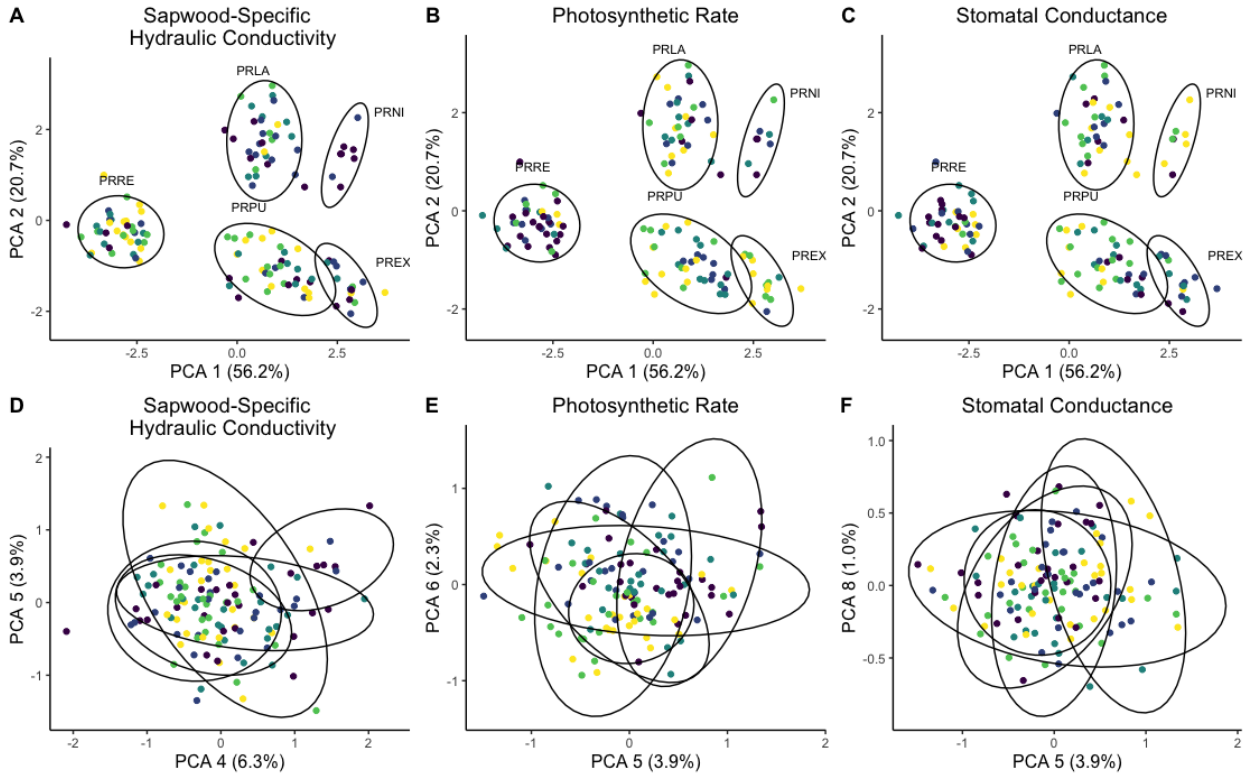

Figure 5: Visualizing variation in relative performance arising from different combinations of structural traits, for a subset of performance traits (Ks, or sapwood-specific hydraulic conductivity: A and D; Photosynthetic rate: B and E; Stomatal conductance: C and F). For each panel, individuals from our empirical dataset are plotted with respect to their position in multivariate structural trait space. For A, B, and C individuals are plotted using the first two principal components (PC1 and PC2). For D, E, and F individuals are plotted in the structural trait space that is most aligned with performance (i.e., the PC axes that are most parallel with the regression vector for each performance trait). The color of the points reflects the relative performance of each individual, corresponding to one of five ordered categories (Low, Medium Low, Medium, Medium High, and High). The confidence ellipses correspond to species groupings. PRLA: *P. laurifolia*, PRNI: *P. nitida*, PREX: *P. eximia*, PRPU: *P. punctata*, and PRRE: *P. repens*.

Consistent with the univariate examination of among species structural trait variation (Figure 2), we see that when plotted with respect to PC1 and PC2 (the top two axes of trait variation), species are well differentiated in structural trait space (Figure 5, top row). In contrast,

when we plot individuals in structural trait space that most closely reflects structural trait variation associated with the functional axis describing performance (Figure 5, bottom row), we see that species are weakly differentiated, if at all.

Figure 5 also illustrates that individuals with different combinations of structural traits (different positions in PCA space) can have similar performance (the same color) and that there are many different combinations of traits that can lead to performance in the highest (or lowest) quintile. Returning to the example of sapwood-specific hydraulic conductivity (K_s), we see that all species (other than *P. nitida*) have individuals with K_s in the highest quintile (e.g., high relative performance) and that all five of the species have individuals with K_s in the lowest quintile (e.g., low relative performance). The same pattern is repeated across all six physiological performance traits measured.

Implications for Trait-Mediated Species Coexistence and Community Ecology

Basic principles of functional ecology hold that species subject to similar selection pressures should have similar phenotypes, but basic principles of community ecology hold that species should exhibit trait differences along at least one niche axis in order to coexist. Thus, principles of functional ecology suggest that species should share traits that allow them to survive in a particular environment (Keddy 1992), while principles of community ecology suggest that species should differ in ways that allow them to coexist (Chesson 2000; HilleRisLambers et al. 2012). Environmental filtering may explain the oft-observed association between community-weighted mean trait values and environments (Ackerly and Cornwell 2007) and evidence of phylogenetic underdispersion in studies evaluating the relative phylogenetic diversity in local community assemblages (Webb 2000; Webb et al. 2002; Mayfield and Levine 2010). On the other hand, there is also substantial evidence of local trait differences within communities that

may promote coexistence (Cavender-Bares et al. 2004*a*, 2004*b*; Kraft et al. 2008; Swenson and Enquist 2009).

The Marks and Lechowicz (2006) 'alternative designs' model may allow us to resolve this apparent contradiction. Traits may covary in many different ways to achieve similar performance, permitting the persistence of species that display high trait diversity within a community and shared environment that are functionally very similar. These trait differences promote coexistence through niche differentiation while minimizing fitness differences (Adler et al. 2007; Umaña et al. 2016). Given the complex nature of how traits interact with one another to affect performance (Worthy et al. 2020; Funk et al. 2021), the trait space where performance is roughly equivalent may be extremely large (Marks and Lechowicz 2006; Laughlin 2014; Laughlin and Messier 2015).

CONCLUSION

In this paper we show that when the major axes of trait variation are largely orthogonal to the functional axis there may be relatively little variation in functional performance. A paucity of variation in functional performance arises even if there is both a strong relationship between the traits of individual organisms and their performance, and substantial variation among individuals in those traits. To the extent that long-term co-existence among species requires similar levels of performance within a given habitat, we therefore expect the axis of functional performance to be orthogonal to major axes of trait variation. Interestingly, Engen and Saether (2021) recently demonstrated a similar phenomenon in the evolution of multivariate phenotypic traits subject to natural selection. Specifically, they showed that the G matrix (the additive genetic covariance) evolves such that at evolutionary equilibrium the eigenvector associated with the smallest eigenvalue is parallel to the selection gradient. In other words, within a single population natural

468 selection acts to eliminate genetic variation along axes aligned with fitness. Similarly, we
469 anticipate that competitive interactions among species will act to eliminate phenotypic variation
470 along axes aligned with functional performance.
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