

The complexity of trait–environment performance landscapes in a local subtropical forest

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Summary

- That functional traits should affect individual performance and, in turn, determine fitness and population growth, is a foundational assumption of trait-based ecology. This assumption is, however, not supported by a strong empirical base.
- Here, we measured simultaneously two individual performance metrics (survival and growth), seven traits and 10 environmental properties for each of 3981 individuals of 205 species in a 50-ha stem-mapped subtropical forest. We then modelled survival/growth as a function of traits, environments and trait × environment interactions, and quantified their relative importance at both the species and individual levels.
- We found evidence of alternative functional designs and multiple performance peaks along environmental gradients, indicating the presence of complicated trait × environment interactions. However, such interactions were relatively unimportant in our site, which had relatively low environmental variations. Moreover, individual performance was not better predicted, and trait × environment interactions were not more likely detected, at the individual level than at the species level.
- Although the trait × environment interactions might be safely ignored in relatively homogeneous environments, we encourage future studies to test the interactive effects of traits and environments on individual performances and lifelong fitness at larger spatial scales or along experimentally manipulated environmental gradients.

Introduction

The trait-based approach has emerged as a promising way to understand the mechanisms of species coexistence and processes of community assembly (McGill *et al.*, 2006; Laughlin *et al.*, 2012; Kraft *et al.*, 2015; Lusk & Laughlin, 2017), to predict the distribution of organisms along environmental gradients (Chapin *et al.*, 1993; Westoby *et al.*, 2002), and to explain the relationship between biodiversity and ecosystem functioning (Lavorel & Garnier, 2002; Cadotte, 2017). This approach is built on the assumption that ‘functional’ traits should affect individual performance (e.g. survival, growth and reproduction), which in turn determine fitness and population growth (Violle *et al.*, 2007; Laughlin & Messier, 2015; Shipley *et al.*, 2016; Struckman *et al.*, 2019; Treurnicht *et al.*, 2020). The entire discipline of trait-based ecology will be at risk if this foundational assumption is not reinforced by a strong empirical base (Shipley *et al.*, 2016), which is still weak and fragmentary. For instance, those studies that empirically tested this assumption have reported typically

weak or nonexistent trait–performance relationships (e.g. Poorter *et al.*, 2008; Kraft *et al.*, 2010; Wright *et al.*, 2010; Adler *et al.*, 2014; Paine *et al.*, 2015).

One important reason why traits alone might poorly predict performance is that the effects of traits on individual performance should depend on the environment (Laughlin & Messier, 2015; Yang *et al.*, 2018; Swenson *et al.*, 2020), because no organism would have optimal adaptation to all relevant environments at the same time (i.e. a Darwinian demon). Recently, a few empirical studies have detected significant interactive effects between some traits and environments on individual performance (Blonder *et al.*, 2018; Laughlin *et al.*, 2018; Zirbel & Brudvig, 2020). For example, specific leaf area is positively related to survival probability at low soil C : N ratio, but negatively correlated to survival probability at high soil C : N ratio (Laughlin *et al.*, 2018). However, these studies consider only interactions between one trait and one environment, ignoring the multidimensional nature of phenotypic traits and environments (Laughlin, 2014; Laughlin & Messier, 2015). Therefore, testing the interactive effects of multiple traits and environments via the inclusion of higher-order trait × trait × environment × environment interactions is an

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important next step towards understanding the effects of whole-organism phenotypes on individual performance in different environments (Laughlin *et al.*, 2018). Specifically, the inclusion of such higher-order interactions between traits and environments enables us to explore performance landscapes (mapping performance on multiple trait axes) and the possibility of multiple optima along environmental gradients (Laughlin & Messier, 2015). Each optimum represents an alternative functional design (a specific trait combination) of approximately equal performance in a given environment (Marks & Lechowicz, 2006). To our knowledge, Worthy *et al.* (2020) is the only example to date that has empirically tested higher-order trait \times trait \times environment interactions and found evidence of alternative designs and multiple growth performance peaks. That study did not consider other performance metrics besides growth nor the multidimensional nature of the environment. Therefore, more comprehensive studies that test the interactive effects of multiple traits and multiple environments on different measures of individual performances are necessary.

One practical barrier that hinders the empirical test of trait \times environment interactions (especially the higher-order interactions) is the difficulty of obtaining sufficient data regarding individual performances, traits and environments for accurate estimation of numerous parameters (Laughlin *et al.*, 2018). Therefore, it is not enough to just simply identify such significant trait \times environment interactions, as done in previous studies (Blonder *et al.*, 2018; Laughlin *et al.*, 2018; Worthy *et al.*, 2020; Zirbel & Brudvig, 2020). It is also necessary to explicitly quantify the relative importance of such trait \times environment interactions to individual performance, because this tells us how much information one might lose when ignoring these complicated trait \times environment interactions. If trait \times environment interactions contribute little information to the prediction of individual performance, we can ignore these interactions without introducing substantial bias of estimating trait–performance relationships. For example, these interactions might be safely ignored in sites with relatively homogenous environments because the importance of trait \times environment interactions for predicting plant performance would logically increase with the heterogeneity of environments. Otherwise, trait \times environment interactions would be necessary despite the challenge of obtaining sufficient data. However, there is still a lack of empirical studies quantifying the relative importance of trait \times environment interactions to know when such interactions can be safely ignored.

Another reason for the surprisingly weak trait–performance relationships reported so far is the shortcut of characterising all individuals of a species with its species mean trait value (Yang *et al.*, 2018; Swenson *et al.*, 2020). This shortcut implicitly assumes that interspecific trait variation is far greater than intraspecific trait variation. However, intraspecific trait variation, arising from phenotypic plasticity and genetic diversity, has been acknowledged as a substantial source of trait variation in a growing number of studies (e.g. Albert *et al.*, 2010; Messier *et al.*, 2010; Siefert *et al.*, 2015). Moreover, phenotypic plasticity may enable individuals of a species to adjust their trait values to a certain extent in order to better adapt to their local environments (Gratani, 2014), and thus trait–performance relationships will

likely be stronger when evaluated at the individual level (Yang *et al.*, 2018; Swenson *et al.*, 2020). However, few studies have empirically tested trait–performance relationships at both the species and individual levels to see if the models using individual level traits would outperform the ones using species mean traits (but see Liu *et al.*, 2016), and further tested if trait \times environment interactions are more likely to be detected at the individual level than at the species level.

In this study, we measured two performance metrics (survival and growth), seven traits and 10 environmental properties for each of 3981 individuals of 205 species in a 50-ha stem-mapped subtropical forest plot. Using this large dataset, we modelled size-dependent individual survival/growth as a function of traits, environments and their interactions (including the higher-order ones) at both the species and individual levels to address the following questions:

(1) Do alternative functional designs (multiple performance peaks) exist in a given environment and (if exist) how do they shift along multiple environmental gradients?

A single optimum for a given environment and different optima for different environments are often assumed in single trait and environment analyses (Enquist *et al.*, 2015; Laughlin, 2018). With the inclusion of higher-order trait \times trait \times environment \times environment interactions, alternative functional designs are expected for a given environment and either same or different optima are possible for different environments.

(2) What is the relative importance of the trait \times environment interactions to individual survival and growth?

Their relative importance is expected to decline with decreasing environmental heterogeneity and might be safely ignored in relatively homogenous environments.

(3) Are individual survival and growth better predicted, and trait \times environment interactions more likely detected, at the individual level than at the species level?

This would be true when intraspecific trait variation is substantial responding to the changing environments.

Materials and Methods

Study site

The study was conducted in a 50-ha forest dynamic plot within the Heishiding Provincial Nature Reserve (23°27'N, 111°52'E; altitude: 150–927 m asl), Guangdong Province, southern China. The region has a subtropical moist monsoon climate with a mean annual temperature of 19.6°C and mean annual precipitation of c. 1740 mm. The monthly mean temperature ranges from 10.6°C in January to 28.4°C in July, and the precipitation falls predominantly (79%) from April to September. The vegetation, characterised by an evergreen broadleaved forest, is dominated by the *Lauraceae*, *Fagaceae* and *Theaceae* families.

Demographic data

The 50-ha plot (1000 m \times 500 m) was established following the ForestGEO (<https://www.forestgeo.si.edu>) protocol in 2011.

The first census was completed in 2013 with all free-standing individuals with diameter at breast height (DBH) more than 1 cm being tagged, mapped, measured and identified to species. About 273 000 free-standing stems belonging to 245 species, 160 genera and 71 families were recorded. The second census was finished in 2017, in which we recorded the status (0 for dead and 1 for alive) and DBH of all individuals recorded in the first census. The individual relative growth rate (RGR) was calculated as $[\log(\text{DBH}_2) - \log(\text{DBH}_1)]/5$, where DBH_1 and DBH_2 are DBH recorded in the two censuses.

Functional traits

We measured seven traits including specific leaf area (SLA), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), leaf dry matter content (LDMC), leaf area (LA), wood density (WD) and wood dry matter content (WDMC), on 3981 individuals of 205 species randomly distributed within the 50-ha plot (Supporting Information Fig. S1). Details on how these traits were sampled and measured can be found in our previous studies (Chen, 2015; He & Deane, 2016; He & Biswas, 2019). These traits have been reported to have effects on survival and growth rates (Poorter *et al.*, 2008; Kraft *et al.*, 2010; Wright *et al.*, 2010; Adler *et al.*, 2014). For example, light-demanding species with high growth and mortality rates tend to have larger SLA and LNC, but smaller WD than shade-tolerant species with low growth and mortality rates (Adler *et al.*, 2014). We performed principal component analyses for

Environmental conditions

In total, 625 surface soil samples (0–10 cm depth), randomly distributed within the 50-ha plot, were collected during the summer of 2016. Nine soil properties for each soil sample were measured with detailed methods shown in Table S1. Two orthogonal soil properties (Fig. 1b), soil organic matter (SOM) and soil acidity (pH), were selected in the following analyses. Soils with higher SOM had more total nitrogen, total phosphorus and available nitrogen, while soils with higher pH had more available phosphorus, available potassium and higher sand content. In addition, the understory light availability was estimated using hemispherical photography at 2352 places randomly distributed within the 50-ha plot (Zhao & He, 2016). The SOM, soil pH and light availability were interpolated to grids of 10 m × 10 m using the Ordinary Kriging in the AUTOMAP package (Hiemstra *et al.*, 2009) to estimate the environmental conditions in which the individuals were located; predictions in the grids that contained observations were replaced with the average of the observations in the grids (Fig. S1).

Data analysis

To explore interactive effects of multivariate traits and multivariate environments, we modelled individual performance (Z , survival or growth) as a function of: (1) a size effect (DBH), (2) main effects of two traits (T_1 and T_2) and two environments (E_1 and E_2), as well as (3) their two-way, (4) three-way, and (5) four-way interactions with a general form:

$$\begin{aligned} Z = & \alpha + \gamma_{\text{species}} + \delta_{\text{quadrat}} + \beta_1 \cdot \text{DBH} + \beta_2 \cdot T_1 \times T_2 \times E_1 \times E_2 \\ = & \underbrace{\alpha + \gamma_{\text{species}} + \delta_{\text{quadrat}}}_{\text{random effects}} + \underbrace{\beta_1 \cdot \text{DBH}}_{\text{size effect}} + \underbrace{\beta_2 \cdot T_1 + \beta_3 \cdot T_2 + \beta_4 \cdot E_1 + \beta_5 \cdot E_2}_{\text{main effects}} + \\ & \underbrace{\beta_6 \cdot T_1 : T_2 + \beta_7 \cdot T_1 : E_1 + \beta_8 \cdot T_1 : E_2 + \beta_9 \cdot T_2 : E_1 + \beta_{10} \cdot T_2 : E_2 + \beta_{11} \cdot E_1 : E_2}_{\text{two-way}} + \\ & \underbrace{\beta_{12} \cdot T_1 : T_2 : E_1 + \beta_{13} \cdot T_1 : T_2 : E_2 + \beta_{14} \cdot T_1 : E_1 : E_2 + \beta_{15} \cdot T_2 : E_1 : E_2 + \beta_{16} \cdot T_1 : T_2 : E_1 : E_2}_{\text{three-way}} \end{aligned}$$

these traits and found that the first two principal components captured 64% variation of the seven traits (Fig. 1a). One dimension runs from individuals with ‘conservative’ leaves (low SLA, LNC and LPC, and high LDMC) to individuals with ‘acquisitive’ leaves (high SLA, LNC and LPC, and low LDMC), correlated with the world-wide leaf economics spectrum (Wright *et al.*, 2004; Shipley *et al.*, 2006; Díaz *et al.*, 2016). The other dimension runs from individuals with low LA, high WD and WDMC to individuals with high LA, low WD and WDMC. This negative relationship between LA and WD has been reported in some previous studies (Cavender-Bares *et al.*, 2004; Pickup *et al.*, 2005; Wright *et al.*, 2007), probably because individuals with lower wood density usually have higher hydraulic conductivity and thus can transport more water to support larger leaves (Wright *et al.*, 2007).

We built linear mixed models of individual performance, treating survival (0 for death and 1 for survival) as a binomial-family model with a logit link function and growth (log-transformation of RGR) as a Gaussian-family model with an identity link function, respectively. Two random effects were considered. First, we included random intercepts across species (γ_{species}) to account for species-level differences in survival and growth that were unrelated to the traits. Second, we divided the 50-ha plot into 1250 (20 m × 20 m) quadrats and included random intercepts across quadrats (δ_{quadrat}) to account for spatial autocorrelation. We computed the R^2 -marginal (variance explained by all the fixed effects) and R^2 -conditional (variance explained by both fixed and random effects) using the function `r.squaredGLMM` in the `MUMIN` package (Zuur *et al.*, 2009). We further partitioned the R^2 -marginal to quantify the relative contribution of the size effect

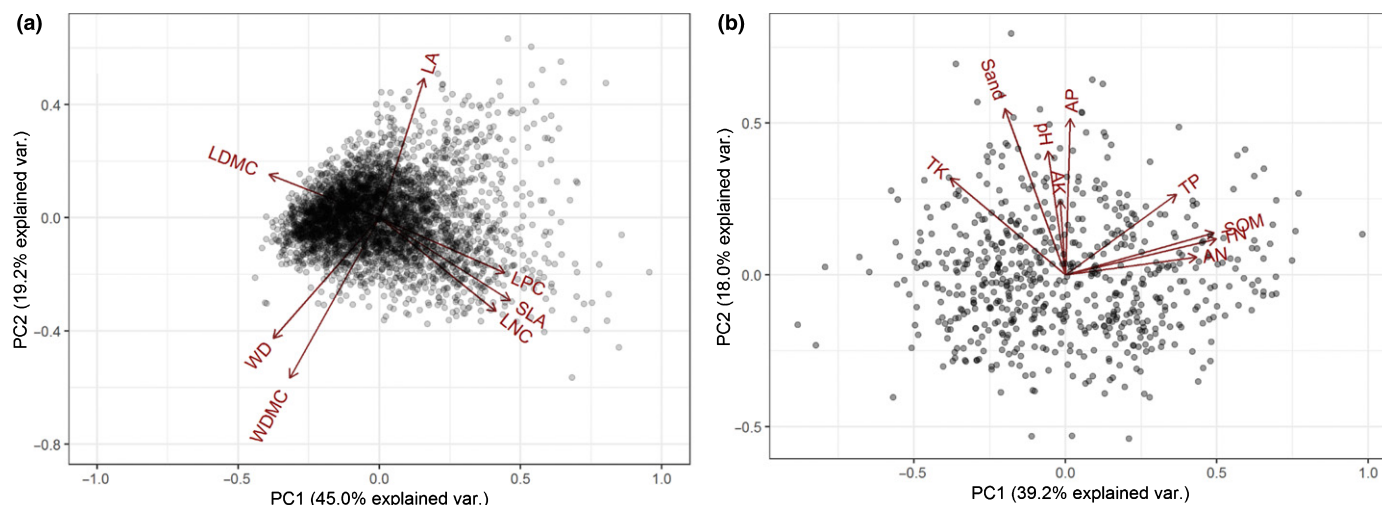


Fig. 1 Principal component analyses of seven traits (a) and nine soil properties (b). The seven traits, that is leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), wood density (WD) and wood dry matter content (WDMC), were simultaneously measured on 3981 individuals of 205 species within the 50-ha forest plot. The first two principal components explain c. 64% of total trait variation. The nine soil properties, that is soil pH, soil organic matter (SOM), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), available potassium (AK) and sand content (Sand), were measured for 625 soil samples randomly collected within the 50-ha forest plot. The first two principal components explained c. 58% of total soil variation.

(DBH), main effects of two traits and two environments, and their two-way, three-way and four-way interactions to the variance explained by fixed effects (Notes S1).

The above analyses were repeated for 36 models with different combinations of two independent traits (T_1 and T_2) and two independent environments (E_1 and E_2) for individual survival and growth, respectively. The first trait of the pair (T_1) was selected from the four traits relating to the first dimension (SLA, LNC, LPC and LDMC) and the second trait of the pair (T_2) was selected from the three traits relating to the second dimension (LA, WD and WDMC) (Fig. 1a). The two environments (E_1 and E_2) were the pairwise combinations of SOM, pH and light. The predictors DBH, LA, SLA, LNC and LPC and light availability were log-transformed to better approximate normality and all fixed predictors were then scaled to unit variance before analyses. To control the false discovery rate, we adjusted the P -values for each parameter estimation of 36 models using the Benjamini–Hochberg correction (Benjamini & Hochberg, 1995; Chen *et al.*, 2017). All these models were run at both the species and individual levels. To explore the occurrence of alternative functional designs and multiple performance peaks, we constructed 3D plots (performance landscapes) displaying how logit-survival or log-RGR varied along with two trait axes at four extreme environmental conditions (combinations of minimum and maximum observed values of the two environmental variables used in the model) in the PLOT3D package (Soetaert, 2019). All analyses were done in R v.3.6.2 (R Core Team, 2019).

Results

Summary of individual performance models

The standardised coefficients, their significance and model fit statistics of the 36 models ($Z \approx \text{DBH} + T_1 \times T_2 \times E_1 \times E_2$) for

survival and growth at both the species and individual levels are summarised in Tables S2–S5. Individual size (DBH) was always positively correlated with survival probability but negatively correlated with RGR (Tables S2–S5). Out of the 36 survival models, most of them detected significant main effects (of traits rather than environments), but only a few models detected significant two-way, three-way and four-way interactions at both the species and individual levels (Table 1). Modelling survival probability at the individual level did not detect more trait \times environment interactions (except for the three-way interactions) than at the species level (Table 1). Out of the 36 growth models, most of them detected the significant main effects of traits or environments and their two-way interactions, but a few models detected significant three-way and four-way interactions (Table 1). Modelling RGR at the individual level did not increase the detection of two-way, three-way or four-way interactions than at the species level. In addition, both survival and growth were only slightly better modelled (the R^2 -marginal and R^2 -conditional were higher) at the individual level than at the species level in most cases (Tables S2–S5).

Performance landscapes at extreme environmental conditions

We selected one survival model and one growth model with significant four-way interaction as an example to display the performance landscapes and explore the occurrence of functional alternative designs and performance peaks along environmental gradients. For the survival model with a significant four-way interaction between LNC, WDMC, SOM and pH at the species level, we found two survival peaks in each of the four extreme environments (Fig. 2). Specifically, in environments with minimum observed values of SOM and pH (or maximum SOM and pH), the survival probability peaked for individuals of high LNC

Table 1 The number of survival and growth models (out of 36 models) that detected a significant size effect (diameter at breast height, DBH), main effects (T_1 , T_2 , E_1 or E_2), two-way (T_1 : T_2 , T_1 : E_1 , T_1 : E_2 , T_2 : E_1 , T_2 : E_2 or E_1 : E_2), three-way (T_1 : T_2 : E_1 , T_1 : T_2 : E_2 , T_1 : E_1 : E_2 or T_2 : E_1 : E_2) or four-way (T_1 : T_2 : E_1 : E_2) interactions at the species and individual levels, respectively.

| Predictors | Survival | | Growth | |
|---|----------------------|----------------------|-----------------------|-----------------------|
| | Species level | Individual level | Species level | Individual level |
| DBH | 36 | 36 | 36 | 36 |
| Main effects (T_1 , T_2 , E_1 , E_2) | 27 (15, 12, 0, 0) | 33 (15, 24, 0, 0) | 20 (3, 4, 0, 19) | 29 (18, 3, 0, 22) |
| Two-way (T_1 : T_2 , T_1 : E_1 , T_1 : E_2 , T_2 : E_1 , T_2 : E_2 , E_1 : E_2) | 3 (0, 2, 1, 0, 0, 0) | 0 (0, 0, 0, 0, 0, 0) | 20 (0, 9, 0, 8, 0, 4) | 18 (5, 6, 0, 5, 0, 6) |
| Three-way (T_1 : T_2 : E_1 , T_1 : T_2 : E_2 , T_1 : E_1 : E_2 , T_2 : E_1 : E_2) | 1 (0, 0, 1, 0) | 8 (0, 2, 5, 1) | 2 (0, 2, 0, 0) | 0 (0, 0, 0, 0) |
| Four-way (T_1 : T_2 : E_1 : E_2) | 1 | 0 | 2 | 2 |

There are four terms of main effects, six terms of two-way interactions and four terms of three-way interactions in each survival and growth model. The numbers outside the brackets indicate the number of models that detected at least one significant term and the numbers inside the brackets indicate the number of models that detected each of the significant terms.

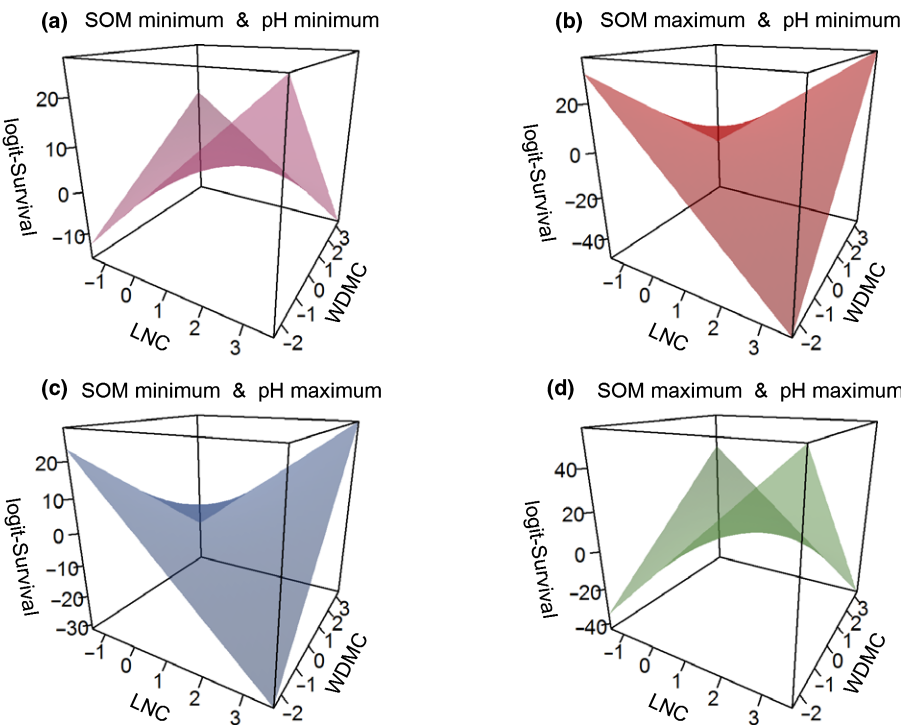


Fig. 2 The survival landscapes involving leaf nitrogen concentration (LNC) and wood dry matter content (WDMC) at four extreme environmental conditions with minimum or maximum observed values (a–d) of soil organic matter (SOM) and pH.

and low WDMC as well as for individuals of low LNC and high WDMC (Fig. 2a,d). In environments with maximum SOM and minimum pH (or minimum SOM and maximum pH), the survival probability peaked for individuals of low LNC and low WDMC as well as for individuals of high LNC and high WDMC (Fig. 2b,c). For the growth model with a significant four-way interaction between SLA, WD, pH and light at the species level, we also found two growth peaks in each of four extreme environments (Fig. 3). In environments with minimum observed values of pH and light (or maximum pH and light), the RGR peaked for individuals of low SLA and WD as well as for individuals of high SLA and WD (Fig. 3a,d). While in environments with maximum pH and minimum light (or minimum pH and maximum light), the RGR peaked for individuals of low SLA and high WD as well as for individuals of high SLA and low WD (Fig. 3b,c).

Relative importance of trait \times environment interactions

On average, the fixed and random effects explain *c.* 30% of the variation in survival and growth at both the species and individual levels (Fig. 4). We further portioned the variance explained by fixed effects to estimate the relative contribution of the size effect (DBH), the main effects of two traits and two environments and their interactions. For the survival models analysed at the species level, the explained variance due to the size effect (DBH), main effects of two traits and two environments and their interactions (sum of two-way, three-way and four-way interactions) were, on average, 41%, 43% and 16%, respectively (Fig. 4a). The results at the individual level were generally the same as the results at the species level (Fig. 4b). However, the trait \times environment interactions on average accounted for less than 5% of the explained variance of the growth models

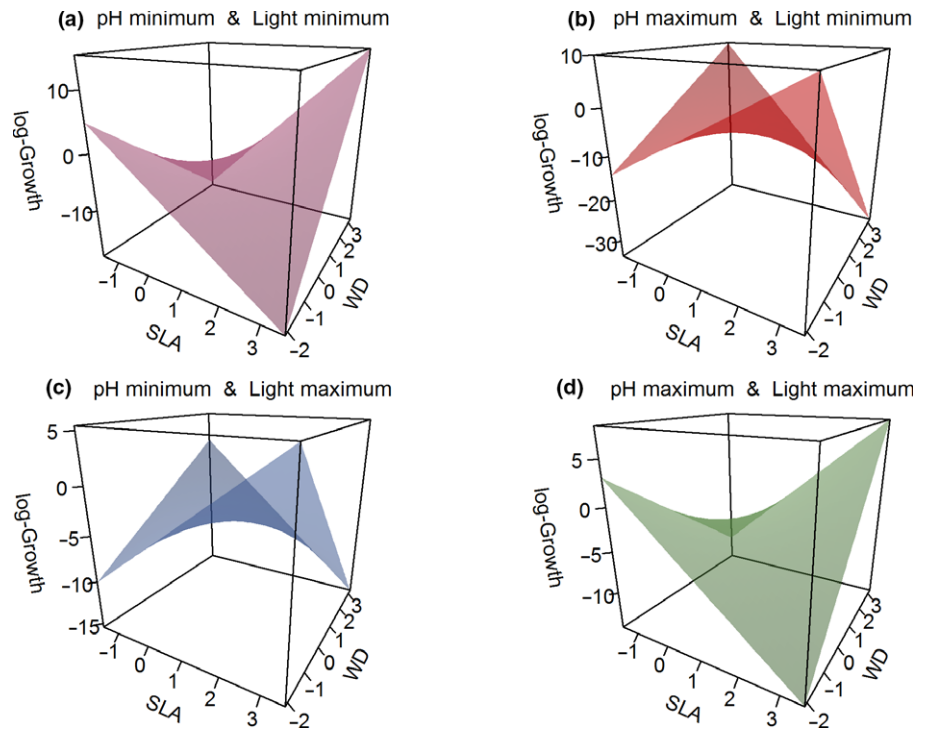


Fig. 3 The growth landscapes involving specific leaf area (SLA) and wood density (WD) at four extreme environmental conditions with minimum or maximum observed values (a–d) of pH and light.

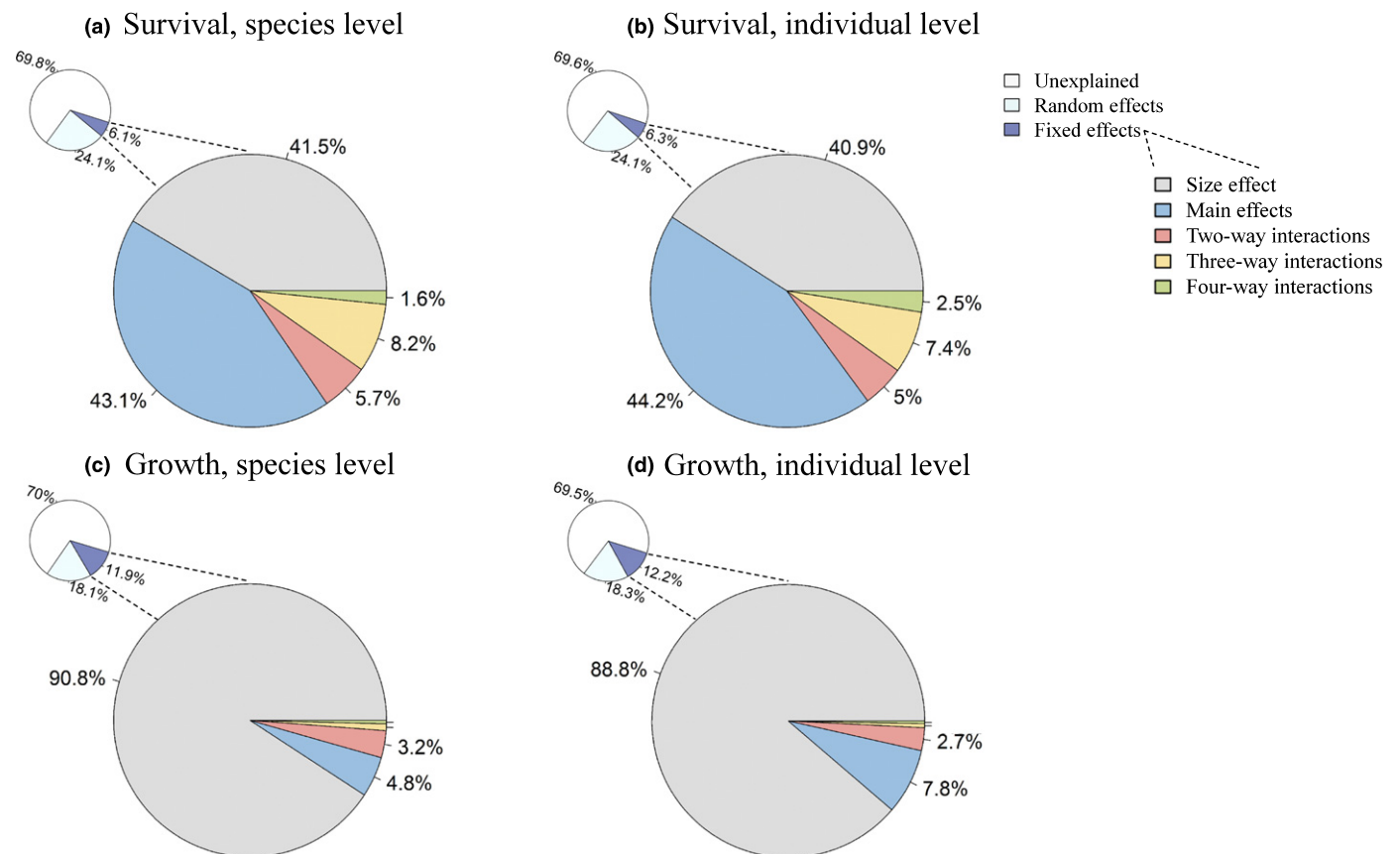


Fig. 4 The average contributions of fixed and random effects to variance in survival and growth at both the species and individual levels (a–d) summarised from Supporting Information Tables S2–S6. The fixed effects include size effect (diameter at breast height, DBH), main effects of two traits and two environments as well as their two-way, three-way and four-way interactions.

regardless of at the species or individual level (Fig. 4c,d). The size effect (DBH) accounted for the majority (*c.* 90%) of the explained variance of the growth models (Fig. 4c,d).

Discussion

Despite the importance of trait \times environment interactions to individual performance and the resulting population dynamics and composition of communities (Laughlin & Messier, 2015; Shipley *et al.*, 2016), such interactions have been empirically tested in only a few studies (Blonder *et al.*, 2018; Laughlin *et al.*, 2018; Worthy *et al.*, 2020; Zirbel & Brudvig, 2020). By measuring the two individual performance metrics (survival and growth), seven functional traits and 10 environmental conditions for thousands of individuals in a subtropical forest, we have been able to explicitly test for more complicated interactions at both the species and individual levels. Because of the high levels of statistical power provided by our data (Notes S2; Fig. S2), we detected a few significant two-way (e.g. an interaction between LDMC and SOM on individual survival at the species level), three-way (e.g. an interaction between LPC, pH and light on individual survival at the species level), and four-way interactions (e.g. an interaction between LNC, WDMC, SOM and pH on individual survival at the species level) involving the survival and growth models at both the species and individual levels (Tables 1, S2–S5).

Two-way (one trait \times one environment) interactions had been reported to affect individual survival probability (Laughlin *et al.*, 2018), seedling establishment (Zirbel & Brudvig, 2020) and multiple demographic rates (Blonder *et al.*, 2018). With the inclusion of three-way interactions between two traits and one environment, Worthy *et al.* (2020) found alternative functional designs and multiple growth peaks and they shifted along environmental gradients. In our study, we found multiple performance peaks, not only for growth but also for survival, in a few models with significant three-way and four-way interactions (Table 1). As examples illustrated in 3D plots (Figs 2, 3), the performance landscapes became more complicated in the presence of significant four-way interactions. First, the existence of alternative functional designs and multiple performance peaks (Figs 2, 3) means that there is not a single optimal trait (or trait combination) value for an environment. Given this, the correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits (Laughlin *et al.*, 2018), which requires higher-order moments of community-level trait distributions like community-weighted variances to be considered (Shipley, 2010; Loranger *et al.*, 2018). Second, the alternative functional designs and multiple performance peaks shifted along environmental gradients and thus the same strategy might be favoured in contrasting environments (Figs 2, 3). This surprising result contrasts with common expectations that different optima should be favoured in different environments and that environmental heterogeneity increases functional diversity (Stark *et al.*, 2017). Finally, different performance landscapes for survival and growth can obscure our understanding of how traits affect lifelong fitness (Caswell, 1989). Future studies should

integrate effects of traits on different measures of performance to explore the overall fitness landscapes and estimate population growth (Struckman *et al.*, 2019).

The presence of trait \times environment interactions (especially the three-way and four-way interactions) points to the potential for the types of complications described above. Such interactions, however, contributed a relatively small proportion of the total explained variance in most cases in our plot (Table S6; Fig. 4). This is good news because it means that trait–performance relationships might be simple in many situations and we may not lose much information if we simply ignore these complicated interactions. If this is generally true, then the estimated trait–performance relationships without considering traits \times environment interactions in many prior studies (e.g. Poorter *et al.*, 2008; Kraft *et al.*, 2010; Adler *et al.*, 2014) did not introduce large errors in their estimates. The above conclusion must be qualified, because the importance of trait \times environment interactions would logically increase with increasing environmental heterogeneity. We suspect that the small proportion of significant trait \times environment interactions and their generally small contributions to individual performance in our study, is due to the fact that our study was conducted within a 50-ha plot in a well established forest that had low environmental variation relative to other studies. The coefficients of variance of SOM, soil pH and light availability are lower in our plot, relative to a pine forest in Arizona (Laughlin *et al.*, 2018), a tropical rainforest in Xishuangbanna (Worthy *et al.*, 2020) and abandoned fields in southwestern Michigan (Zirbel & Brudvig, 2020) (Table S7). In addition, significant trait \times temperature and trait \times precipitation interactions on individual survival were also found (Laughlin *et al.*, 2018), but temperature and precipitation were often assumed to be the same at local scales like in our study. Although trait \times environment interactions might be safely ignored in relatively homogeneous environments at local scales, we encourage future studies to test the interactive effects of traits and environments on individual performance at larger spatial scales (e.g. across forest sites) or along experimentally manipulated environmental gradients. Another, but less likely, reason for the unimportance of trait \times environment interactions is that these commonly measured traits failed to effectively capture the individual response to the environments (Yang *et al.*, 2018). If this was the case, the inclusion of more relevant trait \times environment interactions should improve our predictions of individual performance.

Phenotypic plasticity enables individuals of a species to adjust their traits to better adapt to local environments (Gratani, 2014), thus trait–performance relationships can be greatly improved (Liu *et al.*, 2016) and trait \times environment interactions should be more likely to be detected at the individual level rather than at the species level. In contrast with our expectations, we did not observe this in our study (Tables 1, S2–S5). This also might be due to the small environmental variation in our plot. Individual adaptation to relatively homogeneous local environments led to much smaller intraspecific trait variation relative to interspecific trait variation (Fig. S3), therefore few benefits were obtained when considering this relatively small intraspecific trait variation at the individual level. In this case, characterising trait–

performance relationships at the species level were similarly effective to that at the individual level. However, we expect that intraspecific trait variation should be more substantial and play a more important role in studies confronting more heterogeneous environments at larger scales (Bolnick *et al.*, 2011; Violle *et al.*, 2012; Siefert *et al.*, 2015).

Our study conducted a comprehensive test of the trait–performance relationship in a subtropical forest by simultaneously considering multiple performance metrics, interactions between multivariate traits and multivariate environments at both the species and individual levels. Although some traits and environments were found to have significant interactive effects on individual performance, they were not very important and inclusion of intraspecific variation did not improve the detection and importance of these interactions. We encourage future studies to test the interactive effects of traits and environments on different performance metrics at larger spatial scales (e.g. across forest sites) or along experimentally manipulated environmental gradients, and further integrate different measures of performance to estimate their effects on lifelong fitness and population growth.








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Author contributions

YL and CC conceived the project. YJ synthesised the data and conducted the analyses with inputs from YL, CC and BS. YL wrote the manuscript with input from CC, BS and YJ. BL is responsible for the census data. DH, YC, DIR-H, WL and KZ collected the data of leaf morphological traits, leaf chemical traits, stem traits, soil properties and light availability, respectively. YL and YJ contributed equally to this work.

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Data availability

Data associated with this study are deposited in the TRY Plant Trait Database: <https://www.try-db.org/TryWeb/Data.php#68>.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Distribution of 3981 sampled individuals within the 50-ha forest plot with interpolated soil organic matter (SOM), soil pH and light availability to grids of 10 m × 10 m using the Ordinary Kriging.

Fig. S2 The chance of detecting every simulated effect given different sample sizes at four levels of β and three levels of σ .

Fig. S3 Trait variance explained by interspecific variation and intraspecific variation plus measurement error.

Notes S1 R^2 -marginal partitioning.

Notes S2 Power analysis.

Table S1 Details of measurements of soil properties in the Heishiding plot.

Table S2 The standardised coefficients, their significance, and model fit statistics for 36 survival models ($Z \approx \text{DBH} + T1 \times T2 \times E1 \times E2$) including different trait (T) and environment (E) combinations analysed at the species level.

Table S3 The standardised coefficients, their significance, and model fit statistics for 36 survival models ($Z \approx \text{DBH} + T1 \times T2 \times E1 \times E2$) including different trait (T) and environment (E) combinations analysed at the individual level.

Table S4 The standardised coefficients, their significance, and model fit statistics for 36 growth models ($Z \approx \text{DBH} + \text{T1} \times \text{T2} \times \text{E1} \times \text{E2}$) including different trait (T) and environment (E) combinations analysed at the species level.

Table S5 The standardised coefficients, their significance, and model fit statistics for 36 growth models ($Z \approx \text{DBH} + \text{T1} \times \text{T2} \times \text{E1} \times \text{E2}$) including different trait (T) and environment (E) combinations analysed at the individual level.

Table S6 The contributions of the size effect (DBH), main effects of two traits (T1 and T2) and two environments (E1 and

E2) as well as their two-way, three-way and four-way interactions to the total explained variance of survival and growth at both the species and individual levels.

Table S7 Coefficients of variance (standard deviation/ mean) of soil organic matter (SOM), soil pH and light availability in our and other studies.

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