Received: 28 September 2023 | Accepted: 10 July 2024

DOI: 10.1111/1365-2435.14624

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Functional traits and ecological niches as correlates of the interspecific growth–mortality trade-off among seedlings of 14 tropical tree species

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Funding information
The Joint Fund of the National Natural Science Foundation of China-Yunnan Province, Grant/Award Number: U1902203; Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Grant/Award Number: 151C53KYSB20200019; The Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDB31000000; National Natural Science Foundation of China, Grant/Award Number: 32160268

Handling Editor: Katie Field

Abstract

1. The interspecific trade-off between growth versus mortality rates of tree species is thought to be driven by functional biology and to contribute to species ecological niche differentiation. Yet, functional trait variation is often not strongly correlated with growth and mortality, and few studies have investigated the relationships of both traits and niches, specifically encompassing above and belowground resources, to the trade-off itself. These relationships are particularly relevant for seedlings, which must often survive resource limitation to reach larger size classes.
2. We investigated the functional basis of the interspecific growth–mortality trade-off and its relationship with ecological niches for seedlings of 14 tree species in a tropical forest in southwest China.
3. We found evidence for an interspecific growth–mortality trade-off at the seedling stage using 15 functional traits and 15 ecological niche variables. None of the organ-level traits correlated with growth, mortality, nor the trade-off, whereas specific stem length (SSL), a biomass allocation trait, was the only trait to have a significant correlation (positive). Moreover, light-defined niches were not correlated with growth, mortality or the trade-off, but soil-defined niches did. Species at the faster growth/higher mortality end of the trade-off were associated with higher fertility defined by lower soil bulk density and slope, and higher soil organic matter concentration and soil total nitrogen.
4. Our findings indicate the importance of stem elongation and soil fertility for growth, mortality and their trade-off at the seedling stage in this Asian tropical forest. Our findings contrast with analogous studies in neotropical forests showing the importance of photosynthesis-related leaf traits related to insolation. Therefore, the functional drivers of demographic rates and trade-offs, as well as their consequences for ecological niches, can vary among forests, likely

owing to differences in biogeography, canopy disturbance rates, topography and soil properties. Moreover, the effects of functional trait variation on demographic rates and trade-offs may be better revealed when biomass allocation is accounted for in a whole-plant context.

KEYWORDS
relative height growth rate, resource allocation strategies, seedlings, specific stem length, tropical rainforest

1 | INTRODUCTION

One of the best documented life history trade-offs in trees is the interspecific trade-off between growth and mortality rates, and evidence supporting this trade-off has been broadly found among tree species in both tropical and temperate forests and at different life stages from seedlings to adult trees (Kitajima, 1994; Kitajima & Poorter, 2008; Kobe, 1996; Masaki et al., 2021; Metz et al., 2023; Poorter et al., 2008; Russo et al., 2008, 2021; Wright et al., 2010). The growth–mortality trade-off is thought to be defined by the demographic consequences of adaptation to heterogeneously available resources. At one end of the axis are inherently faster-growing species, with physiologies enabling rapid resource acquisition and allocating more resources to rapid growth, a strategy that is favourable under resource-rich conditions; at the other end is inherently slower-growing species with more conservative resource use strategies, associated with greater investment in defence and tolerance of resource limitation, maintaining higher survival in resource-depleted environments (Coley et al., 1985; Kitajima, 1994; Loehle, 1988). Because there are survival costs of fast growth in stressful environments (Rose et al., 2009; Russo et al., 2008), and conversely, slower-growing species can be outcompeted in resource-rich environments (Lusk & Matus, 2000; Schreeg et al., 2005), the phenotypes and ecological niches of tree species should align with their position along the growth–mortality trade-off (Kitajima, 1994; Kobe et al., 1995; Wright et al., 2010). Studies of the growth–mortality trade-off, however, have not considered whether certain functional traits are more important correlates of the trade-off than others, nor the multiple above and belowground dimensions of species' ecological niches. In this study, we compare the strength of functional traits as putative drivers of the growth–mortality trade-off of tree seedlings and its consequences for species' multidimensional niches.

The hierarchy of biological organization suggests that tree growth and mortality rates should have a functional basis and therefore should correlate with functional traits, but this is often not the case (Iida & Swenson, 2020; Lasky et al., 2015; Paine et al., 2015; Poorter et al., 2008; Yang et al., 2018). One explanation is that there are dimensions of function that are not captured by commonly measured organ-level traits, like specific leaf area (SLA) and wood density (WD) (Iida & Swenson, 2020; Yang et al., 2018). Many organ-level traits may not be directly mechanistically linked to growth or survival, but related to multiple functions in a phenotypically integrated plant (Marks & Lechowicz, 2006), which means that organ-level traits must be considered in the context of whole-plant biomass allocation, since growth and survival operate at the level of individuals (Iida & Swenson, 2020; Yang et al., 2018). These contingencies are potentially at the root of the weak correlations often observed between organ-level traits and vital rates.

Here, we compare the strength of the relationships of biomass allocation versus organ-level traits with growth rate, mortality rate and the growth–mortality trade-off. We define biomass allocation traits as traits quantifying how biomass is distributed among, not within, organs, whereas organ-level traits are traits that quantify how the organ is built, not how much of it is built. Biomass allocation traits, like leaf area ratio (LAR) or leaf mass fraction (LMF), can exhibit stronger relationships with growth and mortality rates than organ-level traits, particularly among juvenile trees (Kitajima, 1994; Umana et al., 2021). This may be because organ-level traits are often indirectly connected with multiple physiological processes, whereas biomass allocation traits are more informative about how resources are distributed within plants, which may be more directly linked to demographic performance (Adler et al., 2014; Sterck et al., 2011). For example, specific stem length (SSL) offers a more direct measure of the height growth consequences of biomass allocation to the stem, as higher SSL means less biomass is invested per unit of stem elongation, which is essential for trees at juvenile stages in closed canopy forests (Poorter et al., 2012). The analogous organ-level trait, wood density (WD), has several more diffuse links with growth and survival, as it is related to hydraulic capacity, mechanical support and pest defence (Chave et al., 2009; King et al., 2006; Kitajima et al., 2012; Reich, 2014).

Interpretation of the consequences of the growth–mortality trade-off for ecological niches has largely focused on shade-tolerance niches and traits related to carbon capture in forests with relatively frequent canopy disturbances and a wide range of understory light levels (Hubbell, 2001; Kitajima, 1994; Kobe et al., 1995; Metz et al., 2023; Wright et al., 2010). Species at the faster-growth end of the trade-off axis are more light-demanding and have functional traits optimized for higher light-use efficiency and fast growth, but have lower survival in shade than species at the slower-growth end (Kitajima, 1994; Kobe et al., 1995). However, other environmental dimensions, such as soil properties and topography, often correlated with resource availability, are also key axes of niche differentiation (Baltzer et al., 2005; Gunatilleke et al., 2006; Kenfack et al., 2014; Potts et al., 2002), implying that species' positions along the growth-mortality trade-off may align with niche dimensions beyond light.

Soil properties have been shown to affect the growth–mortality trade-off (Baraloto et al., 2005; Dent & Burslem, 2009; Fine et al., 2006; Russo et al., 2008), growth and mortality rates (Baraloto et al., 2006; Fine et al., 2004; Fortunel et al., 2016; Russo et al., 2005), and functional trait variation (Baltzer et al., 2005; Katabuchi et al., 2012; Liu et al., 2014; Weemstra et al., 2021) and may be of similar importance as insolation for juvenile trees (Umana et al., 2020), particularly in forests on less fertile soils and with less frequent canopy disturbances. Specialists of less fertile, well-drained soils have greater water-use efficiency, lower dark respiration rate (Baltzer et al., 2005) and greater investment in physical and chemical defences of leaves (Fine et al., 2006), which come at the cost of fast growth, but enable tolerance of resource limitation. Here, we quantify ecological niches with respect to multiple dimensions (Hutchinson, 1957) and evaluate their relationships to growth, mortality and the growth–mortality trade-off of tree seedlings.

In this study, we evaluated putative functional drivers of interspecific variation in growth, mortality and the growth–mortality trade-off among tree seedlings and their relationships with multidimensional ecological niches. We used univariate and multivariate analyses of data on height growth and mortality rates, 15 functional traits, and 15 ecological niche variables of naturally recruited seedlings of 14 tree species in a closed-canopy tropical rainforest in southwest China. We addressed the following specific research questions: (Q1) Is there evidence for an interspecific growth–mortality trade-off among these species at the seedling stage? Is variation in species' growth and mortality rates and species' position along the interspecific growth–mortality trade-off (Q2) more strongly correlated with organ-level or biomass allocation traits and (Q3) associated with ecological niche dimensions other than light? We hypothesized that if variation in species' resource allocation strategies and environmental heterogeneity are the drivers of the variation in growth and mortality rates, then traits and niches that influence growth and mortality rates should also influence their trade-off relationship because trade-offs equalize species' relative fitness (Hubbell, 2001). We also predicted that the functional traits related to biomass allocation would be more strongly correlated with growth, mortality and the growth–mortality trade-off than organ-level traits and that species at the faster-growth end of the trade-off axis would exhibit higher specific stem length and leaf area ratio, but lower root mass fraction. We also expected that species at the faster-growth end of the trade-off axis would occupy more resource-rich ecological niches and that soil properties would be important in defining these niches, because the forest in our study has relatively low rates of canopy disturbance producing relatively uniform deep shade in the understory (Deng, 2022).

2 | MATERIALS AND METHODS

2.1 | Replication statement

Scale of inference	The scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Seedling community	Quadrats	500 quadrats
Seedling community	Growth rate Mortality rate	All species with ≥100 seedlings
Seedling community	Ecological niches	All species with ≥100 seedlings
Seedling community	Functional traits	All species with ≥100 seedlings, 3–5 individuals per species

2.2 | Study site and seedling dataset

Our study was conducted in the 20-ha (400 m × 500 m) Xishuangbanna Forest Dynamics Plots (XFDP), located in Yunnan Province, Southwestern China (21°37′08″ N, 101°35′07″ E) (Figure S1). This forest emergent layer height of nearly 50–60 m is dominated by the largest basal area individuals of *Parashorea chinensis* (Dipterocarpaceae), the main canopy layer (nearly 30 m high) was dominated by *Pometia tomentosa*, *Sloanea tomentosa*, *Garcinia cowa* and *Pittosporopsis kerrii* in the 2007 census, the XFDP contained 468 woody species (Cao et al., 2008). The elevational range of the XFDP is 709–869 m, and its total annual rainfall (1493 mm) is strongly seasonally distributed between the rainy (May to October) and dry (November to April) seasons (Cao et al., 2008). The XFDP was established in 2007 using the standardized methods of the Center for Tropical Forest Science (CTFS). XFDP is characterized by a dense and closed canopy without strong disturbance events such as typhoons or anthropogenic logging (Deng, 2022). A full description of the site's climate and floristic composition can be found in Cao et al. (2008).

During 2010, a total of 500 seedling quadrats (2 m × 2 m) were established in the center of each 20 m × 20 m subplot in XFDP. Between January and April 2010 all free-standing woody plants with height ≥20 cm and diameter <1 cm in the seedling quadrats were tagged and identified to species. Height was defined as stem length in cm from the ground to the tallest apical growing point. Seedling quadrats were re-censused for survival and height for previously tagged individuals and new seedling recruits each year from 2011 to 2015.

2.3 | Functional trait measurements

In 2015, we haphazardly selected three to five healthy seedlings per species from the area surrounding XFDP and harvested them by carefully removing them from the soil while preserving as much of the root system as possible. The heights of all harvested seedlings were close to each species median height in our seedling plot, and they no longer had cotyledons, making them similar in stage to the seedlings in the XFDP seedling quadrats. We measured 10 functional traits on these seedlings following standardized protocols (Cornelissen et al., 2003) (Table S1). Each seedling individual was divided into roots, stems and leaves, and the fresh mass of each organ was recorded. We selected one to three fully expanded, healthy leaves per seedling for leaf-level trait measurements. After removing petioles, leaves were scanned using a digital scanner (Canon 5600F Canon Inc., Tokyo, Japan), and leaf area was estimated using R package LeafArea. Leaf thickness (mm) was measured on laminar intercostal tissue, avoiding major veins with an electronic digital micrometre on fresh leaves (CANY Co., Shanghai, China), leaf chlorophyll content was estimated with a hand-held SPAD-502 chlorophyll meter (Minolta Camera Co, Japan). Leaves, stems and roots were dried to a constant weight at 70°C for over 72 h, and measured for the total dry mass (g) of each organ. Leaf area (LA), leaf chlorophyll content index (CHL), leaf thickness (LT), leaf dry matter content (LDMC), specific leaf area (SLA) are organ-level traits related to leaf structure and resource acquisition, and leaf area ratio (LAR), leaf mass fraction (LMF), stem mass fraction (SMF), specific stem length (SSL) and root mass fraction (RMF), are biomass allocation traits related to whole-plant resource allocation strategies (Table 1) (Poorter et al., 2012; Umana et al., 2015; Worthy et al., 2020).

We also conducted measurements of seed mass (SM) and stem wood density (WD). SM was measured using seeds collected in seed traps within the XFDP (Yang, 2010). Wood density was measured on wood samples collected from adult tree trunks using the water displacement method. We determined the fresh volumes (cm^3) of wood samples, and their dry mass was determined after oven-drying at 70°C for 72 h. WD was calculated as the ratio of dry mass to fresh volume (Table 1) (Swenson & Enquist, 2008). Since these functional traits are likely to covary, we also conducted a principal component analysis (PCA) on the species' means for each functional trait data to derive orthogonal axes representing multivariate trait variation (Trait PC1, Trait PC2 and Trait PC3).

2.4 | Ecological niches of species

We characterized the ecological niches of seedlings of each species using data on 10 soil properties, two topographic variables and

TABLE 1 Descriptions, abbreviations and units of 12 functional traits and 13 ecological niche variables measured on seedlings of 14 tree species.

	Functional traits	Abbreviation	Unit
Organ-level traits	Leaf area	LA	cm^2
	Leaf chlorophyll content	CHL	SPAD
	Leaf dry matter content	LDMC	g g^{-1}
	Leaf thickness	LT	mm
	Specific leaf area	SLA	cm^2 g^{-1}
	Seed mass	SM	g
	Wood density	WD	g cm-^{3}
Biomass allocation traits	Leaf area ratio	LAR	cm^2 g^{-1}
	Leaf mass fraction	LMF	g g^{-1}
	Specific stem length	SSL	cm g^{-1}
	Stem mass fraction	SMF	g g^{-1}
	Root mass fraction	RMF	g g^{-1}
	Ecological niche variables	Abbreviation	Unit
Soil niches	Soil available nitrogen	AN	mg kg^{-1}
	Soil available phosphorous	AP	mg kg^{-1}
	Soil available potassium	AK	mg kg^{-1}
	Soil bulk density	BD	g cm^{-3}
	Soil organic matter concentration	OMC	%
	Soil pH	pH	—
	Soil total nitrogen	TN	g kg^{-1}
	Soil total phosphorous	TP	g kg^{-1}
	Soil total potassium	TK	g kg^{-1}
	Soil volumetric water content	SVWC	%
Topographic niches	Elevation	Elevation	m
	Slope	Slope	°
Light niche	Light availability	Light	%

canopy openness collected in each of the 500 seedling quadrats in the XFDP plot. Soil pH, organic matter content (OMC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), available potassium (AK) and bulk density (BD) within each sample were measured, as described in Appendix S1. Topographic variables were elevation and slope, and calculated using standard methods (Wu et al., 2016). The XFDP plot is divided into 500 20×20 m subplots with a seedling quadrat at the centre of each subplot. The elevation of each seedling quadrat was estimated as the mean of values at each of the four corners of the 20×20 m subplots. The slope was calculated as the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three of its corners. Soil volumetric water content (%) (SVWC) was measured using time-domain reflectometry (Theta probe MPM-160B, ICT International Pty Ltd., Armidale, New South Wales, Australia) at a soil depth of 0–5 cm at three randomly chosen locations around each seedling quadrat. The measurements for each seedling quadrat were taken over seven consecutive rain-free mornings during the dry season of 2013. The mean of the three measurements was used as the soil moisture for each seedling quadrat. Hemispherical photographs were used to estimate understory light availability for each seedling quadrat. The pictures were taken using a Nikon Coolpix 4500 with a Nikon FC-E8 Fisheye Converter lens in January 2014 under conditions of dry vegetation and uniform skylight. We used the Gap Light Analyser software (GLA, version 2.0) to analyse the images and quantify canopy openness. 90% of seedling quadrats within a range of canopy openness between 0.29% and 3% (Wu et al., 2016).

Based on the above environmental variables, we used conditional probability to quantify the local ecological niches of each species at the seedling stage (Itoh et al., 2010). The conditional probability of species occurrence (E) for a given environmental variable x, $p(E|x)$ represents the probability that a focal species exists at a selected location when the environmental variable at that location equals x. The $p(E|x)$ values are not affected by the frequency distribution of x within a study plot. In our case, x represents the canopy openness and soil environmental factors. We assumed that the ecological niches of each species would be the environment with the greatest probability of occurrence, which happens when $p(E|x)$ reaches its maximum, which was determined by number of occurrences of the species with respect to the environmental variables. To quantify species' multivariate niches, we performed a PCA based on the soil and topographic variables (Niche PC1 and Niche PC2).

2.5 | Estimation of growth and mortality rates

We used the census data from the 500 seedling quadrats to estimate species' growth and mortality rates. To increase accuracy in the estimation of vital rates, we used all species with ≥100 seedlings in 2010 (the initial census). In the final seedling dataset, there were a total of 5364 seedlings, representing 14 species with a range of growth forms, maximum heights and shade tolerances (Table S2). The relative height growth rate of each seedling (RGR, cm year^{-1}) was calculated as $(\log[H_1]-\log[H_0])/T$, where H_0 and H_1 is the height in cm of a seedling alive in the 2010 and 2013 censuses, respectively, and T is the number of years between censuses (Hunt, 1982). We were interested in estimating RGR in the absence of physical damage (e.g., falling trees) or large measurement errors, which can cause large negative growth rates that can bias the mean growth rate downward for reasons unrelated to ecological strategies. We therefore excluded individuals with absolute height change between 2013 and 2010 <−10 cm. With the seedlings alive in 2013, we estimated the annual mortality rate (%/year) from 2013 to 2015 for each species as $(\log[N]-\log[S])/T$, where N is the number of seedlings alive in the 2013 census, S is the number of those seedlings that survived until the 2015 census, and T is the number of years between censuses.

2.6 | Testing for the interspecific growth–mortality trade-off

To address Q1, we evaluated the evidence for the interspecific growth–mortality trade-off using species' RGR and mortality rates. Previous studies quantified the interspecific growth–mortality trade-off by estimating species' capacity for fast growth as the 95th quantile of growth rate, and species' mortality at slow growth as the mortality rate of the 25% of the slowest-growing trees (Hubbell, 2001; Wright et al., 2010). We evaluated whether detection of the trade-off is robust to these decisions, using Pearson's correlations between the 85th, 90th and 95th quantiles of RGR (RGR_{85}, RGR_{90} and RGR_{95}) and the mortality rate of the 20%, 25%, and 30% of the slowest growing seedlings (M_{20}, M_{25} and M_{30}) for each species. The strongest correlation was between RGR_{90} and M_{30} (Figure S2), so we used this combination to define the interspecific growth–mortality trade-off. We assessed the relationship between RGR_{90} and M_{30} using standardized major axis regression (SMA) using the 'smatr' function (smatr R package; Warton et al., 2012). We also examined the trade-off in an evolutionary context using phylogenetic independent contrasts with 'pic' function (ape R package; Paradis et al. (2004)), based on a previously published phylogeny for these species (Wu et al., 2016).

2.7 | Relationships of traits and niches with growth, mortality and the trade-off

To address Q2 and Q3, we used three approaches. First, SMA was used to explore the relationships of species-specific functional trait values and ecological niches with RGR90 and M30. Second, we used the species' values for the first component (PC1) of a principal components analysis of species' RGR_{90} and M_{30} to define species' position along the interspecific growth–mortality trade-off axis, as in Wright et al. (2010). SMA was used to test functional traits, ecological niches, Trait PC1–PC3 and Niche PC1 and PC2 with the trade-off PC1 values across species. Third, we used multivariate analyses to fit functional trait and ecological niche driver variables to the growth–mortality trade-off ordination using the 'envfit' (linear) and 'ordisurf' (non-linear) functions in R package vegan (Oksanen et al., 2011). In our case, the ordination space is defined by a PCA of RGR_{90} and M_{30}. The linear analysis regresses driver variables onto an ordination by finding the vector direction in the ordination space that has a maximal correlation with the driver variables (Jongman et al., 1995; Rüger et al., 2018). The non-linear analysis is analogous, but uses a generalized additive model to account for nonlinearity in the relationships. The significance of the fitted vectors was assessed using a permutation-based test in which the observed values were compared with those from 999 permutations. Model selection using *F*-statistics from analysis of variance (ANOVA) was used to identify whether the linear or non-linear model was more supported by the data. The linear was more supported than the non-linear model for all functional traits and ecological niche variables, except for LAR, SMF and OMC (Tables S3 and S4). All analyses were conducted in the R statistical programming language version 4.0.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Interspecific growth–mortality relationship

We found evidence for the interspecific growth–mortality relationship at the seedling stage, since there was a significant positive relationship between RGR_{90} and M_{30} among the 14 species in our study ($R^2=0.45$, $p=0.008$) (Figure 1). Furthermore, the relationship between RGR_{90} and M_{30} remained unchanged when phylogenetic-independent contrasts were used ($R^2=0.48$, $p=0.008$) (Figure S3). The first principal component (PC1) accounted for 84% of the total variation of growth and mortality rates and was positively correlated with both rates (Figure 2). Most species fell along a well-defined axis of increasing RGR_{90} with increasing M_{30}, with one exception, *Dichapetalum gelonioides*, a moderately shade tolerant, midstory tree species (Table S2) that had the slowest RGR_{90}, but the second-highest M_{30}.

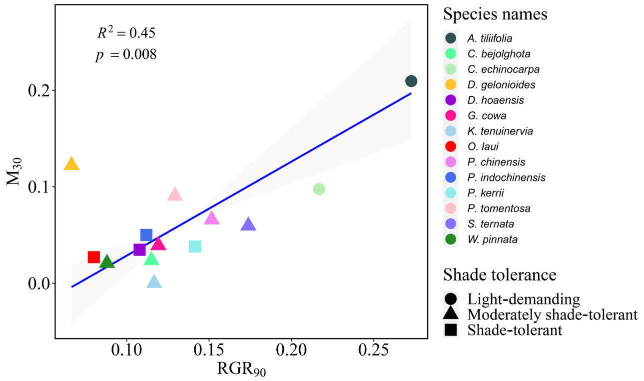

FIGURE 1 The growth–mortality trade-off at the seedling stage for 14 tree species in the Xishuangbanna forest dynamics plot, China. The capacity for fast height growth is the 90th percentile of relative height growth rate (RGR_{90}), and the slow-growth mortality rate is the rate of the 30% slowing seedlings (M_{30}) and were significantly correlated ($r=0.67$, $p<0.01$). The grey ribbon shows the 95% confidence interval for the growth–mortality trade-off relationship based on an standardized major axis regression fit (Slope = 1.02, upper and lower 95% confidence intervals of 1.61 and 0.65, $R^2=0.45$, $p=0.008$). See Table S2 for species information and Figure S2 for a robustness analysis of the interspecific growth–mortality trade-off.

3.2 | Relationships of traits and niche variables with growth, mortality and the growth–mortality trade-off

The first three principal component axes for traits (Trait PC1, Trait PC2 and Trait PC3) accounted for 66% of the total trait variation across all species (Table S5). Trait PC1 was highly associated with LA, LT and LMF, whereas Trait PC2 was highly associated with SLA, LAR and RMF, and Trait PC3 was associated with CHL, LDMC and LMF (Table S5). The first two principal component axes for niches (NichePC1 and Niche PC2) together accounted for 63% of the total variation (Table S6). Niche PC1 was negatively associated with TK and SVWC, Niche PC2 was negatively associated with AN, AP and TP (Table S6). Only one functional trait (SSL) and variables related to soil fertility (BD, OMC, TN, slope and Niche PC2) were significantly related to growth rates (Figure 3a–f; Table 2). SSL alone showed a significant negative relationship with mortality rates (Figure 3g; Table 2). The growth–mortality ordination (trade-off PC1) was also strongly correlated with SSL and very weakly with LMF and the multivariate Trait PC1 (Figures 2a and 3h; Table 2). This ordination was also associated with more fertile soils, as suggested by a positive correlation with TN and a negative correlation with BD, topographic slope and Niche PC2 (Figures 2b and 3i–l; Table 2). Species at the fast growth/high mortality end of the growth–mortality trade-off axis were associated with lower SMF, and higher LAR and OMC based on a nonlinear analysis (Figure S4a–c; Table 2).

4 | DISCUSSION

Using data on 5 years of seedling censuses, we found evidence for the interspecific growth–mortality trade-off at the seedling stage among 14 co-occurring tree species in a tropical forest in Asia. The existence of the trade-off is thought to be attributable to interspecific variation in functional traits (King et al., 2006; Kitajima, 1994; Metz et al., 2023; Osazuwa-Peters et al., 2014; Sterck et al., 2006; Wright et al., 2010) and resource allocation strategies (Russo et al., 2021). Our study supports the latter hypothesis, as we found little evidence that the trade-off was correlated with organ-level trait variation. Instead the interspecific growth–mortality trade-off for these seedlings was strongly related to allocation-based functional traits. Specifically, the trade-off was linearly related to SSL and LMF and nonlinearly related to LAR and SMF.

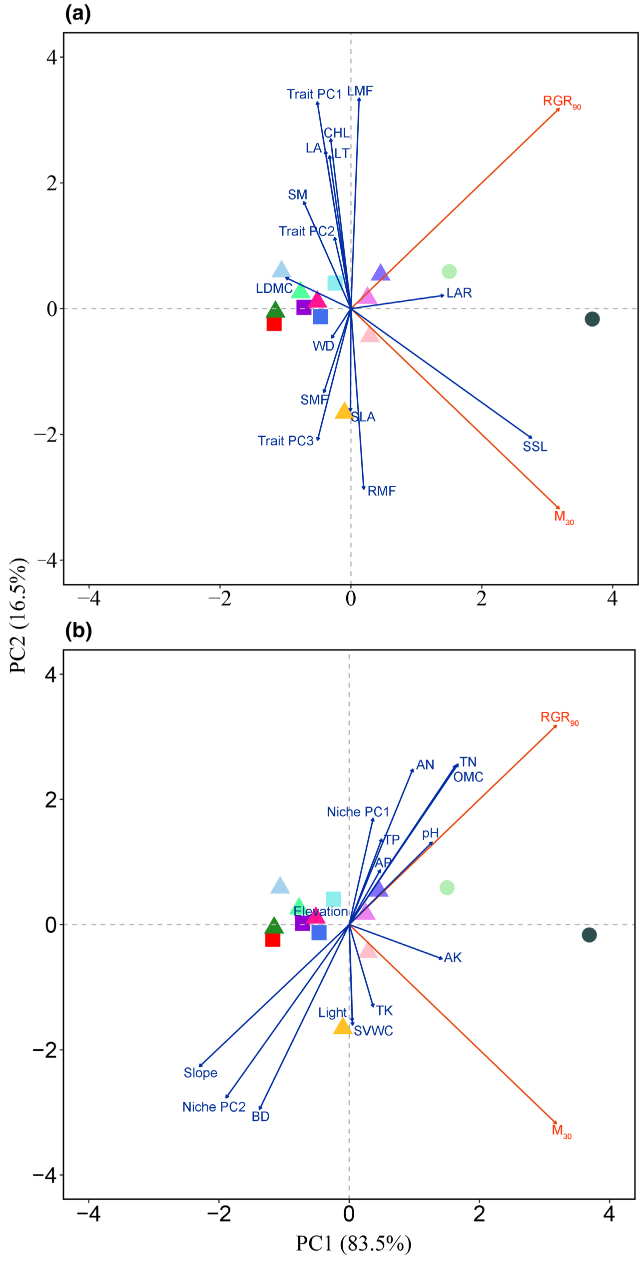

FIGURE 2 Ordination plot of species growth and mortality (PC1 and PC2) with respect to functional traits and ecological niches based on a linear model for seedlings of 14 species in the Xishuangbanna forest dynamics plot, China. The linear regression analysis finds the direction in the growth–mortality ordination space that has maximal correlation with the driver variables (Jongman et al., 1995), which in our case are the functional traits (a) and ecological niche variables (b). The direction and length of the vectors for each trait and niche variable were determined by the envfit function in the vegan package (Oksanen et al., 2011), indicating the direction of the gradient and the strength of the correlation, respectively. The interspecific growth–mortality relationship (PC1) was estimated based on the species' 90th quantile of relative growth rate in height (RGR_{90}) and the mortality rate of the 30% slowest growing individuals (M_{30}) for each species. See Table S2 for species information and Table 1 for information about functional traits and ecological niche variables. Symbol colours and shapes match those in Figure 1.

Only SSL was also related to growth and mortality rates (analysed separately). SSL represents the seedling height growth achieved per unit mass invested in the stem, and has been found to be a central organizing trait for plant (Rao et al., 2023). In our study, species with higher SSL were strongly associated with the faster growth/higher mortality end of the trade-off axis, reflecting the importance of this growth-related trait for surviving in the understory of this closed-canopy forest. The nonlinear relationships of LAR and SMF to the trade-off suggest that functional contributions of these traits to growth and mortality relationships are likely to depend in complex ways on other phenotypic traits. This nonlinearity may also explain why functional trait relationships with demography show considerable inconsistency across studies. Our finding that interspecific variation in organ-level traits was not strongly associated with the trade-off axis nor growth and mortality rates analysed separately is consistent with some studies (Poorter et al., 2008; Wright et al., 2010; Yang et al., 2018). But inconsistent with others finding that variation in SLA and WD was significantly associated with seedling demographic rates and trade-offs (Browne et al., 2022; Kitajima, 1994; Metz et al., 2023).

Inconsistency across studies in functional trait-demographic rate relationships may also be explained by variation across sites in the relative importance of particular environmental factors for plant fitness and, thus, of the traits that mediate those phenotype–environment interactions. Studies of the growth–mortality trade-off among tree species have often focused on light availability and the consequences for species ecological niches with respect to shade tolerance and intolerance (Kitajima, 1994; Kobe, 1996; Philipson et al., 2014). However, we found that growth, mortality and the trade-off were not related to ecological niches defined by light, but rather by variation in belowground resources, consistent with Baraloto et al. (2006) and Russo et al. (2005, 2008). In our study, species at the faster growth/higher mortality end of the trade-off were associated with more fertile soils defined by lower soil BD and slope, and higher OMC and TN.

Our study supports suggestions that, to predict tree demographic rates and putative drivers of trade-offs, organ-level functional traits should be considered along with allocation in a whole-plant perspective, since demographic rates operate at the individual level (Yang et al., 2018). Moreover, a multidimensional conception of tree species' niches including not only light, but also topography and soil fertility is necessary to fully capture the consequences of demographic trade-offs for species distributions at the seedling stage.

4.1 | Interspecific growth–mortality trade-off

The interspecific growth–mortality trade-off is thought to be driven by unavoidable compromises between alternative functions related to resource allocation at the organ and whole-plant levels (Grubb, 1977; Rüger et al., 2018; Wyckoff & Clark, 2002). The trade-off is defined by an axis of variation from resource-acquisitive

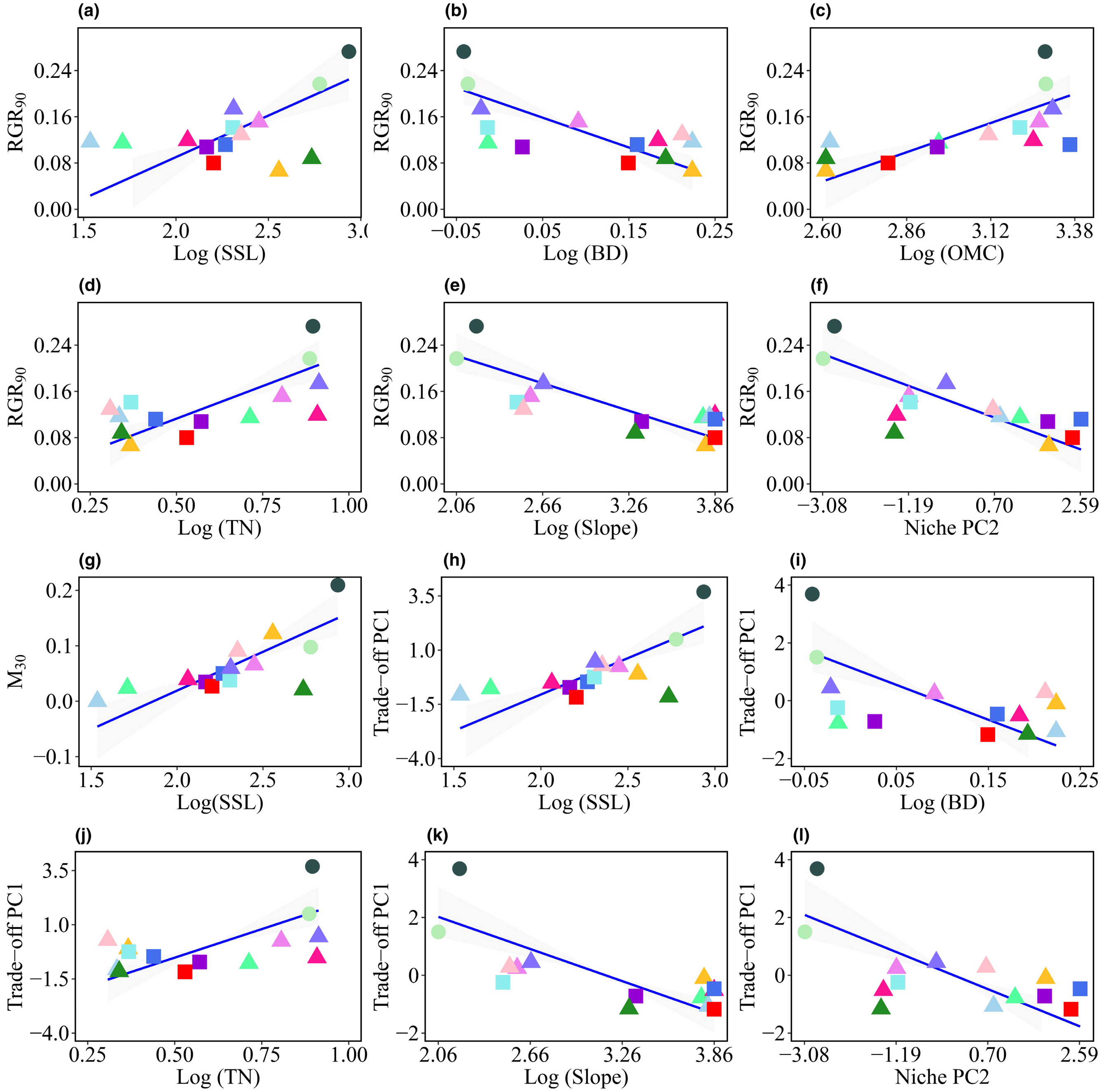

FIGURE 3 Functional trait and ecological niche correlates of seedling growth and mortality rates and the growth–mortality trade-off across 14 species in the Xishuangbanna forest dynamics plot, China. Relationships of specific stem length (SSL), soil bulk density (BD), soil organic matter concentration (OMC), soil total nitrogen (TN), slope and Niche PC2 with RGR_{90} (a, b, c, d, e, f). And SSL with M_{30} (g). SSL, BD, TN, slope and Niche PC2 with the interspecific growth–mortality trade-off axis (h, i, j, k, l). SSL, BD, OMC, TN and slope are plotted on the natural log scale. See Table S2 for species information and Table 1 for information about functional traits and ecological niche variables. Symbol colours and shapes match those in Figure 1.

species with higher growth and mortality rates that usually are found in habitats with ample resources to resource-conservative species thought to have greater stress tolerance, and hence higher survival despite occupying more resource-limited habitats (Diaz et al., 2004; Inman-Narahari et al., 2014; Kitajima & Meyers, 2008; Russo et al., 2008; Sterck et al., 2006). As in previous studies in species-rich forests (Rüger et al., 2020, Russo et al., 2021), we found that most species were at the more resource conservative end of the trade-off axis, with the exception of just two light-demanding species (*A. tiliifolia* and *C. echinocarpa*) found at the more acquisitive end, which makes sense since canopy gaps are often rare in closed-canopy forests experiencing milder disturbance regimes, such as in XFDP. One species, however, did not fall along the interspecific growth–mortality trade-off axis,

TABLE 2 Relationships of species' growth rates, mortality rates and the interspecific growth–mortality trade-off with functional traits and ecological niches for seedlings of 14 tree species.

		SMA		Multivariate analyses	
	Traits or niche variables	RGR$_{90}$	M$_{30}$	Trade-off PC1	r^2
Organ-level traits	LA	<0.01 (<0.01)	0.14 (<−0.01)	−0.15	0.31
	CHL	0.01 (<0.01)	0.14 (<−0.01)	−0.11	0.36
	LDMC	0.03 (−0.64)	0.05 (−0.62)	−0.89	0.06
	LT	<0.01 (0.78)	0.12 (−0.76)	−0.13	0.29
	SLA	0.02 (<−0.01)	0.02 (<0.01)	<−0.01	0.13
	SM	0.02 (<0.01)	0.14 (<−0.01)	0.39	0.01
	WD	0.01 (−0.66)	<0.01 (−0.65)	−0.53	0.16
Biomass allocation traits	LMF	0.12 (0.70)	0.05 (−0.68)	0.03	**0.55***
	LAR†	0.08 (<0.01)	0.07 (<0.01)	0.98	0.10
	SMF†	0.07 (−0.96)	<0.01 (−0.93)	−0.29	0.09
	SSL	**0.32* (0.01)**	**0.58** (0.01)**	**0.80**	**0.58****
	RMF	0.02 (−0.66)	0.11 (0.64)	0.06	0.40
Multivariate traits	Trait PC1	<0.01 (0.03)	0.25 (−0.02)	−0.15	**0.54****
	Trait PC2	<0.01 (−0.03)	0.03 (−0.03)	−0.21	0.06
	Trait PC3	0.14 (−0.04)	<0.01 (−0.04)	−0.23	0.22
Soil niches	AN	0.29 (<0.01)	0.03 (<0.01)	0.36	0.35
	AP	0.04 (<0.01)	0.01 (<0.01)	0.48	0.04
	AK	0.07 (<0.01)	0.10 (<0.01)	0.93	0.11
	BD	**0.46** (−0.47)**	0.07 (−0.45)	**−0.42**	**0.52****
	OMC†	**0.43* (<0.01)**	0.12 (<0.01)	**0.54**	**0.45***
	pH	0.16 (0.05)	0.07 (0.05)	0.69	0.16
	TN	**0.44** (0.11)**	0.12 (0.11)	**0.54**	**0.46***
	TP	0.08 (0.32)	0.00 (0.31)	0.34	0.10
	TK	<0.01 (0.01)	0.06 (<0.01)	0.27	0.09
	SVWC	0.01 (<0.01)	0.02 (<0.01)	0.03	0.12
Topographic niches	Elevation	<0.01 (<−0.01)	<0.01 (<−0.01)	−1.00	0.01
	Slope	**0.51** (<−0.01)**	0.23 (<−0.01)	**−0.71**	**0.51****
Light niche	Light	0.01 (−0.02)	0.02 (0.02)	0.02	0.11
Multivariate niches	Niche PC1	0.08 (0.02)	<0.01 (0.02)	0.21	0.14
	Niche PC2	**0.54** (−0.02)**	0.16 (−0.02)	**−0.56**	**0.55****

Note: Univariate analyses used standardized major axis regression (SMA) to evaluate the relationships of each trait and Trait PC1–PC3 and each niche and Niche PC1–PC2 with the 90th quantile of relative height growth rate (RGR$_{90}$) and the mortality rate of the 30% of the slowest growing seedlings (M$_{30}$), using species-specific values. The R^2 is given, along with the estimate of the slope of demographic rate as a function of traits or niches in parentheses, and the probability (p) is indicated by asterisks (* corresponds to $p < 0.05$; ** corresponds to $p < 0.01$). Multivariate analyses used models to regress trait variables onto the growth–mortality trade-off ordination to find the vector direction in the growth–mortality ordination space that has a maximal correlation with the driver variables. The values in the column, 'Trade-off PC1' represent the relationship of the trait or niche variables with the interspecific growth–mortality trade-off axis based on cosines: Values closer to 1 indicate that direction of the relationships between the trait or niche and Trade-off PC1 axis are similar, values closer to −1 indicate that they vary in opposite directions, and values near zero mean they are little to no relationship of directions. The r^2 represents the amount of variation in the trait or niche that is explained by the trade-off, and significance is assessed with a permutation-based test. If the r^2 is statistically significant, yet the value of trade-off PC1 near zero, this suggests that this trait or niche related to the second axis of the growth–mortality relationship. Statistics from linear models are reported for all traits, the non-linear model provided a better fit to the SMF, LAR and OMC relationship with the trade-off (indicated by †) (Figure S4). Significant parameter estimates are indicated in bold, with * indicating significance at <0.05, and ** indicating significance at <0.01. See Table 1 for abbreviations.

D. gelonioides. It is not unusual that some species deviate from the expected trade-off axis, and in some cases, this may be explained by particular combinations of functional properties of the species that may allow them to 'escape the trade-off' (sensu Russo et al., 2010) or by stochastic or environmentally driven variation in demographic rates.

4.2 | Biomass allocation traits and soil-defined niches are related to the interspecific growth–mortality trade-off

Functional traits are thought to be a fundamental driver of variation in plant performance, such as growth, mortality and reproduction (McGill et al., 2006; Reich, 2014). However, this is only true to the extent that they are reliable proxies for integrated physiological processes operating at the whole-plant level (Adler et al., 2014; Yang et al., 2018). Our study suggests that organ-level traits may not always be reliable proxies, as we found that only biomass allocation traits (SSL, LAR and SMF) had significant relationships with the trade-off, and only SSL was positively related to growth and mortality rates at the seedling stage in a tropical forest in southwest China. Species achieving greater stem elongation per unit mass had faster growth and higher mortality rates, and were at the more acquisitive end of the trade-off axis, suggesting that these species prioritize resource allocation to the non-photosynthetic organ stem during the early life stages. LAR had no significant relation to growth or mortality rates individually in our study, in contrast with other studies (Umana et al., 2021), although it did vary nonlinearly with the growth–mortality trade-off. Our results indicate that the biomass allocation trait, SSL, may be important for seedlings in deeply shaded understories of closed-canopy forests with low rates of disturbance. However, the trait determinates of the interspecies growth–mortality trade-off may vary with ontogenetic stage. For example, although the SSL may be a more important functional trait for seedlings to grow rapidly in height and position their leaves in better light environments in closed canopy forests, other traits, especially organ-level traits like WD and SLA may be more important for adult trees (Iida & Swenson, 2020; Visser et al., 2016).

SSL is related to WD, which has been found to correlate with growth, mortality, and the trade-off at the seedling stage (Kitajima, 1994, Philipson et al., 2014). However, SSL is distinct from WD and is more functionally related to seedling growth, as it is a measure of the mass investment required for stem elongation and is thus directly related to the efficiency of height growth (Poorter et al., 2012; Umana et al., 2021). Moreover, SSL may act as a hub trait with respect to phenotypic integration by integrating the trade-off between stem construction cost and carbon gain from leaves (Kleyer et al., 2019; Rao et al., 2023). For young trees, height growth is essential because tree height partly governs light capture in closed-canopy forests (Bin et al., 2022). However, wood is costly to construct and does not directly contribute to photosynthesis, so species with an acquisitive strategy should maximize their stem elongation rate by investing the minimal amount of mass per unit length of stem that is required to support their crown and display leaves for light capture (Poorter et al., 2012).

Species with higher RGR_{90} and strong growth–mortality trade-off were associated with more fertile soils, as suggested by a positive correlation with OMC and TN and a negative correlation with BD and slope (Figure 3b–e), this is consistent with previous studies that higher soil nitrogen is associated with faster seedlings growth rates (Umana et al., 2021) and promotes greater plant biomass allocation to leaves (Santiago et al., 2012). BD is an important physical property of soil, offering a comprehensive reflection of the soil's overall fertility (Saini, 1966). Variation in BD is linked with soil porosity, which in turn is correlated with soil permeability, water-holding capacity, organic matter concentrations and the ability of plant roots to access soil nutrients (Bengough, 2003; Weil & Brady, 2017). Species with higher BD have been observed to allocate more biomass to root elongation, thus limiting the height growth (Ola et al., 2018). Areas of the study forest with shallower slope tend to have higher belowground resource availability, which would favour faster growth strategies (Liu et al., 2014; Reich, 2014).

Many studies have shown that light heterogeneity and canopy disturbance rates have a strong effect on growth–mortality trade-offs (Baraloto et al., 2005; Hubbell, 2001; Kobe et al., 1995; Russo et al., 2021; Wright et al., 2010) and growth and mortality rates (Umana et al., 2020, 2021; Wu et al., 2016). However, we did not observe a significant effect of canopy openness on the seedling growth–mortality trade-off (Table 2). That may be because the canopy disturbance rates in our forest are relatively low and these dominant species show higher allocation towards stems to increase and enhance light-capture ability access to the scarce light resources available in the understorey, so light availability may be a less important factor shaping ecological niches at the seedling stage in this forest. The two light-demanding species in our study had faster growth and higher mortality rates than the other species, which were more shade-tolerant. The more light-demanding species also had higher SSL and were found in more fertile, indicating an acquisitive strategy with greater allocation to faster growth which is favoured in more fertile soils (Russo et al., 2005; Worthy et al., 2020). This relationship highlights the critical that soil properties and topography play in tree demography.

Our results differ from some studies of transplanted or naturally recruited seedlings from primarily neotropical forests, which suggest that organ-level traits, especially those related to photosynthesis, WD and light-based niches, were correlates of the trade-off (Kitajima, 1994; Metz et al., 2023; Philipson et al., 2014). While identical traits and niche variables were not investigated in these studies, the contrasting results suggest that the putative functional drivers of the trade-off and its consequences for ecological niches are likely to vary, depending on biogeography, climate, topography and soil properties. The study forest is characterized by low canopy disturbance rates and producing very shaded understories and a high degree of topographic variation (Deng, 2022). Other tropical forests can have more open canopies owing to more frequent disturbances or severe droughts or previous logging activities (e.g., Condit et al., 1995; Zimmerman et al., 1994). While it is recognized that demographic rates have a functional basis and that trade-offs are universal (Stearns, 1992), growth and mortality rates still depend on the local environmental conditions, which means that trade-offs may not always be observed (Russo et al., 2021; Van

Noordwijk & Dejong, 1986) or may have different functional drivers and consequences for ecological niches. Thus, environmental differences and compositional variation due to different phylogeographic histories, combined with contrasting abilities of traits to function as reliable proxies for whole-plant physiological processes, are likely to cause site-to-site variation in the strength of relationships of demographic rates and trade-offs with functional traits and ecological niche variables.

5 | CONCLUSIONS

For the seedlings in this Asian tropical forest, we found that traits related to biomass allocation, rather than organ-level traits, have stronger associations with growth rates, mortality rates and their trade-off, which correlated with ecological niches defined by soil properties and topography, rather than light. While allocation-based traits can be directly measured in younger trees, a challenge for trait-based plant ecology is to develop tractable quantitative approaches, such as allometric approximations (e.g., Waring & Powers, 2017) and imaging-based approaches (Burt et al., 2018), to directly measure resource allocation-based traits in adult trees in order to compare the functional-drivers of demographic trade-offs across life stages.

AUTHOR CONTRIBUTIONS

C.Z., L.L. and S.E.R. conceived and designed the study. C.Z., R.G. and L.L. collected the data. C.Z. analysed the data, with help from S.E.R. All authors wrote the manuscript.

ACKNOWLEDGEMENTS

This study was funded by the Strategic Priority Research Program of Chinese Academy of Sciences (XDB31000000), the Joint Fund of the National Natural Science Foundation of China-Yunnan Province (U1902203), Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (151C53KYSB20200019) and the National Natural Science Foundation of China (32160268). We thank Liqing Sha for soil data collection. We thank all of the people who have contributed to the establishment of and data collection in the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot.

CONFLICT OF INTEREST STATEMENT

Sabrina E. Russo is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper. The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the figshare: https://doi.org/10.6084/m9.figshare.26264681 (Zhang et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Abbreviation, calculation, unit, mean, minimum and maximum values of twelve functional traits measured on seedlings of 14 tree species in the 20-ha Xishuangbanna forest dynamics plot.

Table S2: Taxonomic and ecological characteristics of the species included in this study (species with ≥100 seedlings in the 2010 census) in the 20-ha Xishuangbanna forest dynamics plot.

Table S3: Model selection based on analyses of variance comparing the linear and non-linear analysis of functional traits with respect to the ordination of growth and mortality rates across species.

Table S4: Model selection based on analyses of variance comparing the linear and non-linear analysis of ecological niche variables with respect to the ordination of growth and mortality rates across species.

Table S5: The loadings of each functional trait onto the first three components (PC1, PC2, and PC3) from a principal components analysis (PCA) of twelve functional traits measured on seedlings of 14 species in the 20-ha Xishuangbanna forest dynamics plot in China.

Table S6: The loadings of environmental variables onto the first two components (PC1 and PC2) of a principal components analysis (PCA) of 12 ecological niche variables measured in seedling quadrats in the 20-ha Xishuangbanna forest dynamics plot in China.

Figure S1: Geographical location of the 20-ha Xishuangbanna forest dynamic plot in southern China, with dark green indicating forested regions (left). Locations of seedling subplots in the Xishuangbanna plot (right).

Figure S2: Robustness analysis of the interspecific growth-mortality trade-off for seedlings across 14 tree species in the Xishuangbanna forest dynamics plot, China.

Figure S3: Left: phylogenetic relationships of 14 seedling species included in this study from the Xishuangbanna forest dynamics plot in southern China (based on Wu et al., 2016). Phylogenetic independent contrasts of RGR_{90} and M_{30} for seedlings of 14 tree species in this study.

Figure S4: Ordination plot of species growth and mortality (PC1 and PC2) with respect to functional traits and ecological niches area based on a nonlinear model for seedlings of 14 species in the Xishuangbanna forest dynamics plot, China.

How to cite this article: Zhang, C., Gu, R., Lin, L., & Russo, S. E. (2024). Functional traits and ecological niches as correlates of the interspecific growth–mortality trade-off among seedlings of 14 tropical tree species. *Functional Ecology*, *38*, 1888–1901. https://doi.org/10.1111/1365-2435.14624