SCIENCE CHINA
Life Sciences

•RESEARCH PAPER•

https://doi.org/10.1007/s11427-021-2135-3

Functional trait space and redundancy of plant communities decrease toward cold temperature at high altitudes in Southwest China

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Received April 7, 2022; accepted May 31, 2022; published online July 20, 2022

Plant communities in mountainous areas shift gradually as climatic conditions change with altitude. How trait structure in multivariate space adapts to these varying climates in natural forest stands is unclear. Studying the multivariate functional trait structure and redundancy of tree communities along altitude gradients is crucial to understanding how temperature change affects natural forest stands. In this study, the leaf area, specific leaf area, leaf carbon, nitrogen, and phosphorous content from 1,590 trees were collected and used to construct the functional trait space of 12 plant communities at altitudes ranging from 800 m to 3,800 m across three mountains. Hypervolume overlap was calculated to quantify species trait redundancy per community. First, hypervolumes of species exclusion and full species set were calculated, respectively. Second, the overlap between these two volumes was calculated to obtain hypervolume overlap. Results showed that the functional trait space significantly increased with mean annual temperature toward lower altitudes within and across three mountains, whereas species trait redundancy had different patterns between mountains. Thus, warming can widen functional trait space and alter the redundancy in plant communities. The inconsistent patterns of redundancy between mountains suggest that warming exerts varying influences on different ecosystems. Identification of climate-vulnerable ecosystems is important in the face of global warming.

leaf trait, plant community, hypervolume, redundancy, altitude, natural forest

Citation: Zhang, L., Liu, X., Sun, Z., Bu, W., Bongers, F.J., Song, X., Yang, J., Sun, Z., Li, Y., Li, S., et al. (2022). Functional trait space and redundancy of plant communities decrease toward cold temperature at high altitudes in Southwest China. Sci China Life Sci 65, https://doi.org/10.1007/s11427-021-2135-3

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INTRODUCTION

Many ecosystems are affected by ongoing global warming, but the range of possible outcomes is still under discussion because different ecosystems may respond differently (Engler et al., 2011; Turner et al., 2020). In particular, forested ecosystems may be disrupted from their current stable state (Albrich et al., 2020; Scheffer, 2009). Throughout this process, the ecosystem functional traits of communities will be altered initially because of changes in species composition with temperature, which can consequently affect ecosystem stability (Fay et al., 2008; Imbert et al., 2021; Pillar et al., 2013). Community functional trait space and species trait redundancy, which reveal community niche occupation, are confounding elements that reflect ecosystem functional trait structure. However, how functional trait space and species trait redundancy systematically change under different temperatures is unclear, especially in natural forest stands. Thus, our study aims to fulfill this gap in a mountainous area in China to provide possible evidence of natural systems.

Ecosystem functional trait space, i.e., niche occupation, can be estimated by the functional traits that comprise plant communities (Denelle et al., 2019; Hu et al., 2021; Norberg, 2004). As the leaf economics spectrum reflects aboveground strategies for a tree species (Rees et al., 2001; Silvertown, 2004), five leaf traits, namely, leaf size expressed as leaf area (LA), leaf area per unit mass (SLA), leaf nitrogen content, phosphorous content, and carbon content per unit mass (LN, LP and LC, respectively), are usually used to represent important axes of functional trait space in tree communities (Diaz et al., 2016; Gong et al., 2020; Swenson et al., 2011; Wright et al., 2004). In the present study, we quantify the volumes of functional trait space via a joint consideration of these five traits to represent the functional trait space of communities (i.e., hypervolumes) (Cornwell et al., 2006).

Species trait redundancy, which indicates similar niche occupation between co-occurring species (Elmqvist et al., 2003; Lawton and Brown, 1993), is an important ecological concept (Walker, 1992). Redundant species reduce the chance of functional loss in a community because of the loss of a single species, thereby ensuring the stability of a community (Carmona et al., 2016). Species trait redundancy has positive effects on ecosystem stability and resilience at a single trophic or multi-trophic level (Kang et al., 2015; Pillar et al., 2013; Sanders et al., 2018). Stepwise exclusion of one species after another from a community can be performed to evaluate the functional redundancy of a species (i.e., species sustain similar functions) (Jax, 2005; Naeem, 2002). The degree of change in functional trait space (in terms of volume overlap) after species exclusion indicates the functional redundancy of each excluded species in the community, i.e., species trait redundancy (Fetzer et al., 2015).

As mountainous ecosystems provide natural gradients of temperature (Ma et al., 2010), plant communities in different altitudes open a unique opportunity to understand how community functional trait space and species trait redundancy change in response to temperature variations. Accordingly, this study focuses on plant communities located at an altitudinal gradient ranging from 800 to 3,800 m in Yunnan Province, Southwest China (Figure 1) and aims to understand how altitude and the associated environmental factors affect community trait structures. Moreover, this study is conducted at the individual level to estimate trait structure (Kohli and Jarzyna, 2021). Therefore, 1,590 individual trees from 171 species belonging to 55 families are sampled in this study.

In this study, we predict that functional trait space and redundancy decline with altitude because of the habitat filtering effect (Figure 2) (Cornwell and Ackerly, 2009; Diaz et al., 1998). We first hypothesize that the environmental filtering effect becomes stronger with lower temperature as the altitude increases, which leads to fewer species passing the filter and a constrained functional trait space at high altitudes (Figure 2A). Second, low altitudes are warmer and generally support more species than cold environments at high altitudes (Whittaker, 1960; Whittaker et al., 2001). Therefore, we hypothesize that co-occurring species at high altitudes share less functional trait space than species at low altitudes because the cold temperature at high altitudes constrains available resources, leading to the divergent niche occupation of different species (bigger interspecific trait variation but smaller intraspecific trait variation) (Figure 2B).

RESULTS

Trait differences among mountains and altitude within mountains

Values of all five traits differed among mountains (Figure S1 in Supporting Information). Radar plots show clearly that the three mountains differed in the mean values of LA, SLA, LC, LN, and LP (Figure 3A). Within mountains, the values of LA, SLA, LC, LN, and LP differed among altitudes, but the trait values across altitudes were inconsistent (Figure 3B–D, Figure S2 in Supporting Information).

Functional trait space across temperatures and altitudes

Functional trait space (hypervolume sizes, an estimation of multidimensional trait space based upon the principal component axis (PCA) values of all traits) consistently increased with increasing temperature and decreased with increasing altitude significantly (Figure 4A–B and Figure S3A in Supporting Information, Table 1 and Table S3 in Supporting

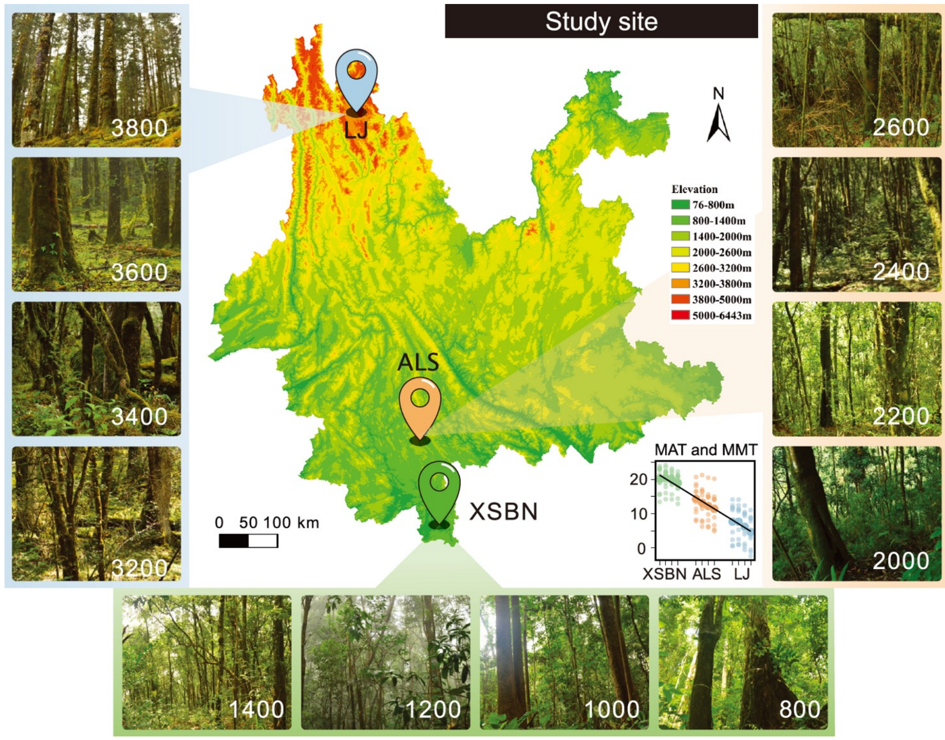

Figure 1 Locations of the three study mountains in Yunnan Province, Southwest China (Source: Geospatial Data Cloud) and corresponding forest landscapes in 12 altitudes located in the three mountains (photos were taken in September 2014). Mean annual temperature (MAT, bigger points) of each altitude was highly correlated with altitude (R^2=0.99). The correlation of MAT and mean monthly temperature (MMT, smaller points) with altitude was shown.

Information). In addition, functional trait space significantly increased with temperature and decreased with altitude across the three mountains (Figure 4C, Table 2).

Species trait redundancy across temperatures and altitudes

Within mountains, species trait redundancy showed different patterns (Figure 5A–B, Table 1 and Table S3 in Supporting Information). Across mountains, species trait redundancy (hypervolume overlap) increased across the whole temperature range and decreased along the altitudinal gradient (Figure 5C, Table 2). In XSBN and LJ, species trait redundancy significantly increased with temperature and decreased with altitude. In ALS, species trait redundancy decreased with temperature and increased with altitude.

DISCUSSION

Functional trait space across temperatures and altitudes

Our first hypothesis that low temperatures at high altitudes filter out species and constrain functional trait space (leaf trait space estimated by hypervolume) was supported across the whole mountain ranges and within each mountain (Figure 4 and Figure S3 in Supporting Information, Tables 1, 2, and Table S3 in Supporting Information). Thus, cold environments at high altitudes generally constrain the variation in leaf trait space of plant communities within and across different ecosystems. This phenomenon leads to a convergence of resource usage (low hypervolumes), which is in agreement with the results obtained from the high-altitude region of the western Himalayas (Thakur and Chawla, 2019). Altitudinal gradients are often analogous to latitudinal gradients (Rahbek, 1995), and our results are similar to those of studies that found decreased functional trait space for plants (Swenson et al., 2012) and mammals (Safi et al., 2011) at the high latitudes. This phenomenon suggests that when studying different ecosystems on a large spatial scale, altitude and latitudinal effects need to be addressed separately because they can cause similar patterns.

Context dependency is an important consideration in trait-based ecology (Catford et al., 2022). Our results highlight this because community functional trait space shifts considerably more with altitude in LJ compared with the other mountains. This result may be due to the strong environmental filtering effect of winter temperatures dropping to zero in LJ (Figure 1).

Similar to the findings of a previous grassland-based work (De Boeck et al., 2007), the present results indicate that warming can widen functional trait space, enhance divergent resource usage and, therefore, partially compensate for the

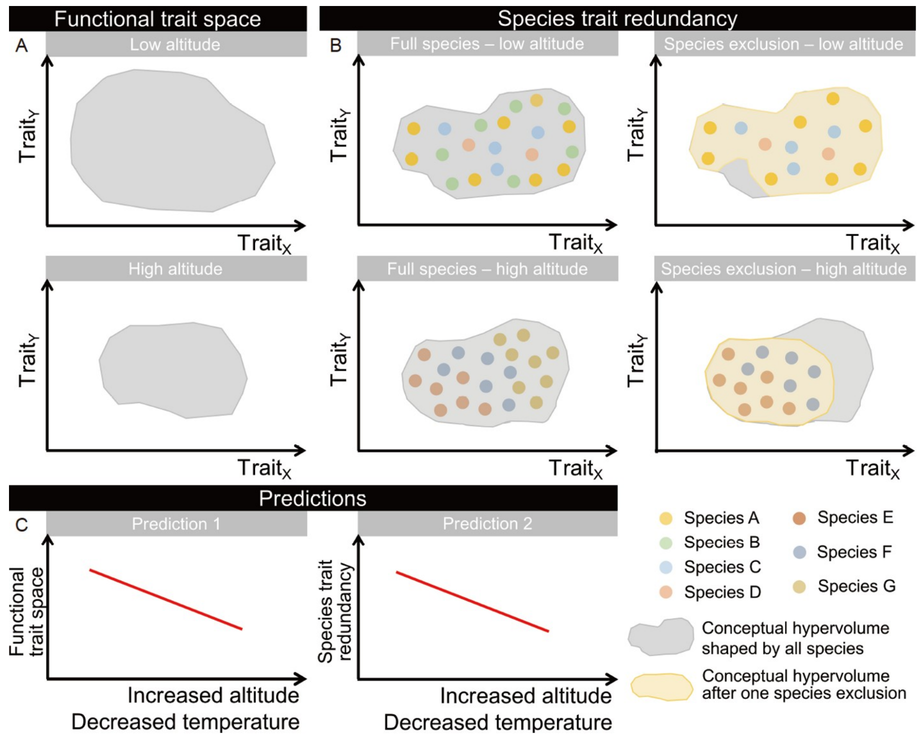

Figure 2 Conceptual illustration of differences in functional trait space (hypervolume) (A) and species trait redundancy (hypervolume overlap) (B) between low and high altitudes (i.e., high and low temperatures), and predictions of functional trait space and species trait redundancy change with temperature and altitude (C). Hypothetical two-dimensional hypervolumes are presented to represent functional communities at low and high altitudes. A, Tree communities at low altitudes (high temperatures) occupy a large functional trait space because of warmer conditions than those at high altitudes (low temperatures). B, Hypervolume overlap between species exclusion and full species. A community at a low altitude (high temperature) is composed of species A, B, C, and D, whereas a community at a high altitude (low temperature) is composed of species E, F, and G. Species at low altitudes are redundant to each other, while species at high altitudes are relatively unique to each other. Species exclusion at low altitudes reduces the hypervolume size less compared with species exclusion at high altitudes. C, We predict that with increasing altitude and decreasing temperature, functional trait space decreases because of constrained environmental conditions. We also predict that with increasing altitudes, species trait redundancy decreases because low altitudes have warm conditions, which may support functionally redundant species. At high altitudes, the cold environment becomes harsh, which could lead to less functionally redundant species.

loss of productivity due to community shifts. Moreover, if warming widens functional trait space and resource usage, additional niche space, especially in cold environments, could become available and could be occupied by species with an affinity to warmer temperatures, which consequently facilitate a shift in plant community structure and composition (Zellweger et al., 2020).

Species trait redundancy changes across temperature and altitudes

Our second hypothesis that low temperatures at high altitudes lead to less species trait redundancy was not completely supported by the results (Figure 5 and Figure S3 in Supporting Information, Tables 1, 2, and Table S3 in Supporting Information). In most cases, species trait redundancy increased toward the high temperature of low altitude within mountains. However, the patterns of redundancy with temperature and altitude differed between mountains. This finding suggests that the divergence or convergence of species functioning in different ecosystems is not universal. The response of species trait redundancy to climate can be context-dependent (Catford et al., 2022). For example, in ALS, the redundancy decreased with temperature and increased with altitude, whereas the opposite relationship was observed in the two other mountains. This phenomenon suggests that in ALS, species share similar functional trait space in cold environments at high altitudes. In XSBN and LJ, species use a unique functional trait space and thus are divergent in cold environments at high altitudes. Nevertheless, warming alters the redundancy in plant communities. In general, redundancy is limited in cold environments at high altitudes. Therefore, within different mountains, the redundancy of communities may not change consistently with future warming. However, we can expect redundancy to increase generally with temperature. Communities with high species trait redundancy should, in principle, be resilient to species extinction as functionally similar species replace those lost (Eisaguirre et al., 2020; Fonseca and Ganade, 2001; Sanders et al., 2018). Therefore, high-altitude plant communities are likely to be functionally vulnerable, and these ecosystems should be preserved primarily. A collaborative work that covers altitude gradients across East and Southeast Asia (Brearley et al., 2019) is warranted to further elucidate species trait re-

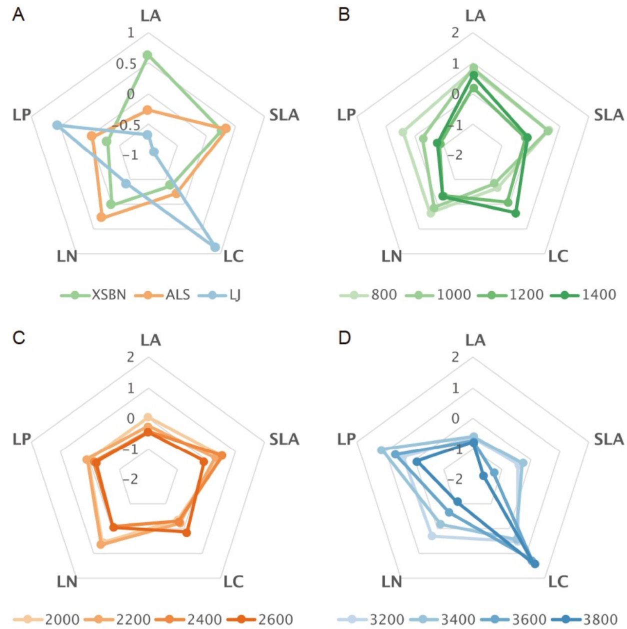

Figure 3 Mean trait values across mountains and altitudes within mountains. Mountains are identified with different colors and altitudes within each mountain with various shades of colors. The polygons connect scaled values (mean=0 and SD=1) for each trait for the (A) three mountains and (B–D) altitudes within XSBN (B), ALS (C), and LJ (D), respectively. See Figures S1 and S2 in Supporting Information for significant differences between mountains and altitudes within mountains per trait.

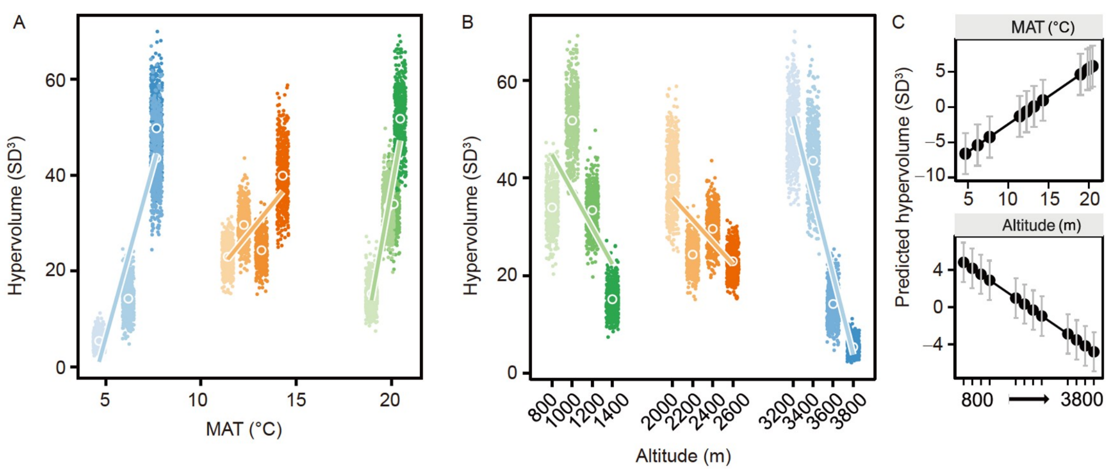

Figure 4 Functional trait space (hypervolume) across the 12 altitudes and corresponding mean annual temperature (MAT). A and B, hypervolumes constructed from the first three PCA axes from all five traits (leaf area, specific leaf area, carbon content, nitrogen content, and phosphorous content) (Table 1). Each small individual solid dot represents one functional trait space of the altitude, and the mean values of each altitude are indicated by large solid dots. Regression lines are shown for each mountain. C shows predicted means and standard errors based on linear mixed models (Table 2). The green gradient represents XSBN, the orange gradient represents ALS, and the blue gradient represents LJ.

dundancy in mountainous ecosystems across latitudes.

MATERIALS AND METHODS

Site description

This study was conducted at 12 altitudinal levels ranging from 800 m to 3,800 m across three sites in Yunnan Province, Southwest China (Figure 1). Three major climatic zones are recognized: tropical (ca. 800 m), subtropical (ca. 2000 m), and subalpine (ca. 3000 m). The first four altitudinal levels are located in Mengla, Xishuangbanna (21°48′N, 101°56′E), which is covered with a monsoon evergreen broad-leaved forest. The mean annual precipitation is 1,521.9 mm, and the mean annual temperature (MAT) is approximately 21°C (Li and Zhu, 2005). The middle four altitudinal levels are located in the Ailao Mountain Nature Reserve (23°9′N, 100°88′E), which is covered by moist evergreen broad-leaved forest. The mean annual precipitation is 1931 mm with a MAT of approximately 11.3°C (Liang

Table 1 Linear models for effects of mean annual temperature (MAT) and altitude on the functional trait space and species trait redundancy of all traits within Xishuangbanna (XSBN), Ailao Mountain (ALS), and Lijiang (LJ), respectively. MAT and altitude were independent variables, while functional trait space and species trait redundancy were dependent variables. t value and corresponding adjusted R^2 are given. Bold letters indicate a significant effect. ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$

	Site	*n*	MAT		Altitude	
			t	R^2	*t*	R^2
Functional trait space	XSBN	2,000	93.43	**0.82*****	−34.27	**0.37*****
	ALS	2,000	39.91	**0.44*****	−37.67	**0.42*****
	LJ	2,000	104.54	**0.85*****	−113.5	**0.87*****
Species trait redundancy	XSBN	133	11.84	**0.51*****	−3.18	**0.065****
	ALS	106	−6.45	**0.28*****	5.86	**0.24*****
	LJ	33	4.82	**0.41*****	−4.39	**0.36*****

Table 2 Linear mixed models for effects of mean annual temperature (MAT) and altitude on the functional trait space and species trait redundancy across mountains. MAT and altitude were set as fixed factors, while site was set as a random effect to account for the biotic and abiotic difference among sites. All variables were scaled. t and P values are given. Bold letters indicate significant effect ($P<0.05$)

	n	MAT		Altitude	
		t	*P*	*t*	*P*
Functional trait space	6,000	103.2	**<0.001**	−81.7	**<0.001**
Species trait redundancy	272	2.96	**<0.05**	−2.98	**<0.05**

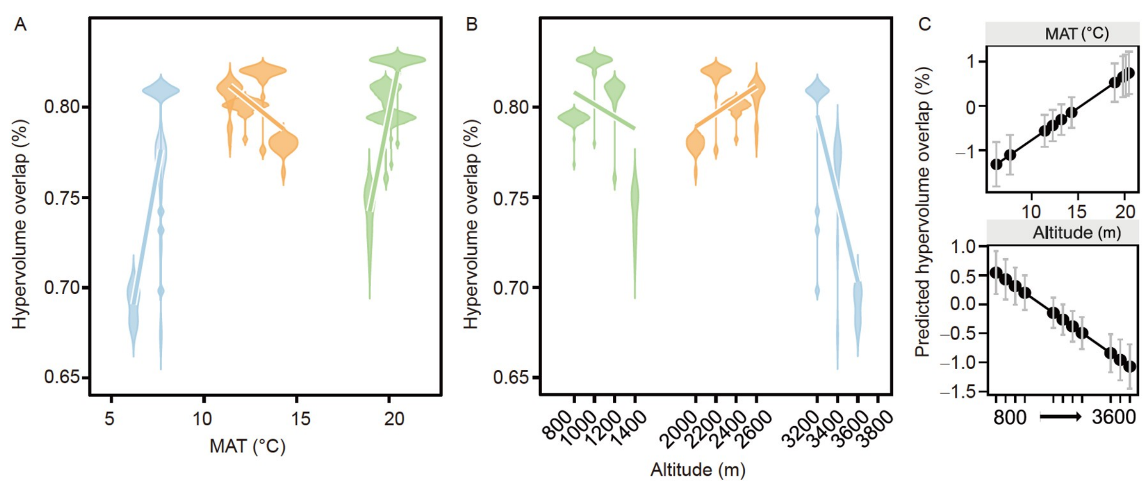

Figure 5 Species trait redundancy (hypervolume overlap) across the 11 altitudes and corresponding mean annual temperature (MAT). A and B, hypervolume overlaps between one species exclusion and full species per altitude calculated from first three PCA axes from all five traits (leaf area, specific leaf area, carbon content, nitrogen content, and phosphorous content) (Table 1). Regression lines are shown for each mountain. C, predicted means and standard errors based on linear mixed models (Table 2). Green represents XSBN, orange represents ALS, and blue represents LJ.

and Gong, 2013). Both sites have distinct dry and wet seasons. The highest four altitudinal levels are located in the subalpine coniferous forest in Yulong Snow Mountain Nature Reserve in Lijiang (26°86′N, 100°25′E). The mean annual precipitation is 935 mm with a MAT of approximately 5.5°C (Li et al., 2016). Detailed descriptions of the three locations are given in Table S1 in Supporting Information.

Leaf trait measurements

At each altitude, we constructed four 20 m×20 m plots. In total, 48 plots were sampled across the three mountains. All woody trees with a diameter at breast height >5 cm (1,590 individuals in total) were sampled and identified to the species level. Four to five undamaged healthy leaves were collected per tree. The total leaves were scanned, and individual LAs (cm^2) were determined. Leaves were then oven-dried for 48 h at 70°C to estimate total dry leaf weight. SLA ($cm^2\ g^{-1}$) was calculated as total LA divided by total dry leaf weight. LC ($mg\ g^{-1}$) and LN ($mg\ g^{-1}$) were determined using the CHNOS Elemental Analyzer Vario EL III (Elementar Analysensysteme GmbH, Hanau, Germany). LP ($mg\ g^{-1}$) was determined using an Inductively Coupled Plasma Atomic Emitted Spectrometer (iCAP 6300 ICP-OES Spectrometer, Thermo Fisher, USA).

Multivariate hypervolume construction

Multivariate hypervolumes were constructed to estimate the multidimensional trait space of tree communities at different altitudes. All individuals in four plots per altitude were pooled together to calculate the variation of trait values at each altitude. A principal component analysis was performed on the scaled (mean=0 and SD=1) trait values for leaf traits at the individual level to create a set of independent axes and construct the hypervolume (Blonder et al., 2014; Hutchinson, 1957). LA, LN, and LP were log-transformed before scaling. Individuals' scores on the first three (for LA, SLA, LC, LN, and LP, together explained 88.6% of variation) PCA axes were used as independent "integrated trait" values. A maximum of three PCA axes were selected for hypervolume construction because the dimensions used for hypervolume construction must be less than the number of log(individuals). An equal number (85 individuals, the least sampled fragments) of individuals were randomly sampled, with replacement (Lamanna et al., 2014), to compare functional trait space (i.e., hypervolume sizes) of tree communities across altitudes. This procedure was simulated 500 times by bootstrapping to create the variability for comparing functional trait space among altitudes (Bittebiere et al., 2019; Bongers et al., 2020; Gardener, 2014). Hypervolumes were constructed by the "hypervolume_gaussian" function, assuming default settings (Silverman bandwidth estimation and 95% probability threshold), in the R package "hypervolume," version 2.0.12 (Blonder et al., 2014; Blonder et al., 2018).

To evaluate the species trait redundancy of communities, we calculated the overlap between the hypervolumes of a subset with one species excluded and the full species set per altitude. First, hypervolumes of the species excluded and the full species set were constructed separately. Thus, at each altitude, each species was excluded one by one, and the rest of the species (individuals) were used for hypervolume construction. As species exclusion reduced the available individuals, an equal number of 60 individuals (the minimum number of individuals when a species was excluded) were selected for the hypervolume construction in both species exclusion and full species set. The overlap of the hypervolumes between species exclusion and full species was evaluated using the multidimensional variation of Sorensen similarity (twice the volume of intersection of two hypervolumes divided by the sum of the two volumes). The whole procedure was simulated 500 times. A high hypervolume overlap between one species exclusion and full species indicated that this species was redundant to another species in the community. A low value of overlap suggests a big unique contribution of such species to the multidimensional trait space to the community. In other words, this species has low redundancy in the community, leading to a big shift in multidimensional trait space after the exclusion of this species. An averaged species trait redundancy in each community was used to represent redundancy at the community level. No redundancy was calculated at 3,800 m because there were only two species, of which one species had only one individual.

Statistical analysis

One-way ANOVAs with post-hoc tests (Tukey's HSD in R) were performed to compare the mean trait values between altitudes within and across mountains. Linear models were used with temperature and altitude as independent variables and functional trait space or species trait redundancy as dependent variables to test if functional trait space and species trait redundancy changed with temperature and altitude within mountains. Linear mixed models were then used to test the changes in functional trait space and species trait redundancy with temperature and altitude as fixed factors and site as the random factor (varying intercept, fixed slopes) to control for unmeasured biotic and abiotic differences. The basic model had the form:

$$y_{i,s}=\alpha+\beta x_{i,s}+\gamma_s+\varepsilon_{i,s},$$

where y is the functional trait space or species trait redundancy at altitude (or temperature) i in site s; α is the overall mean functional trait space or species trait redundancy; β is the parameter adjusting the effect of altitude (or temperature) x; γ denotes the random effect of the site; and ε is the residual error.

All variables were scaled in linear mixed models. The temperature was indicated by MAT and the coldest mean monthly temperature. All statistical analyses were performed in R 4.0.3.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

Acknowledgements *This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31000000), the National Natural Science Foundation of China (31870409, 32061123003), the National Science and Technology Ministry Major Project (2017YFA0605103), CAS Interdisciplinary Innovation Team (JCTD-2018-06), the Youth Innovation Promotion Association CAS (2019082) and the National Science Foundation of the United States (DEB-2029997). We acknowledge the local helpers involved in setting up the plots and collecting data.*

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The supporting information is available online at https://doi.org/10.1007/s11427-021-2135-3. The supporting materials are published as submitted, without typesetting or editing. The responsibility for scientific accuracy and content remains entirely with the authors.