Variation Patterns of Woody Plant Functional Traits in the Tropical Cloud Forest of Bawangling, Hainan Island (Postprint)

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Abstract

Investigating variation in plant functional traits facilitates understanding of the mechanisms and strategies by which plants adapt to their environment, and provides a basis for predicting species distribution and environmental change. In the Hainan Bawangling tropical cloud forest, 21 permanent 20 m × 20 m plots were established and subdivided into 336 subplots of 5 m × 5 m. Functional traits (leaf area, LA; leaf dry weight, LDW; leaf mass per area, LMA; chlorophyll content, Chl; leaf thickness, LTh; wood density, WD) were measured for all individual trees and shrubs with a diameter at breast height greater than 5 cm, along with soil nutrient content. Variance partitioning was employed to quantify the magnitude of functional trait variation at individual, intraspecific, interspecific, and community levels, and to examine the influence of soil nutrients on trait variation. The results indicated that the ranges of explained variance for LA, LDW, LMA, CHl, LTh, and WD at individual, intraspecific, interspecific, and community levels were 0.06–0.47, 0.09–0.35, 0.35–0.72, and 0–0.07, respectively. Across these hierarchical levels, interspecific variation in functional traits was greatest, while community-level variation was minimal. Stepwise regression analysis revealed that functional trait variation at different scales was closely associated with soil organic matter, nitrogen, and phosphorus contents.

Full Text

Variation in Woody Plant Functional Traits of the Tropical Cloud Forests in Bawangling, Hainan Island

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Abstract

Studying variation in plant functional traits helps us understand how plants adapt to environmental conditions and provides a basis for predicting species distributions and environmental changes. We established twenty-one 20 m × 20 m plots, subdivided into 336 subplots of 5 m × 5 m, in the tropical cloud forests of Bawangling, Hainan Island. Functional traits—including leaf area (LA), leaf dry weight (LDW), leaf mass per area (LMA), leaf chlorophyll content (Chl), leaf thickness (LTh), and wood density (WD)—were measured for all trees and shrubs with diameter at breast height (DBH) $\geq$ 5 cm, along with soil nutrient contents in all plots. The magnitude of variation in each functional trait was assessed at individual, within-species, among-species, and community levels using variance decomposition analysis, while relationships between soil nutrients and functional traits were examined using stepwise linear regression. Results showed that the ranges of explained variance for LDW, LMA, Chl, LTh, LA, and WD were 0.06–0.47, 0.09–0.35, 0.35–0.72, and 0–0.07 at the individual, within-species, among-species, and community levels, respectively. This indicates that functional trait variation was highest at the among-species level and lowest at the community level. Stepwise regression analysis showed that changes in functional traits at all studied scales were significantly correlated with soil organic matter, nitrogen, and phosphorus.

Keywords: tropical cloud forest; functional traits; variation; soil factors

Introduction

Plant functional traits typically refer to biological characteristics that affect plant survival, reproduction rate, and ultimate fitness. These traits reflect interactions between organisms and between organisms and their environment at individual, community, and ecosystem levels, advancing community ecology from qualitative description and complex models toward quantitative and parsimonious approaches. Plant functional traits are closely related to environmental conditions, with different traits reflecting different ecological strategies and influencing species assembly processes in communities. The magnitude of functional trait plasticity varies among species, and the effects of environmental filtering on functional traits are related to both spatial scale and community organization level. Community organization levels include individual, within-species, among-species, and community scales, which help researchers explain ecological patterns and processes.

Most scholars consider among-species functional trait variation as the primary approach for functional trait studies. However, recent findings indicate that within-species functional trait variation is also very important, potentially being more sensitive to environmental conditions than among-species variation and playing a significant role in community ecology. Some researchers argue that studying functional traits at the community level can place environmental factors and functional traits within the same system to explain plant adaptation mechanisms. Although many studies have sought potential sources of functional trait variation across various community organization levels, controversy remains regarding the relative magnitude of variation at each level.

Tropical cloud forests refer to forests in humid tropical regions that are frequently shrouded in clouds and fog. These forests experience strong mountain winds, and soil water content is often saturated. Compared with typical low-altitude tropical forests, tropical cloud forests have significantly shorter tree heights and smaller diameters, often with crooked trunks, high proportions of simple leaves, and rich in endemic and endangered species. Affected by environmental filters such as low air temperature and low soil phosphorus, Hainan Island' s tropical cloud forests are mainly distributed on mountain tops or ridges above 1200 m in forested areas. Plants in tropical cloud forests have smaller specific leaf area and height than low-altitude forest plants, suggesting that patterns of functional trait variation may differ from low-altitude vegetation in tropical regions.

Taking the tropical cloud forest in Bawangling, Hainan as our study object, we measured functional traits including leaf dry weight, leaf chlorophyll content, leaf thickness, and wood density for all individuals with DBH $\geq$ 5 cm in each 20 m $\times$ 20 m plot, as well as soil organic matter, total nitrogen, and available nitrogen content. We then used variance decomposition to quantify the magnitude of trait variation at individual, among-species, and community levels, and explored relationships between soil nutrients and functional trait variation at different community organization scales. We hypothesized that: (1) functional traits of tropical cloud forest plants would show different magnitudes of variation across community organization scales, with the largest variation at the among-species level; and (2) soil factors would significantly affect functional trait variation across community organization scales.

1. Study Site Description

The study site is located in Bawangling Nature Reserve (18°50 -19°05 N, 109°05 -109°25 E), with an elevation range of 100–1654 m. The region has a tropical monsoon climate with distinct wet and dry seasons. The average annual temperature at 100 m is 23.6°C, with annual precipitation of 1677.1 mm. Soils transition from latosol (mountain red soil) at lower elevations to mountain yellow soil and mountain meadow soil at higher elevations. Vegetation types distributed along the elevation gradient include tropical lowland rainforest, tropical montane rainforest, tropical montane evergreen forest, and tropical montane dwarf forest. Bawangling' s tropical cloud forests are mainly distributed as island-like patches on Yajia Songding and Songlingding peaks, with dominant species including *Pinus fenzeliana*, *Distylium racemosum*, *Rhododendron moulmainense*, *Syzygium buxifolium*, and *Engelhardia roxburghiana*. The average tree height is approximately (4.79 $\pm$ 2.80) m.

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2. Species Survey Methods

We established 21 plots of 20 m $\times$ 20 m in the tropical cloud forests of Yajia Songding and Songlingding in Bawangling, covering a total area of 0.84 hm^2. Plots were spaced 10–11 m apart. Each plot was subdivided into 5 m $\times$ 5 m subplots. For all trees and shrubs with DBH $\geq$ 5 cm, we measured DBH using a diameter tape and recorded species names. Specimens that could not be identified in the field were collected and taken to the laboratory for expert identification. Plot information is summarized in .

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3. Selection and Measurement of Functional Traits

We selected functional traits that reflect plant carbon accumulation, photosynthetic rate, and resistance to environmental stress: leaf area (LA), leaf dry weight (LDW), leaf mass per area (LMA), leaf chlorophyll content (Chl), leaf thickness (LTh), and wood density (WD). Leaf mass per area reflects the adaptation ability of cloud forest plants to low temperature and thin soil conditions, as well as their competitive ability for light and space resources. Wood density reflects growth rate and the ability to resist pathogens and physical damage. Leaf chlorophyll content is related to photosynthetic rate and carbon accumulation, while leaf thickness reflects mechanical strength and responses to low temperature and strong wind conditions in tropical cloud forests.

Functional traits were measured for all trees and shrubs with DBH $\geq$ 5 cm (excluding gymnosperms). For each plant individual, we selected 3–5 fully expanded, mature, sun-exposed leaves from the canopy edge. Leaf thickness was measured as the thickness between the edge and midrib (avoiding veins) using a digital caliper (SF2000, Guilin, China). Chlorophyll content was measured using a portable chlorophyll meter (SPAD-502 Plus, Konica Minolta, Japan). Leaf area was measured with a leaf area meter (LI-COR 3100C, LI-COR, USA). Leaves were then oven-dried at 70°C for 72 hours and weighed to obtain leaf dry weight. LMA was calculated as the ratio of leaf dry weight to leaf area.

From each plant, we cut a 10 cm branch segment, removed the bark, and measured volume using the water displacement method. The branch was then oven-dried at 70°C for 72 hours and weighed. Wood density was calculated as the ratio of dry weight to volume. Previous studies have shown strong correlations between branch and trunk wood density for trees in Bawangling tropical forests, allowing us to use branch density as a non-destructive proxy that avoids damage from tree coring.

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4. Soil Sampling and Nutrient Measurement

Soil samples were collected from the center of each 5 m × 5 m subplot. After removing surface litter, we collected soil from 0–20 cm depth, placed it in labeled bags, and transported it to the laboratory. Samples were air-dried and sieved for analysis. Soil organic matter was measured using the high-temperature external heating potassium dichromate volumetric method. Total nitrogen was determined by the Kjeldahl method. Total phosphorus was measured using $HClO_4$-H_2SO_4 digestion followed by ascorbic acid reduction colorimetry. Available nitrogen was determined by alkali diffusion method, and available phosphorus by acid ammonium fluoride extraction [32].

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5. Data Analysis Methods

To normalize the data, all functional trait values were $\log_{10}$-transformed before analysis. We used restricted maximum likelihood (REML) in the "lme" package of R 3.1.3 to perform variance component analysis for functional traits at individual, within-species, among-species, and community levels. The analysis model was structured as: `varcomp.LMA <- varcomp(lme(log(LMA) ~ 1, random = ~1 | Plot/Species/Tree/leaf or stem, data = d, na.action = na.omit), 1)`. This allowed us to quantify the magnitude of trait variation at different organizational scales.

To analyze relationships between functional traits and soil nutrients, we conducted stepwise linear regression with soil organic matter, total nitrogen, and available nitrogen as independent variables, and leaf area, leaf dry weight, leaf mass per area, chlorophyll content, leaf thickness, and wood density at individual, within-species, among-species, and community levels as dependent variables. Model selection was based on coefficient of determination (R^2) and P-values. All analyses and figures were generated using R [33].

Results

1. Variation in Functional Traits at Individual, Within-Species, Among-Species, and Community Levels The average species richness was 25.80 ± 6.00 per 20 m × 20 m plot, with community similarity of 0.58 ± 0.10. The explained variance for the six functional traits at different scales showed consistent patterns: among-species variation was largest, while community-level variation was smallest. For leaf dry weight, the explained variance was 0.47 at the among-species level, 0.43 at the within-species level, and 0.06 at the individual level. For leaf mass per area, variance was 0.57–0.72 among-species, 0.58 within-species, and 0.26 at the individual level. Chlorophyll content showed 0.35–0.72 among-species, 0.34 within-species, and 0.06 at the individual level. Leaf thickness variation was 0.21–0.30 among-species, 0.06–0.09 within-species, and 0.00–0.01 at the individual level. Wood density variation was 0.35 among-species, 0.09 within-species, and 0.00 at the individual level.

Frequency distribution patterns of functional traits in each plot were consistent with those across all plots. When the among-species level was removed from the model, most of its variance component was added to the within-species level, with some added to the community level, but the overall pattern of variation remained consistent.

2. Relationships Between Functional Trait Variation and Soil Nutrients Functional trait variation at all scales was closely related to soil organic matter, nitrogen, and phosphorus. At the within-species level, leaf traits were primarily correlated with soil organic matter content, while wood density variation was mainly related to soil phosphorus and nitrogen. At the among-species level, stem traits were related to both soil organic matter and nitrogen/phosphorus. At the community level, leaf traits were correlated with organic matter, but wood density showed no significant relationship with soil nutrients. Specific relationships are detailed in and

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Discussion

1. Variation in Functional Traits Across Different Scales The six functional traits showed different magnitudes of variation across community organization scales, with the largest variation at the among-species level and the smallest at the community level. This indicates that among-species functional trait variation has the greatest influence on overall trait patterns. Among-species variation may be related to both genetic and environmental factors. Studies have detected significant phylogenetic signals in traits such as LMA and LTh, indicating strong phylogenetic conservatism. The evolutionary history of functional traits significantly influences their development, and associations between

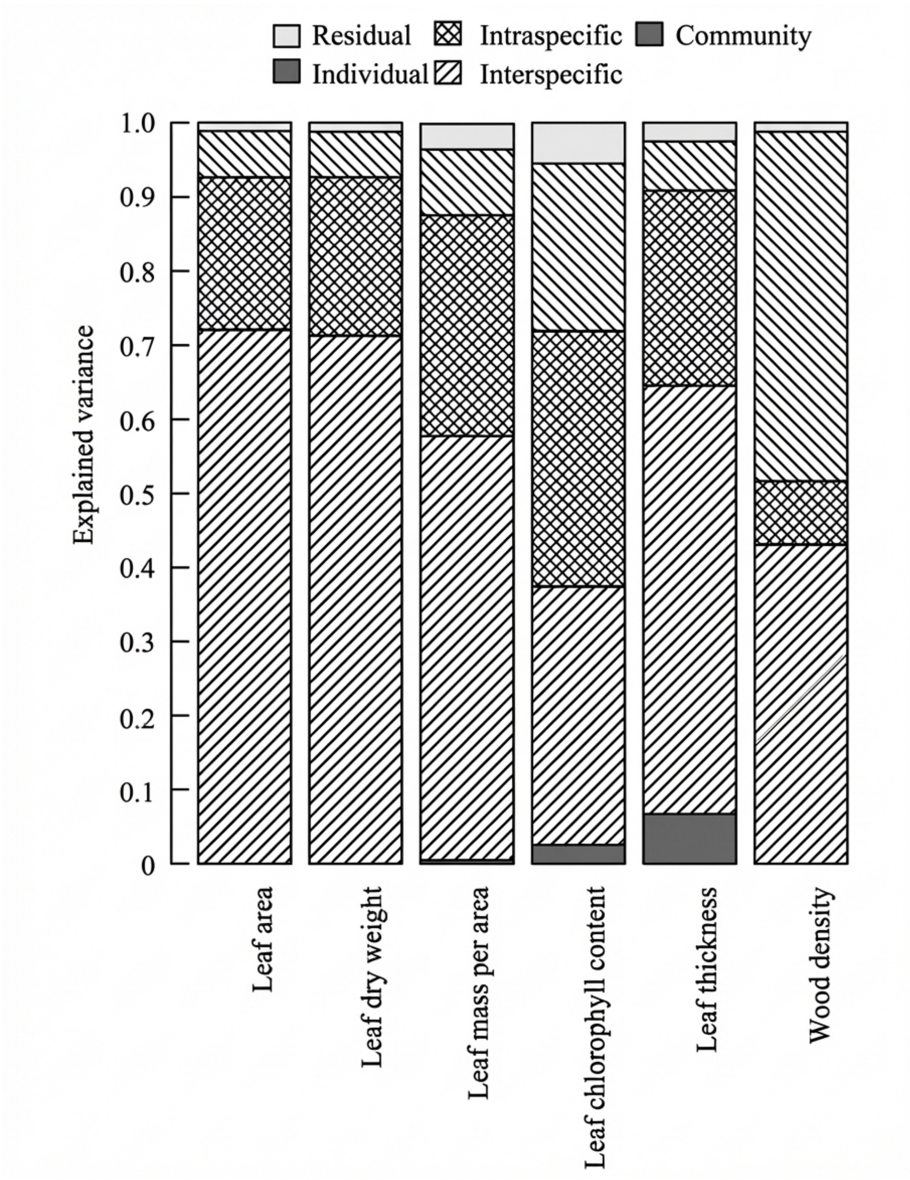

Figure 1: Figure 2

traits reflect phylogenetic relationships that facilitate functional coordination for survival in variable environments.

The high among-species variation in tropical cloud forests may also be strongly influenced by environmental conditions. Distributed above 1200 m elevation, these forests experience dramatic environmental gradients, with plants subjected to low air temperature and low soil phosphorus stress. Soil nutrients significantly affect among-species functional traits, consistent with the view that functional trait variation is primarily expressed at the among-species level. Community-level functional trait variation was smallest, likely due to relatively high similarity among communities (0.58 ± 0.10), which reduces the impact of species turnover on functional trait changes. However, community-level variation remains an important source of trait change, directly linking environmental factors to functional traits in ecosystems and providing an important approach for analyzing plant ecological strategies and environmental adaptation.

Contrary to our first hypothesis, within-species variation was slightly smaller than among-species variation but larger than individual and community-level variation. This pattern is consistent with other studies showing that within-species functional trait variation is an important source of trait change. Within-species variation arises primarily from phenotypic plasticity and genetic diversity. In the variable environment of tropical cloud forests, plants adjust their attributes through phenotypic plasticity to adapt to complex conditions, which helps expand species distribution ranges along environmental gradients.

2. Effects of Soil Factors on Plant Functional Traits Consistent with our second hypothesis, functional trait variation at individual, within-species, among-species, and community scales was closely related to soil organic matter, nitrogen, and phosphorus, although the specific effects varied by trait and scale. At the within-species level, leaf traits were generally correlated with soil organic matter content, while wood density variation was mainly related to soil phosphorus and nitrogen. At the among-species level, stem traits were related to both organic matter and nitrogen/phosphorus. At the community level, leaf traits correlated with organic matter, but wood density showed no significant relationship with soil nutrients.

Soil organic matter contains abundant nitrogen (N) and phosphorus (P), which are important components of leaf dry matter and structure. Leaf area and dry matter content are therefore closely related to soil organic matter. In nutrient-poor environments, plants often adopt conservative nutrient-use strategies. Tropical cloud forests have low soil phosphorus content, and plants with high LMA and leaf thickness can better adapt to such conditions. Chlorophyll content is influenced by both light adaptation and mineral elements, especially nitrogen deficiency, which can block chlorophyll biosynthesis or accelerate decomposition, reducing photosynthetic pigment content and rate. Wood density was positively correlated with soil organic matter and available nitrogen, likely because strong winds in tropical cloud forests favor slow-growing trees with high wood density. Soil phosphorus was negatively correlated with wood density, possibly because plants can use limited phosphorus to synthesize structural materials for stems, while available nitrogen can be directly absorbed to synthesize wood fibers and lignin, enhancing stem hardness.

References

[1] Ackerly DD. Community assembly, niche conservatism, and adaptive evolution in changing environments. International Journal of Plant Sciences, 2003, 164(S3): S165-S185.

[2] Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, Van Der Heijden MGA, Pausas JG, Poorter H. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany, 2003, 51(4): 335-380.

[3] Poorter L, Marksteijn L. Seedling traits determine drought tolerance of tropical tree species. Biotropica, 2008, 40(3): 321-331.

[4] Westoby M, Wright IJ. Land-plant ecology on the basis of functional traits. Trends in Ecology & Evolution, 2006, 21(5): 261-268.

[5] McGill BJ, Enquist BJ, Weiher E, Westoby M. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution, 2006, 21(4): 178-185.

[6] Vile D, Shipley B, Garnier E. Ecosystem productivity can be predicted from potential relative growth rate and species abundance. Ecology Letters, 2006, 9(9): 1061-1067.

[7] Long WX, Zang RG, Ding Y. Air temperature and soil phosphorus availability correlate with trait differences between two types of tropical cloud forests. Flora-Morphology, Distribution, Functional Ecology of Plants, 2011, 206(10): 896-903.

[8] Long WX, Zang RG, Schamp BS, Ding Y. Within- and among-species variation in specific leaf area drive community assembly in a tropical cloud forest. Oecologia, 2011, 167(4): 1103-1113.

[9] Long WX, Schamp BS, Zang RG, Ding Y, Huang YF, Xiang YZ. Community assembly in a tropical cloud forest related to specific leaf area and maximum species height. Journal of Vegetation Science, 2015, 26(3): 513-523.

[10] Cavender-Bares J, Keen A, Miles B. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology, 2006, 87(S7): S109-S122.

[11] Messier J, McGill BJ, Lechowicz MJ. How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters, 2010, 13(7): 838-848.

[12] McGill BJ. Exploring predictions of abundance from body mass using hierarchical comparative approaches. The American Naturalist, 2008, 172(1): 88-101.

[13] Burns KC. Patterns in specific leaf area and the structure of a temperate heath community. Diversity and Distributions, 2004, 10(2): 105-112.

[14] Cornwell WK, Ackerly DD. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs, 2009, 79(1): 109-126.

[15] Albert CH, Thuiller W, Yoccoz NG, Douzet R, Aubert S, Lavorel S. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Functional Ecology, 2010, 24(6): 1192-1201.

[16] Paine CET, Baraloto C, Chave J, Hérault B. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. Oikos, 2011, 120(5): 720-727.

[17] Bolnick DI, Amarasekare P, Aráujo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution, 2011, 26(4): 183-192.

[18] Lebrija-Trejos E, Pérez-García EA, Meave JA, Bongers F, Poorter L. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology, 2010, 91(2): 386-398.

[19] Swenson NG, Weiser MD. Plant geography upon the basis of functional traits: an example from eastern North American trees. Ecology, 2010, 91(8): 2234-2241.

[20] Bubb P, May I, Miles L, Sayer J. Cloud Forest Agenda. Cambridge, UK: UNEP-World Conservation Monitoring Centre, 2004.

[21] Zang RG, Tao JP, Li CY. Within community patch dynamics in a tropical montane rain forest of Hainan Island, South China. Acta Oecologica, 2005, 28(1): 39-48.

[22] Jiang YX. Community characteristics of tropical montane evergreen forest and tropical montane dwarf forest in Bawangling, Hainan Island. Biodiversity Science, 2011, 19(5): 558-566.

[23] Williams-Linera G. Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. Biodiversity & Conservation, 2002, 11(10): 1825-1843.

[24] Liu YH. Studies on community ecology and biogeography of mossy dwarf forests on mountain tops in Yunnan [D]. Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 2007.

[25] Long WX, Huang YF, Xiang YZ. Environmental characteristics of tropical cloud forests in Bawangling, Hainan during the rainy season. Chinese Journal of Plant Ecology, 2011, 35(2): 137-146.

[26] Baraloto C, Paine CET, Patiño S, Bonal D, Hérault B, Chave J. Functional trait variation and sampling strategies in species-rich plant communities. Functional Ecology, 2010, 24(1): 208-216.

[27] Chaturvedi RK, Raghuvanshi AS, Singh JS. Leaf attributes and tree growth in a tropical dry forest. Journal of Vegetation Science, 2011, 22(5): 917-931.

[28] Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, De Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, Van Der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany, 2013, 61(3): 167-234.

[29] Bu WS, Zang RG, Ding Y. Field observed relationships between biodiversity and ecosystem functioning during secondary succession in a tropical lowland rainforest. Acta Oecologica, 2014, 55: 1-7.

[30] Soil Agricultural Chemistry Committee of Chinese Soil Society. Routine Analysis Methods of Soil Agricultural Chemistry. Science Press, 1983.

[31] R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing, 2009.

[32] Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. Ecological consequences of genetic diversity. Ecology Letters, 2008, 11(6): 609-623.

[33] Vasseur F, Violle C, Enquist BJ, Granier C, Vile D. A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. Ecology Letters, 2012, 15(10): 1149-1157.

[34] Grady KC, Laughlin DC, Ferrier SM, Kolb TE, Hart SC, Allan GJ, Whitham TG. Conservative leaf economic traits correlate with fast growth of genotypes of a foundation riparian species near the thermal maximum extent of its geographic range. Functional Ecology, 2013, 27(2): 428-438.

[35] Ackerly DD. Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. The American Naturalist, 2004, 163(5): 654-671.

[36] Cao K, et al. Phylogenetic signal of functional traits and its effects on community structure in Gutianshan woody plants. Biodiversity Science, 2013, 21(5): 564-571.

[37] Ackerly DD, Reich PB. Convergence and correlations among leaf size and

function in seed plants: a comparative test using independent contrasts. American Journal of Botany, 1999, 86(9): 1272-1281.

[38] Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. The worldwide leaf economics spectrum. Nature, 2004, 428(6985): 821-827.

[39] Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. Towards a worldwide wood economics spectrum. Ecology Letters, 2009, 12(4): 351-366.

[40] Jung V, Violle C, Mondy C, Hoffmann L, Muller S. Intraspecific variability and trait-based community assembly. Journal of Ecology, 2010, 98(5): 1134-1140.

[41] Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. Oecologia, 1998, 114(4): 471-482.

[42] Wright IJ, Westoby M, Reich PB. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. Journal of Ecology, 2002, 90(3): 534-543.

[43] Verhoeven AS, Demmig-Adams B, Adams III WW. Enhanced employment of the xanthophyll cycle and thermal energy dissipation in spinach exposed to high light and N stress. Plant Physiology, 1997, 113(3): 817-824.

[44] Effects of nitrogen deficiency on gas exchange, chlorophyll fluorescence, and chloroplast ultrastructure in Buddha' s hand. Journal of Zhejiang University (Agriculture and Life Sciences), 2009, 35(3): 307-314.

[45] Wright IJ, Reich PB, Westoby M. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology, 2001, 15(4): 423-434.

**** Information of 21 plots
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** Distribution of the study sites
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** Variance partitioning for the six functional traits across individual, within-species, among-species, and community levels
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** Density distribution of functional traits
[FIGURE:4] Variance partitioning for the six functional traits across individid-

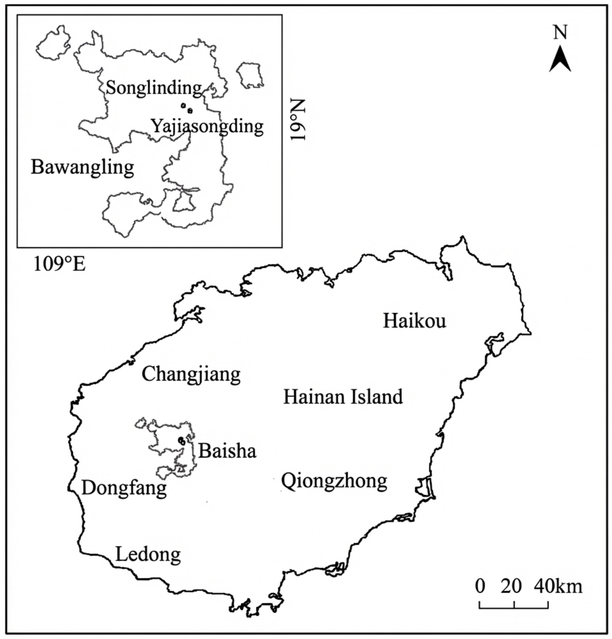

Figure 2: Figure 1

ual, within-species, and community levels
**** Stepwise regression analysis of functional traits with soil nutrients

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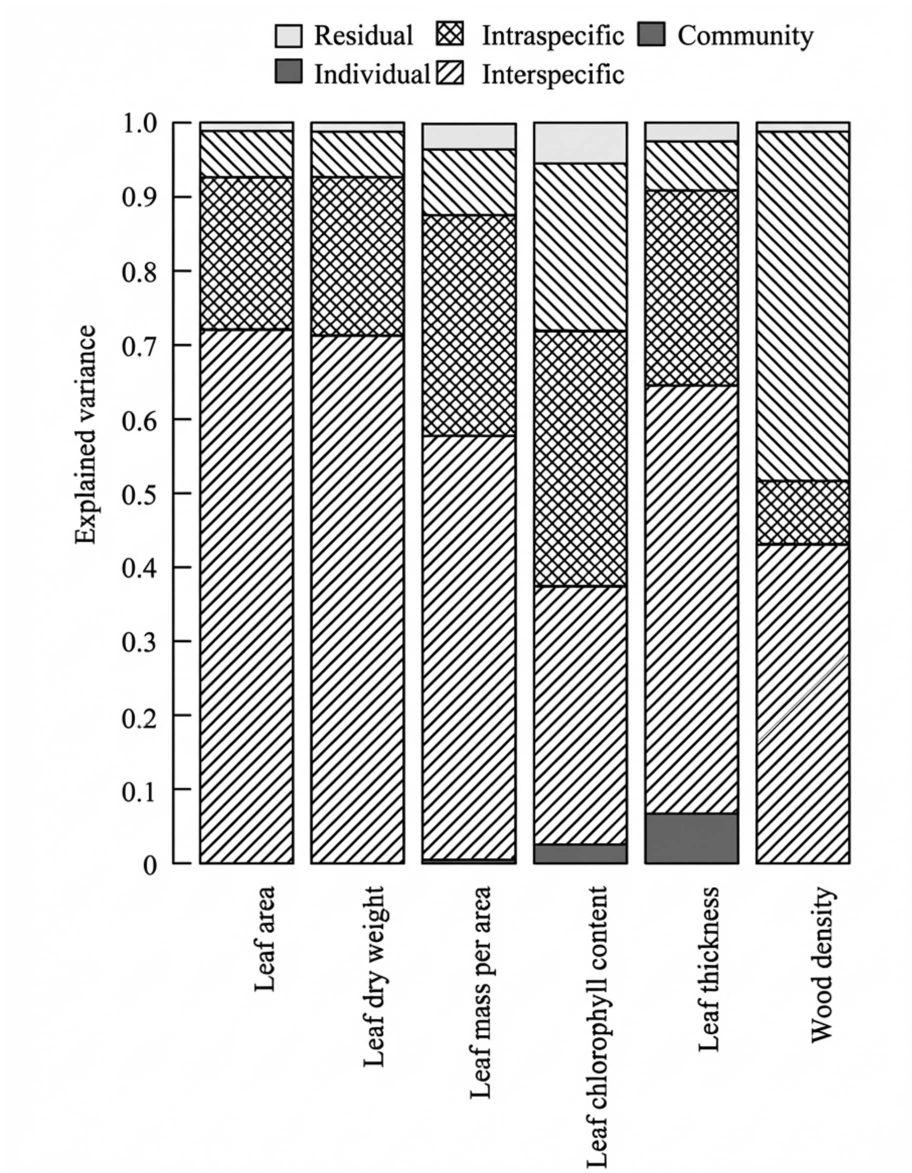

Figure 3: Figure 2

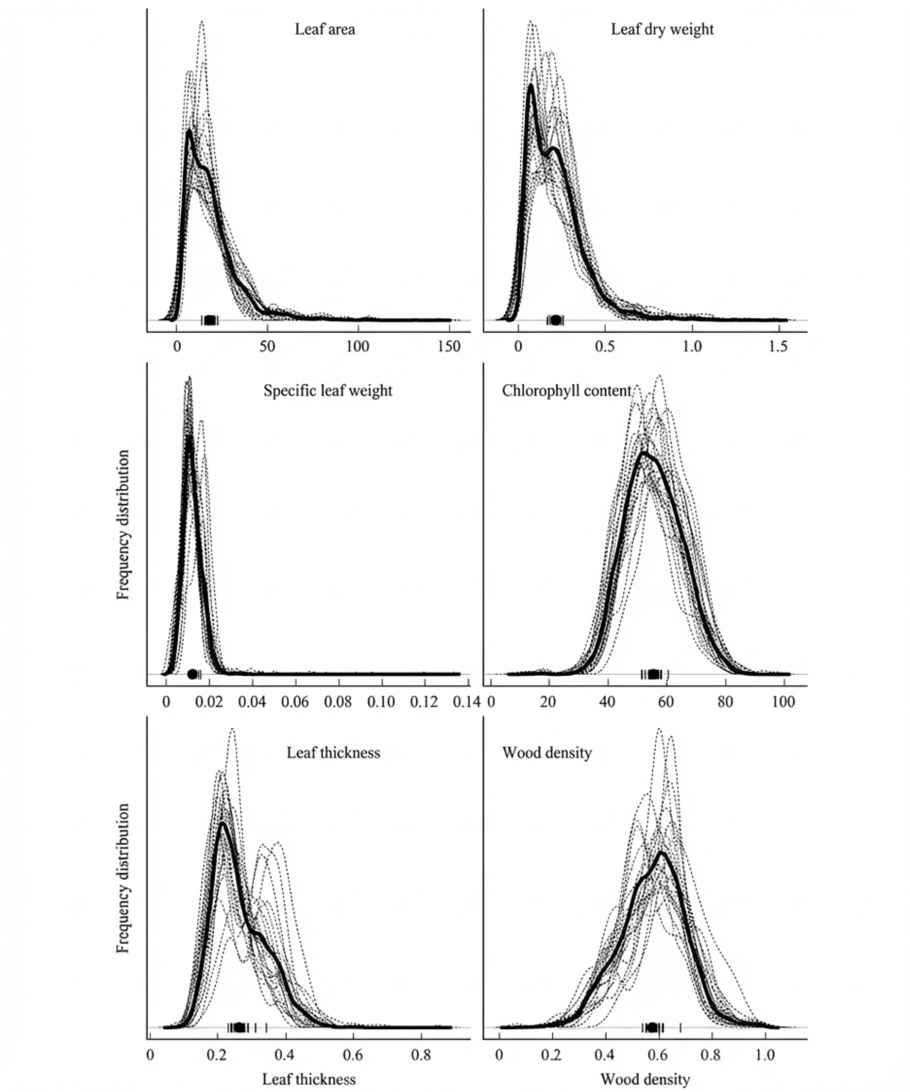

Figure 4: Figure 3