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华东师范大学

博士后研究工作报告

题目 ：浙东常绿阔叶林树种的种内性状变异与整合：格局与后果

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浙东常绿阔叶林树种的种内性状变异与整合：格局与后果

Intraspecific Trait Variation and Integration in Tree Species of Evergreen Broadleaf Forests in eastern Zhejiang province: Patterns and Consequences

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内 容 摘 要

植物结构和功能的多样性是生态学和进化生物学长期以来的重大问题之一。多维表型空间的概念为解答此一问题提供了一个支点。不过，以往关于该问题的探讨更多偏重跨种间的层次，种内性状变异与整合的意义还是有待深入发掘。

第 1 章简单撮述了涉及表型空间结构的关键概念，标举了种内性状变异与整合目前尚待研究的几个重要方面，并在此背景下提出了本项目试图解答的主要问题。

在第 2 章中，我以天童国家森林公园 604 株耐阴性树种黄丹木姜子（*Litsea elongata*）为材料，揭示了 8 种功能性状（叶面积、比叶面积、叶含水率、叶氮含量、叶磷含量、比枝长、枝含水率和休伯值）随树木大小变异的趋势，并比较了幼树和成树两个发育阶段性状标度关系（性状 x 的单位增量将伴随性状 y 的多少增量）的差异。结果显示，相对成树，幼树的树叶一般面积更大，更纤薄（即比叶面积更大），枝条更细长（比枝长更大），表明幼树的经济策略倾向低投入快收益型；但是幼树的叶氮含量却并比老树更低，这可能是因为耐阴性常绿树种的叶氮偏于投入组织建构而并不完全用于光合作用。多数性状两两之间的标度关系在两个发育阶段是基本一致的，表明树木生长发育过程中性状协变关系基本受控于统一的经济学和生物物理学法则，而成树和幼树在多维表型空间的位置分化被约束在这些标度轨迹的两端。

在第 3 章中，我以普陀山岛（湿润、缺磷）和泗礁岛（干旱、富磷）216 株硬叶树种柃木（*Eurya japonica*）为材料，检视了不同环境压力下叶性状协变关系的异同。结果显示，性状相关矩阵在两种生境条件下是显著同构的(Mantel $r > 0.5$)，都反映出展叶效率（主要反映在比叶面积上）和水分利用效率（主要通过 $\delta^{13}C$ 衡量）之间的功能权衡。然而，在干旱、富磷的生境，气孔导度仅与叶面积、厚度、比叶面积相关；而在湿润、缺磷的生境，气孔导度仅仅与单位面积的叶氮含量相关。水分利用效率与单位面积叶氮、磷含量的显著关系发生于干旱环境，不出现在湿润环境。这些性状协变关系的生境间差异表明，缺水和缺磷条件下植物叶表型整合的路径分别倾向优化保水形态和充分利用养分，寓示叶经济谱反映的光合收益速率–周期间的权衡并非塑造植物策略的刚性限制。同时，这也意味着

表型整合的结构作为一个高阶“性状”对植物维持有效策略的意义十分重大。

在第 4 章中，我以宁波各区县共 70 个常绿阔叶林群落为材料探究了种内性状变异如何影响群落水平的性状协变进而调控环境梯度上的多样性格局。结果发现，如果假设各物种仅有一个“平均”表型而不存在种内变异，物种间的性状整合度将显著提高，表明种内性状变异具有提高群落表型空间（也即功能生态位空间）维数的作用。不论是否考虑种内变异，土壤越贫瘠，群落表型空间的维数越低，从而降低物种多样性和功能多样性，表明在恶劣环境条件下实现最优功能必须以其他多方面的功能为代价，如此方能形成有效策略。尤为重要的是，表型整合度与物种数的负关系相对假设不存在种内变异的情形更为明显，表明物种的分布和共存至少部分取决于种内性状变异的幅度。

概而言之，本项目对于亚热带常绿阔叶林功能多样性乃至物种多样性的动力源有崭新的发现，并强调通过种内性状变异与整合深化理解生物多样性格局及其背后的功能权衡。

关键词：群落构建；环境胁迫子；功能权衡；生态位；植物经济谱；表型整合；性状标度；树木大小

Abstract

The diversity of plant forms and functions has long been an overarching theme in ecology and evolutionary biology. The notion of multidimensional phenotypic space provides a pivot for this very theme. However, because the theme has been largely constrained at the across-species level, the relevancy of intraspecific trait variation and integration in functional ecology is yet to be demonstrated.

In chapter 1, I briefly summarized the key concepts pertaining to the architecture of phenotypic space and outlined some important aspects of intraspecific trait variation and integration that are currently unclear. With these backgrounds available, I raised my core questions.

In chapter 2, I evaluated how individual traits and whether bivariate trait scaling relationships within evergreen species vary with tree size. Eight morphological, stoichiometric and hydraulic traits for 604 individual plants of a shade-tolerant species, *Litsea elongata*, were measured in a subtropical evergreen stand in Tiantong Forest Park, eastern China. Individual trait values were regressed against tree basal diameter to evaluate size-dependent trait variations. Standardized major axis regression was employed to examine the trait scaling relationships and to test whether there was a common slope and elevation in the trait scaling relationships across size classes. Results showed that small trees tended to have larger, thinner leaves and longer, slenderer stems than large trees, indicating an acquisitive economic strategy in juvenile trees. Leaf nitrogen concentration increased with plant size, probably due to a high ratio of structural to photosynthetic nitrogen in evergreen leaves of large trees. Bivariate trait scaling was minimally modified by tree size despite the elevation of some relationships differed between size classes. These results suggest that there exist common economic and biophysical constraints on intraspecific trait covariation independent of tree size, and that small and large trees tend to be located at two opposite ends of an intraspecific plant economic spectrum.

In chapter 3, I examined how multiple phenotypic traits in evergreen tree species are integrated to accomplish proper functions under specific stressors. Ten leaf traits (stomatal conductance, relative chlorophyll concentration, lamina area, perimeter/area ratio, specific leaf area, leaf water content, leaf thickness, leaf carbon isotope ratio, leaf nitrogen and phosphorus concentration) for 216 individual trees of a sclerophyll

species, *Eurya japonica*, were measured in the Zhoushan Archipelago, eastern China, to examine how the structures of trait correlation (i.e., phenotypic integration) vary between two habitats with contrasting moisture and phosphorus (P) availability. Overall, the trait correlation matrices were similar between the two habitats under study (Mantel $r > 0.5$), reflecting a consistent tradeoff between leaf outspreading (i.e., leaf area/mass ratio) and water-use efficiency (measured by $\delta^{13}C$). Stomatal conductance was correlated with leaf area, thickness and area/mass ratio only in the dry, P-rich habitat, whereas it was robustly correlated with leaf P per unit area in the wet, P-poor habitat. Moreover, leaf water-use efficiency was robustly correlated with leaf P and N per unit area in the dry habitat, but not so in the low-P one. The varied trait correlation structures pinpoint the pathways of strategic compromise in sclerophyll species under contrasting stressors. This study also highlights the importance of phenotypic integration as an emergent "trait" in sustaining viable strategies.

In chapter 4, I explored how intraspecific trait variability alters the strength of trait integration and eventually modulates biodiversity along environmental gradients. To this end, I measured nine functional traits (leaf area, specific leaf area, leaf and stem dry-matter content, leaf nitrogen and phosphorus contents, specific stem length, Huber value and maximum height) paired with site-specific soil fertility for 70 woody communities in subtropical Chinese forests. All species-by-site combinations were sampled to ensure a sufficient representation of intraspecific trait variation across sites. Community-level trait integration was quantified from the variance of eigenvalues of the trait correlation matrix. The direct and/or indirect effects of soil fertility and trait integration on species richness and trait diversity were assessed through path analyses. Trait integration quantified from both inter- and intraspecific variances was on average 21.7% weaker than that from only interspecific variance, indicating a crucial role of intraspecific trait variability in promoting niche dimensionality. Whether accounting for intraspecific variation or not, less fertile sites had stronger trait integration, which in turn depressed both taxonomic and functional diversity, supporting the assumption that higher environmental stress demanding stronger tradeoffs among multiple functions in viable strategies. Importantly, the negative association between trait integration and species richness became stronger when accounting for intraspecific variation, suggesting that species distribution and occurrence can be a consequence of intraspecific trait variability.

Altogether, this research program sheds light on the forces underlying functional (and taxonomical) diversity in subtropical evergreen broadleaf forests. It also highlights the importance of intraspecific trait variability in understanding functional tradeoffs underlying biodiversity patterns.

keywords: community assembly; environmental stressor; functional tradeoff; niche; plant economic spectrum; phenotypic integration; trait scaling; tree size

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