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Leaf trait covariation and its controls: quantitative data analysis for trait-based modelling

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New-generation vegetation models represent plant functional diversity by sampling from continuous trait distributions. This approach requires information on trait variation, trait-trait covariation and trait-environment relationships. Extensive field data (483 species at 48 sites across China) are used to characterize the dimensions of leaf-trait covariation and their relationships to climate. Leaf area (LA), specific leaf area (SLA), nitrogen per area (Narea), dry-matter content (LDMC) and carboxylation (Vcmax) and electron-transport (Jmax) capacities (adjusted to 25˚C) were measured, and internal-to-ambient CO_2 ratio (χ) was derived from δ13C measurements. Principal components analysis was used to infer total trait-variation patterns, and redundancy analysis to quantify the effects of climate, site and stratum. Four dimensions were identified: LA, χ, the leaf economics spectrum (SLA versus LDMC and Narea), and Vcmax and Jmax. Across sites, LA and χ covary with moisture index; SLA increases while LDMC and Narea decline with latitude; LDMC and LA decline with altitude. But within-site variation shows similar patterns to total trait variation, and accounts for about half of it. Trait-based models should assign coexisting plants a range of leaf-trait values sampled from a four-dimensional continuum, while allowing community-mean trait values to respond adaptively to environmental gradients.