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Coordination of physiological and structural traits in Amazon forest trees

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Our aim was to examine interactions between structural and physiological trait characteristics for Amazon forest trees and to determine if integrated trait dimensions can be identified. Data on leaf and leaflet size, the ratio of leaf area to sapwood area ($\Phi_{\rm LS}$) were obtained for 1040 trees species located in 53 tropical forest plots across across the Amazon Basin and incorporated into an analysis using an index of diffusional limitations to photosynthetic CO_2 assimilation based on carbon isotope ratios and previously acquired data on species maximum height ($H_{\rm max}$), seed size, leaf mass per unit area ($M_{\rm A}$), foliar nutrients and branch xylem density ($\rho_{\rm x}$).

Where appropriate, responses were first partitioned into genetic and environmental effects. Strong bivariate relationships were observed for a many of the genetic and environmentally dependent trait components. For example, for the derived genetic components, leaf size is significantly correlated with foliar nitrogen and phosphorus concentrations, with $\Phi_{\rm LS}$ also correlating with foliar [N] and [P] as well as negatively with $M_{\rm A}$. Negative associations were also found between $\rho_{\rm x}$ and foliar [P] and [K] and with a positive relationship between $\rho_{\rm x}$ and $M_{\rm A}$. Both $M_{\rm A}$ and seed size increase with $H_{\rm max}$.

As there was evidence of different bivariate relationships between the measured traits for species associated with low versus high fertility soils, we utilised a common principal components (CPC) method to reveal associations embedded in the trait variance-covariance matrix, this analysis effectively allowing the PCA eigenvalues to vary between the two soil fertility dependent groups. This analysis identified five significant integrated trait dimensions for Amazon forest trees. The first involves primarily cations, foliar carbon and $M_{\rm A}$ and seems to be associated with differences in foliar construction costs. The second relates to the classic "leaf economic spectrum" of plant resource utilisation. but with increased individual leaf areas and a higher $\Phi_{\rm LS}$ newly identified components. The third dimension relates primarily to increasing $H_{\rm max}$ and involves greater $M_{\rm A}$ (primarily attributed to increased leaf thicknesses) with reductions in $\Phi_{\rm LS}$ and with carbon isotopes suggesting a general decline in the ratio of leaf internal to ambient carbon dioxide concentrations with increasing $H_{\rm max}$. Although species from high fertility sites had higher eigenvector values for these first three dimensions, the final two dimensions were found to be more important for low fertility soil associated species. The fourth dimension showed seed size and $\Phi_{\rm LS}$ to be negatively correlated (with the fifth dimension linking together a range of shade tolerance characteristics such as low $H_{\rm max}$, greater seed size and high wood densities. Also associated with this dimension (which was virtually insignificant for high fertility soil associated species) were increased $M_{\rm A}$, higher foliar [C] and greater diffusional limitations for CO_2 diffusion.

Environmental conditions were also found to influence the structural traits examined with $\rho_{\rm x}$ decreasing with increased soil fertility but decreasing with increased temperatures. This soil fertility response appears to be synchronised with increases in foliar nutrient concentrations and reductions in foliar [C]. Leaf and leaflet area and $\Phi_{\rm LS}$ are less responsive to the environment than $\rho_{\rm x}$, although there was some evidence of both $\Phi_{\rm LS}$ and $\rho_{\rm x}$ decreasing as precipitation increases.

We conclude that physiological and structural traits coordinate in distinct ways for tropical tree species, but that the nature of this association may differ according to a species preferred soil fertility "niche" and with the nature of these associations somewhat modified by a species' actual growth environment.