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Deciphering climate, soil and phylogenetic controls on leaf nitrogen and phosphorus stoichiometry of terrestrial plants-V1

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As an important aspect of the leaf economic spectrum, leaf nitrogen (N) and phosphorus (P) concentrations are key traits that shape plant growth and function and reflect evolutionary history. Their patterns across the globe have been interpreted as being reflective of controls by climate, soil fertility, and atmospheric N and P deposition. Yet, recent research has emphasized an overriding importance of species identity and phylogeny in determining stoichiometry. This limits the applicability of methods for predicting global patterns in foliar stoichiometry from environmental covariates and implies that stoichiometry responses to global environmental change are limited by the rate of species replacement.

Here, we investigated these contrasting views. We established a comprehensive global data set of 36,413 paired observations of leaf N and P concentrations with their specific phylogenetic taxonomy and 46 environmental covariates. For leaf N, we identified the most important predictors being N deposition, irradiance, temperature of the coldest month, atmospheric CO₂, elevation, mean annual vapor pressure deficit, and aluminum saturation of the soil solution. For leaf P, the predictors are N deposition, temperature of the coldest month, aridity index, atmospheric CO₂, soil phosphorus concentration, annual mean ratio of actual over potential evapotranspiration, multi-day average stomatal conductance, available water storage capacity and precipitation of the driest month. Together, the predictors explain 46% and 33% of leaf N and P variations respectively in the data aggregated by sites, using a Random Forest model. Using linear models on the full non-aggregated data and not accounting for interactions between predictors, species identity explains the largest portion of observed variations in individual-level foliar N (50.4%) and P (33.9%), while environmental covariates explain only 3.8%, and 2.8%, respectively.

A trait gradient analysis reconciles these contrasting results and suggests more within-species variations in response to the environment as would be expected from the results of the linear models. We found (i) that the genetic variation or environmentally-induced plasticity in foliar N and P within species is substantial for most species, (ii) that species' distributions cover a wide range of environments as expressed by site-level mean leaf N and P, and (iii) that variations of leaf N and P stoichiometry across sites are not merely emerging as a result of distinct species present at different sites. This challenges the notion of a fixed biogeochemical niche occupied by individual species and suggests that plants mediate their stoichiometry in response to their environment, and potentially to global environmental change. This insight also provides the basis for a robust spatial upscaling of foliar N and P, using global fields of environmental covariates as predictors. Our global predictions also suggest that the highest foliar N concentration occurs in cold and dry climates and at high-elevation.