**Optimal photosynthetic strategies**

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**Abstract**

Leaf traits collectively offer valuable insight into a plant’s photosynthetic strategy under varying environmental conditions. Eco-evolutionary optimality (EEO) theory can be used to predict photosynthetic trait variation, offering insight into the underlying mechanisms beyond what can be gleaned from data alone. EEO has been used to explore mechanisms underlying the variation in individual photosynthetic traits across space and time. Here, I extend this approach to examine global variability in biochemical, stomatal, chemical, and morphological traits that collectively define a photosynthetic strategy. The first principal component, explaining 51.3% of global variability in optimal traits, was defined by differences in C3 and C4 plants with C4 plants displaying faster rates of optimal photosynthesis and greater optimal intrinsic water use efficiency. This reflects the unique, fast-efficient strategy employed by C4 plants. The second principal component (36.1%) was defined by a correlation between optimal photosynthetic nitrogen use efficiency and optimal stomatal conductance. This was common across all plant types, with increasing aridity driving lower optimal stomatal conductance and nitrogen use efficiency. This follows expectations from photosynthetic least-cost theory where plants are thought to adopt inefficient nitrogen use to lower water use in dry environments. Optimal leaf mass per area acted as an important separator between C3 deciduous and C3 evergreen plants, despite similar strategy distribution within both groups. This reflects the need for evergreen plants to expend greater costs on leaf construction to increase leaf lifespan. Optimal photosynthetic strategy distributions remained similar under a simulated high temperature, high CO2 environment. However, optimal C4 and C3 strategies were not as divergent as under present-day conditions, particularly in low aridity environments. The results indicate that EEO theory can reproduce patterns of photosynthetic strategies across global gradients, while also revealing new insights into the clustering of these strategies. These results can be used to better understand photosynthetic trait data and, ultimately, physiological functioning of plants under present-day and future conditions.

**Keywords**

Eco-evolutionary optimality, carbon assimilation, photosynthetic capacity, stomatal conductance, leaf nitrogen

**Introduction**

Photosynthesis is the process by which plants assimilate carbon dioxide (CO2) from the atmosphere into sugars to support tissue growth and maintenance. Because of the ubiquity of plants on Earth, photosynthesis is the largest flux of CO2 between the atmosphere and the Earth’s surface. To perform photosynthesis, plants must use water and nutrient resources from the soil and, as a result, photosynthetic physiology can have large impacts on terrestrial biogeochemical cycling as well as partitioning of energy between sensible and latent heat. Thus, photosynthesis is the backbone of many of the terrestrial ecosystem services on which humans rely.

Not all plants perform photosynthesis similarly. For instance, while many plants use the C3 system for photosynthesis, morphological and physiological changes have led to some species using other systems, such as C4 and crassulacean acid metabolism (CAM) photosynthesis. Additionally, within these groups of photosynthetic types, photosynthetic traits can vary widely over space and time, from near instantaneous to evolutionary time scales.

The method by which an individual performs photosynthesis can be viewed the result of many traits that describe various aspects of the photosynthetic process. These include morphological, biochemical, stomatal, and chemical traits. For instance, leaf mass per area (LMA) is a morphological trait that reflects structural investment in leaves. Biochemical traits can be used to understand investment in and output from photosynthetic enzymes. Stomatal traits reflect water use for photosynthesis and trade-offs between carbon intake and water loss. Chemical traits can be indicative of nutrient use for photosynthetic processes. While many correlations between individual photosynthetic traits have been found, it is not clear that trait combinations across all traits can be defined by a single axis of variation.

Classic, theoretical models of photosynthesis provide a starting point for understanding photosynthetic functioning through the lens of traits. For instance, the Farquhar, von Caemmerer, and Berry (1980) model of C3 photosynthesis…

Eco-evolutionary optimality (EEO) is a powerful tool for quantifying optimal traits to better understand and predict trait variation over space and time. EEO has long been used for understanding photosynthetic traits, in particular. Recent developments have led to simple, theory-based models for predicting variation in morphological, biochemical, stomatal, and chemical traits that are important for photosynthesis. These models have…

EEO models of individual photosynthetic traits now allow for muti-trait analyses to better understand the makeup and variability in optimal photosynthetic strategies globally. Strategy here is defined as trait combinations that reflect how a leaf of a given type of plant uses resources to assimilate carbon in a given environment. Here, we use a model that integrates multiple, optimal single-trait estimations to simulate multiple optimal traits across the land surface of the Earth for C3 deciduous, C3 evergreen, and C4 plants. We then assess the clustering of optimal traits to explore the distribution of optimal photosynthetic strategies, as well as the environmental drivers they are correlated with. We hypothesize that …

**Methods**

**Results**

**Discussion**