

Predicting ecosystem productivity based on plant community traits

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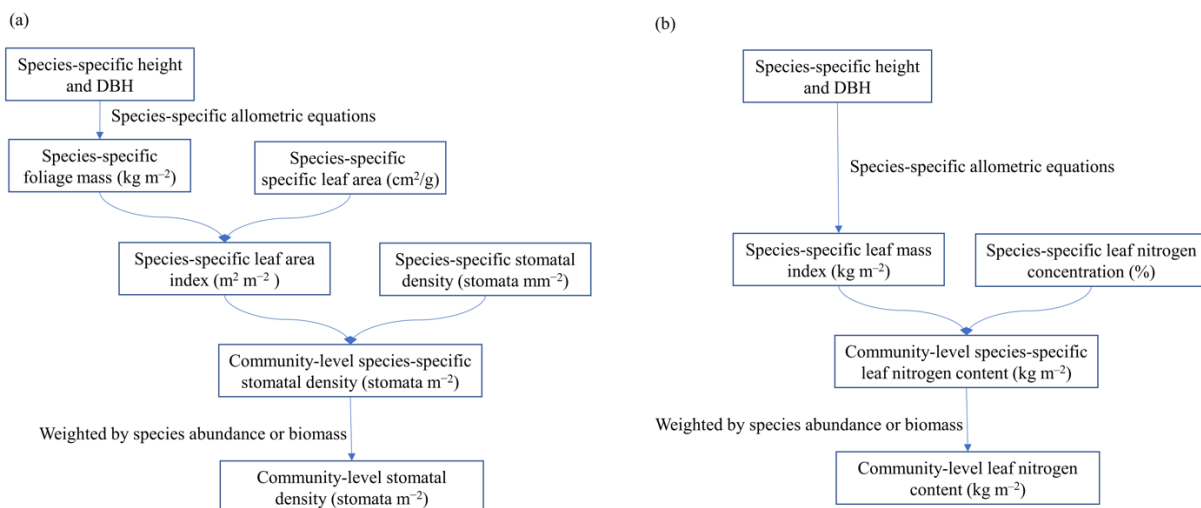


Figure S1. Schematic diagram for the derivation of ecosystem/community-level traits from individual or species level traits. Here, LAI can be derived from a straightforward method using a statistically significant leaf sample from the plant canopy, measuring the leaf area of each sample plot, and dividing it by the plot land surface area [S1].

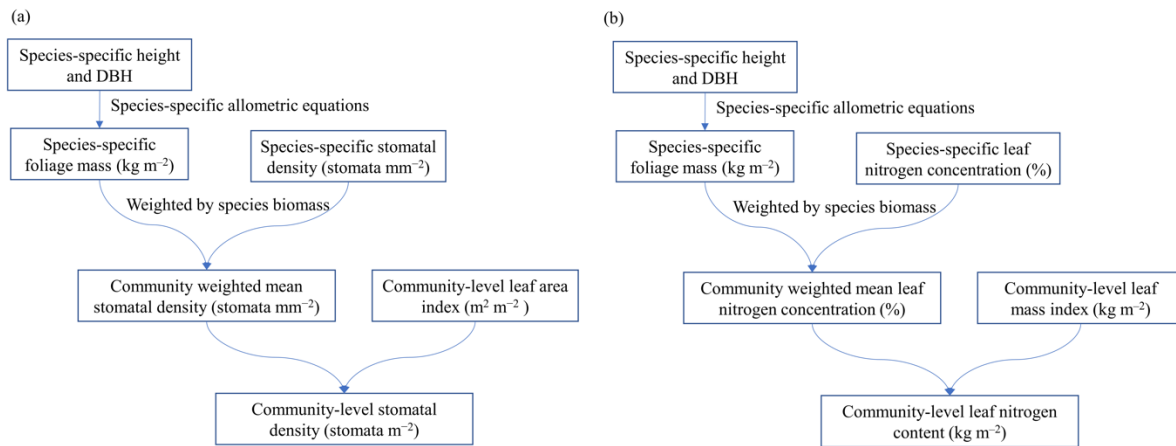


Figure S2. Schematic diagram for the derivation of ecosystem/community-level traits from community weighted mean traits. Here, LAI can be derived from an indirect method measuring canopy geometry or light extinction and correlating it to LAI [S1].

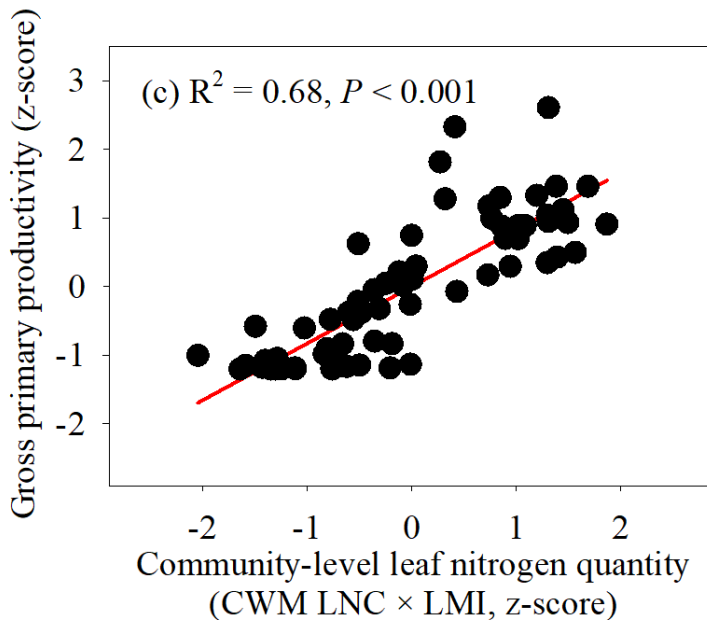


Figure S3 Relationships between community-level traits of nitrogen and ecosystem productivity. All fits in R using the ordinary least squares method (*lm* function in R), and all variables were standardized (z-score, mean = 0, SD = 1) prior to analysis. Community-level traits are derived from the formula 1.1 in Box 2.

Appendix 1. Derivation of the inverse production function

In the derivation that follows, all parameters and variables are understood to be defined on a ground-area basis; that is, they are ecosystem-level quantities.

GPP can be understood in terms of two processes occurring in series: the diffusion of CO_2 from the atmosphere to chloroplasts, and the assimilation of that CO_2 by the photosynthetic machinery. Diffusion into leaves is described by

$$P = g(c_a - c_i) \quad (1),$$

where g is the conductance for CO₂ diffusion from the atmosphere to the chloroplast, c_a is ambient CO₂ mole fraction, and c_i is intercellular CO₂ mole fraction. Photosynthetic assimilation of CO₂ by chloroplasts can be described by

$$P = k(c_i - \Gamma) \quad (2),$$

where k is the "biochemical conductance", determined by photosynthetic capacity and light availability as discussed below, and Γ is the CO₂ compensation point. Equation 2 was given by Farquhar, Buckley and Miller [S2] (their Eqn 19) and has been previously employed elsewhere (e.g., Farquhar and Sharkey [S3]), and can be interpreted as a simplification of the biochemical model of Farquhar et al. (Farquhar, von Caemmerer and Berry [S4]; hereafter the FvCB model). The full FvCB model is

$$P = \min \left\{ \frac{J(c_i - \Gamma_*)}{4(c_i + 2\Gamma_*)}, \frac{V_m(c_i - \Gamma_*)}{c_i + K'} \right\} - R_d \quad (3),$$

where J is potential electron transport rate, V_m is maximum carboxylation velocity, Γ_* is the photorespiratory CO₂ compensation point, K' is the effective Michaelis constant for carboxylation, and R_d is the rate of mitochondrial respiration in the light. Assuming that $R_d \ll P$ (in which case $\Gamma \approx \Gamma_*$) and setting the expressions for P in Eqns 2 and 3 equal to one another (e.g., $k(c_i - \Gamma) = J(c_i - \Gamma)/4(c_i + 2\Gamma) \rightarrow k = J/4(c_i + 2\Gamma)$) leads to the following expressions, which suggest that the biochemical conductance, k , should be proportional to J or V_m ;

$$k = \frac{J}{4(c_i + 2\Gamma)} \quad \text{or} \quad k = \frac{V_m}{c_i + K'} \quad (4).$$

where the first and second expressions apply when photosynthesis is limited by electron transport or carboxylation, respectively.

Two important points arise from Eqn 4:

(i) When averaged over a day or longer, k should depend to some degree on both light intensity (which affects J directly) and nitrogen investment in photosynthetic enzymes (which affects both J and V_m).

(ii) At long time scales that subsume diurnal and seasonal fluctuations in c_i , k should scale approximately inversely with atmospheric CO₂ concentration, c_a , because c_i (in the denominators of Eqn 4) will scale with c_a , all else being equal.

To a good approximation, c_i tends to hover around 70% of c_a in C3 plants and around 40% of c_a

in C4 plants Wong, Cowan and Farquhar [S5] ; i.e., $c_i \approx 0.7 \cdot c_a$ or $0.4 \cdot c_a$. Adopting this simplification sacrifices some subtleties of the nonlinearity in the FvCB model, but is useful for the purpose of creating a scalable production model, as shown below.

We suggest that these three drivers of k – nitrogen, light, and CO_2 – can be compactly modeled by writing

$$k = \left(\frac{V_m J}{V_m + J} \right) \cdot \frac{1}{rc_a + M} \quad (5),$$

in which r is either 0.7 (for C3 plants) or 0.4 (for C4 plants), and M is an *effective bulk Michaelis constant* that lies somewhere between the values of $2\Gamma^*$ and K' . The term in parentheses in Eqn 5 heuristically combines the influences of both J and V_m in Eqn 4. The term at right ($rc_a + M$) is an estimate of the average influence of c_i in Eqn 4.

Note as well that J can be modeled as (e.g., Farquhar and Wong [S6])

$$J = \frac{J_m \phi i}{J_m + \phi i} \quad (6),$$

in which J_m is the maximum potential electron transport rate or *electron transport capacity*, ϕ is the maximum quantum yield of electrons, and i is the absorbed irradiance. Applying Eqn 6 to Eqn 5 gives

$$k = \left(\frac{V_m \frac{J_m \phi i}{J_m + \phi i}}{V_m + \frac{J_m \phi i}{J_m + \phi i}} \right) \cdot \frac{1}{rc_a + M} = \left(\frac{1}{\frac{1}{\phi i} + \frac{1}{J_m} + \frac{1}{V_m}} \right) \cdot \frac{1}{rc_a + M} \quad (7),$$

Applying Eqn 7 to Eqn 2 gives

$$P = \left(\frac{1}{\frac{1}{\phi i} + \frac{1}{J_m} + \frac{1}{V_m}} \right) \left(\frac{c_i - \Gamma}{rc_a + M} \right) \quad (8),$$

Equation 8 represents the biochemical "demand" for CO_2 , whereas Eqn 1 represents the diffusive "supply" of CO_2 (*sensu* Farquhar and Sharkey [S3]). These demand and supply constraints on photosynthesis can be combined by setting Eqn 8 equal to Eqn 1, to give

$$\left(\frac{1}{\frac{1}{\phi i} + \frac{1}{J_m} + \frac{1}{V_m}} \right) \left(\frac{c_i - \Gamma}{rc_a + M} \right) = g(c_a - c_i) \quad (9),$$

Solving Eqn 9 for c_i gives

$$c_i = \frac{g c_a \left(\frac{1}{\phi_i} + \frac{1}{J_m} + \frac{1}{V_m} \right) + \frac{\Gamma}{r c_a + M}}{g \left(\frac{1}{\phi_i} + \frac{1}{J_m} + \frac{1}{V_m} \right) + \frac{1}{r c_a + M}} \quad (10),$$

Applying this expression for c_i to Eqn 1 gives

$$P = g \left(c_a - \frac{g c_a \left(\frac{1}{\phi_i} + \frac{1}{J_m} + \frac{1}{V_m} \right) + \frac{\Gamma}{r c_a + M}}{g \left(\frac{1}{\phi_i} + \frac{1}{J_m} + \frac{1}{V_m} \right) + \frac{1}{r c_a + M}} \right) \quad (11),$$

which can be rearranged to give

$$P = \frac{g(c_a - \Gamma)}{g(r c_a + M) \left(\frac{1}{\phi_i} + \frac{1}{J_m} + \frac{1}{V_m} \right) + 1} \quad (12),$$

(Note that applying Eqn 10 to Eqn 8 instead of Eqn 1 would lead to the same solution; not shown.)

The next step is to link the parameters in Eqn 12 to the supplies of key resources that limit photosynthesis: namely, water, nitrogen and light. First, we note that J_m and V_m are very tightly coordinated across leaves and even across species, such that $J_m \approx z \cdot V_m$ (where z is a scaling factor, approximately 2.1; Wullschleger, 1993. This simplifies Eqn 12 to

$$P = \frac{g(c_a - \Gamma)}{g(r c_a + M) \left(\frac{1}{\phi_i} + \frac{j}{V_m} \right) + 1} \quad (13),$$

where $j \equiv 1/z + 1$. Second, we assume that V_m is proportional to leaf N content, N :

$$V_m = \chi' N \quad (14),$$

where χ' is an empirical coefficient (e.g., Evans [S7]). Third, we note that incident irradiance is a fraction (f_{par}) of the value above the canopy (i_o):

$$i = f_{\text{par}} i_o \quad (15).$$

Fourth, note that diffusive conductance, g , is related to canopy transpiration, E , as

$$E = 1.6gD = K(\psi_{soil} - \psi_{leaf}) \quad (16),$$

where D is evaporative demand (VPD, expressed as a mole fraction), K is the hydraulic conductance between the soil and leaf, ψ_{soil} is soil water potential and ψ_{leaf} is leaf water potential (note that K in Eqn 16 is unrelated to K' in Eqn 4). Solving Eqn 16 for g gives

$$g = \frac{K(\psi_{soil} - \psi_{leaf})}{1.6D} \quad (17),$$

Applying 14, 15 and 17 to Eqn 12 gives

$$P = \frac{\frac{K(\psi_{soil} - \psi_{leaf})}{1.6D} (c_a - \Gamma)}{\frac{K(\psi_{soil} - \psi_{leaf})}{1.6D} (rc_a + M) \left(\frac{1}{\phi f_{par} i_o} + \frac{1}{\chi N} \right) + 1} \quad (18),$$

where $\chi \equiv \chi'/j$. Further rearrangement gives

$$P = \frac{(c_a - \Gamma)}{\frac{1.6D}{K(\psi_{soil} - \psi_{leaf})} + (rc_a + M) \frac{1}{\phi f_{par} i_o} + (rc_a + M) \frac{1}{\chi N}} \quad (19),$$

Equation 19 expresses and generalizes an idea that can be traced back at least to Farquhar and Sharkey (1982), in which biochemical constraints on photosynthesis are interpreted as being analogous to, and additive with, diffusional constraints. More generally, all constraints on photosynthesis can be thought of, in some sense, as "resistances" to CO_2 uptake. The denominator of Eqn 19 includes three such resistances. The first, involving D and K , represents diffusive (stomatal) constraints; the second, involving N , represents biochemical (photosynthetic capacity) constraints; and the third, involving i_o , represents energetic (light) constraints. Each of these terms includes both environmental factors (ψ_{soil} , D , c_a , i) and biological traits (K , ψ_{leaf} , Γ , M , χ , ϕ , f_{par}).

The additivity of the resistances in the denominator of Eqn 19 suggests a novel approach to predicting P based on traits and environmental factors, which focuses on the *inverse* of P rather than P itself. Taking the reciprocal of P gives an expression in which the diffusional, biochemical and energetic constraints are additive:

$$\frac{1}{P} = \frac{1}{c_a - \Gamma} \left(\frac{1.6D}{K(\psi_{soil} - \psi_{leaf})} + (rc_a + M) \left(\frac{1}{\phi f_{par} i_o} + \frac{1}{\chi N} \right) \right) \quad (20).$$

Note that, in the absence of limitations caused by the plant's finite capacity to capture available resources from the environment, the photosynthetic resource quantities (transpiration rate E , canopy nitrogen content N , and incident irradiance i) approach the environmental availabilities

of those resources (respectively, precipitation, E_o ; total ecosystem N, N_o ; and irradiance above the canopy, i_o). Then $1/P$ approaches its minimum value, $1/P_o$ (i.e., P approaches its maximum value, P_o):

$$\frac{1}{P_o} = \frac{1}{c_a - \Gamma} \left(\frac{1.6D}{E_o} + (rc_a + M) \left(\frac{1}{\phi i_o} + \frac{1}{\chi N_o} \right) \right) \equiv \frac{1}{P_o} \quad (21).$$

(Note that $K(\psi_{soil} - \psi_{leaf})$ has been replaced with E_o in Eqn 21, reflecting the premise that $E = E_o$.) This suggests the following formulation:

$$\frac{1}{P} = \frac{1}{c_a - \Gamma} \left(\frac{1.6D}{E_o} \left(\frac{E_o}{K(\psi_{soil} - \psi_{leaf})} \right) + (rc_a + M) \left(\frac{1}{\phi i_o} \left(\frac{1}{f_{par}} \right) + \frac{1}{\chi N_o} \left(\frac{N_o}{N} \right) \right) \right) \quad (22),$$

Equation 22 can be written more succinctly as

$$\frac{1}{P} = \frac{1}{P_w \cdot \epsilon_w} + \frac{1}{P_i \cdot \epsilon_i} + \frac{1}{P_n \cdot \epsilon_n} \quad (23),$$

or, re-inverting $1/P$,

$$P = \frac{1}{\frac{1}{P_w \cdot \epsilon_w} + \frac{1}{P_i \cdot \epsilon_i} + \frac{1}{P_n \cdot \epsilon_n}} = \frac{P_w P_i P_n}{\frac{P_i P_n}{\epsilon_w} + \frac{P_w P_n}{\epsilon_i} + \frac{P_w P_i}{\epsilon_n}} \quad (24),$$

in which the terms on the right-hand side are related to underlying environmental variables or plant traits:

$$P_w = \frac{E_o(c_a - \Gamma)}{1.6D}, \quad \epsilon_w = \frac{K(\psi_{soil} - \psi_{leaf})}{E_o} \quad (25),$$

$$P_n = \left(\frac{c_a - \Gamma}{rc_a + M} \right) \chi N_o, \quad \epsilon_n = \frac{N}{N_o} \quad (26),$$

$$P_i = \left(\frac{c_a - \Gamma}{rc_a + M} \right) \phi i_o, \quad \epsilon_i = f_{par} \quad (27).$$

Equation 23 is the *Inverse Production Function* or IPF. The terms P_w , P_n and P_i can be understood as follows: their respective *reciprocals* ($1/P_w$, $1/P_n$, and $1/P_i$) represent the minimum diffusional, biochemical and energetic constraints, respectively, possible for a given environment (i.e., a given E_o , N_o and i_o). we refer to P_w , P_n and P_i as *production potentials*. The terms ϵ_w , ϵ_n and ϵ_i can be understood as *acquisition efficiencies*. For example, ϵ_w is the ratio of actual water use ($K(\psi_{soil} - \psi_{leaf})$) to the maximum water use theoretically possible in this environment (E_o). The

acquisition efficiencies are dimensionless and range between zero and unity; a value of unity means all of the available resource has been acquired.

The IPF bears a superficial resemblance to the traditional production function, with production potentials each multiplied by acquisition efficiencies. We note that the conventionally defined "resource use-efficiencies" (e.g., light use efficiency) are implicit in the IPF, and emerge when the expression is re-inverted to give P , and then rearranged. For example, light-use efficiency would be P divided by the actual light use:

$$\frac{P}{i} = \frac{P}{f_{par} i_o} = \left(\frac{c_a - \Gamma}{r c_a + M} \right) \frac{\phi}{1 + \frac{P_i \epsilon_i}{P_w \epsilon_w} + \frac{P_i \epsilon_i}{P_n \epsilon_n}} \quad (28).$$

The complex interactions among P_i , P_w , P_n , ϵ_i , ϵ_w and ϵ_n in the denominator of Eqn 28 illustrate why it is difficult to interpret or predict resource-use efficiencies, particularly within the paradigm of a production theory that focuses explicitly on only one resource: namely, a given resource-use efficiency depends not only on the production potential and acquisition efficiency for that resource, but also on the production potentials and acquisition efficiencies for the other two resources.

It is important to recognize that the Inverse Production Function was derived from process-based descriptions of diffusional (Eqn 1) and biochemical and energetic (Eqn 3, the FvCB model of photosynthesis) constraints on photosynthesis. That is, the form of Eqn 23 was not adopted on *ad hoc* or conceptual grounds: rather, it is an *identity*, at least within the limits of the accuracy of the underlying biophysical models and simplifying assumptions. It is in fact a simplification of the FvCB model, with minor additional rearrangements to highlight the relationships between resource availability and actual resource acquisition.

The IPF makes a prediction that may seem somewhat counterintuitive to those familiar with the FvCB photosynthesis model. Whereas FvCB seems to predict that photosynthesis is the lesser of two limiting factors (Eqn 3), the IPF suggests photosynthesis is simultaneously co-limited by three limiting factors. The resolution to this seeming paradox has two parts. Firstly, this interpretation of FvCB is not quite right: in actuality, FvCB always predicts that photosynthesis is simultaneously limited by at least two factors (g and either V_m or J), and under electron transport-limited conditions, by three (g , J_m and I ; i.e., water, nitrogen, and light). Secondly, we combined the two non-stomatal limitations in FvCB (carboxylation and electron transport) in Eqn 5, based on the idea that both of these factors will tend to limit photosynthesis to various degrees when averaged over a long-time frame, as is the context of this model.

Supplemental references

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