

Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences

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Appendix F: Mixtures effects thanks to differences in light extinction abilities.

This appendix demonstrates with a simple classical model how variability in light extinction coefficients among species interacts with the functional form (convexity) of the light extinction process to produce diversity effects on light capture. We assume that light extinction through a cover of leaves of species i with leaf area index L and extinction coefficient k_i obeys Beer's law (Monsi & Saeki, 1953):

$$I_{mono,i} = I_0 \exp(-k_i L) = f(k_i L) \tag{F.1}$$

where I_0 and I_i are incident and ground level PAR ($W.m^{-2}$) and $f(x) = I_0 e^{-x}$.

Let there be a polyculture composed of S species that form S distinct vegetation layers overtopping each other with respective leaf area index LAI_i such that $\sum_i LAI_i = L$. Ground level PAR

is given by:

$$I_{poly} = I_0 \prod_{i=1}^S \exp(-k_i LAI_i) = f\left(-\sum_{i=1}^S k_i LAI_i\right) \quad (\text{F.2})$$

If leaves from the same polyculture were rearranged to create S juxtaposed monocultures, each occupying a proportion LAI_i of ground area and thus each having a leaf area index of L , the average ground level PAR would write:

$$\overline{I_{mono}} = \frac{1}{L} \sum_{i=1}^S LAI_i I_{mono,i} = \sum_{i=1}^S \frac{LAI_i}{L} f(k_i L) > f\left(\sum_{i=1}^S k_i LAI_i\right) = I_{poly} \quad (\text{F.3})$$

4 since f is strictly convex and $\sum_{i=1}^S LAI_i/L = 1$ (Jensen's inequality). Note that the inequality
holds only if k_i s differ from each other. Therefore, with total leaf area held constant, polycultures
6 capture more light than expected from the average monoculture performance weighted by each
species' contribution in the mixture.

Taylor expansions around $\bar{k}L$, where $\bar{k} = \frac{1}{L} \sum_{i=1}^S LAI_i k_i$ denotes the weighted mean, yield:

$$\overline{I_{mono}} - I_{poly} \approx \frac{1}{2} f(\bar{k}L) L \sum_{i=1}^S LAI_i (k_i - \bar{k})^2 = \frac{1}{2} f(\bar{k}L) L^2 V \quad (\text{F.4})$$

8 Diversity effects thus decrease with the mean (\bar{k}) but increase with the variance of light extinction
coefficients ($V = \sum LAI_i (k_i - \bar{k})^2 / L$). In other words, diversity effects are stronger for mixtures
10 including many species that capture only a small amount of light and a few species that strongly
reduce PAR. With no effects on total leaf area, this type of diversity effects cannot be 'transgressive',
12 that is polyculture cannot capture more light than the 'best' monoculture, since $\bar{k} \leq \max k_i$.
However, thanks to a trade-off between height growth and shade tolerance or to overyielding,
14 polycultures may achieve a larger total leaf area than monocultures and capture more light than

their ‘best’ constituent monoculture.

In reality and in the spatially explicit light interception model we use in the main text, neither do monocultures form a homogeneous layer nor are polycultures laid out in perfectly distinct layers. In our spatially explicit model, the sky hemisphere is divided in discrete regions r with specific PAR I_r . The PAR reaching a point P on the ground surface is calculated as $I(P) = \sum_r I_r \prod_{k(r)} CO_{k(r)}$ where k iterates over trees that intersect light rays joining P and the center of the sky region r and CO_k denotes tree’s k ‘crown openness. Therefore, I can be written

$$I(P) = \sum_r I_r \prod_{i=1}^S CO_i^{q_i(r)} = \sum_r I_r \exp \left(\sum_{i=1}^S q_i(r) \log CO_i \right) \quad (\text{F.5})$$

16 where i iterates over species and $q_i(r)$ is the number of crown of species i that are hit by rays joining
the sky region r and P . Since $q \geq 1$, $I(P)$ is, like f with light extinction coefficients, a convex
18 function of crown openness. The same basic principles as before apply and even in the absence of
strict “multilayering”, the closer to the horizon light rays are, the more likely they are to intersect
20 crowns of multiple species and generate the diversity effects of the type analyzed in this appendix.
As a corollary, differences in crown architecture that maximize the number of multispecific crown
22 hits per rays r will facilitate this type of diversity effects.

Literature cited

- ²⁴ Monsi, M. & Saeki, T. (1953). Über den lichtfaktor in den pflanzengesellschaften und seine bedeutung für die stoffproduktion. pp. 22–52.