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Supplementary Information for

How functional traits influence plant growth and shade tolerance across the life-cycle

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Supporting Information Text

Additional details on the `FF16` growth model in the `plant` package

In this paper we use the `FF16` growth model from the package `plant` (1), which is accessed via R (2). A full derivation of the Eqs. from the main text are described is provided in Appendix of (1), see also (3). Below we repeat some additional details from (1), so that readers have a complete picture of the model.

The `FF16` physiological model includes default values for all needed parameters (Table S1). Species are known to vary considerably in many of these parameters, such as ϕ, ρ, ν, and ω; so by varying parameters one can account for species differences. When altering a parameter in the model, however, one must also consider whether there are trade-offs linking parameters. This is achieved via a hyper-parameterisation function.

Hyper-parameterisation of the `FF16` model via traits. `plant` allows for the hyper-parameterisation of the `FF16` physiological model via plant functional traits: this enables simultaneous variation in multiple parameters in accordance with an assumed trade-off. The hyper-parameterisation function used in the current analysis differs slightly from that in (1). The functions implemented are as follows.

Seed mass. Effects of the trait seed mass, are naturally embedded in the equation determining fecundity and the initial height of seedlings. In addition, we let the accessory cost per seed be a multiple of seed size, $\alpha_{\mathrm{f3}} = \beta_{\mathrm{f1}}\omega$, as empirically observed (4).

Nitrogen per unit leaf area. Photosynthesis per unit leaf area and respiration rates per unit leaf mass (or area) are assumed to vary with leaf nitrogen per unit area, ν. The calculation of respiration rates is already described above. To calculate the average annual photosynthesis for a leaf, we integrate the instantaneous rate per unit leaf area over the annual solar trajectory, using a rectangular-hyperbolic photosynthesis light response curve,

$$p(\nu, E) = \frac{1}{365\mathrm{d}} \int_0^{365\mathrm{d}} \frac{Y(t) + A_{\max} - \sqrt{(Y(t) + A_{\max})^2 - 4\beta_{\mathrm{lf2}} Y(t) A_{\max}}}{2\beta_{\mathrm{lf2}}} \mathrm{d}t, \qquad [1]$$

where $A_{\max}$ is the maximum photosynthetic capacity of the leaf, β_{lf2} is the curvature of the light response curve, $Y(t) = \beta_{\mathrm{lf3}} I(t)$ is the initial yield of the light response curve, with β_{lf3} being the quantum yield parameter, $I(t) = k_{\mathrm{I}}\, I_0(t)\, E$ is the intensity of light on the leaf surface, and $I_0(t)$ is light incident on a surface perpendicular to the sun's rays directly above the canopy at time t. The profile of $I_0(t)$ is given by a solar model adapted from (**?**).

We allow for the maximum photosynthetic capacity of the leaf to vary with leaf nitrogen per unit area, as

$$A_{\max} = \beta_{\mathrm{lf1}} \left(\frac{\nu}{\nu_0}\right)^{\beta_{\mathrm{lf5}}}, \qquad [2]$$

where β_{lf1} and β_{lf5} are constants. The relationships is normalized around ν_0, the global mean of leaf nitrogen per unit area.

Leaf mass per unit area. The trait leaf mass per unit area, denoted by ϕ, directly influences growth by changing $\mathrm{d}A_{\mathrm{l}}/\mathrm{d}M_{\mathrm{a}}$. In addition, we link ϕ to the rate of leaf turnover, based on a widely observed scaling relationship from (5) (Fig. S1),

$$k_{\mathrm{l}} = \beta_{\mathrm{kl1}} \left(\frac{\phi}{\phi_0}\right)^{-\beta_{\mathrm{kl2}}}. \qquad [3]$$

This relationship is normalised around ϕ_0, the global mean of ϕ. This allows us to vary β_{kl1} and β_{kl2} without displacing the relationship from the observed mean.

We also vary the mass-based leaf respiration rate so that it stays constant per unit leaf area and varies with ϕ and nitrogen per unit leaf area ν, as empirically observed by (5),

$$r_{\mathrm{l}} = \frac{\beta_{\mathrm{lf4}}\, \nu}{\phi}. \qquad [4]$$

Wood density. The trait wood density, denoted by ρ, directly influences growth by changing $\mathrm{d}A_{\mathrm{l}}/\mathrm{d}M_{\mathrm{a}}$. As for ϕ, these relationships are normalized around ρ_0, the global mean of ρ. By default, β_{kI2} and β_{ks2} are set to zero, so these linkages only become present when these parameters are set to something other than their default values.

The rate of sapwood respiration per unit volume is assumed to be constant, so sapwood respiration per unit mass varies as

$$r_{\mathrm{s}} = \frac{\beta_{\mathrm{rs1}}}{\rho}, \qquad [5]$$

where β_{rs1} is a default rate per volume of sapwood. Similarly, the rate of bark respiration per unit mass varies as

$$r_{\mathrm{b}} = \frac{\beta_{\mathrm{rb1}}}{\rho}, \qquad [6]$$

with $\beta_{\mathrm{rb1}} = 2\beta_{\mathrm{rs1}}$.

Implementation of hyper-parameterisation function. The hyper-parameterisation function used in this analysis is implemented as follows:

```
function(
                                lma_0=0.1978791,
                                B_kl1=0.4565855,
                                B_kl2=1.71,
                                rho_0=608.0,
                                B_dI1=0.01,
                                B_dI2=0.0,
                                B_ks1=0.2,
                                B_ks2=1.25, #0.0,
                                B_rs1=4012.0,
                                B_rb1=2.0*4012.0,
                                B_f1 =3.0,
                                narea=1.87e-3,
                                narea_0=1.87e-3,
                                B_lf1=5120.738 * 1.87e-3 * 24 * 3600 / 1e+06,
                                B_lf2=0.75,
                                B_lf3=0.04,
                                B_lf4=21000*0.75,
                                B_lf5=0.5,
                                k_I=0.5,
                                latitude=0) {
  assert_scalar <- function(x, name=deparse(substitute(x))) {
    if (length(x) != 1L) {
      stop(sprintf("%s must be a scalar", name), call. = FALSE)
    }
  }
  assert_scalar(lma_0)
  assert_scalar(B_kl1)
  assert_scalar(B_kl2)
  assert_scalar(rho_0)
  assert_scalar(B_dI1)
  assert_scalar(B_dI2)
  assert_scalar(B_ks1)
  assert_scalar(B_ks2)
  assert_scalar(B_rs1)
  assert_scalar(B_rb1)
  assert_scalar(B_f1)
  assert_scalar(narea)
  assert_scalar(narea_0)
  assert_scalar(B_lf1)
  assert_scalar(B_lf2)
  assert_scalar(B_lf3)
  assert_scalar(B_lf4)
  assert_scalar(B_lf5)
  assert_scalar(k_I)
  assert_scalar(latitude)

  function(m, s, filter=TRUE) {
    with_default <- function(name, default_value=s[[name]]) {
      rep_len(if (name %in% colnames(m)) m[, name] else default_value,
              nrow(m))
    }
    lma       <- with_default("lma")
    rho       <- with_default("rho")
    omega     <- with_default("omega")
    narea     <- with_default("narea", narea)

    ## lma / leaf turnover relationship:
    k_l   <- B_kl1 * (lma / lma_0) ^ (-B_kl2)

    ## rho / mortality relationship:
```

```
d_I  <- B_dI1 * (rho / rho_0) ^ (-B_dI2)

## rho / wood turnover relationship:
k_s  <- B_ks1 *  (rho / rho_0) ^ (-B_ks2)
k_b <- k_s

## rho / sapwood respiration relationship:

## Respiration rates are per unit mass, so this next line has the
## effect of holding constant the respiration rate per unit volume.
## So respiration rates per unit mass vary with rho, respiration
## rates per unit volume don't.
r_s <- B_rs1 / rho
# bark respiration follows from sapwood
r_b <- B_rb1 / rho

## omega / accessory cost relationship
a_f3 <- B_f1 * omega

## Narea, photosynthesis, respiration

assimilation_rectangular_hyperbolae <- function(I, Amax, theta, QY) {
  x <- QY * I + Amax
  (x - sqrt(x^2 - 4 * theta * QY * I * Amax)) / (2 * theta)
}

## Photosynthesis  [mol CO2 / m2 / yr]
approximate_annual_assimilation <- function(narea, latitude) {
  E <- seq(0, 1, by=0.02)
  ## Only integrate over half year, as solar path is symmetrical
  D <- seq(0, 365/2, length.out = 10000)
  I <- plant:::PAR_given_solar_angle(plant:::solar_angle(D, latitude = abs(latitude)))

  Amax <- B_lf1 * (narea/narea_0) ^  B_lf5
  theta <- B_lf2
  QY <- B_lf3

  AA <- NA * E

  for (i in seq_len(length(E))) {
    AA[i] <- 2 * plant:::trapezium(D, assimilation_rectangular_hyperbolae(
                                k_I * I * E[i], Amax, theta, QY))
  }
  if(all(diff(AA) < 1E-8)) {
    # line fitting will fail if all have are zero, or potentially same value
    ret <- c(last(AA), 0)
    names(ret) <- c("p1","p2")
  } else {
    fit <- nls(AA ~ p1 * E/(p2 + E),
              data.frame(E = E, AA = AA),
              start = list(p1 = 100, p2 = 0.2))
    ret <- coef(fit)
  }
  ret
}

# This needed in case narea has length zero, in which case trapezium fails
a_p1 <- a_p2 <- 0 * narea
## TODO: Remove the 0.5 hardcoded default for k_I here, and deal
## with this more nicely.
if (length(narea) > 0 || k_I != 0.5) {
```

```
      i <- match(narea, unique(narea))
      y <- vapply(unique(narea), approximate_annual_assimilation,
                  numeric(2), latitude)
      a_p1  <- y["p1", i]
      a_p2  <- y["p2", i]
    }

    ## Respiration rates are per unit mass, so convert to mass-based
    ## rate by dividing with lma
    ## So respiration rates per unit mass vary with lma, while
    ## respiration rates per unit area don't.
    r_l  <- B_lf4 * narea / lma

    extra <- cbind(k_l,                # lma
                   d_I, k_s, k_b, r_s, r_b, # rho
                   a_f3,               # omega
                   a_p1, a_p2,         # narea
                   r_l)                # lma, narea

    overlap <- intersect(colnames(m), colnames(extra))
    if (length(overlap) > 0L) {
      stop("Attempt to overwrite generated parameters: ",
           paste(overlap, collapse=", "))
    }

    ## Filter extra so that any column where all numbers are with eps
    ## of the default strategy are not replaced:
    if (filter) {
      if (nrow(extra) == 0L) {
        extra <- NULL
      } else {
        pos <- diff(apply(extra, 2, range)) == 0
        if (any(pos)) {
          eps <- sqrt(.Machine$double.eps)
          x1 <- extra[1, pos]
          x2 <- unlist(s[names(x1)])
          drop <- abs(x1 - x2) < eps & abs(1 - x1/x2) < eps
          if (any(drop)) {
            keep <- setdiff(colnames(extra), names(drop)[drop])
            extra <- extra[, keep, drop=FALSE]
          }
        }
      }
    }

    if (!is.null(extra)) {
      m <- cbind(m, extra)
    }
    m
  }
}
<environment: 0x7f9512489620>
```

Table S1. Core parameter of the `FF16` physiological model.

Description	Symbol	Unit	Code	Value
Plant construction				
Crown-shape parameter	η		`eta`	12
Leaf mass per area	ϕ	$\mathrm{kg\,m^{-2}}$	`lma`	0.1978791
Wood density	ρ	$\mathrm{kg\,m^{-3}}$	`rho`	608
Sapwood area per unit leaf area	θ		`theta`	0.0002141786
Height of plant with leaf area of 1m^2	α_{l1}	m	`a_l1`	2.17
Exponent of relationship between height and leaf area	α_{l2}		`a_l2`	0.5
Root mass per unit leaf area	α_{r1}	$\mathrm{kg\,m^{-2}}$	`a_r1`	0.07
Ratio of bark area to sapwood area	α_{b1}		`a_b1`	0.17
Production				
Leaf photosynthesis per area	α_{p1}	$\mathrm{mol\,yr^{-1}\,m^{-2}}$	`a_p1`	151.1778
Saturation of leaf photosynthesis per area	α_{p2}		`a_p2`	0.2047162
Yield = fraction of carbon fixed converted into mass	α_{y}		`a_y`	0.7
Biomass per mol carbon	α_{bio}	$\mathrm{kg\,mol^{-1}}$	`a_bio`	0.0245
Leaf respiration per mass	r_{l}	$\mathrm{mol\,yr^{-1}\,kg^{-1}}$	`r_l`	198.4545
Fine-root respiration per mass	r_{r}	$\mathrm{mol\,yr^{-1}\,kg^{-1}}$	`r_r`	217
Sapwood respiration per mass	r_{s}	$\mathrm{mol\,yr^{-1}\,kg^{-1}}$	`r_s`	6.598684
Bark respiration per mass	r_{b}	$\mathrm{mol\,yr^{-1}\,kg^{-1}}$	`r_b`	13.19737
Turnover rate for leaves	k_{l}	$\mathrm{yr^{-1}}$	`k_l`	0.1521952
Turnover rate for sapwood	k_{s}	$\mathrm{yr^{-1}}$	`k_s`	0.2
Turnover rate for bark	k_{b}	$\mathrm{yr^{-1}}$	`k_b`	0.2
Turnover rate for fine roots	k_{r}	$\mathrm{yr^{-1}}$	`k_r`	1
Fecundity				
Seed mass	ω	kg	`omega`	0.000038
Height at maturation	H_{mat}	m	`hmat`	15
Maximum allocation to reproduction	α_{f1}		`a_f1`	0.8
Parameter determining rate of change in $r(x, m_{\mathrm{l}})$ around H_{mat}	α_{f2}		`a_f2`	10

Table S2. Parameters for hyper-parameterisation of the `FF16` physiological model.

Description	Symbol	Unit	Code	Value
Leaf turnover				
Global average leaf mass per area	ϕ_0	$\mathrm{kg\,m^{-2}}$	`lma_0`	0.1978791
Rate of leaf turnover at average leaf mass per unit leaf area, ϕ_0	β_{kl1}	$\mathrm{yr^{-1}}$	`B_kl1`	0.4565855
Scaling exponent for ϕ in leaf turnover	β_{kl2}		`B_kl2`	1.71
Sapwood turnover				
Global average wood density	ρ_0	$\mathrm{kg\,m^{-3}}$	`rho_0`	608
Rate of sapwood turnover at average wood density, ρ_0	β_{ks1}	$\mathrm{yr^{-1}}$	`B_ks1`	0.2
Scaling exponent for ρ in sapwood turnover	β_{ks2}		`B_ks2`	1.25
Photosynthesis				
Leaf nitrogen per unit leaf area	ν	$\mathrm{kg\,m^{-2}}$	`narea`	0.00187
Global average nitrogen per unit leaf area	ν_0	$\mathrm{kg\,m^{-2}}$	`narea_0`	0.00187
Potential CO_2 photosynthesis at average leaf nitrogen, ν_0	β_{lf1}	$\mathrm{mol\,d^{-1}\,m^{-2}}$	`B_lf1`	0.8273474
Curvature of light response curve	β_{lf2}		`B_lf2`	0.75
Quantum yield of leaf photosynthesis (CO_2 per unit photosynthetically active radiation)	β_{lf3}		`B_lf3`	0.04
Scaling exponent for leaf nitrogen in maximum leaf photosynthesis	β_{lf5}		`B_lf5`	0.5
Respiration				
CO_2 respiration per unit leaf nitrogen	β_{lf4}	$\mathrm{mol\,yr^{-1}\,kg^{-1}}$	`B_lf4`	15750
CO_2 respiration per unit sapwood volume	β_{rs1}	$\mathrm{mol\,yr^{-1}\,m^{-3}}$	`B_rs1`	4012
CO_2respiration per unit bark volume	β_{rb1}	$\mathrm{mol\,yr^{-1}\,m^{-3}}$	`B_rb1`	8024

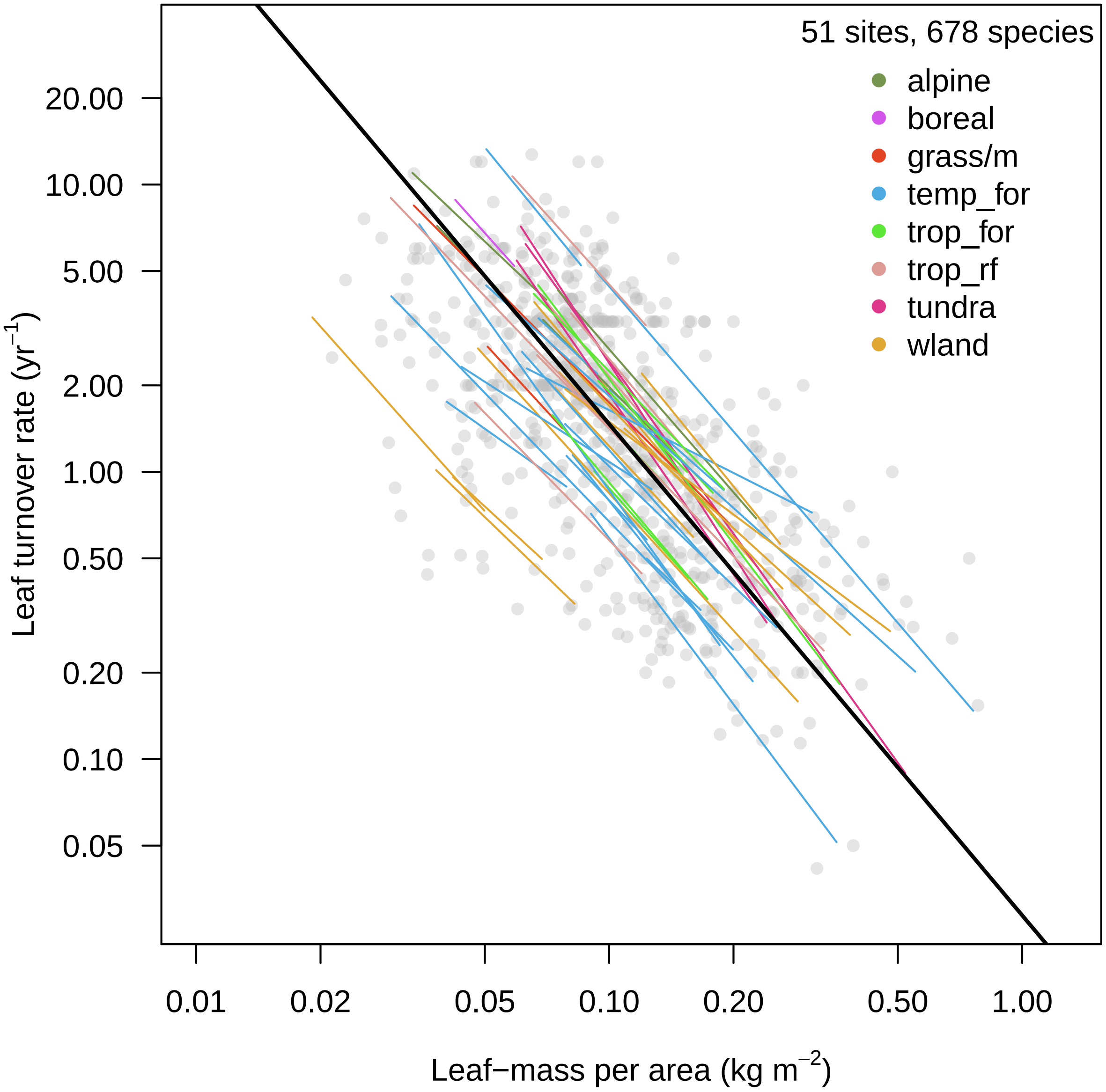

Fig. S1. Leaf turnover decreases with leaf-mass per unit leaf area. Data from (5) for 678 species from 51 sites, each point giving a species-average. Lines show standardised major axis lines fitted to data from each site, with intensity of shading adjusted according to strength of the relationship.

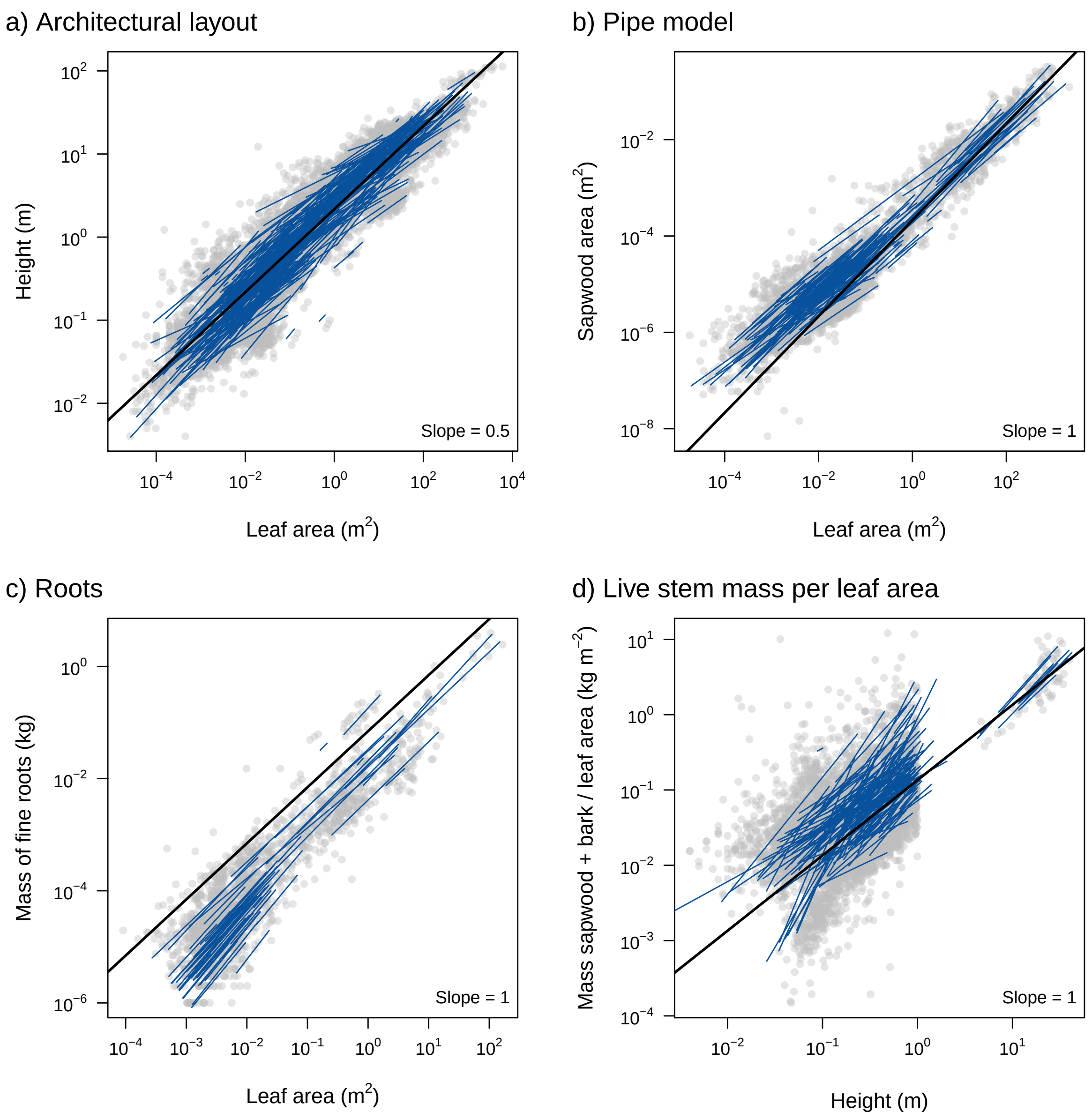

Fig. S2. Assumptions of a functional balance model for plant construction. Each dot is a single plant from the BAAD (6). Blue lines show standardised major axis lines fit to different species. The black line shows the relationship assumed in this paper, with slope given by the functional-balance assumptions in Table 4 from main text.

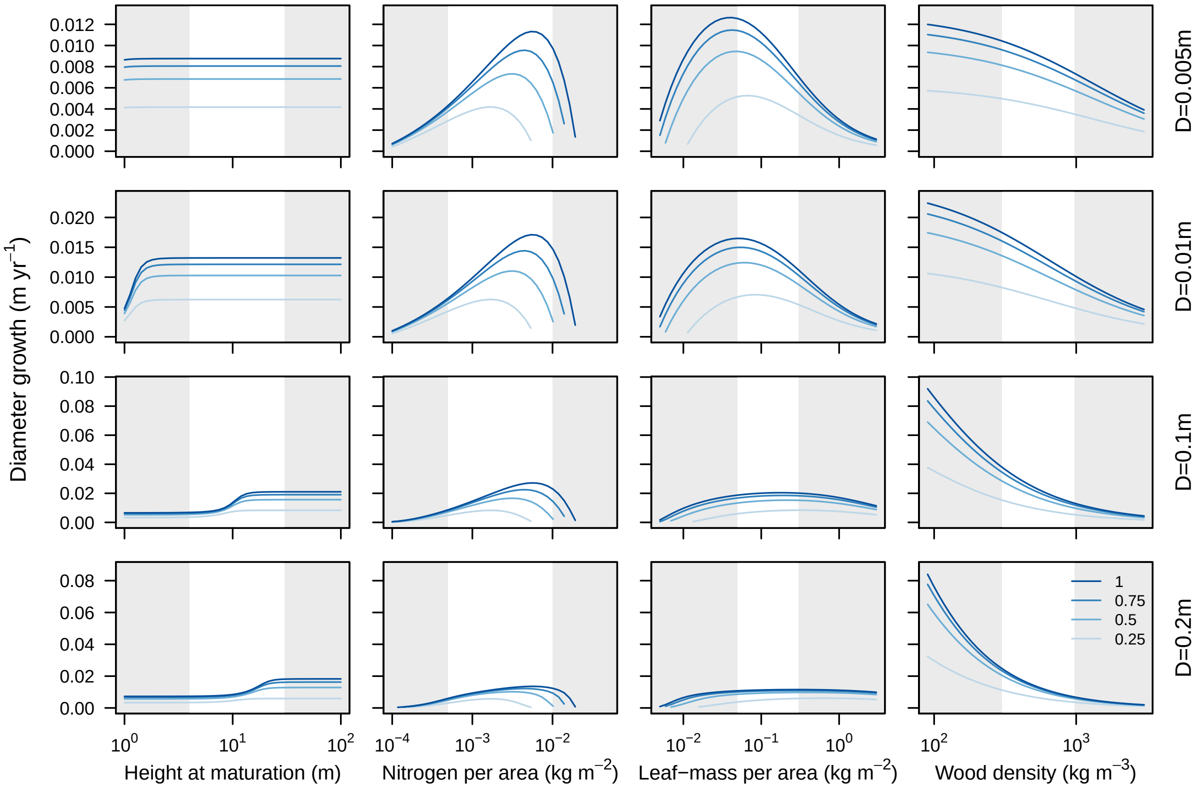

Fig. S3. Effect of four traits on stem-diameter growth rate for different-sized plants. Growth rates were simulated using the `plant` model, applying the trade-offs describing in Table 3. Each panel shows how growth is influenced by a different trait for plants of a given height, and across a series of canopy openness values from completely open (light blue, $E = 1$) to heavily shaded (dark line, $E = 0.25$). For any given value of trait and E, plants were grown to the desired stem-diameter and their growth rate estimated. Changes in trait-growth relationships are summarised in Table 5.

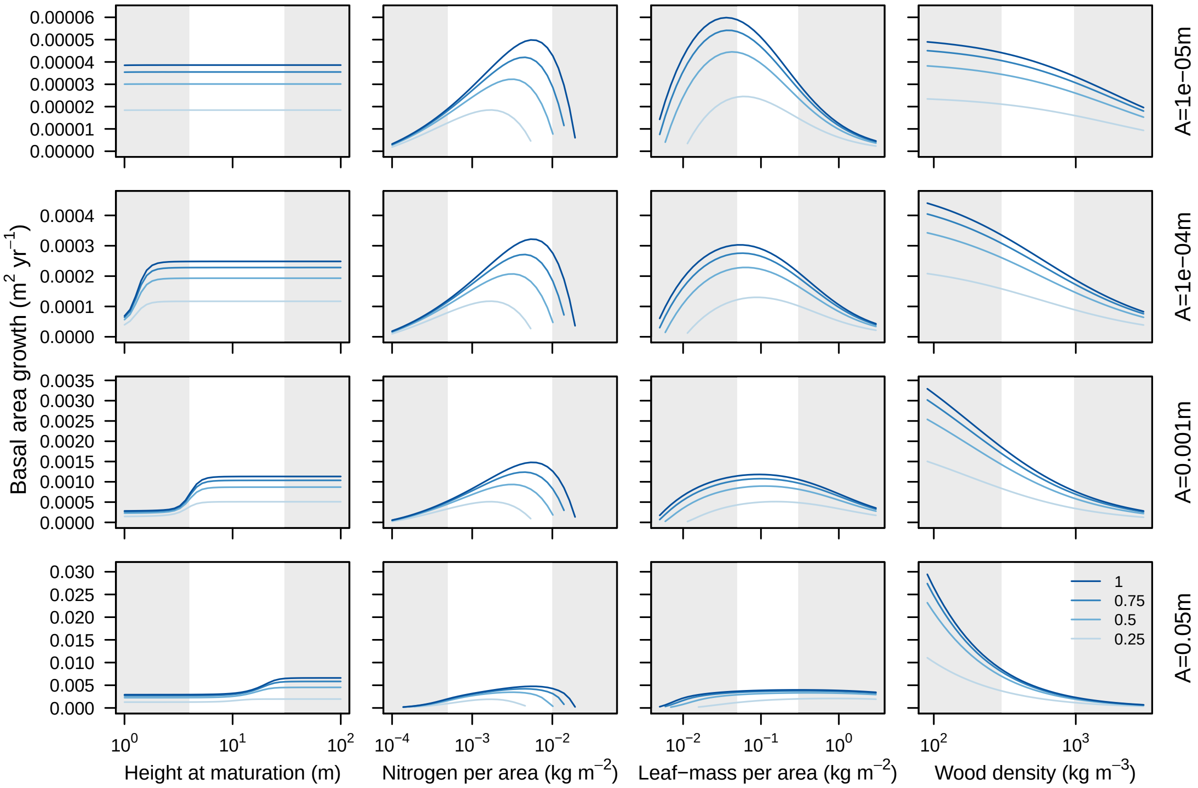

Fig. S4. Effect of four traits on stem-area growth rate for different-sized plants. Growth rates were simulated using the `plant` model, applying the trade-offs describing in Table 3. Each panel shows how growth is influenced by a different trait for plants of a given height, and across a series of canopy openness values from completely open (light blue, $E = 1$) to heavily shaded (dark line, $E = 0.25$). For any given value of trait and E, plants were grown to the desired stem-area and their growth rate estimated. Changes in trait-growth relationships are summarised in Table 5.

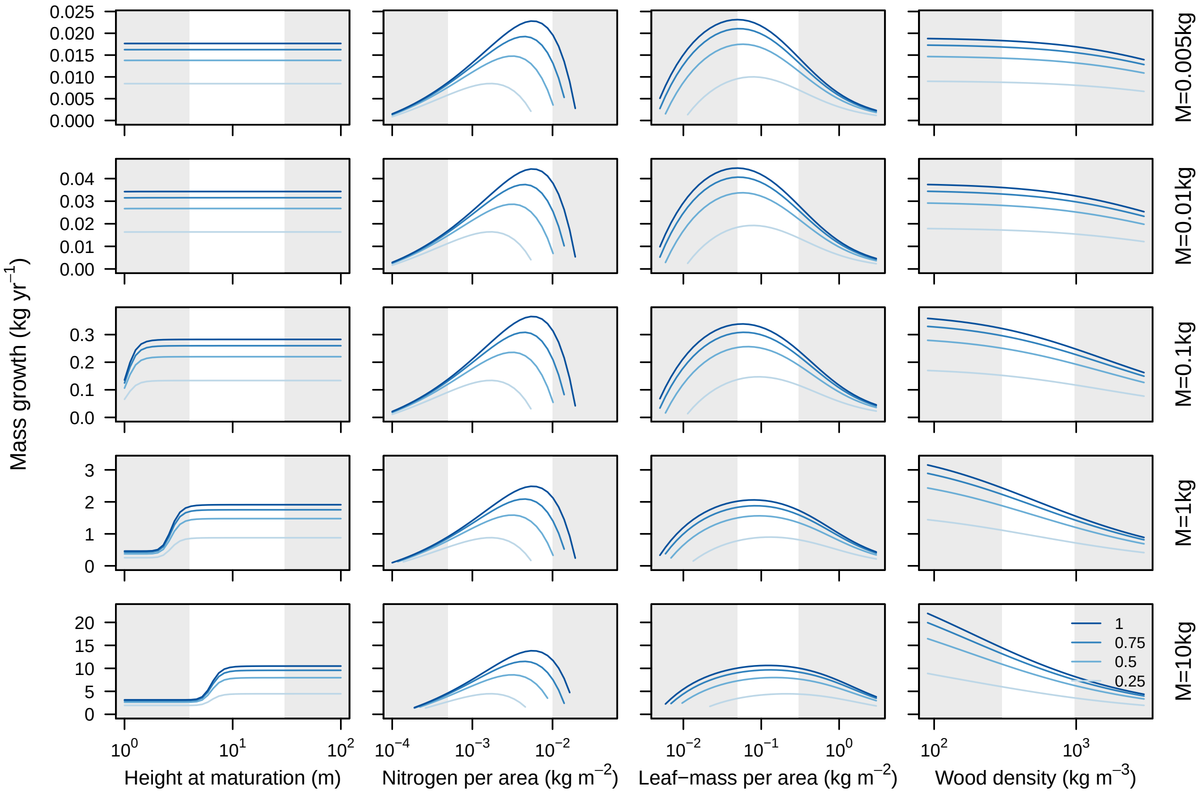

Fig. S5. Effect of four traits on plant mass growth rate for different-sized plants. Growth rates were simulated using the `plant` model, applying the trade-offs describing in Table 3. Each panel shows how growth is influenced by a different trait for plants of a given height, and across a series of canopy openness values from completely open (light blue, $E = 1$) to heavily shaded (dark line, $E = 0.25$). For any given value of trait and E, plants were grown to the desired mass and their growth rate estimated. Changes in trait-growth relationships are summarised in Table 5.

References

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4. Henery M, Westoby M (2001) Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* 92:479–490.
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