Title:

Habitat adaptation mediates the influence of leaf traits on canopy productivity: evidence from a tropical freshwater swamp forest

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ABSTRACT

Functional traits offer generalizability to the prediction of ecosystem processes such as production, and community-weighted mean trait values are increasingly used for such predictions. However, the underlying causal direction between traits and ecosystem processes are often indirect and sometimes even tenuous. In this study, we aimed to uncover underlying causal mechanisms between traits, habitat adaptation and canopy productivity. We used canopy production data estimated from leaf litter traps, and trait and habitat association data obtained from 40 permanent vegetation plots in the Nee Soon catchment in Singapore, which contains a heterogeneous mix of freshwater swamp and dry-land tropical forests. Mean canopy production across the catchment was estimated to be 768 g m^{-2} $year^{-1}$, which is similar to other tropical dry-land forests in the region. Fortnightly per-basal-area canopy production was found to be consistently lower in swamp than non-swamp plots, and positively correlated with monthly mean temperature. Structural equation models fitted to data of canopy production, leaf traits, plot type (swamp versus non-swamp), basal areas and habitat adaptations of 69 tree species–plot combinations suggested that tree species possessing leaf traits associated with more conservative resource acquisition strategies, viz., low specific leaf area, high leaf C:N ratio, and thicker leaves, are better adapted to stressful, waterlogged swamp conditions, but that this adaptation also reduces canopy—and likely total—net primary productivity. These observations suggest that the stressful conditions of waterlogged, anoxic swamp habitats significantly reduce the rate at which nutrients are cycled by communities found in such environments.

KEYWORDS

Functional traits, litterfall, peat, primary productivity, Southeast Asia, waterlogged soil

INTRODUCTION

Primary production is a fundamental process of ecosystems, and a key contributor to their nutrient cycling and carbon sequestering efficacies. Tropical forests constitute the largest global terrestrial carbon sink (Pan and others 2011). To date, most studies of tropical forest net primary productivity (NPP) utilize correlative approaches to extrapolate NPP estimates across vast expanses of forests which share superficial similarities (e.g., wet versus dry tropical forests) (Clark and others 2001). However, correlative approaches rely heavily on the assumption that tree communities in any given forest patch conform largely to a well-defined set of "forest types" to which specific NPP values can be attached. In reality, forest tree communities vary structurally and compositionally in a countless number of ways, as a result of both anthropogenic and non-anthropogenic phenomena (Whitmore 1988). Litterfall, a measure of canopy production which is a major component of NPP, has long been known to scale proportionately with forest structural attributes such as stand basal area (Turnbull and Madden 1983), while the effects of compositional differences on NPP are evident from NPP's relationships with forest successional stage (Goulden and others 2011) and plant functional traits (Reich 2012). Reliable predictive models thus need to be based upon a mechanistic, bottom-up understanding of the drivers of primary production in tropical forests (Trugman and others 2019).

Plant functional traits are measurable morpho-physio-phenological attributes that affect species fitness through effects on growth, reproduction and survival (Violle and others 2007), and offer the ecological generality necessary for predicting across diverse biogeographical regions (McGill and others 2006). They are increasingly being recognized to be correlated with ecosystem processes, and can be considered as important predictors of ecosystem processes such as productivity (Garnier and others 2004; Finegan and others 2015; Funk and others 2017). For example, plants with resource-acquisitive traits (e.g., high specific leaf area

[SLA] and leaf nitrogen content [LNC], low wood density, etc.) have high instantaneous leaf-level photosynthetic capacity and growth rates when resource stresses are low, which translates to positive correlations between community-weighted mean (CWM) SLA and LNC with aboveground NPP at the stand level (Garnier and others 2004; Reich 2014). Since the allocation to canopy production is a relatively constant proportion of total NPP (Malhi and others 2011), canopy production should also appear to be closely associated with functional traits.

In addition to facilitating some ecosystem processes, functional traits also moderate the interactions of species with their environment and other species, and are thus closely associated to the life history trade-offs and habitat adaptation of species (Keddy 1992; Diaz and others 1998). Functional traits may facilitate the adaptation of species to certain habitats and/or be limited by physiological constraints imposed by the abiotic conditions of habitats (Keddy 1992; Diaz and others 1998; Fortunel and others, 2014; Gonzalez-M and others 2020). For example, resource-acquisitive species will be better able to exploit abundant resources in early successional habitats than conservative species, and traits associated with acquisitive strategies facilitate these species' adaptation to forest gaps, edges, or disturbances (Reich 2014). On the other hand, abiotic stressors imposed by environments often select for resource conservative traits.

Wetland forests (e.g., floodplain forests of South America, or peat swamp forests and freshwater swamp forests of Southeast Asia) are stressful environments for trees to grow in because the waterlogged conditions result in anoxic and unstable substrates that hinder root respiration and structural stability of trees (Corner 1978; Kozlowski 1997). Many of the tree species in these swamp forests exhibit ecophysiological or anatomical traits such as aerenchyma, lenticilate bark and stilt/prop roots, that confer obvious adaptive advantages to growth in the unstable and anoxic substrates of such habitats (Corner 1978; Kozlowski 1997).

Mori and others (2019) also found that species associated with nutrient-poor blackwater floodplain forest (‘igapo’) had lower SLA, LNC, leaf dry matter content, and branch wood density compared with congeners associated with nutrient-rich white-water floodplain forest (‘varzea’). This suggest that, even within stressful waterlogged conditions, other concurrent stresses such as low nutrient availability can further reduce the dominance of the more acquisitive trait syndromes and favour more conservative resource acquisition strategies (Moor and others 2017).

If a close relationship exists between functional traits and habitat adaptation, and functional traits are known to directly or indirectly affect ecosystem processes such as productivity, then habitat adaptation, functional traits and productivity must be causally interconnected such that habitat adaptation and productivity are also linked to each other, whether directly or indirectly. Indeed, this is supported by some empirical observations. For example, in a tropical montane forest in Hainan Island in southern China, the community-weighted mean (CWM) wood density and SLA were found to mediate the environmental effects of terrain convexity, soil organic matter and exchangeable base on aboveground carbon (Bu and others 2019). However, the investigation of the trait–environment–productivity relationship should ideally be conducted at the species rather than the community level, and within causal rather than correlative frameworks. However, links between production and plant traits have been mostly examined at the stand level using CWM values, and the causal links between species-level trait values, species habitat adaptation and the productivity of individual species remain poorly established.

In this study, we aimed to first describe the total canopy production in swamp and non-swamp areas within a freshwater swamp forest in Singapore. Next, we aimed to determine the causal pathways giving rise to observed differences in canopy productivity in 25 tree species monitored in our surveys. We identified nine possible causal pathways linking canopy productivity to the traits and habitat adaptation and expressed these as nine unique biological hypotheses (Fig. 1). Habitat adaptation and functional traits may jointly (biological hypotheses i‒iii; Fig. 1) or singly (biological hypotheses iv and v; Fig. 1) constrain and/or determine the primary productivity of species; either habitat adaptation or functional traits may mediate the effect of each other on the primary productivity of species (biological hypotheses vi and vii; Fig. 1); or no causative relationship may exist at all between habitat adaptation and primary productivity, or between functional traits and primary productivity (biological hypotheses viii‒x; Fig. 1). At the same time, habitat adaptation may also constrain functional traits (i.e., environmental filtering; biological hypotheses ii, vii & ix; Fig. 1), or functional traits may facilitate adaptation on habitat types (biological hypotheses i, vi & viii; Fig. 1). We compared models representing these nine biological hypotheses to determine the most likely causal mechanism driving canopy productivity.

MATERIALS & METHODS

Study site

The study was conducted in ten 20 × 20-m permanent vegetation plots established in the Nee Soon catchment (NSFSF; 1°23'27.3"N, 103°48'35.5"E) that contains the last substantial tract of intact freshwater swamp forest in Singapore. Five of these plots (hereafter ‘swamp plots’) occurred within swamp conditions, i.e., with open water bodies (swamp streams and/or pools) found within them, while the remaining five plots (known hereafter as ‘non-swamp plots’) occurred in well-drained areas within the same catchment in which open water bodies did not occur. The ten plots had been established earlier as part of a larger study involving 40 plots used for the monitoring of forest tree communities in the NSFSF (Chong 2016; Chong and others 2018; in review). All trees above 5 cm diameter at breast height (DBH) were identified and measured in these plots. Detailed descriptions of the locations and establishment procedures of the forty plots are provided in Chong and others (2016; 2018; in review).

Weather data were obtained from historical daily records published by the Meteorological Society of Singapore, National Environment Agency (weather.gov.sg). This agency maintains 63 weather stations located across the country. Rainfall data were obtained from the Upper Peirce station (1°22'12.0"N, 103°48'18.0"E) located closest to the NSFSF, or from the Mandai station (1°24'13.0"N, 103°47'23.3"E) if data from the Upper Peirce station were unavailable. As daily temperature data were not available from both of these stations, these were obtained from the next nearest station located in Khatib (1°25'02.3"N, 103°49'29.6"E).

Leaf litter collection

Each of the ten monitored plots were divided into four equal 10 × 10 m quadrants, and a 1 m × 1 m leaf litter trap was set up as close to the center of each quadrant as possible, while being positioned to ensure that the trap opening was unobstructed by saplings and lianas. The design of the litterfall traps was adapted from Muller-Landau and Wright (2010). Nylon netting with a 2-mm mesh size was used to line the trap openings, and this netting was suspended approximately one meter above ground level in all traps. Litter was collected every two weeks over a period of one year, from August 2018 to July 2019.

Collected leaves were sorted and identified to species where possible. A species was considered to be a major litter-contributing species if it contributed to at least ten leaves and 5 g of leaf litter dry mass in at least three biweekly collections; for contribution of species, see Table S1. The designation of major (or minor) litter-contributing species was necessary because it was impossible to track and measure the leaf production of all species present in all collections; our approach thus allowed the prioritization of litter species identification for the dominant canopy species and the more ecologically important litter-producers. For each major litter-contributing morphospecies, the fresh mass (g) of all leaves was measured, and subsequently the fresh mass and oven-dried mass (dried at 60°C for at least seven days until a constant dry weight was attained) of a subsample of five leaves was measured. The dry-to-fresh mass ratio from this subsample was then multiplied to the total fresh mass (g) of that species to estimate the total dry mass (g) of the collected leaves. Separately, leaves for minor litter-contributing and unidentified species, as well as twigs (diameter < 2 cm) of all species, were oven-dried and weighed. The reproductive litter fraction, inclusive of fruit and flower parts, and coarse wood were excluded in this study.

In total, 95 morphospecies of leaves were sorted from the litter, of which 38 could be confidently identified as tree species, with 36 of these tree species also occurring within the ten plots in which litter traps were established (Table S1).

Leaf trait measurement

Leaf traits were measured from 25 tree species whose leaves could be identified from leaf litter collections. To do this, five mature sun leaves (i.e., leaves that were fully developed under unshaded conditions) were collected from each of five individuals of each species in the plots. Individuals of each species were collected from both swamp and non-swamp conditions whenever possible. Mature individuals of some species only occurred in one type of habitat, but for those found in both habitat types, preliminary analyses had shown that the measured leaf traits did not differ significantly between individuals of the same species that were found in swamp or non-swamp conditions (Appendix A of the Supporting Information). Four leaf traits were measured: specific leaf area (SLA, $cm^2\ g^{-1}$), leaf dry matter content (LDMC, $mg\ g^{-1}$), leaf thickness (LT, mm) and leaf carbon:nitrogen mass ratio (C:N). The former three traits were measured according to standard protocols described in Pérez-Harguindeguy and others (2013), while elemental carbon and nitrogen composition of leaves were obtained using a vario MICRO cube elemental analyser (Elementar, Langenselbold, Germany) from powdered samples ground in a Rommelsbacher EGK 200 coffee grinder (Dinkelsbühl, Germany) from fresh leaves that had been dried in a 60°C oven for at least a week.

Statistical analysis—total canopy production

The first analysis was done with the first aim of the study in mind: to describe the total canopy production in swamp and non-swamp areas within our study site. Total dry mass (g) of leaf litterfall per plot per collection, excluding leaves from liana species (which may be rooted outside of the plot area), was divided by the summed basal area (m^2) of all trees within the plot with DBH > 5 cm to obtain a fortnightly per-basal-area canopy production value (units: grams of litterfall per year per square-meter of plot per square-meter basal area of the species). This assumes that the vast majority of leaf litter collected in leaf litter traps was produced by trees within the plots, an assumption that was largely supported by the data (Fig. S1). This per-basal-area canopy production value was then log-transformed and modelled using generalised additive mixed-effects models (GAMM) with Gaussian errors. Four weather variables were included in models, namely, (i) mean daily rainfall over the 30-day duration preceding the collection date (mm), (ii) mean daily temperature over the 30-day duration preceding the collection date (°C), (iii) minimum daily temperature over the 30-day duration preceding the collection date (°C), and (iv) maximum daily temperature over the 30-day duration preceding the collection date (°C). These were modelled against the fixed effects of plot condition (swamp or dry), a thin plate spline fitted over the date of collection, six weather variables, the interactions between plot condition and either of these four weather variables, and the random intercept of plot number to control for repeated collections across individual plots. GAMMs were fitted using the R package “gamm4” (Wood and Scheipl 2020). Multimodel inference was performed using Akaike’s information criterion with correction for small sample size (AICc) on models representing all possible fixed effect combinations, with the criteria that models were not allowed to contain more than one temperature-related weather main effect term.

Statistical analysis—species canopy productivity

The next analysis was used to address the second aim of the study: to determine the causal pathways giving rise to observed differences in canopy productivity between swamp and non-swamp areas. This was done by explicitly modelling the basal area–canopy production relationship of litter-contributing tree species, many of which were found in both plot types. Canopy productivity of 25 tree species in each plot for which trait data could be collected was calculated by dividing litterfall dry weight (g m^{-2}) by the duration over which that species' litterfall had been monitored (fraction of a year), and thus took the units of g m^{-2} year^{-1}. The canopy production (ρ) of species i in plot j is expected to scale with its total basal area within that plot (A_{ij}):

$$\rho_{ij} = b_i A_{ij}^{\lambda_i} \qquad (Eqn. 1)$$

where λ_i represents a species-specific scaling exponent and b_i, a species-specific productivity constant. The parameter λ_i relaxes the assumption of a linear relationship between production and basal area for all species, while b_i may be understood as 'specific productivity' of a species after accounting for the number and sizes of individuals present. This specific productivity can be further hypothesized to be a function of intrinsic (such as leaf traits [z] and/or habitat adaptation [here "swamp indicator value", see below; SIV]) and/or extrinsic (such as habitat conditions [x]) factors. Thus Eqn. 1 may be rewritten as:

$$\ln \rho_{ij} = b_0 + b_x x_j + b_{SIV} SIV_i + b_z z_i + \lambda_i \ln A_{ij} + \epsilon_j \qquad (Eqn. 2)$$

Accordingly, the log-transformed canopy production value of each monitored tree species in each plot ($\ln \rho_{ij}$; a total of 69 species–plot combinations) was modelled against the log-transformed basal area of that respective species–plot combination ($\ln A_{ij}$) using linear mixed-effects models, with plot as random intercept and the scaling parameter λ_i as a random slope for each species. The other fixed effects included in component models of canopy production were all possible combinations of habitat adaptation (SIV_i), leaf traits (z_i), or plot type (x_j; swamp or non-swamp). As earlier analyses had demonstrated a consistent association between basal area and canopy production (Appendix B of the Supplementary information), models excluding this variable were not considered in the model selection process.

As we were interested in determining causal pathways rather than mere correlations, the above-described models of canopy production were then integrated into structural equation models (SEMs), together with models of habitat adaptation and leaf traits, in path configurations representing nine different biological hypotheses (Fig 1). SEMs provide a framework for developing and evaluating complex causal hypotheses (Grace 2006). SEMs were fitted using the R package "piecewiseSEM" (Lefcheck 2016), a local estimation-type SEM which does not include latent variables. In such SEMs, the explanatory variables in individual component models may be interpreted as having a causative effect on other explanatory variables, i.e., an explanatory variable in one component model (e.g., habitat adaptation) may also be a dependent variable in its own component model, thus making this variable an intermediate node in a causal chain.

Habitat adaptation was estimated by calculating the degree of association of each tree species with swamp habitats, which was obtained from tree data from all 40 plots (i.e., the ten plots in which leaf litter was collected plus 30 other plots in which leaf litter was not collected; Chong et al. in review). We used the indicator value developed by Dufrêne and Legendre (1997) to estimate the degree to which a species is associated with the swamp habitat type. This swamp indicator value (SIV) was calculated using the "indval" function in the "labdsv" R package:

$$SIV_i = f_i \times a_i \qquad (Eqn. 3)$$

$$f_i = \frac{\sum_{j \in swamp} p_{ij}}{n_{swamp}} \qquad (Eqn. 4)$$

$$a_i = \frac{\dfrac{\sum_{j \in swamp} A_{ij}}{n_{swamp}}}{\dfrac{\sum_{j \in swamp} A_{ij}}{n_{swamp}} + \dfrac{\sum_{j \in non-swamp} A_{ij}}{n_{non-swamp}}} \qquad (Eqn. 5)$$

where p_{ij} is the presence or absence (1/0) of tree species i in plot j; A_{ij} is the total basal area of tree species i in plot j; and n is the number of plots which are swamp or non-swamp in nature. SIV is a product of the fidelity, f_i (Eqn. 4) and specificity, a_i (Eqn. 5) of the focal species towards the swamp habitat type (Dufrene & Legendre, 1997). Thus, species which both occur frequently in swamp plots (high fidelity) and seldom in non-swamp ones (high specificity) would have high SIV values. SIV was calculated for each of the 25 monitored tree species, and used as a proxy of habitat adaptation in the SEMs.

Leaf traits were also included in the SEMs as direct or indirect causes of habitat adaptation and/or canopy productivity (Fig. 1a). However, not all measured leaf traits may play deterministic roles in relationships with habitat adaptation and/or canopy productivity. Furthermore, the number of species for which data could be collected (*n* = 25) was insufficient for complex models involving multiple leaf traits. We thus used six different representations of leaf traits in SEMs: (i) LT, (ii) LDMC, (iii) SLA, (iv) C:N ratio, or a composite measure of all four leaf traits—viz., the (v) first or (vi) second principal components of the scaled values of the four leaf traits (Fig. 4a). Only one of these six possible measures of leaf traits were used in any one SEM. Component models of SIV and leaf traits were all fitted using weighted least squares regression models, with model weights corresponding to the inverse of the number of plots in which each tree species was found. For example, if a species was found in four (of the ten) plots, each leaf trait or SIV observation from that species would have a weight of only 0.25.

Models corresponding to the nine biological hypotheses (Fig. 1) were fitted using each of the six measures of leaf traits, resulting in a total of 108 SEMs, which were then ranked using AIC for d-sep tests (also known as d-sep AIC; (Shipley 2013)) with correction for small sample size. All statistical analyses were performed in R ver. 3.4.0 (R Core Team 2017).

RESULTS

Total canopy production

A total of 30.7 kg of leaf litter dry mass was collected from the 40 monitored leaf litter traps over the one-year survey duration of this study, translating to a canopy production rate across plots of 768 ± 48 g m^{-2} $year^{-1}$ (mean ± SE). Total canopy production was not significantly different between swamp and non-swamp plots whether the leaves of liana species—which may sometimes be rooted outside the plot—were included ($t = 1.33$, df = 8, p-value = 0.221; Fig. 2a) or excluded ($t = 0.49$, df = 8, p-value = 0.639; Fig. 2a). However, when liana-excluded canopy production was divided by the total basal area of trees with DBH >5 cm in plots, a significant difference between swamp and non-swamp plots was evident ($t = 6.81$, df = 8, p-value < 0.001; Fig. 2b).

The most parsimonious model of fortnightly, liana-excluded, per-basal-area canopy production contained the term plot condition (swamp or non-swamp), mean daily temperature over the 30-day duration preceding the collection date, and date of collection. This model had an adjusted R^2 value of approximately 75%, and very strong support from the data, receiving > 90% of the model weights and an AICc value that was 5.47 units smaller than the next best model. Swamp conditions were found to have a strong negative effect on plot per-basal-area canopy production, with non-swamp plots producing approximately 2.01 times (95% CI = [1.57, 2.57]) more leaf litter than swamp plots (Fig. 3a). Mean daily temperature in the 30-day duration preceding the collection date was the strongest weather predictor of canopy production, with warmer weathers predicting higher canopy production (coefficient = 0.40, 95% CI = [0.27, 0.53]; Fig. 3).

Species canopy productivity

The top (ΔAICc < 2) SEM models contained only two models which both correspond to biological hypothesis vi—the hypothesis that leaf traits give rise to habitat adaptations which in turn constrain canopy productivity (Fig. 1). In the most parsimonious model (i.e., the one ranked first, with ΔAICc = 0), leaf traits were represented by SLA. SLA had a negative effect on SIV, i.e., tree species with lower SLA were more likely to be confined to swamp habitats (coefficient = −0.29; 95% CI = [−0.41, −0.17]). Swamp adaptation (SIV) in turn had a weak negative effect on canopy productivity (coefficient = −1.67; 95% CI = [−4.37, 1.04]). Thus, SLA had a positive (−0.29 × −1.67 = 0.48) indirect effect on canopy productivity.

The second-, fifth-, eighth- and ninth-ranked models (Table 1) were identical to the first in all respects (they all constitute the biological hypothesis vi), except that different leaf traits took the place of SLA in the model. PC1 (second-ranked model) had a positive effect on SIV (coefficient = 0.07; 95% CI = [0.04, 0.11]) and thus a negative (−0.12) indirect effect on canopy productivity; LT (fifth-ranked model) had a strong positive effect on SIV (coefficient = 1.20; 95% CI = [0.44, 1.95]) and thus a strong negative (−1.99) indirect effect on canopy productivity; C:N ratio (seventh-ranked model) had a positive effect on SIV (coefficient = 0.009; 95% CI = [0.004, 0.013]) and thus a negative (−0.01) indirect effect on canopy productivity. All models considered, biological hypothesis vi had the greatest support from the data, with a summed Akaike weight of 61.3%—far greater than the summed Akaike weights of the other competing biological hypotheses (Fig. 5).

As expected, the effect of basal area on canopy production was also strongly positive, with an estimated effect of 0.93 (95% CI = [0.61, 1.25]) in the top-ranked model, and a similar estimate across all models. Variance of the basal area random slope parameter was also very small, indicating little if any difference in the basal area–canopy production slope between species. On the other hand, models containing the term plot type (as a fixed effect in the canopy production component model) were generally poor fits to the data. The highest ranked model containing the plot type term had a ΔAICc value of 11.51 and a weight of only 0.001 (Table 1).

DISCUSSION

Our study of canopy production in a catchment in Southeast Asia containing tropical freshwater swamp forest showed that canopy production across both swamp and non-swamp conditions is similar to that in other tropical dry-land forests in the region (768 ± 48 g m^{-2} $year^{-1}$ in our study; 770 ± 40 g m^{-2} $year^{-1}$ in Gunung Palung National Park of West Kalimantan, Indonesia (Paoli and Curran 2007) and 530 g m^{-2} $year^{-1}$ in Pasoh Forest Reserve in Peninsular Malaysia (Kira and others 1998). This also appears to be relatively close to canopy production in both seasonally-flooded Amazonian forests (753–1027 g m^{-2} $year^{-1}$; Hasse, 1999) and the low nutrient systems of Southeast Asian peat swamp forest (554 ± 49 g m^{-2} $year^{-1}$ in Rahajoe & Kohyama [2003]; 460 ± 50 g m^{-2} $year^{-1}$ in Saragi-Sasmito and others [2019]; both from Kalimantan).

However, studies of canopy production between forests often disregard the surrounding stand structure and biomass. After accounting for differences in basal areas across swamp and non-swamp plot types in our study, we found that per-basal-area canopy production was significantly lower in swamp than in non-swamp areas. To understand why this was so, we examined the canopy productivity of 25 tree species which were adapted to swamp conditions to different degrees. Given that the total basal areas of swamp plots are generally higher than that of non-swamp plots across this catchment (Chong and others, under review), it was necessary to account for the confounding difference in stand structure. SEMs were fitted to canopy productivity, leaf traits, plot type (swamp versus non-swamp), tree basal areas and habitat adaptations of these tree species. The scaling of canopy production with plot-level species basal area was almost linear—similar to the finding by Turnbull and Madden (1983)—and invariant across species, justifying the simple normalization of canopy production by dividing by basal area. In addition to demonstrating the importance of accounting for size and abundance of the trees (represented by the plot-level basal area) when modelling canopy production, these SEMs show that the environmental condition of plot type (swamp versus non-swamp) is a poor predictor of canopy production. Instead, the intrinsic factors of leaf traits, while ultimately important in determining canopy productivity, were mediated by swamp adaptation. Leaf traits associated with a more conservative resource acquisition strategy, viz., low SLA, high leaf C:N ratio, and thicker leaves (Lavorel and Garnier, 2002; Wright and others, 2004), appeared to facilitate tree adaptation in swamp conditions, and such an adaptation had a weakly negative effect on the canopy productivity of tree species. These findings suggest that tree species possessing suites of traits associated with conservative resource acquisition strategies are better able to adapt to swamp conditions; and that this adaptation also leads to a reduction in canopy—and likely total—net primary productivity (Reich and others, 2014; Shipley and others, 2005; Shipley and others, 2006; Wright and others, 2004). We also found that canopy production in our study site was highest immediately after warmer temperatures—a finding that is consistent with many other studies from the tropics (E.g., Mexican tropical deciduous forests: Martinez-Yrizar and Sarukhan, 1990; Indian mangroves: Rani and others, 2016; Bornean evergreen rainforests: Nakagawa and others 2019; Kitayama and others, 2021)—likely because leaf metabolic activities and senescence were sped up under such weather conditions. These findings may have significant implications for large-scale modelling (Smith and others 2014) and prediction of carbon-cycling processes in hydrologically heterogeneous environments such as mangroves, tropical swamp forests, and riparian habitats.

Habitat adaptation mediates the influence of leaf traits on canopy productivity

Leaf traits are often used to predict forest productivity (Reich 2012; Funk and others 2017). However, our study shows that leaf traits may not directly influence canopy productivity, but rather facilitate or hinder a species' inherent ability to survive in swamp conditions, which in turn affects its canopy productivity. This does not mean that traits cannot affect ecosystem processes directly, or that there exist no other factors mediating the relationship between traits and habitat adaptation, or between habitat adaptation and productivity. Indeed, our SEMs showed that commonly measured leaf traits were eventually associated with canopy productivity in directions that were both expected by a priori hypotheses and mostly consistent with other empirical studies which employed simple correlative approaches: SLA (Luo and others, 2005; Finegan and others, 2015) had an indirect positive effect on canopy production, while leaf thickness and C:N ratio (Luo and others, 2005) had an indirect negative effect; LDMC (Smart and others, 2017) had an indirect positive effect, but in our study this effect was very weak and inconclusive.

Functional traits offer generalizability to the prediction of ecosystem processes such as productivity (Lavorel and Garnier, 2004), but the underlying causal links between traits and ecosystem processes are often indirect and sometimes even tenuous (Funk and others 2017; Zirbel and others 2017). Our findings suggest that the inclusion of mediating variables, such as habitat adaptation, can both increase the predictive ability of models as well as provide a better understanding of the mechanisms underlying ecosystem processes such as canopy production. We propose that future studies examine more possible intermediate causal nodes mediating the trait–ecosystem process relationship since the somewhat weak effect of habitat adaptation on canopy production in our study suggests that additional sources of variation may remain unaccounted for in our models, and that continuous, quantitative measures of habitat adaptation/association such as the one calculated in this study be more often used in future studies.

Although the biological hypotheses best supported by the data (biological hypotheses vi and i; Fig. 4) both strongly suggested that habitat adaptation mediates the influence of leaf traits on canopy productivity, there was still some support for the alternative hypothesis that habitat adaptation constrained leaf traits, which then had a direct effect on canopy productivity—as predicted by biological hypotheses ii and vii. That is, although most leaf traits were the underlying causes for species' abilities/propensities to be associated with swamp habitats, there was some evidence that this relationship also worked in the opposite direction, particularly for the leaf trait of LDMC (the sixth-ranked model; Table 1). It is likely that some degree of reciprocity exists in the relationship between traits and habitat adaptation (e.g., through environmental filtering; Kraft and others, 2015; Bu and others, 2019), although reciprocal effects are often difficult to model using most SEMs. Given these limitations, our study is only able to demonstrate that the primary direction of causality is in the direction of traits towards habitat adaptation.

Another inference that can be drawn from our analyses is that, at small spatial scales (here, within a single catchment), intrinsic factors (traits, and their effects through habitat adaptation) are better predictors of canopy production than extrinsic factors (such as hydrological condition). This conclusion was not affected by whether the data were analyzed using SEMs (as shown here in the Results section) or linear models (see Appendix B of the online supporting information). While environmental factors such as annual precipitation and temperature are good predictors of NPP when it is compared across biomes, our study shows that, within the confines of a single catchment, the rate at which individual trees produce and shed their leaves is dependent more on their specific predispositions rather than the environmental conditions in which they are found growing.

Implications for resource acquisition strategies

Our findings suggest that the adaptations that allow plants to tolerate stressful waterlogged conditions also reduce their ability to employ fast resource acquisition strategies or competitive and/or ruderal ecological strategies (Moor and others 2017). This is in direct contrast with that of Pan and others (2020), who found using global plant trait datasets that wetland plant species possess traits associated with more resource-acquisitive strategies than dryland plant species. However, Pan and others (2020) did not control for confounding differences in abiotic conditions and vegetation physiognomy between habitats from which species in their study originated, and the study seemed to contain more data from temperate herbaceous wetlands than tropical forested ones. At a global scale, such herbaceous species would occur on the more acquisitive end of the leaf economics spectrum when compared against a random selection of plant species across all known terrestrial ecosystems (Díaz and others 2016). In contrast, we specifically compared tree species occurring in swamp and non-swamp habitats within a single tropical catchment, allowing a surgical isolation of the variable of interest: adaptation to waterlogged swamp forest conditions. Our results are also well supported by observations made by other authors. Lugo and others (1988; 1989; 1990) note that sclerophylly (a conservative resource acquisition strategy, and a suite of traits of which leaf thickness is one of the main) is commonly observed in wetland plant species, particularly those found in nitrogen- and phosphorus-poor soils; such species are especially dominant in wetland communities in South Africa (Sieben and others 2017) and Australia (Finlayson and Oertzen, 1993). Sclerophylly and other conservative resource acquisition traits also appear to characterize Malaysian peat swamp forest tree species (Yule and Gomez, 2008; Ong and others, 2015). More studies should be conducted to ascertain if waterlogging stress universally favours ecologically-conservative resource acquisition strategies independently of the availability of other resources such as light and nutrients.

Implications for nutrient cycling and carbon sequestration

Our recent study from the same forest that was used in this study also reported that leaf litter decomposition rate in waterlogged areas of the catchment was significantly lower than that in well-drained areas (Lam and others, 2021). This means that, in swamp areas of the catchment which are dominated by swamp-adapted species, canopy production rates would tend to be slightly lower, but these leaves would generally decompose much slower on/in the forest floor/pools. Thus, the stressful conditions of waterlogged, anoxic swamp habitats significantly reduce the rate at which nutrients are cycled (both production and decomposition processes) by communities found in such environments. Furthermore, organic matter accumulation and, consequently, net carbon sequestration in swamp forests would have to depend on how much the reduction in production is outweighed by reduced rates of decomposition. Our study also indirectly suggests that transition zones or swamp edges may be where organic matter accumulates the greatest, as tree species which are not well adapted to swamp conditions, and thus possess higher intrinsic canopy productivities, establish on the lower stress non-swamp edges and deposit large amounts of leaf litter into swamp areas, although this remains an untested hypothesis. Regardless, the findings of this study have important consequences for ecosystem functioning and community dynamics within the highly heterogeneous environments of swamp forests. Understanding the effect of different extents and scales of spatial heterogeneity on ecosystem processes and/or community dynamics in tropical swamp forests should thus be a focus of future research.

DATA AVAILABILITY STATEMENT

We intend to archive our data on Figshare upon the acceptance of the manuscript for publication.

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TABLES

Table 1. Top ten models, and the top model containing the term *Plot type*, of the underlying relationships between habitat adaptation (swamp indicator value [*SIV*]), canopy production, basal area (*BA*) and leaf traits (leaf thickness [*LT*], leaf dry matter content [*LDMC*], leaf C:N ratio [*CNratio*], standard leaf area [*SLA*], and the first/second principal component of these four traits combined [*PC1/PC2*]). The column *formulae* describes component linear models in each SEM, with causal variables to the right and effect variables to the left of tilde signs (~). *Biol. Hypo.* = Biological hypotheses represented graphically in Fig. 1a; *W* = model weight.

Model rank	Formulae	Biol. Hypo.	R^2	Fisher's C	AICc	ΔAICc	W
1	Canopy production ~ BA + SIV SIV ~ SLA	vi	35.55 24.10	0.383	27.09	0.00	0.313
2	Canopy production ~ BA + SIV SIV ~ PC1	vi	35.55 21.82	1.469	28.41	1.32	0.162
3	Canopy production ~ BA + SIV + SLA SIV ~ SLA	i	34.86 24.10	0.173	29.78	2.69	0.082
4	Canopy production ~ BA + LDMC LDMC ~ SIV	vii	33.21 3.77	2.849	30.08	2.98	0.071
5	Canopy production ~ BA + SIV SIV ~ LT	vi	35.55 12.49	3.027	30.30	3.20	0.063
6	Canopy production ~ BA + SIV + PC1 SIV ~ PC1	i	36.36 21.82	0.627	30.34	3.25	0.062
7	Canopy production ~ BA + SIV + LDMC LDMC ~ SIV	ii	35.37 3.77	0.743	30.49	3.39	0.057
8	Canopy production ~ BA + SIV SIV ~ CNratio	vi	35.55 18.25	3.651	31.05	3.96	0.043
9	Canopy production ~ BA + SIV SIV ~ PC2	vi	35.55 6.06	4.758	32.39	5.30	0.022
10	Canopy production ~ BA + SIV + LT SIV ~ LT	i	35.98 12.49	2.453	32.59	5.50	0.020
…							
25	Canopy production ~ BA + CNratio + Plot type CNratio ~ SIV	iv	33.40 18.25	–	38.61	11.51	0.001

FIGURE LEGENDS

Fig. 1 (a) Causal pathways representing the underlying relationships linking leaf traits, canopy production and habitat adaptation. The nine possible groups of pathways constitute nine different biological hypotheses which can be expressed as SEMs, as done in this study. Models are grouped by their topologies for ease of reference. ∅ denotes a null model, i.e., the variable does not interact with the other variables in a causal relationship.

Fig. 2 (a) Comparison of total (blue bars) and liana-excluded (green bars) canopy production between swamp and non-swamp plots. (b) Comparison of liana-excluded, per-basal-area canopy production between swamp and non-swamp plots. In both panels, data are represented by means ± standard errors (error bars). $n = 5$.

Fig. 3 (a) Basal area-normalized fortnightly vegetative litter production over the study duration in each plot (points) and as predicted by the GAMM model (solid lines; shaded regions represent confidence intervals of prediction). Blue symbols represent data and predictions from swamp plots, while green/brown symbols represent those from non-swamp plots. (b) The number of rain days in a month during the same period.

Fig. 4 (a) First and second principal component axes, representing a combined 85.8% of total variance, of the functional traits of the 25 tree species examined in this study. Green arrows and text represent the loadings of the four functional traits on the two principal component axes, and black text represent the species first and second principal component scores. Species which are found close to each other in the figure are more similar in the four measured traits (e.g., CSQ and GWA are similar all four traits), and species which are found in the same direction of a trait vector have larger values of that same trait (e.g., HBR has high SLA). (b) Correlation between SLA and habitat adaptation (SIV) of the same 25 species. The top SEM model predicted that SLA determined the habitat adaptation of tree species in the study. The list of unabbreviated species names is found in Table S1.

Fig. 5 The four biological hypotheses that were best supported by the data and their respective summed Akaike model weights.

FIGURES

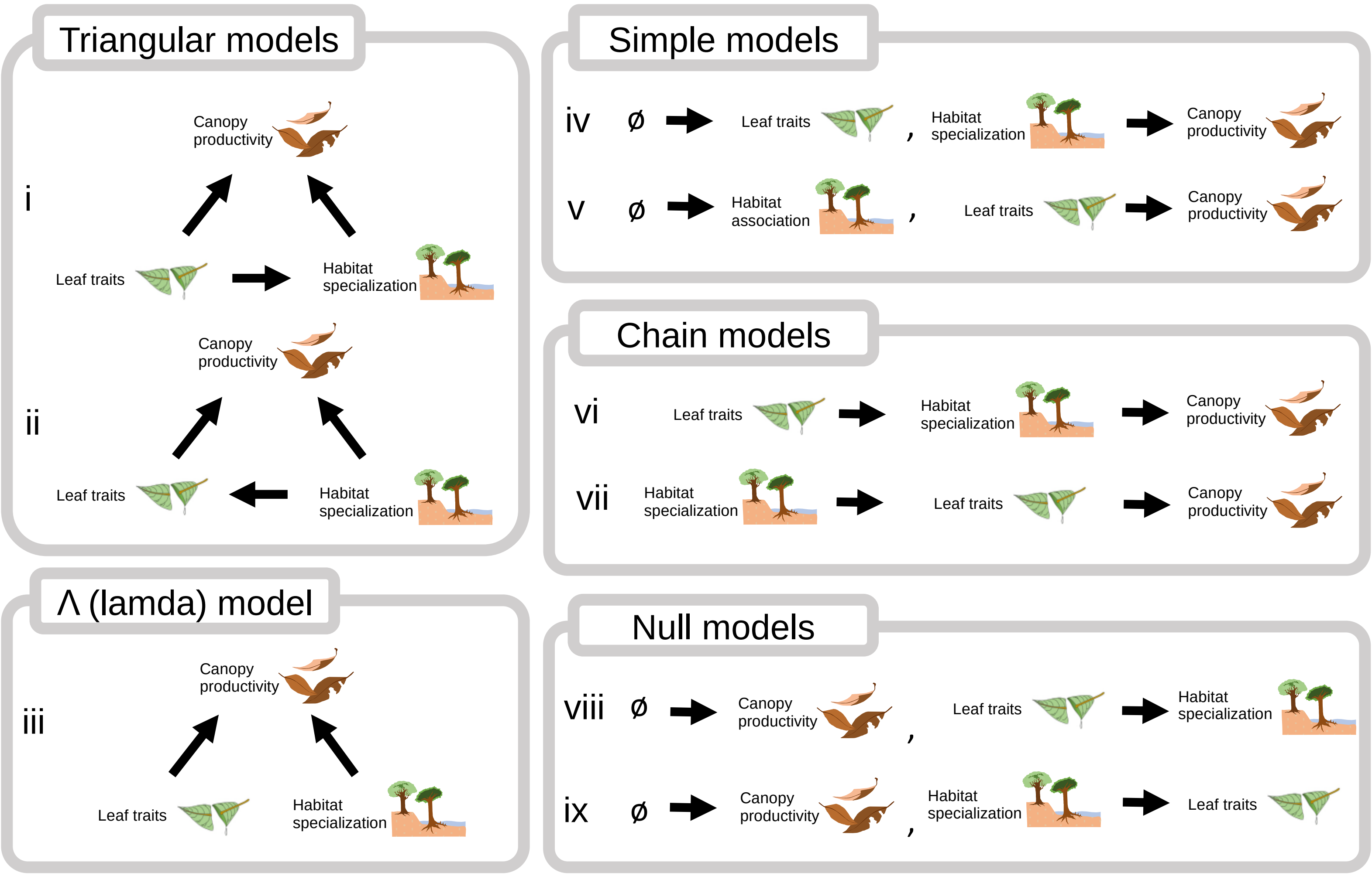

Fig. 1

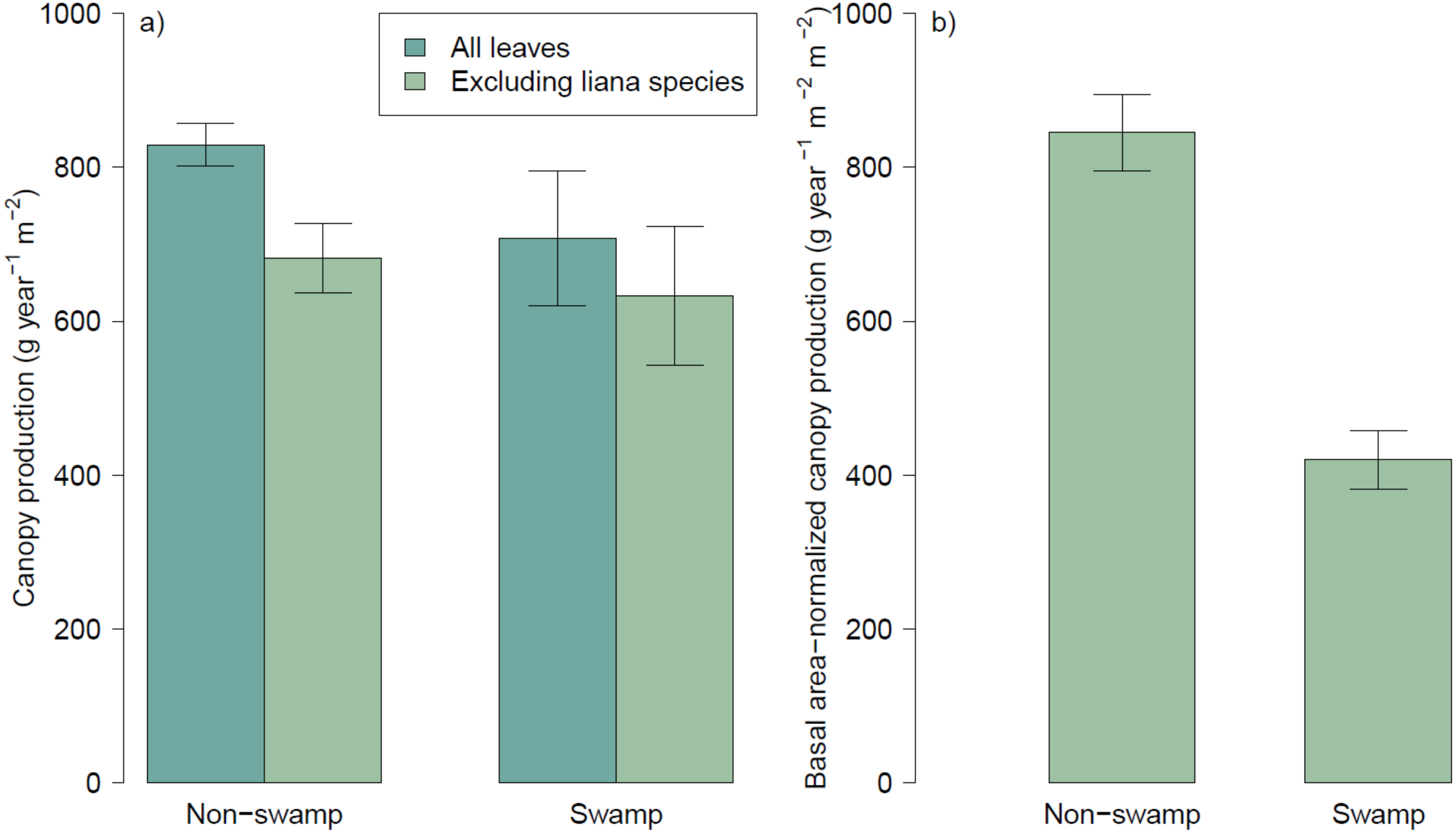
a)
All leaves
Excluding liana species
Canopy production (g year^{-1} m^{-2})
1000
800
600
400
200
0
Non−swamp
Swamp
b)
Basal area−normalized canopy production (g year^{-1} m^{-2} m^{-2})
1000
800
600
400
200
0
Non−swamp
Swamp

Fig. 2

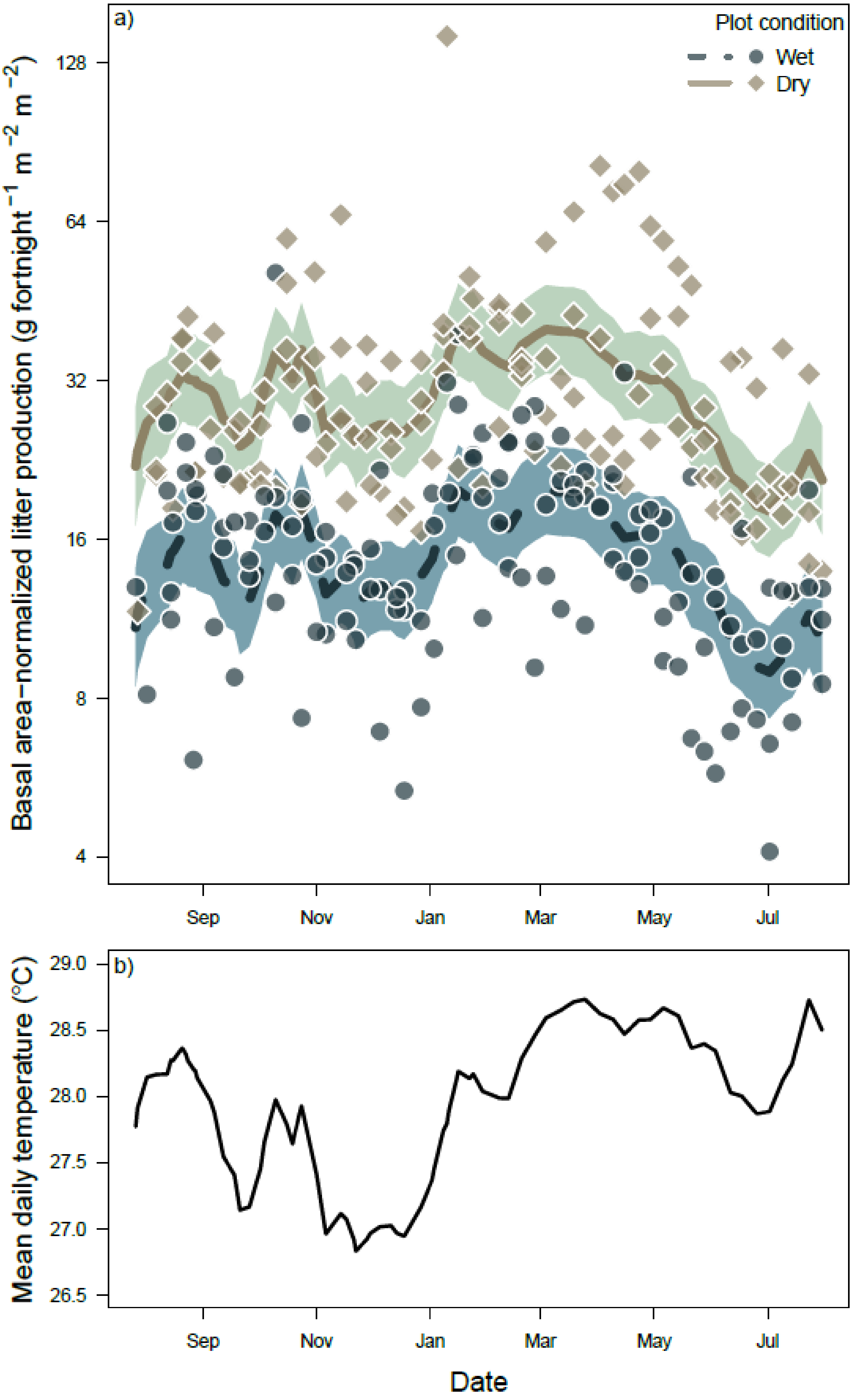
a)
Plot condition
Wet
Dry
Basal area−normalized litter production (g fortnight $^{-1}$ m $^{-2}$ m $^{-2}$)
128
64
32
16
8
4
Sep
Nov
Jan
Mar
May
Jul
b)
Mean daily temperature (°C)
29.0
28.5
28.0
27.5
27.0
26.5
Sep
Nov
Jan
Mar
May
Jul
Date

Fig. 3

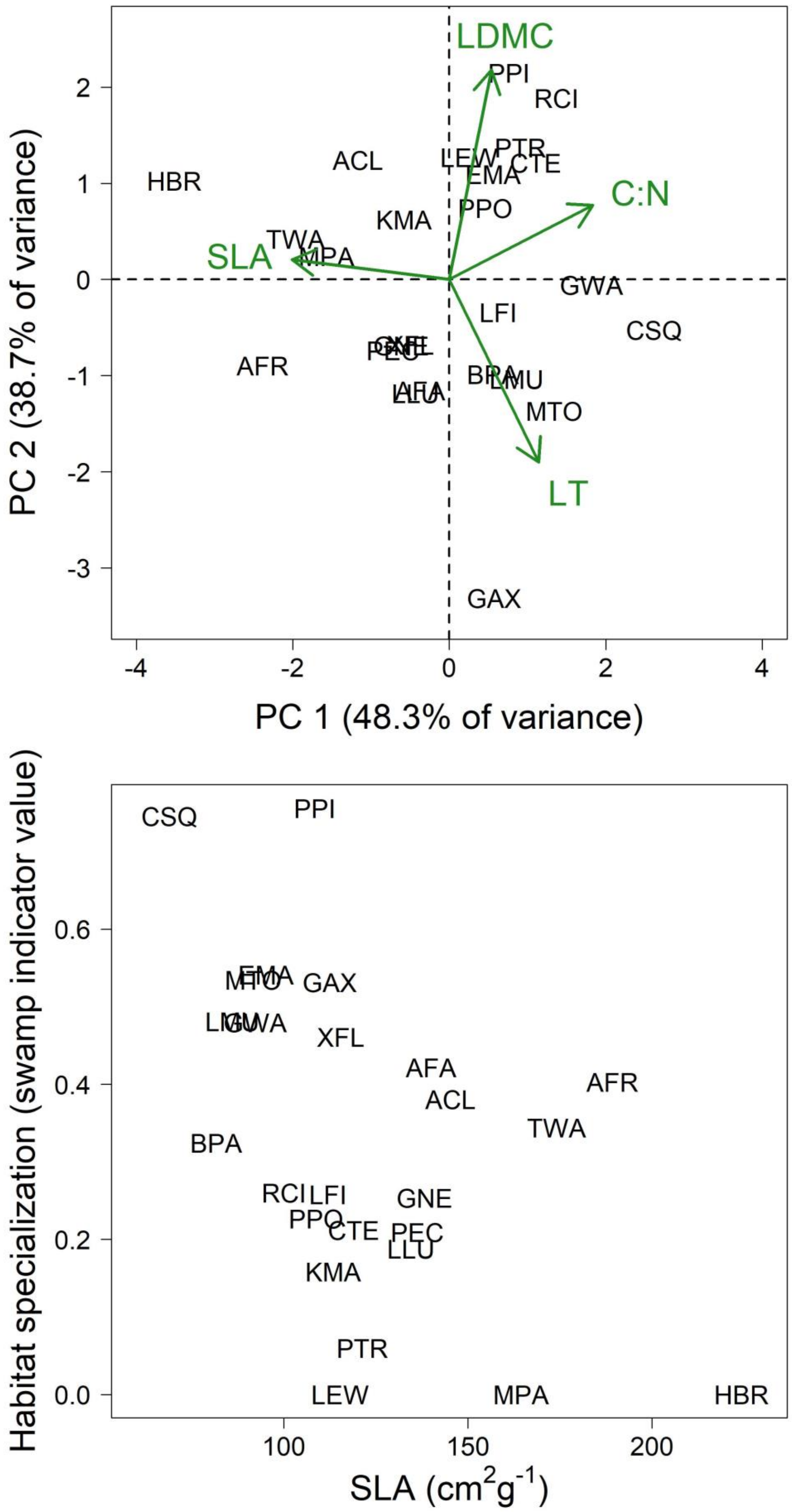
LDMC
C:N
SLA
LT
PPI
RCI
ACL
LEW
PTR
CTE
EMA
HBR
PPO
KMA
TWA
MPA
GWA
LFI
CSQ
GNE
XFL
PEC
AFR
BPA
LMU
AFA
LLU
MTO
GAX
PC 2 (38.7% of variance)
PC 1 (48.3% of variance)
2
1
0
-1
-2
-3
-4
-2
0
2
4
CSQ
PPI
EMA
MTO
GAX
LMU
GWA
XFL
AFA
ACL
AFR
TWA
BPA
RCI
LFI
GNE
PPO
CTE
PEC
LLU
KMA
PTR
LEW
MPA
HBR
Habitat specialization (swamp indicator value)
0.6
0.4
0.2
0.0
100
150
200
SLA (cm²g⁻¹)

Fig. 4

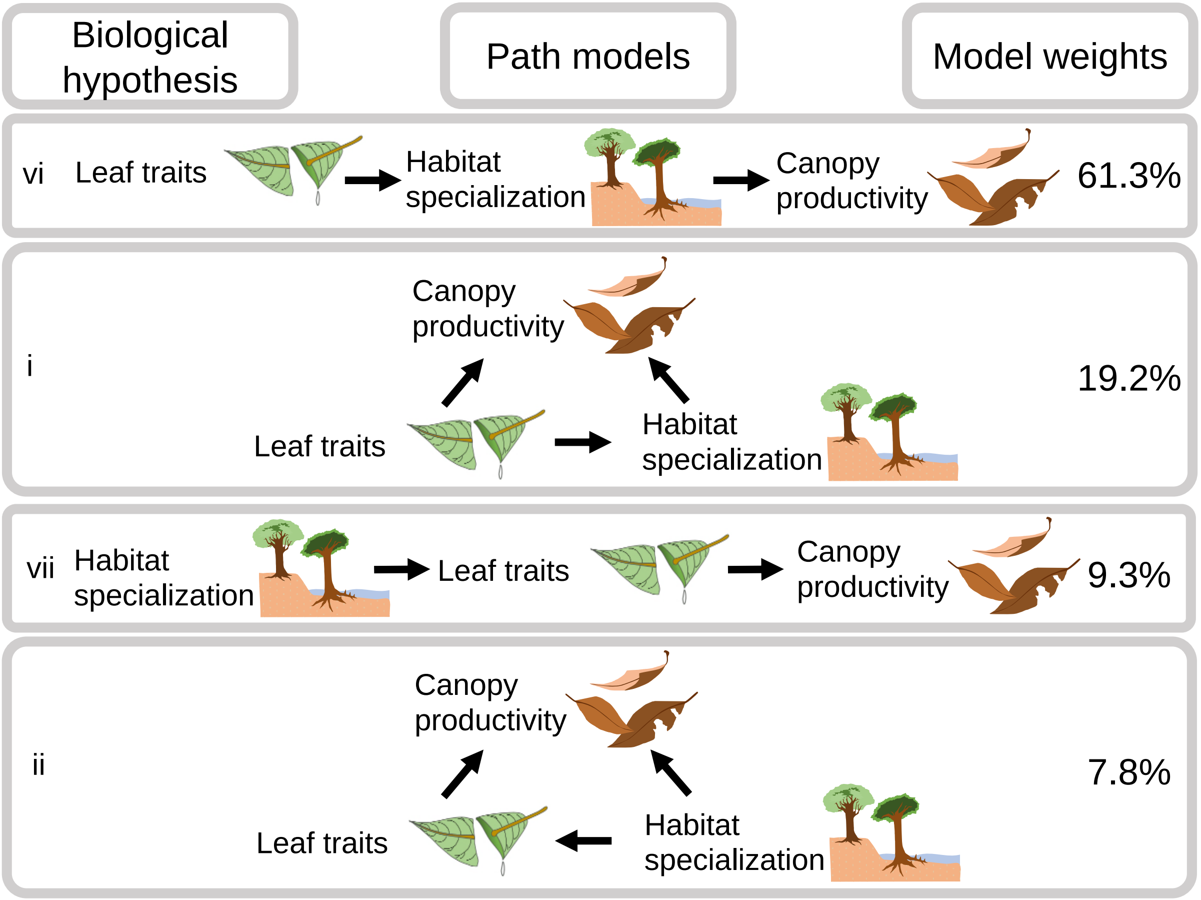
Biological hypothesis
Path models
Model weights
vi
Leaf traits
Habitat specialization
Canopy productivity
61.3%
i
Canopy productivity
Leaf traits
Habitat specialization
19.2%
vii
Habitat specialization
Leaf traits
Canopy productivity
9.3%
ii
Canopy productivity
Leaf traits
Habitat specialization
7.8%

Fig. 5