Elsevier Editorial System(tm) for Ecological Modelling

Manuscript Draft

Manuscript Number: ECOMOD-20-404

Title: How does leaf functional diversity affect the light environment in forest canopies? An in-silico biodiversity experiment

Article Type: Research Paper

Keywords: biodiversity effect; functional diversity; plant traits; radiative transfer modelling; light; energy budget

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Abstract: The interaction of shortwave radiation with vegetation drives basic processes of the biosphere, such as primary productivity, species interactions through light competition, and energy fluxes between the atmosphere, vegetation, and soil. Here, we aim to understand the effects of leaf functional trait diversity on canopy light absorption. We focus on the diversity of two functional traits: leaf angle distribution (LAD) and leaf optical properties (LOP). We used a 3D radiative transfer model to perform an in-silico biodiversity experiment to study the effects of leaf functional diversity on a light proxy for productivity (the fraction of absorbed photosynthetically active radiation (FAPAR)) and net radiation (shortwave albedo). We found that diverse canopies had lower albedo and higher FAPAR than the average of the corresponding monoculture values. In mixtures, FAPAR was unequally re-distributed between trees with distinct traits: some plant functional types absorbed more light and some plant functional types absorbed less than in monocultures. The net biodiversity effect on absorption was greater when combining plant functional types with more distinct leaf traits. Our results support the mechanistic understanding of overyielding effects in functionally diverse canopies and may partially explain some of the growth-promoting mechanisms in biodiversity-ecosystem functioning experiments. They can further help to account for biodiversity effects in climate models.

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Research Data Related to this Submission

Title: DART simulations and data for figures
Repository: GitHub
https://github.com/PlekhanovaElena/DART_article

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Zurich, 11 May 2020

Manuscript submission

Dear Editor,

We wish to submit an original research article entitled “How does leaf functional diversity affect the light environment in forest canopies? An in-silico biodiversity experiment” for consideration by Ecological Modelling. In this paper, we show that functionally richer and more diverse canopies absorb more shortwave radiation than less diverse canopies and explore the mechanisms behind this effect. Our results support the mechanistic understanding of overyielding effects in functionally diverse canopies and related findings from biodiversity-ecosystem functioning experiments. They further support work towards representing biodiversity effects in earth system models.

We developed a novel in-silico biodiversity experiment using a 3D radiative transfer model, which allowed for a detailed representation of plant-light interactions and testing of plant functional type richness and trait diversity effects. We simulated 3D objects of trees, diverse across two functional traits which are key components driving the plant-light interaction: leaf optical properties and leaf angle distribution. We then calculated and evaluated the fraction of absorbed photosynthetically active radiation (FAPAR) as a proxy for light available for photosynthesis and shortwave albedo which contributes to the energy budget. We found a positive biodiversity effect on the shortwave radiation and light absorption. In mixtures, light was unequally re-distributed between functional types and the absorption was greater when combining plants with more distinct traits.

We believe that this manuscript is in the scope of the Journal Ecological Modelling because it 1) describes a novel in-silico combination of process-based modelling of radiation with the well-established design of biodiversity experiments; and 2) contributes to the understanding of fundamental ecosystem functions related to light interaction.

We confirm that this work is original and has not been published elsewhere, nor is it under consideration for publication elsewhere. We have no conflicts of interest to disclose.

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Thank you for your consideration of our manuscript.

On behalf of the co-authors,
Elena Plekhanova

Highlights

- We combined classical biodiversity experiment design with radiative transfer modelling.
- Leaf functional diversity enhances light absorption in both PAR and shortwave domains.
- Mixtures of plants with more distinct traits absorb more shortwave radiation.

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How does leaf functional diversity affect the light environment in forest canopies? An in-silico biodiversity experiment

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Abstract

The interaction of shortwave radiation with vegetation drives basic processes of the biosphere, such as primary productivity, species interactions through light competition, and energy fluxes between the atmosphere, vegetation, and soil. Here, we aim to understand the effects of leaf functional trait diversity on canopy light absorption. We focus on the diversity of two functional traits: leaf angle distribution (LAD) and leaf optical properties (LOP). We used a 3D radiative transfer model to perform an in-silico biodiversity experiment to study the effects of leaf functional diversity on a light proxy for productivity (the fraction of absorbed photosynthetically active radiation (FAPAR)) and net radiation (shortwave albedo). We found that diverse canopies had lower albedo and higher FAPAR than the average of the corresponding monoculture values. In mixtures, FAPAR was unequally re-distributed between trees with distinct traits: some plant functional types absorbed more light and some plant functional types absorbed less than in monocultures. The net biodiversity effect on absorption was greater when combining plant functional types with more distinct leaf traits. Our results support the mechanistic understanding of overyielding effects in functionally diverse canopies and may partially explain some of the growth-promoting mechanisms in biodiversity-ecosystem functioning experiments. They can further help to account for biodiversity effects in climate models.

Key words:
Biodiversity effect; Functional diversity; Plant traits; Radiative transfer modelling; Light; Energy budget

1. Introduction

Plant functional traits underlie the interaction of plants with their biotic and abiotic environment, and are used to assess the structure, function, and diversity of ecosystems (Bodegom et al., 2014; Cadotte et al., 2011; Garnier et al., 2016; Mokany et al., 2008). In particular, plant biochemical and structural traits such as leaf optical properties and leaf orientation influence how much light is absorbed and reflected by plant canopies and how it is distributed among individual plants. In response to climate change, plant trait space shifts through species loss, migration, and adaptation (Bjorkman et al., 2018; IPBES, 2019; Madani et al., 2018; May et al., 2017), altering plant trait diversity, and hence functional diversity (Wieczynski et al., 2019). Functional diversity may have multiple origins: it can arise from inter- and intraspecific variability as well as variation in growing processes (Fahey et al., 2019; Thomas et al., 2019). Investigating effects of functional diversity offers the possibility to increase the understanding of the mechanisms underlying biodiversity-productivity relationships and to estimate alterations in the shortwave energy budget related to functional trait diversity.

A positive biodiversity-productivity relationship is well-established, with mixed communities producing more yield than monocultures ("overyielding" effect (de Wit, 1960)). This relationship arises from interspecific niche complementarity, but the particular mechanisms remain unclear. The mechanisms proposed include 1) the partitioning of limiting resources among species, which could lead to a greater community-level resource use; 2) selection effects that lead to the dominance of particularly well-performing species; 3) facilitation of the growth of some species by environmental modifications driven by others; and 4) complementarity of biotic interactions (Forrester and Bauhus, 2016; Schöb et al., 2018). Previous studies investigating effects of biodiversity on plant-light interactions were mainly based on field experiments and observational studies (Cardinale et al., 2006), and have shown that plant species mixtures (hereafter referred to as "mixtures") typically absorb more light than monocultures in forest and grassland crop ecosystems (Bauhus et al., 2004; Binkley et al., 1992; Forrester et al., 2012; Gebru, 2015). However, with empirical studies, separating the interlinked mechanisms 1)-4) (see above) and quantifying light use complementarity remains extremely challenging. Therefore, experiments were complemented by growth and statistical modelling approaches. They showed that tree crown complementarity (Williams et al., 2017), crown architecture (Forrester et al., 2018), shape, openness (Sapijanskas et al., 2014), and phenology (le Maire et al., 2013; Rissanen et al., 2019; Zhu et al., 2015) correlate with overyielding. Growth and statistical modelling

approaches are useful for characterising plant growth and establishing the correlation with light absorption, but do not allow for the depiction of small-scale plant-light interactions and to study causal relationships. A process-based physical model with accurate vegetation structure representation that also tracks radiative fluxes could allow for directly linking plant functional diversity to the light environment, but to our knowledge, it has not been used so far.

Plant-light interactions are not only important for processes related to the carbon cycle but also determine the net shortwave radiation, a key component of the Earth's surface energy budget. Vegetation structural complexity has been shown to affect albedo (Hovi et al., 2016; Thompson et al., 2004; Tian et al., 2014) – the fraction of incoming solar radiation reflected by the vegetation. In these studies, variation in structural complexity was represented by increasing plant density or biomass, but they did not explicitly include a more detailed parametrization or analysis of vegetation structural variation, such as functional diversity, which might prove crucial to the improvement of existing land-surface models (Loew et al., 2014; Viskari et al., 2019).

Functional diversity is a promising concept to improve mechanistic understanding and predict biodiversity-productivity relationships and plant-light interactions (Ebeling et al., 2014; Zhu et al., 2015). Three traits determine canopy-light interactions: leaf optical properties (LOP), leaf angle distribution (LAD), and leaf area index (LAI) (Asner, 1998; Xiao et al., 2014). While LAI is connected to variation in biomass, the other two describe canopy structure, with LOP representing biochemical leaf composition and structure (Jacquemoud et al., 2019), and LAD representing architectural plant characteristics.

Here, we aim to demonstrate how functional diversity affects vegetation-light interactions in forest communities. We focus on LAD and LOP diversity effects on 1) the albedo of canopies as an indicator of shortwave energy fluxes, and 2) the canopy-integrated measure and vertical distribution of the fraction of absorbed photosynthetically active radiation (FAPAR) as an indicator of light available for photosynthesis.

To investigate these relationships, we combined a classical experimental design following biodiversity- ecosystem functioning studies with a 3D radiative transfer model (DART: https://dart.omp.eu; Gastellu-Etchegorry et al., 1996) to conduct an in-silico biodiversity experiment.

2. Methods

2.1 Functional diversity terminology

In this study, we chose two diversity metrics that capture the ecological similarity of plant characteristics in relation to the function of plant-light interactions: plant functional type richness and trait diversity.

We refer to plant functional type (PFT) as a group of individuals with similar (in our case, identical) traits (Tsakalos et al., 2019). We define different PFTs along LOP or/and LAD gradients. We use the term PFT richness - in analogy to species richness - to represent the number of PFTs in the canopy. This metric allowed us to utilize the classical biodiversity experimental design that is most often based on species richness gradients, ranging from monocultures to mixed communities (see 2.2 Modelling design, experiments 1-2 for the details).

We refer to trait diversity as the difference between the LOP/LAD values of two PFTs. LOP diversity is represented by the distance between leaf reflectance or leaf absorption values, LAD diversity as the distance between foliage gap fractions of two PFTs. This metric allowed us to study the mechanisms behind the observed PFT richness-absorption relationships (see 2.2 Modelling design, experiment 3 for the details).

2.2 Modelling design

We performed three in-silico experiments. To investigate the effect of PFT richness on the light environment, we first simulated 6 PFTs for LOP or LAD and studied their effects on albedo and FAPAR, including vertical profiles of FAPAR. To study the effect of PFT richness along both LOP and LAD axes simultaneously, we performed the second experiment, where we used a 4 LAD $\times$ 4 LOP factorial design and assessed albedo. In the third experiment, we investigated the effect of the LOP/LAD diversities on the change in absorbed energy by simulating all possible mixtures of 10 PFTs along LAD or LOP gradients.

Experiment 1. We designed an in-silico biodiversity experiment based on 6 PFTs along LAD/LOP gradients arranged on a rectangular regular spaced grid (Fig. 1).

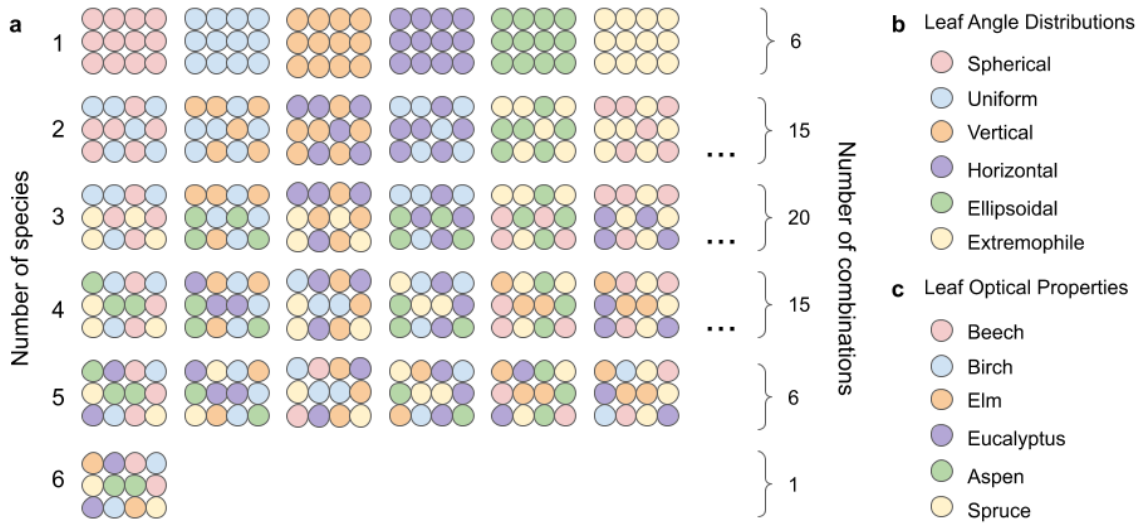


Fig. 1. Modelling design of PFT richness with 6 PFTs. a) Design of a classical biodiversity experiment, where each color represents a species. In our study, species were replaced by PFTs along b) LAD or c) LOP axes (for details on parametrization see Fig. 2 and Supplementary Table 2).

To account for the effects of specific spatial configurations, we used a canopy composed of 60 trees and averaged our results across ten different spatial randomizations for the mixture combinations.

Experiment 2. To simulate communities composed of trees that varied in two traits simultaneously, we used a 4 LAD × 4 LOP factorial design with 16 trait compositions (see Supplementary Fig. 1 for the modelling design).

Experiment 3. To investigate the relationship between differences in traits and the net biodiversity effect, we simulated all possible mixtures of two PFTs (bicultures). For the LOP trait, we varied PFT's leaf reflectance and transmittance from 0 to 1 with interval 0.1 under the restriction of their sum being less or equal to 1. We then calculated the mean values of the net biodiversity effect among all bicultures with a certain difference in transmittance and absorption values. For the LAD trait, we choose gap fraction (the probability of a vertical ray of light passing through the canopy without encountering any plant elements) as a quantitative measure of LAD with fixed LAI. We varied the foliage gap fraction from 0.1 to 1 with the interval 0.1 by choosing the corresponding leaf angle distributions. We then calculated the difference in absorption between mixtures and monocultures for each difference in gap fraction between monocultures.

2.3. Model parametrization

We utilized the discrete anisotropic radiative transfer model (DART, version 5.7.4, Gastellu-Etchegorry et al., 1996) to perform the in-silico biodiversity experiments. The DART 3D radiative transfer model has been shown to accurately represent light scattering and redistribution in the canopy (Gastellu-Etchegorry et al., 2012), and specifically forest canopy radiation (Malenovský et al., 2008; Schneider et al., 2014). The DART model implements a landscape as a 3D matrix of cells with turbid medium and/or triangles and allows for the tracking of radiation fluxes within the 3D canopy, including multiple reflections and mutual shading (Schneider et al., 2014), and calculates radiative budget components.

2.3.1. Plant and canopy representation

Vegetation was represented with 3D models of trees (Fig. 1a), each consisting of a cylindrical trunk and a crown represented by a cloud of triangles (leaves), uniformly distributed within an ellipsoid shape. This representation of the crown allowed us to account for multiple reflections within canopies. We chose an ellipsoid crown shape as it has been shown to closely approximate natural characteristics (Rautiainen et al., 2008). Parameters of individual trees, such as height, trunk diameter etc. (but not LAD and LOP), were fixed at the values representing average *Betula pendula* characteristics from Hovi et al., (2016) (see Supplementary Table 1 for details). To test different diversity scenarios, we simulated a 3D forest scene (30 m $\times$ 50 m, with 1 m voxel size) with a group of 60 regularly distributed trees (Fig. 1b) with different LAD and LOP values (Fig. 1c and d; Supplementary Table 2 for details of parameterization).

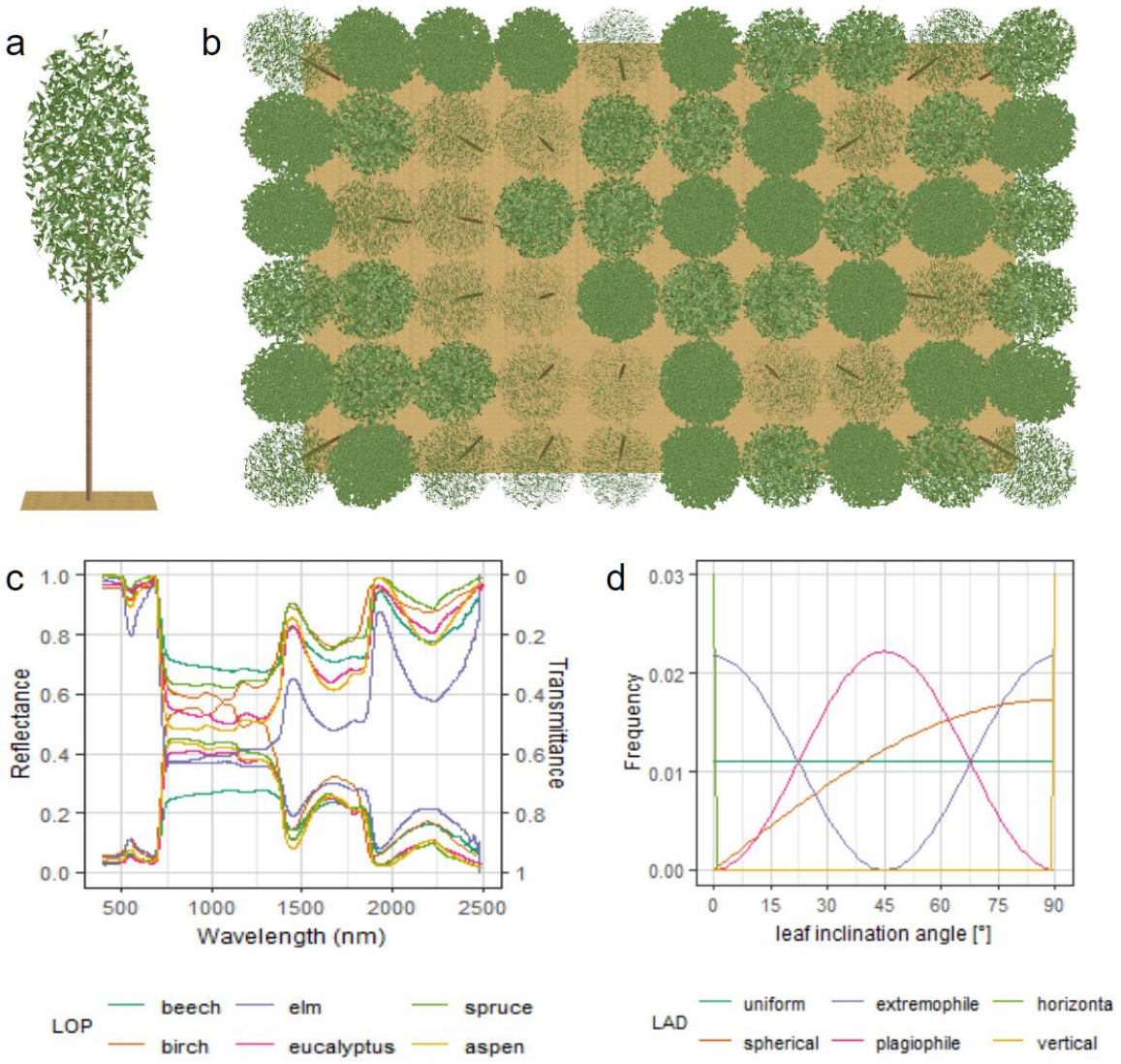


Fig. 2. Plant parameterization. a) 3D representation of a tree in the DART model; b) aerial view of a canopy of 60 trees - 3 PFTs with the following LAD values: uniform, horizontal, and vertical; c) LOP values; d) LAD values. The frequency for the extreme horizontal (vertical) distributions is equal to 1 for 0° (90°).

2.3.2. Background (understory) representation

The total amount of radiation absorbed by a tree canopy is the sum of trunk and foliage absorption before the radiation reaches the background (understory vegetation), and the radiation captured after reflection from the forest floor. To investigate these contributions, we performed our simulations with different optical properties of backgrounds. As a natural background, we took litter optical properties as a representative of forest floor optical properties. We explored the canopy contribution by simulating a black (total absorption) background and understory contribution by subtracting the canopy contribution from the observed FAPAR when assuming a natural, vegetated understory (terminology adopted from

Hovi et al., 2016). Additionally, we performed simulations on a white background in order to gain a greater level of understanding about the processes involved.

2.3.3. Illumination and radiation

The simulations were carried out assuming direct illumination only ("black-sky") and completely isotropic, diffuse illumination ("white-sky"). Black-sky albedo is not dependent on assumptions of atmospheric scattering properties and is commonly used as an input in climate modelling (Herold et al., 2009). Black-sky albedo and FAPAR were simulated for two sun zenith angles: 0° and 30°. The white-sky case was included to represent a diffuse illumination scenario, approximating cloudy days.

Table 1. Parameters of the DART simulation that varied in each run.

Variable	**Type**	**Parameters**
Background, Lambertian optical properties	White	Reflectance = 0
	Black	Reflectance = 1
	Natural	Litter optical properties
Illumination	Direct sun only	Sun zenith angle: 0°, 30°
	Overcast	Diffuse irradiance
Spectral band	Visible	Bands: 400, 500, 600, 700 nm
	Shortwave infrared	Bands: 800-2500 nm, each 100 nm

2.4. Albedo and FAPAR

To approximate canopy reflected shortwave radiation, we calculated the canopy directional-hemispherical and hemispherical-hemispherical albedo (Schaepman-Strub et al., 2006) in the visible and shortwave infrared ranges (λ = 400 nm to 2500 nm, with equal spectral intervals Δλ = 100 nm) (1) at the top of the canopy (1).

$$albedo = \frac{\sum_{\lambda=400\,nm}^{2500\,nm} Exitance\ (\lambda)}{\sum_{\lambda=400\,nm}^{2500\,nm} Irradiance\ (x,\lambda)}, \qquad (1)$$

where $Exitance\ (\lambda)$ is the total hemispherical exitance (W m^{-2} μm^{-1}) for the wavelength λ, and $Irradiance\ (x,\lambda)$ is the spectral irradiance for the wavelength λ, with *x* indicating the directional distribution of the incident radiation (i.e., *x* = *d* for incident mono-directional radiation and *x* = *h* for hemispheric incident radiation).

To quantify the trait diversity effect, we calculated albedo change as the difference between the albedo of the mixture and the average of the albedo values of the corresponding monocultures

$$albedo\ change\ = albedo_{mix} - \frac{1}{\#species}\sum_{\{species\ in\ mixture\}} albedo_{mon},$$

As an approximation of the photosynthetic activity of the plants, we utilized the fraction of absorbed photosynthetically active radiation (FAPAR, where PAR is 400-700 nm). In our study, we were interested in the FAPAR profile of the tree canopy, so we calculated $FAPAR\ (h)$ as the average FAPAR at height h (see (2)).

$$FAPAR\ (h) = \frac{1}{\#\{cells\ (h)\}}\sum_{\{cells\ (h)\}} \frac{\sum_{\lambda=400\ nm}^{700\ nm} Energy\ intercepted\ per\ cell\ (\lambda)}{\sum_{\lambda=400\ nm}^{700\ nm} Irradiance\ of\ upper\ cell\ top\ face\ (x,\lambda)}, \quad (2)$$

where $\{cells\ (h)\}$ is the set of cells within the layer at height h in a single tree space (Supplementary Fig. 2).

Analogous to the albedo change, we calculated FAPAR change:

$$FAPAR\ change = FAPAR_{mix} - \frac{1}{\#species}\sum_{\{species\}} FAPAR_{mon}$$

3. Results

Here we first discuss the PHT richness effects on albedo and FAPAR, then focus on the vertical FAPAR redistribution between PFTs, and finally address the underlying mechanisms of the biodiversity effect.

3.1 Diverse canopies have a lower albedo and higher FAPAR than expected from averaging monocultures

We simulated all combinations of PFTs, realizing all possible PFT richness levels from 2 to 6 levels (see methods for details on experiment design). We found that for the LOP trait, mixtures had 0-0.015 lower albedo than monocultures and for the LAD trait, the difference was 0-0.005 on the natural background (Fig. 3a). The gain in FAPAR was 0-0.0015 for LAD and 0-0.00002 for LOP (Fig. 3b). The diversity effect on albedo and FAPAR was larger with trees standing on the white background and smaller on black background, and LAD mixture results were much more sensitive to the background compared with LOP mixtures (Supplementary Fig. 3). LOP mixture results were not sensitive to illumination conditions,

whereas LAD mixtures had a smaller positive diversity effect with a 30° sun zenith angle (compared with 0°) and under overcast conditions (compared with direct illumination only), where the sign of the effect depended on the background.

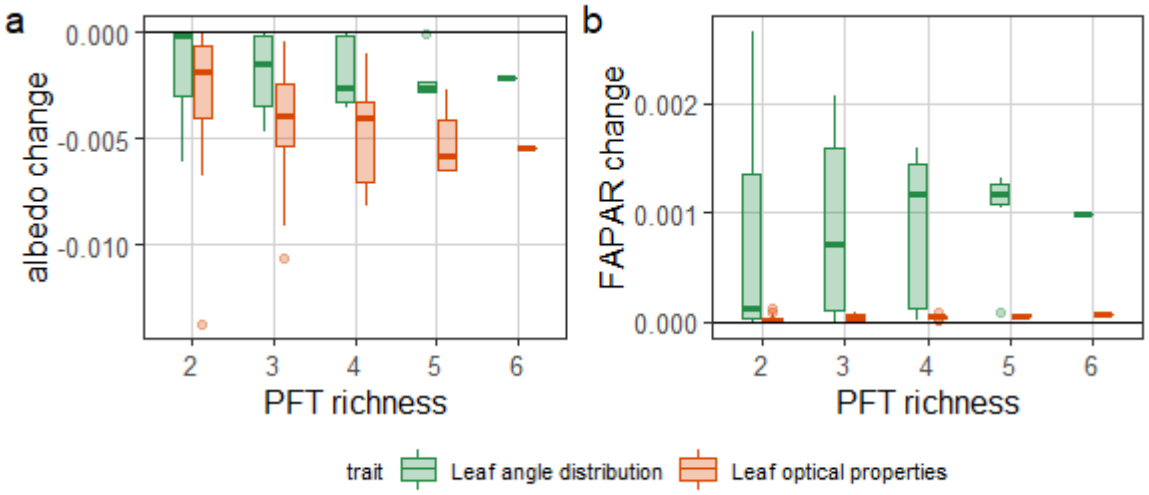


Fig. 3 Albedo (a) and FAPAR (b) change in mixtures compared to monocultures as a function of PFT richness. Results are for natural background, direct sun, and 0° sun zenith angle parameters.

Then, we tested the albedo change in the 2-trait mixtures. We found decreased albedo with increasing PFT richness (Supplementary Fig. 4).

3.2. FAPAR redistribution between PFTs within functionally rich canopies

Does the overall gain in FAPAR imply that each PFT in the mixture will receive more light? The analysis of individual profiles of an average tree of each PFT in different mixtures stressed that some PFTs gained light in mixtures while others lost compared to the same PFTs in monocultures. The LAD experiment shows that a PFT with vertical LAD on average absorbs 40% less in 6-PFTs mixtures than in monocultures, while other PFTs absorb more (Fig. 4). Similar results of a much smaller magnitude were found for the LOP experiment: the PFT with the highest transmittance and lowest absorption in the photosynthetically active domain (with elm and birch optical properties), absorbed 1-2% less light in 6-PFTs mixtures than in the monoculture (Supplementary Fig. 5).

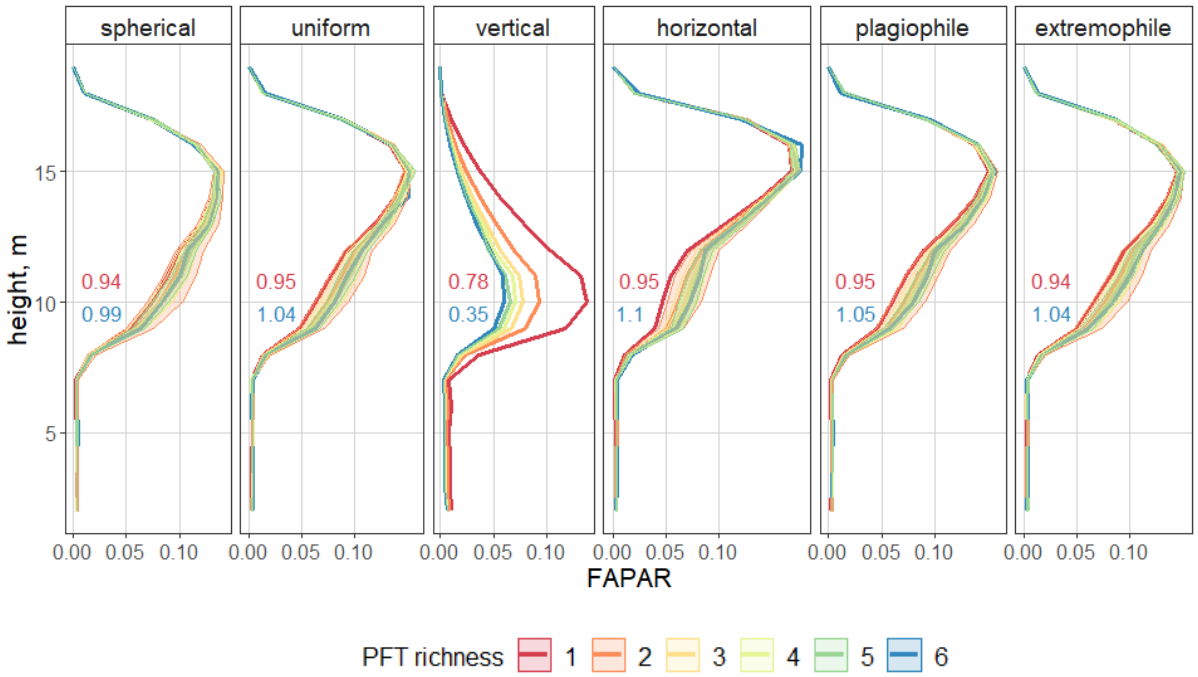


Fig. 4. FAPAR profiles of LAD PFTs in mixtures with different richness. The panels show different trait values, with the colors corresponding to PFT richness (1, red - monoculture; 6, blue - a mixture of 6 PFTs). The margins correspond to 95% confidence intervals; the numbers correspond to mean absorption in monocultures (red) and mean absorption of mixtures of 6 PFTs (blue). Results are for a white background, direct sun, 0° sun zenith angle parameters.

3.3 Why do mixtures absorb more radiation than monocultures?

To investigate the increased absorption in mixtures, we compared all possible mixtures of two PFTs (bicultures) with corresponding monocultures. For the LOP trait, we found that the difference in absorption between mixtures and monocultures positively relates to the leaf absorption and transmittance diversities (Fig 5a). For the LAD trait, it positively relates to the gap fraction diversity. Both LOP and LAD diversity relationships are non-linear.

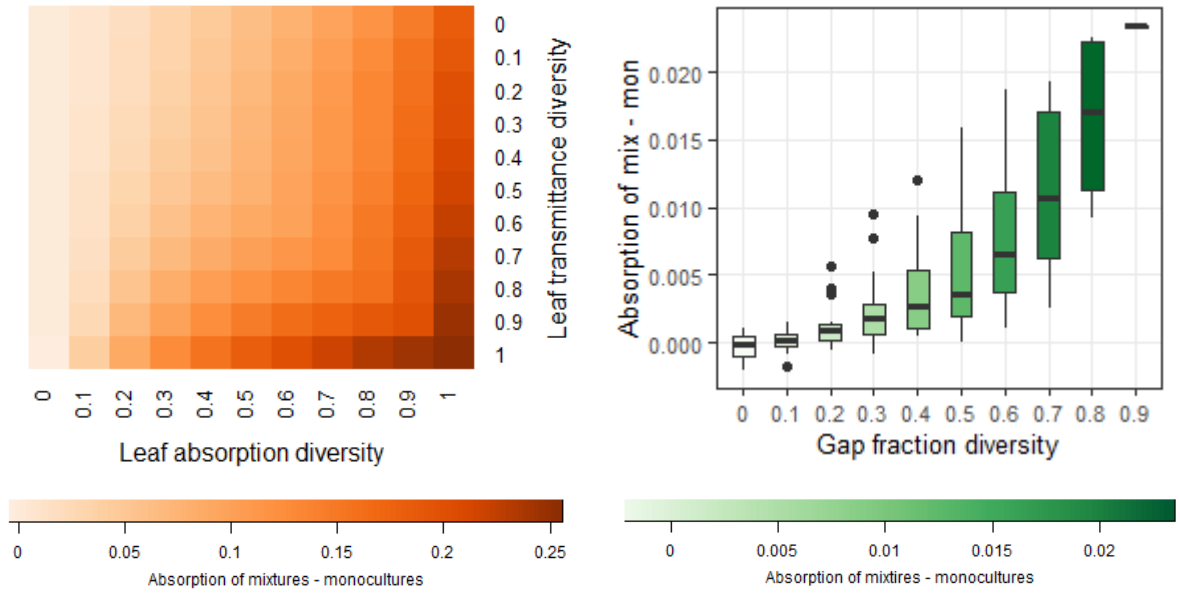


Fig. 5 The change in absorbed radiation in mixtures compared to monocultures as a function of trait diversities a) for LOP represented by leaf absorption and transmittance diversities; b) for LAD represented by the gap fraction diversity. Results are for a white background, direct sun, and 0° sun zenith angle parameters.

4. Discussion

Many experiments have shown that mixed tree stands are more productive than monocultures (Huang et al., 2018). This effect arises from multiple interdependent components, including water, nutrient and light availability, and their use efficiencies, and results in growth-related secondary responses which, in turn, can alter resource acquisition or stand structural diversity (Forrester and Bauhus, 2016). The effects of individual resources are difficult to distinguish, especially for light-related variables that depend on the overall canopy architecture and individual scattering components (leaves, branches, trunk, understory) properties, as well as multiple reflections between these components. Using a 3D radiative transfer model, we were able to isolate the light interception from the growth-related secondary responses.

4.1 LAD and LOP PFT richness decrease albedo and increase FAPAR in mixtures

We found a negative PFT richness-shortwave albedo relationship, which implies that less shortwave radiation is reflected from the canopy back to the atmosphere in more diverse canopies. For the photosynthetically active domain, our results support previous findings that vegetation complexity increases the amount of absorbed radiation in visible and near-infrared wavelength ranges. For tropical forests, phenology was shown to contribute to a

gain of 2-3% in yearly PAR captured by a mixture, compared to the null expectation based on monoculture performance (Sapijanskas et al., 2014). Based on our parametrization, we found a much smaller contribution of LOP PFT richness occurring at one point in time: 0-0.02% gain in instant FAPAR of mixtures (Fig. 3). This relatively small instant increase in FAPAR through time continuously contributes to the increase of light available for photosynthesis (Sapijanskas et al., 2014). This may, in turn, facilitate plant growth and contribute to overyielding, as well as result in multiple growth-related secondary responses associated with increasing biodiversity.

4.2 Sensitivity of the biodiversity effect to different backgrounds and illumination conditions

For LOP trait, PFT richness effects on albedo and FAPAR remained robust on different backgrounds and under different illumination conditions (Supplementary Fig. 3), which suggests that they arise mainly from the multiple scattering of radiation within and between trees and do not depend on the time of day or cloudiness. In contrast, LAD PFT richness effects strongly depend on understory characteristics and illumination (Supplementary Fig. 3). These results are expected, e.g. assuming a vertical LAD and 0° sun zenith angle, most light first hits the understory and is then scattered back up to the canopy. Interestingly, on the black background with the overcast scenario, we see that albedo increases with LAD PFT richness. Our explanation of this exception refers to the decrease of the canopy transmittance due to the trapping of radiation by multiple scattering in more diverse, hence structurally more complex, canopies. Overall, while the LOP PFT richness effect occurs mainly due to the trapping of radiation into the diverse foliage, the LAD PFT richness effect is determined by the amount of radiation scattered from the forest floor.

4.3 Light partitioning in mixtures

Despite the overall gain in FAPAR of mixtures, our findings suggest unequal light partitioning between PFTs in mixtures, meaning some PFTs absorb more light in mixtures, while others absorb less (Fig 4). This inequality can contribute to differences in the growth-related secondary responses of different species in mixtures (Dahlin et al., 2019; Forrester et al., 2018).

4.4 Absorption of mixtures in relation to functional diversity

How does increasing absorption of mixtures depend on functional diversity? We found that combining monocultures with more distinct traits led to a greater gain in the radiation of mixtures (Fig 5). For the LOP, the biodiversity effect is strongly dependent on the LOP diversities, which explains why the FAPAR change is much smaller than albedo change (see

Fig. 1) as the difference between LOP in the visible range is much smaller than in the rest of the spectrum. For the LAD, the highest diversity effect occurs when one of the species has a much higher gap fraction than the other, which is in accordance with our previous conclusion. These findings can help predict light-related biodiversity effects based on the traits of monocultures, and hence contribute to understanding the overyielding effect as well as changes in the shortwave radiative balance of the mixed canopies.

4.5 Assumptions and parametrization

The goal of our analysis was to isolate plant-light interactions and investigate LAD and LOP PFT richness and trait diversity effects in a specifically designed in-silico experiment. To do so, we made several simplifying assumptions, the most important of which we address here. We choose a 3D radiative transfer model (DART), which allows for a detailed representation of vegetation and calculates multiple interactions between light and individual scattering components (Gastellu-Etchegorry et al., 2012). As the DART is not a growth model, it does not allow for the simulation of canopy development. We tracked albedo at the top of the canopy and excluded atmospheric effects. The black and white background parametrization represent extreme scenarios close to the bare soil and full ground snow cover. We employed it to assess the floor and canopy contributions, and complemented it with more realistic forest litter ground optical properties to assess the trend in absorption on different backgrounds. We modelled the sun angles of 0° and 30° and ideal diffuse radiation that represent the sun at noon in central latitudes and idealistic overcast conditions. We used these to assess trends in light absorption under different illumination conditions. To isolate LAD and LOP PFT richness and diversity effects from the growth-related secondary responses, we parameterized all PFTs in monocultures identically to the ones in the mixture. For each PFT, all leaves had the same LOP and simplistic LAD, without variability within one tree, e.g. vertical variability of LAD within canopy. We also assumed identical crown architecture and single-layer canopy to simplify the interpretation of the biodiversity experiment. The effect of crown architecture and spatial complementarity in tree crowns on light overyielding in mixtures was already addressed in multiple studies (Barillot et al., 2014; Forrester et al., 2018; Williams et al., 2017). Although the PFTs do not correspond to different species, they nevertheless allowed us to study trait diversity and richness which can be generalized to inter- and intraspecific variability as well as variation in growing processes (Fahey et al., 2019; Thomas et al., 2019).

Acknowledgments

We thank Maitane Iturrate-Garcia for contributing to conceptualization of the manuscript. We thank DART team in CESBIO (Université de Toulouse) for their constant support with the DART software. This study was supported by the University Research Priority Program on Global Change and Biodiversity of the University of Zurich.

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Funding

This study was supported by the University Research Priority Program on Global Change and Biodiversity of the University of Zurich (URPP-GCB) and the Swiss National Science Foundation (Project no. 178753).

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***Declaration of Interest Statement**

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: