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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 three key functional traits that influence the light-canopy interaction: leaf area index (LAI), 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 absorptance 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.

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., 2020). 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.

Most experimental studies have shown that productivity increases with species diversity; specifically, mixed communities produce more yield than the average monoculture of the same species ("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

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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 absorbtion, 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 LAI, 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, 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 and 2 for the details).

We refer to trait diversity as the distance between the LAI, LOP, or LAD values of two PFTs. LAI diversity was represented by distance in LAI values, LOP diversity by the distance between leaf transmittance or leaf absorptance values, and LAD diversity as the distance between foliage gap fractions of two PFTs. These metrics allowed us to study the mechanisms behind the observed PFT richness-absorptance 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 along the LAI, LAD and LOP gradients and studied their effects on albedo and FAPAR. We then retrieved vertical profiles of FAPAR of different PFTs in the canopy to analyse light redistribution. To study the effect of PFT richness along both LOP and LAD axes simultaneously, we performed a second experiment, where we used a 4 LAD × 4 LOP factorial design and retrieved albedo. In the third experiment, we investigated the effect of the functional trait diversities on the change in absorbed energy. We chose a representation at regular intervals of LAI, LAD and LOP levels as LAI values, gap fraction and leaf reflectance and transmittance, respectively.

Experiment 1. We designed an in-silico biodiversity experiment based on 6 PFTs along LAI, LAD, or LOP gradients arranged on a rectangular regular spaced grid (Fig. 1). We simulated 60 trees along these gradients and repeated this subset in all horizontal directions (see Section 2.3 and Fig. 2 for the details on parametrization).

We chose values of 1–6 for LAI, 1 representing an analogy of the one-leaf model and 6 as maximum realistic LAI for forests (Asner et al., 2003). LAI was parameterized in DART through the foliage density variable (see Supplementary table 4 for the details). Selected LAD values include both realistic and extreme angular distributions, while the set of LOP was chosen from the northern temperate and boreal species with intention to have the most different LOP (see Supplementary Table 2). For the representation of the PFT parametrization see Fig. 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 LAI × 4 LAD factorial design with 16 trait compositions (see Supplementary Fig. 1 for the modelling design). We simulated a scene of 72 trees, as this size allowed us to test 15 out of 16 combinations of the trait richness levels, and for the 16th we took the average across the spatial configuration. The scene was repeated in all horizontal directions.

Experiment 3. To investigate the relationship between differences in traits and the net biodiversity effect, we simulated all possible mixtures of two PFTs (bicultures) along LAI, LAD and LOP gradients. To quantify the differences in trait values, we aimed at a representation at regular intervals along a gradient. The LAI gradient was already represented by the LAI values, so we took bicultures simulated in experiment 1. 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. We varied the foliage gap fraction from 0 to 1 with the interval 0.1 by choosing the corresponding leaf angle distributions (see Supplementary table 3 for details). We then calculated the difference in absorptance between mixtures and monocultures for each difference in gap fraction between monocultures. 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 absorptance values. We simulated the bicultures on the scenes of 4 trees, repeated in all horizontal directions.

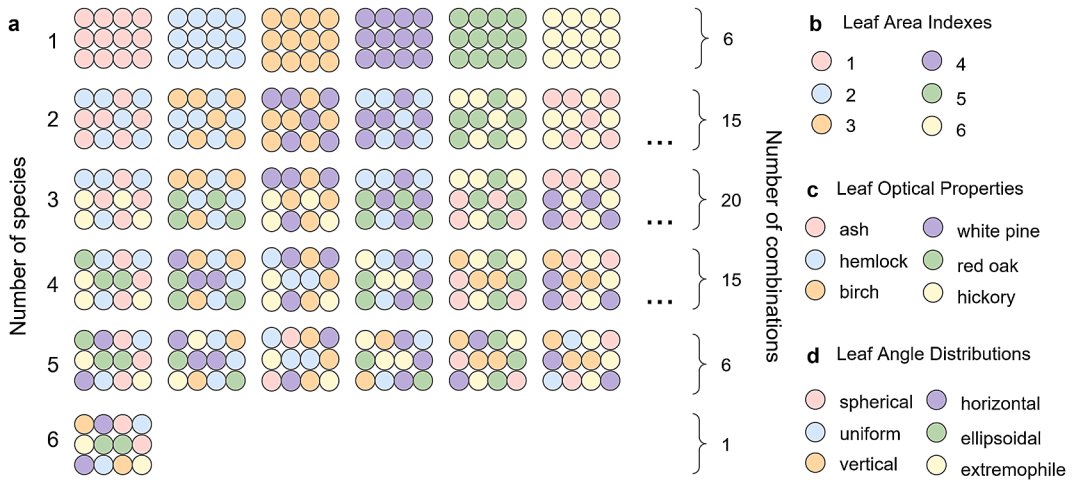

Fig. 1. Modelling design of PFT richness with 6 PFTs. (a) Design of a classical biodiversity experiment, where each colour represents a species. In our study, species were replaced by PFTs along (b) LAI, (c) LOP or (d) LAD axes. Note that the figure only shows subsets of the entire scenes modelled, i.e. we modelled the scenes with 60 trees, repeated in all horizontal directions.

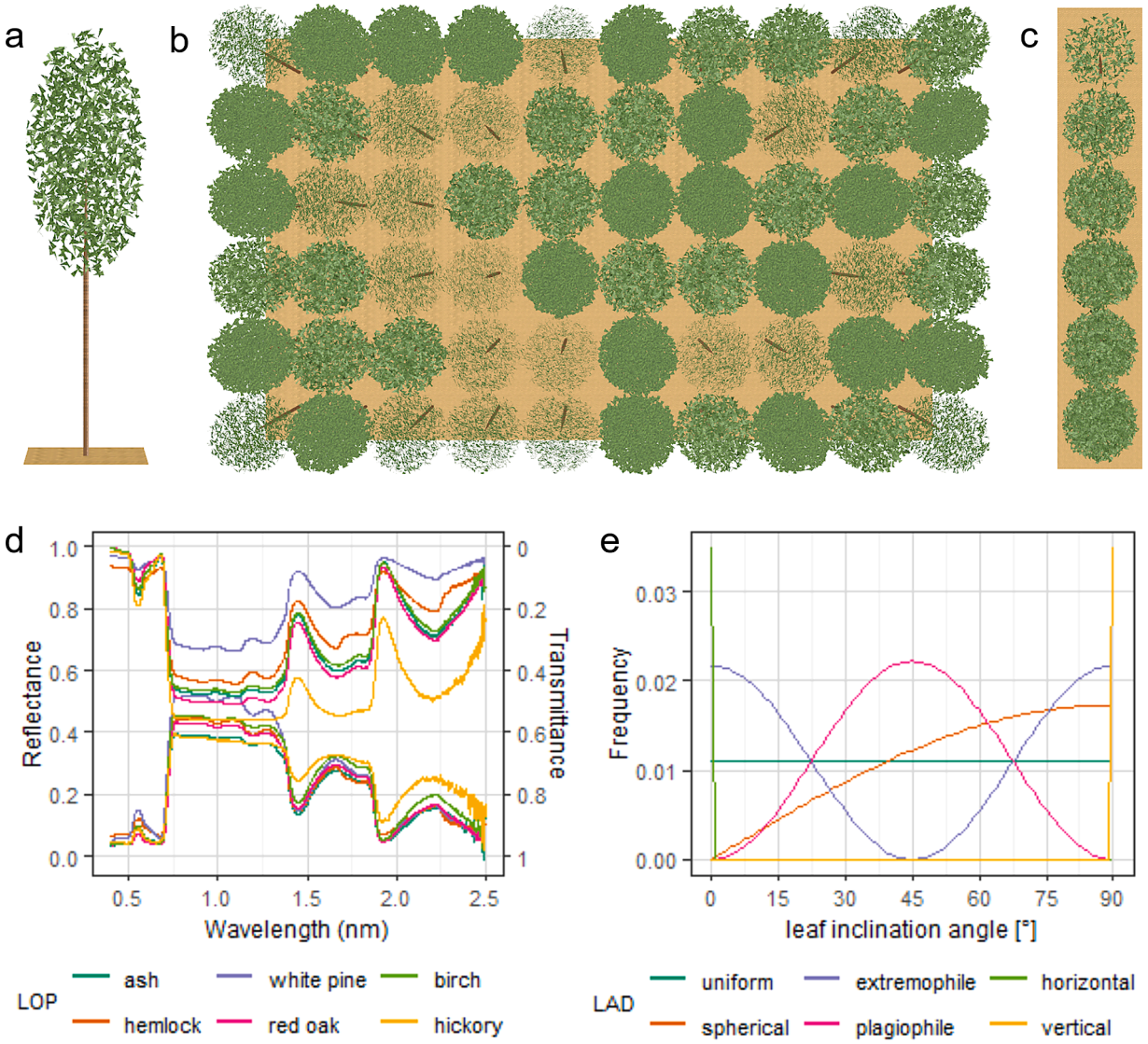

Fig. 2. Plant parameterization. (a) 3D representation of a tree in the DART model; (b) aerial view of a canopy of 60 trees - 3 PFTs with the following LAD values: uniform, horizontal, and vertical; (c) LAI representation - the LAI values are 1–6 from the top to the bottom; (d) LOP values: upper lines correspond to transmittance and the lower lines to reflectance; (e) LAD values. The frequency for the extreme horizontal (vertical) distribution is equal to 1 for 0° (90°)).

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 (see github repository: https://github.com/PlekhanovaElena/DART_article for the simulations and the code for visualisation). 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 LAI, 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 × 50 m, with 1 m voxel size) with a group of 60 regularly distributed trees (Fig. 1b) with different LAI, LAD and LOP values (Fig. 1c–e).

2.3.2. Background (understory) representation

The total amount of radiation absorbed by a tree canopy is the sum of trunk and foliage absorptance 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 to amplify the effect of the understory and better understand the trend of the understory contribution to the overall canopy effect.

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: 400–700 nm, spectral resolution of 50 nm
	Shortwave infrared	Bands: 750–2500 nm, spectral resolution of 50 nm

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 (Lewis and Barnsley, 1994)(). 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.

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 $\Delta\lambda$ = 50 nm) at the top of the canopy ((1).

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

where *Exitance* (λ) 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

$$albedo\ change\ = albedo_{mix} - \frac{1}{\#PFTs} \sum_{\{PFTs\ in\ mixture\}} albedo_{mon}, \quad (2)$$

We refer to albedo change in % as the albedo change divided by the average albedo value of the corresponding monoculture (second term in Eq. (2)). We refer to shortwave absoptance change as minus albedo change.

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 (3)).

$$FAPAR\ (h) = \frac{1}{\#\ \{cells\ (h)\}} \sum_{\{cells\ (h)\}} \frac{\sum_{\lambda\ =\ 400\ \mathrm{nm}}^{700\ \mathrm{nm}} Energy\ intercepted\ per\ cell\ (\lambda)}{\sum_{\lambda\ =\ 400\ \mathrm{nm}}^{700\ \mathrm{nm}} Irradiance\ of\ upper\ cell\ top\ face\ (x,\ \lambda)}, \quad (3)$$

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:

$$FAPAR\ change = FAPAR_{mix} - \frac{1}{\#PFTs} \sum_{\{PFTs\}} FAPAR_{mon} \quad (4)$$

We refer to FAPAR change in % as the FAPAR change divided by the average FAPAR values of corresponding monocultures (second term in Eq. (4)).

3. Results

Here we first discuss the PFT richness effects on albedo and FAPAR,

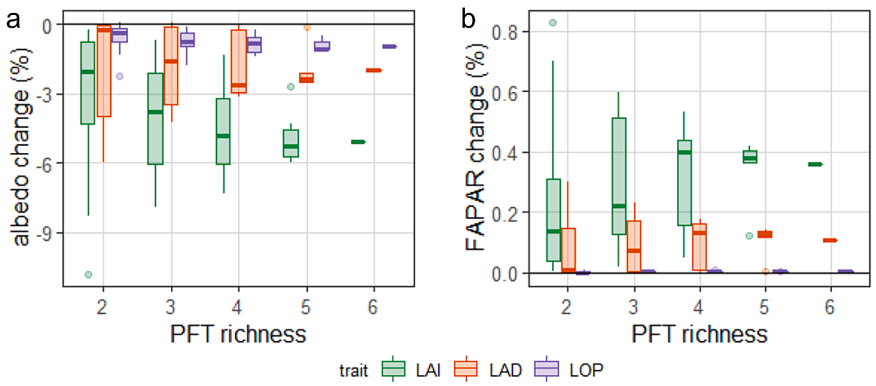

Fig. 3. Albedo (a) and FAPAR (b) change in mixtures compared to monocultures as a function of PFT richness (the results are presented for natural background, direct sun, and 0° zenith angle parameters).

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 (see methods for details on experiment design). The typical value of albedo for the monoculture stands was ~0.17 and of FAPAR ~0.96. We found the highest albedo change for the LAI trait (mixtures had 0.5–6% lower albedo than monocultures), then for the LAD trait (0–4%) and the lowest for the LOP trait (0.2–1.2%) on the natural background (Fig. 3a). The gain in FAPAR was correspondingly highest for LAI (0.02–0.5%), then for LAD (0–0.18%) and lowest for LOP (0–0.01%) (Fig. 3b). We tested different illumination conditions and backgrounds. We found that the biodiversity effect of LOP mixtures was not sensitive to them, whereas LAD mixtures had a smaller positive diversity effect with a 30° sun angle (compared with 0°) and under overcast conditions (compared with direct illumination only), where the sign of the effect depended on the background (Supplementary Fig. 3). LAI mixtures showed very similar results under different illumination conditions on the natural or white background. We then looked at the canopy vs. understory contributions of the observed effect (see Section 2.3.2. for details). The diversity effect on albedo and FAPAR was about twice larger with trees standing on the white background and smaller on black background. LAI and LAD mixture results were much more sensitive to the background compared with LOP mixtures.

We then tested how this difference behaved 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? We looked at individual profiles of an average tree of each LAI and LAD PFT in different mixtures and found that some PFTs gained light in mixtures while others lost compared with the same PFTs in monocultures. The LAI experiment shows that a PFT with LAI = 1 on average absorbed 6% less in 6-PFTs mixtures than in monocultures, while a PFT with LAI = 6 absorbed 4% more (Fig. 4). Similar results were found in the LAD experiment: the PFT with vertical leaves absorbed less light in 6-PFT mixtures, while the PFT with horizontal leaves absorbed more (see Supplementary Fig. 5).

We hypothesized that the observed effect is related to the canopy-understory interactions. For example, the most transparent PFT is transmitting the highest amount of radiation, which is then absorbed either by the same PFT in monocultures or by different PFTs in mixtures, resulting in the observed light partitioning. Alternatively, the effect

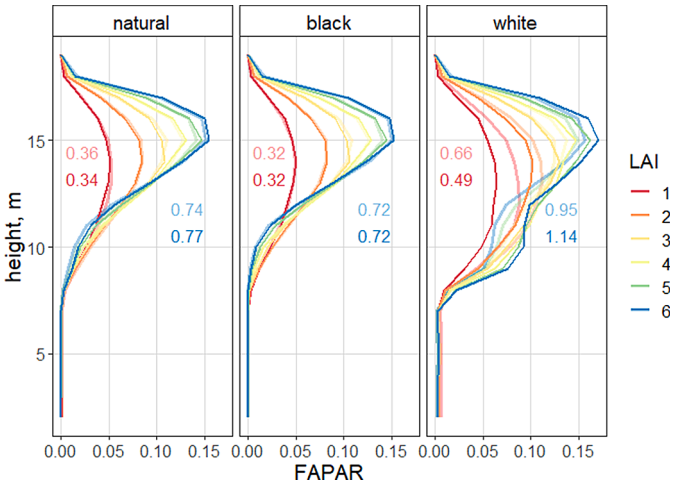

Fig. 4. FAPAR profiles of LAI PFTs in monocultures and same PFT in a 6-PFT mixture on different backgrounds. The panels show different backgrounds (natural, black, white), with the colours corresponding to LAI values and shade to the number of PFTs (light-shade - monoculture; dark-shade – the same PFT in a mixture of 6 PFTs). The numbers correspond to mean absorptance in monocultures (light-red or light-blue) and mean absorptance of in mixtures of 6 PFTs (dark-red or dark-blue) (the results are presented for direct sun, 0° zenith sun angle parameters).(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

could have arisen solely due to multiple reflections between the foliage of different PFTs without understory contribution. To test this hypothesis, we constructed FAPAR profiles of the same PFTs without accounting for the understory reflectance (implementing a black background) and with exaggerated understory reflectance (implementing a white background) (Fig. 4). On the black background the FAPAR profiles were very similar and there was almost no difference between the FAPAR of monocultures and mixtures. On the white background, each PFT absorbed more light, especially in the lower part of the foliage, and the same PFT lost or gained light, but at higher magnitudes.

3.3. Why do mixtures absorb more radiation than monocultures?

In Section 3.1, we showed that combining PFTs with different trait values leads to increased absorptance of shortwave radiation. So we hypothesized that the more distinct PFTs we combine, the bigger this absorptance would be. To test this hypothesis, we first represented the LAI, LAD and LOP PFTs in regular intervals along a gradient to quantify the difference in trait values (see Methods Section 2.2). We then compared the shortwave absorptance of all possible mixtures of two

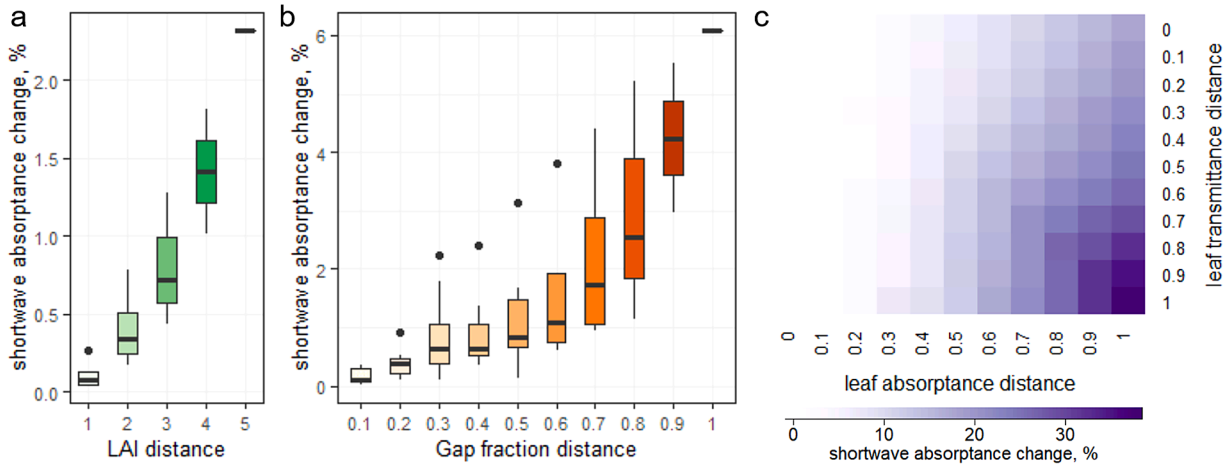

Fig. 5. The change in absorbed radiation in mixtures compared to monocultures as a function of trait diversities (a) for LAI; (b) for LAD represented by the gap fraction diversity (the results are presented for natural background, direct sun, and 0° zenith angle parameters); (c) for LOP represented by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

PFTs (bicultures) with corresponding monocultures. We found that the biodiversity effect increases with the trait distance for all three traits studied (Fig. 5).

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, crown openness was shown to contribute a gain of 0.3–0.8% 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 slightly smaller contribution of LAD and LAI PFT richness occurring at one point in time: 0–0.18% gain in instant FAPAR of mixtures for LAD and 0.02–0.5% for LAI (Fig. 3b). This 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, cloudiness or understory characteristics. 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, whereas under overcast conditions or on the black background this effect would not take place. LAI mixtures show similar positive biodiversity effects under different illumination conditions, but a very small effect on the black background, suggesting the effect arises mainly from the canopy-understory interplay. 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 LAI and LAD PFT richness effects are 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, Supplementary Fig. 5). We observed that the most transparent PFT that absorbed less in monocultures (e.g. LAI = 1 or with vertical LAD) lost light in mixtures, while the least transparent gained light in mixtures (LAI = 6 or with horizontal LAD) and this gain occurred mostly in the lower crown level. We propose the following explanation for this effect: the light is transmitted through the most transparent PFT, is then reflected by the understory, and finally reaches either the same PFT (in monocultures) or mostly other PFTs (in mixtures). Note that in the PAR region, around 95% of the light that reaches the leaves is absorbed, so we expect the most transparent PFT to absorb more light in monocultures than in mixtures.

This explanation implies that the effect mainly arises from the portion of light that is reflected by the understory, so we tested this by simulating different backgrounds. We concluded that this PFT richness effect on light partitioning indeed occurs mainly due to the canopy-understory interactions. 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). It can also create a positive feedback loop for diversification of some traits: e.g. in the light-constrained canopies, the species with the highest LAI would gain light and potentially develop even higher LAI, and the opposite would happen with the species with lowest LAI. As we discuss in the next Section, this diversification would also have an effect on the overall change in albedo and hence the shortwave radiation budget.

4.4. Absorption of mixtures in relation to functional diversity

How does increasing absorptance 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 LAI and LAD, the highest diversity effect occurs when one of the PFTs has a much higher LAI or gap fraction than the other, which is in accordance with our previous conclusion. 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. 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. Robustness of the results

There are several assumptions of the described implementation of the model, which may influence the outcomes, including spatial configuration, a tree parametrization and extreme PFT values. To ensure the spatial robustness of our results, we averaged the results across ten different spatial configurations. We also performed an additional simulation with white spruce tree parametrization (see Supplementary table 5) and obtained very similar results (see Supplementary Figs. 6, 7). Finally, we investigated the effect along the LAD gradient excluding the vertical LAD, which had a strong effect because of extreme transmittance for the vertical radiation. We found similar trends, though of a much smaller magnitude (Supplementary Figs. 8, 9).

4.6. 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 absorptance 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 absorptance under different illumination conditions. To isolate LAI, 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., 2020).

4.7. Conclusion

Our study shows that functionally diverse communities have higher light interception (FAPAR) and reduced albedo through the radiative transfer effects alone, excluding all other effects, like variation in architecture or growth. This suggests that such effects could also be at play in real communities where it is not so straightforward to separate cause and effects.

CRediT authorship contribution statement

Elena Plekhanova: Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Pascal A. Niklaus:** Conceptualization, Methodology, Writing - review & editing. **Jean-Philippe Gastellu-Etchegorry:** Software, Writing - review & editing. **Gabriela Schaepman-Strub:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109394. Please find the code and the DART simulations on the GitHub repository: https://github.com/PlekhanovaElena/DART_article.

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