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LETTER

Enhanced light interception and light use efficiency explain overyielding in young tree communities

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Abstract

Diverse plant communities are often more productive than mono-specific ones. Several possible mechanisms underlie this phenomenon but their relative importance remains unknown. Here we investigated whether light interception alone or in combination with light use efficiency (LUE) of dominant and subordinate species explained greater productivity of mixtures relative to monocultures (i.e. overyielding) in 108 young experimental tree communities. We found mixed-species communities that intercepted more light than their corresponding monocultures had 84% probability of overyielding. Enhanced LUE, which arose via several pathways, also mattered: the probability of overyielding was 71% when, in a mixture, species with higher 'inherent' LUE (i.e. LUE in monoculture) intercepted more light than species with lower LUE; 94% when dominant species increased their LUE in mixture; and 79% when subordinate species increased their LUE. Our results suggest that greater light interception and greater LUE, generated by inter and intraspecific variation, together drive overyielding in mixed-species forests.

Keywords

biodiversity–ecosystem function, complementarity, diversity–productivity, ecophysiology, forest productivity, functional diversity, IDENT, niche partitioning, photosynthetic light-response.

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INTRODUCTION

Studies of natural forests (e.g. Vilà *et al.* 2007; Paquette & Messier 2011; Zhang *et al.* 2012; Mori 2018) and tree-diversity experiments (Grossman *et al.* 2018; Paquette *et al.* 2018) show that diversity often enhances productivity (but see Chisholm *et al.* 2013; Staples *et al.* 2019). Identifying the mechanisms that drive diversity–productivity relationships is critical for predicting the consequences of biodiversity loss on future forest function. Yet, empirically demonstrating biological mechanisms remains rare (Cardinale *et al.* 2011; Niklaus *et al.* 2017). Enhanced productivity in species mixtures relative to monocultures (i.e. overyielding) may arise in many ways, including competitive relaxation via resource partitioning (Richards & Schmidt 2010; Sapijanskas *et al.* 2014; Barry *et al.* 2019), competitive imbalance leading to the dominance of a highly productive species (Yachi & Loreau 2007), facilitation that ameliorates nutrient, microclimatic or light stress (Tilman *et al.* 1997; Cowles *et al.* 2016; Wright *et al.* 2017; Kothari *et al.* 2020), plant–soil interactions that enhance soil resource availability (Reich *et al.* 2012; Cowles *et al.* 2016), and trophic interactions that increase plant fitness (Laforest-Lapointe *et al.* 2017) or reduce herbivory or disease (Jactel & Brockerhoff 2007; Jactel *et al.* 2017). Here we focus on how interactions among trees for a single resource – light – can lead to overyielding in mixed-species forests.

Light powers photosynthesis, carbon assimilation and, thus, plant growth. On average, light access limits carbon assimilation in closed-canopy forests (Tjoelker *et al.* 1995) and limits the growth of individual trees (Pacala *et al.* 1996). Light competition is a critical process shaping forests, affecting composition, structure and dynamics (Bazzaz 1979; Pacala *et al.* 1996; Falster *et al.* 2017). Since light originates from a single source such that taller plants can intercept light before it reaches shorter ones, competition for light is often thought to be asymmetrical with respect to size (Weiner 1990; but see Forrester 2019). However, plants can differ in their interception of light in space and time as well as in their capacity to photosynthesise at different light intensities. Plants also differ in their ability to tolerate stress due to extremes at either end of the light gradient (Givnish 1988; Montgomery 2004). Thus, species partitioning of light may contribute to overyielding in species mixtures – yet, the relative importance of different mechanisms of light partitioning remains relatively unexplored (but see, e.g. Sapijanskas *et al.* 2014; Forrester *et al.* 2018).

To examine how interactions among trees for light may contribute to diversity–productivity patterns in forests, we drew upon the production ecology equation (Monteith 1977; Binkley *et al.* 2004) to articulate what determines overyielding

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from first principles. Specifically, an increase in the light supply, the proportion of light intercepted and/or the efficiency of light use in a mixture relative to monoculture is expected to lead to overyielding (Fig. 1a). Differences among species may result in species mixtures capturing more light and/or using light more efficiently than one species alone; the central premise of the complementarity effect (Niklaus *et al.* 2017).

Greater filling of canopy space has been found in mixed-species assemblages of crops (Zhu *et al.* 2015) and trees (Pretzsch 2014; Jucker *et al.* 2015; Williams *et al.* 2017) – due to both interspecific differences and plasticity in crown shape – leading to increased light interception (Sapijanskas *et al.* 2014; Zhu *et al.* 2015). Species may also vary in their shade tolerance and photosynthetic light-response, enabling species to partition light gradients efficiently within canopies (Valladares & Niinemets 2008), and leading to greater growth in mixtures for the same amount of intercepted light at the community scale. Such partitioning of light gradients is enhanced by the nonlinear relationship between photosynthesis and light intensity. For instance, species with shallower photosynthetic light-response curves – and thus lower dark respiration, maximum photosynthetic rates and light compensation points – might have near-maximal photosynthetic rates at lower light and, in some cases, have higher rates of photosynthesis than other species at low light (Valladares & Niinemets 2008). Differences among or within species in photosynthetic light-responses – combined with the effects of canopy structure on light interception – may lead to the photosynthetic light-response at the canopy scale saturating at a higher irradiance than the response of an individual leaf (Ruimy *et al.* 1995; Hirose 2005).

In mixed-species forests, previous studies have illustrated how inter and intraspecific differences affect light interception (e.g. Sapijanskas *et al.* 2014; Forrester *et al.* 2019). How mixing tree species together enhances community-level light use efficiency has received less attention – and is a central focus of this study. Previous studies that have examined how light use contributes to productivity in mixed-species forests have characterised light use at a stand scale (e.g. Binkley *et al.* 1992) or using models (e.g. Richards & Schmidt 2010; Morin

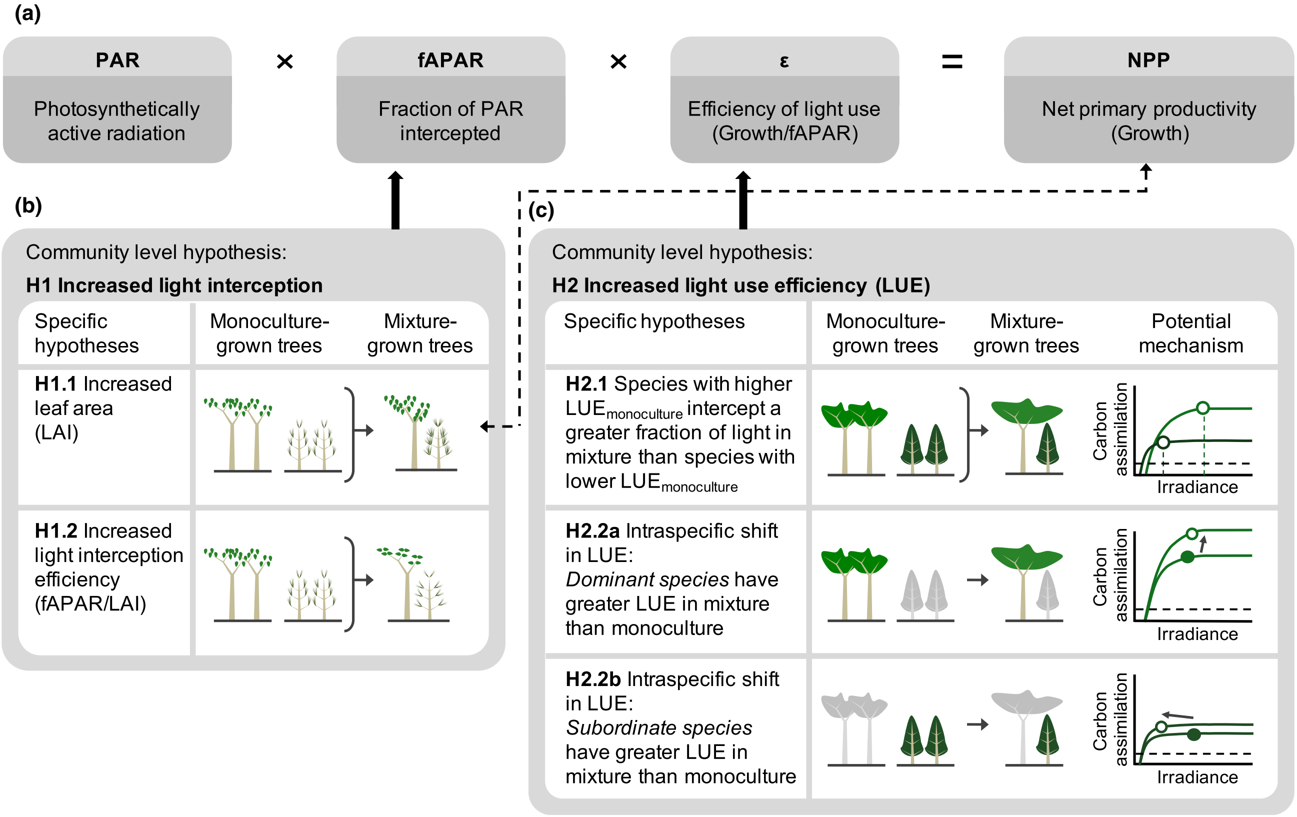

Figure 1 (a) Production ecology equation with respect to light, and hypothesised pathways by which (b) light interception or (c) light use efficiency (LUE) – defined as stem biomass accumulated per year per unit of PAR intercepted by the canopy – may increase within mixed-species communities and increase productivity relative to monocultures. Boxes surround nested hypotheses. Hypotheses apply either to the community level or species level (i.e. rely upon variation among species within communities and subsequently aggregate to the community level). Illustrations show differences within or among species and from monoculture-grown trees to mixture-grown trees that might correspond with hypothesised phenomena and subsequently enhance community level productivity. Hypotheses nested within H2 are also illustrated with simplified photosynthesis-irradiance curves (open circles represent species' per tree relationship within mixture and closed circles within monoculture) to show one set of potential physiological mechanisms by which the hypothesised phenomena might arise. Hypotheses 2.2a-b distinguish among dominant (light green) and subordinate species (dark green); dominant species are defined as those that intercept more light in mixture than expected based on the proportion of trees planted of the given species, and subordinate species are those that intercept less light. Note that increased leaf area might be both a cause and a consequence of increased productivity (indicated by dashed arrow).

et al. 2011; Le Maire *et al.* 2013), not by empirically examining the contributions of individual species within a diverse set of mixtures, as in our study. These earlier studies emphasised how differences among species in shade tolerance may promote productivity – a finding further corroborated by empirical studies (e.g. Haggar & Ewel 1997; Menalled *et al.* 1998; Zhang *et al.* 2012).

Here we examine how light interception alone, or in combination with how efficiently light is used for growth, affects productivity and overyielding in a tree diversity experiment as the communities of young trees undergo canopy closure. For the purpose of this study, we define light use efficiency (LUE) as how much biomass is accumulated per fraction of light intercepted. Over three years during early stand development (years 4–6), we characterised tree growth, light interception and leaf area in 108 communities representing 36 different assemblages (monocultures and mixtures of two and six species). Communities were planted in a common garden; incoming light did not differ among them, and light-driven differences in productivity arose from differences in light interception and/or LUE (Fig. 1a).

We tested a series of nested hypotheses (Fig. 1b and c) for what drives overyielding and examine how these drivers change through early stand development as canopies close. Specifically, we hypothesised that species mixtures overyield because they (H1) intercept more light, and/or (H2) use light more efficiently than the same species on average when grown in monoculture. In turn, increased light interception (H1) may occur through (H1.1) increased leaf area or (H1.2) increased efficiency of light interception, whereby more light is intercepted per leaf area. To examine community-level LUE (H2) in more detail, we examined relationships for species within communities, because the productivity of species within communities sum to community-level productivity. Greater LUE in mixture may occur through (H2.1) efficient partitioning of light among species in a mixture, such that species with higher 'inherent' LUE (as assessed in monoculture) receive a greater fraction of the light intercepted by a mixture than species with lower inherent LUE. Moreover, species might increase their LUE in mixture relative to monoculture (H2.2). Such increases in LUE may occur within (H2.2a) dominant species (i.e. species that intercept a greater fraction of light in the mixture than expected based on their relative proportion of trees) and/or, (H2.2b) subordinate species (i.e. species that intercept a smaller fraction than expected). Finally, as these hypothesised drivers are not mutually exclusive, we evaluated their relative importance to overyielding across all communities within the experiment.

METHODS

Study site

We use an experiment belonging to the International Diversity Experiment Network with Trees (IDENT, Tobner *et al.* 2014) that was established in spring 2010 at the Cloquet Forestry Center (Cloquet, Minnesota, USA, 46° 40' 46" N, 92° 31' 12" W, 382 m.a.s.l.). The site has a mean annual air temperature of 4.8 °C and annual precipitation of 783 mm (averaged over 1973–2008) (Reich *et al.* 2015).

The experiment consists of trees planted 0.4 m apart in a grid pattern to form 2.8 by 2.8 m plots, which we also refer to as 'communities', containing 49 trees. Plots were spaced 1 m apart. Seedlings of 12 common temperate-boreal species were planted, representing six congeneric pairs (one species from North America and one from Europe), six angiosperms and six gymnosperms (Table S1). Here we focused on 36 different assemblages – 12 monocultures, 20 two-species mixtures and four six-species mixtures (species were planted in near-equal proportion within mixtures; Table S2) – replicated across three blocks for a total of 108 plots. To minimise edge effects, we focus on the inside 25 trees within a plot; henceforth, 'plots' or 'communities' refer to this inside portion of the original plot. We report data from years four to six (2013–2015), representing the 4th–6th growing seasons, when canopies were closing.

Productivity

Annual stem biomass growth (Mg ha^{-1} year^{-1}), our measure of productivity, was calculated each year using tree height and basal diameter (5 cm above ground) measured at the growing season end in 2012–2015. Stem biomass (including branches and bark) was estimated with genus-level allometric equations developed from our experiment and comparable studies (see Supplementary Methods: Allometric equations).

Light interception and leaf area

Total light interception by the community on each plot was measured annually in the middle of the growing season (Machado & Reich 1999). On uniformly overcast days, we measured photosynthetically active radiation (PAR) at ground level with a point quantum sensor (LI-190, LI-COR, Lincoln, Nebraska) in August 2013, and with a wand quantum sensor (AccuPAR LP-80, Decagon Devices, Pullman, Washington) in late July or August 2014 and 2015. We took several measurements per plot (44 with the point sensor, four with the wand sensor) and simultaneously recorded PAR in an adjacent open area. The fraction of PAR intercepted by the canopy (fAPAR) on each plot was calculated as one minus the ratio of PAR beneath the canopy to PAR in the open (Parent & Messier 1996).

In addition, we estimated light interception and the leaf area index (LAI, m^2 leaf m^{-2} ground) for each species within plots using a line intercept method (Thomas & Winner 2000; Nock *et al.* 2008) (see Supplementary Methods: Line intercept approach). In brief, we dropped vertical lines through the canopy on each plot in August of each year (when canopies were at peak biomass), and we recorded the angle and species identity of each intercepted leaf (or branchlet for conifers). Light interception was estimated using these data together with the Beer–Lambert law (line-intercept and sensor-based estimates of plot-level fAPAR were comparable, Fig. S1). LAI was calculated as the number of leaves intercepted by one line, adjusting for leaf angle.

Calculations and analyses

Establishing causal relationships between fAPAR, LAI and productivity would require dynamic accounting of carbon assimilation and allocation. Here, as a proxy, we examined relationships between annual productivity and variables (LAI and fAPAR) measured in the same year; relationships with variables measured in the previous year gave similar results (Fig. S2).

For each plot, we assessed net diversity effects (NE) on productivity, LAI and fAPAR, as follows:

$$\mathrm{NE}\,x = x_o - x_e \tag{1}$$

where x_o is the observed value of x (e.g. growth) in the mixed-species plot. x_e is the expected value and was calculated as the sum of each constituent species' (i) value in monoculture (m) (monocultures were matched to mixtures within the same block) weighted by the proportion of trees of $\mathrm{species}_i$ planted in the mixture (p), as follows:

$$x_e = \sum (x_{m,i} \times p_i) \tag{2}$$

NE on stem biomass growth > 0 indicates overyielding and < 0 indicates underyielding.

Relative fAPAR was calculated for each species within each mixed-species plot, as follows:

$$\mathrm{Relative\,fAPAR} = \frac{\left(\mathrm{fAPAR_{species}}/\mathrm{fAPAR_{plot}}\right)}{\left(\mathrm{nt_{species}}/\mathrm{nt_{plot}}\right)} \tag{3}$$

where $\mathrm{fAPAR_{species}}$ is the fraction of light intercepted by the species within the mixed-species plot (see above), $\mathrm{fAPAR_{plot}}$ is the total fraction of light intercepted by the plot, $\mathrm{nt_{species}}$ is the number of trees of the species planted within the plot and $\mathrm{nt_{plot}}$ is the total number of trees planted within the plot (i.e. 25 trees). Species with relative fAPAR >1 were considered dominants and <1 were considered subordinates. We also calculated two efficiency indices to connect light interception, leaf area and productivity. Light interception efficiency (LIE) indicates how much light was intercepted per unit leaf area, as follows:

$$\mathrm{LIE} = \mathrm{fAPAR}/\mathrm{LAI}. \tag{4}$$

Light use efficiency (LUE), as defined here, indicates how much trees grew per unit of light interception, as follows:

$$\mathrm{LUE} = \mathrm{growth}/\mathrm{fAPAR}. \tag{5}$$

where growth is annual stem biomass growth (Mg ha^{-1} year^{-1}).

All statistical analyses were conducted in R (v. 3.5.1) (R Core Team 2018). To examine bivariate relationships between productivity and each of fAPAR, LAI and LIE – as well as between the net diversity effects on productivity and each of these variables – mixed effects models were fitted with the nlme package (Pinheiro *et al.* 2018). Fixed effects were the main predictor variable (e.g. fAPAR), year and their interaction. Random effects were assemblage nested within block. Interactions were assessed with likelihood ratio tests using models fitted with maximum likelihood. We calculated squared Pearson's correlation coefficients (R^2) for each year between the observed values and values predicted from the population-level (fixed effects) model.

Relationships among some variables were nonlinear. However, models with and without nonlinear transformations gave similar relative estimates of model slope or shape and goodness-of-fit among years and variables (Fig. S3, Table S3). In the main text, we present models without nonlinear transformations because we sought to compare the strength and direction of relationships, rather than describe the specific relationship forms.

Multiple logistic regression models to predict whether or not overyielding occurred were fitted using the lme4 package (Bates *et al.* 2015), with additive binary terms for each hypothesised driver (H1, H2.1, H2.2a and H2.2b – the latter two were treated as 'true' if any species within the plot met the criterion). Block was treated as a random effect. Years were modelled separately. We calculated odds ratios (O) and probabilities (O/(1-O)) of overyielding using model coefficients for fixed effects (Quinn & Keough 2002). Probabilities of overyielding for all possible combinations of hypothesised drivers were calculated manually.

RESULTS

Productivity, light interception and leaf area

Communities differed in productivity (annual stem biomass growth; Fig. 2), averaging 3.42 ± 2.42 (mean ± SD among all 108 plots), 5.61 ± 3.65 and 10.03 ± 6.34 Mg ha^{-1} year^{-1} in years four, five and six respectively. Expressed as a fraction of the previously accumulated stem biomass, mean 'relative' productivity was comparable but declined across years (0.87 ± 0.68, 0.79 ± 0.37 and 0.73 ± 0.22). During mid-to-late summer, communities intercepted 75% (± 18%), 93% (± 7%) and 94% (± 6%) of incoming light, in years four to six respectively. LAI also increased over time from 3.2 (±1.7) to 4.5 (± 1.9) and 5.9 (± 2.7). As expected, light interception had a saturating relationship with increasing LAI (Fig. S4).

Relationships between productivity and each of light interception, LAI and LIE differed among years ($L_2 \geq 39.84$, $P < 0.001$; Table S3). Productivity was positively associated with community-level light interception in all years, but light interception explained little variation beyond year four (R^2 = 0.44, 0.17, 0.15) (Fig. 3a, see also Fig. S3). The slope of the relationship between light interception and productivity increased through time, indicating increasing LUE (Fig. 3a). However, LUE differed among communities, particularly in years five and six when many communities intercepted most light but differed in productivity.

Productivity was positively associated with LAI in all years (Fig. 3b), but LAI explained less variation in productivity in year four (R^2 = 0.35) than in years five (R^2 = 0.75) and six (R^2 = 0.71). On average, productivity increased more per unit increase in LAI as the communities aged (evident in the slope of the modelled relationship increasing over time). On average across communities, LIE declined over time (Fig. S4) and was negatively associated with productivity (Fig. 3c).

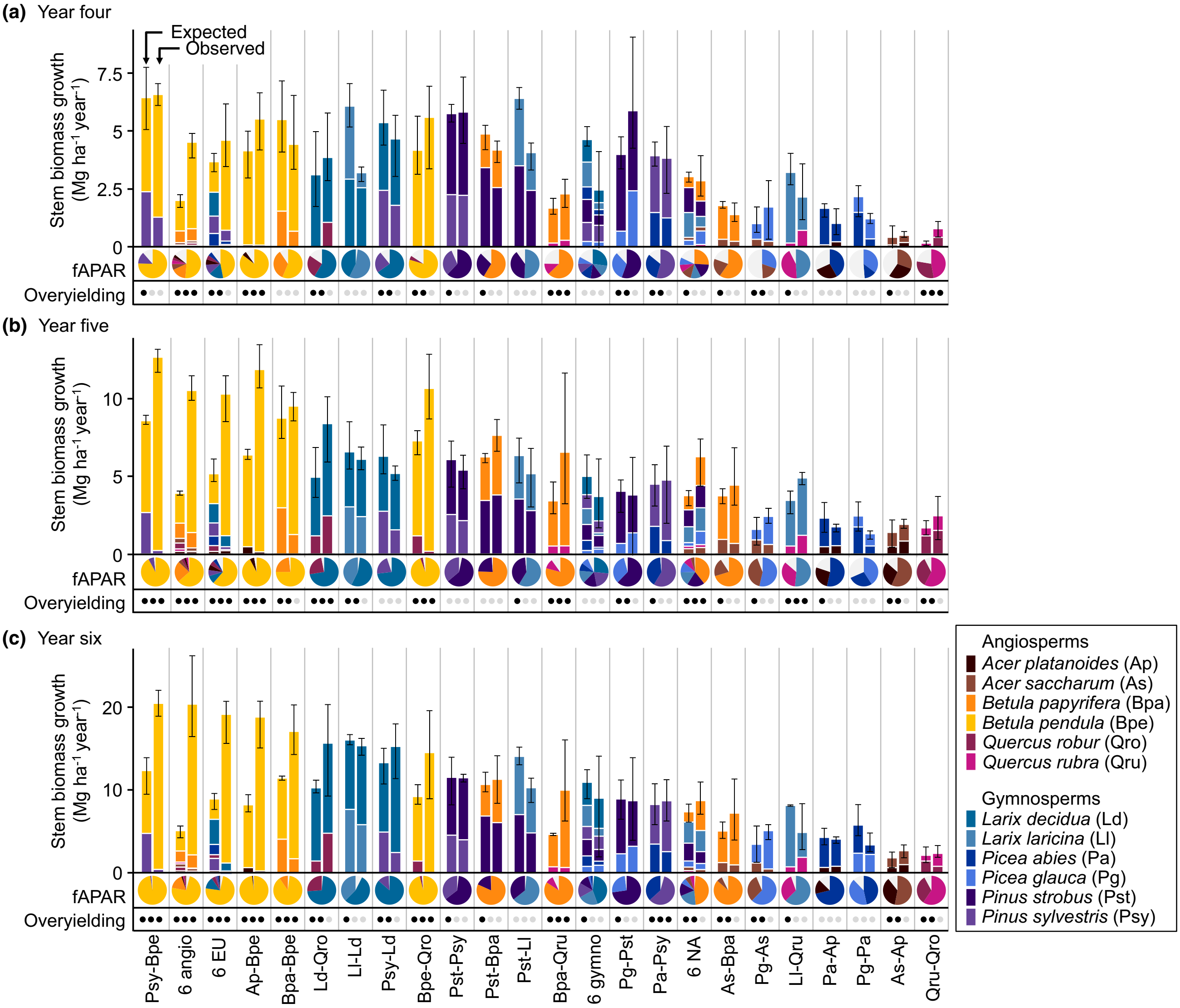

Figure 2 Productivity (as annual stem biomass growth) of each mixed-species community alongside the fraction of light intercepted (fAPAR) in years (a) four, (b) five and (c) six (i.e. the 4th to 6th growing seasons). Error bars show the range of values (minimum and maximum) observed among replicate plots ($n = 3$) of each community. Two stacked bars are shown for each community: 'expected' bars (on left) show species' mean productivity in monoculture scaled by their relative abundance (number of stems planted) in the mixed-species community, and 'observed' bars (on right) show species' mean productivity recorded in the mixed-species community. Bars are stacked according to species' relative fAPAR with dominant species above subordinate. Pie charts show the mean fAPAR by each species within the mixed-species community (estimated with the line-intercept approach); within each pie chart, species are ordered clockwise from most to least fAPAR (starting at top). Light grey represents light not intercepted by the community so that the total fAPAR represented by the pie sums to unity. Circles show the three plots of each mixed-species community with black shading signifying the number that overyielded. 6 EU = six species of European origin, 6 NA = six species of North American origin, 6 gymno = six gymnosperm species, 6 angio = six angiosperm species. Communities arranged from left to right according to the mean observed productivity in the sixth growing season.

Overyielding, light interception and leaf area

Annually, roughly half the mixed-species plots had greater productivity (in absolute terms) than the average of their relevant paired monocultures, demonstrating overyielding (Fig. 2). On average across communities, NE on productivity increased over time from slightly underyielding in year four (0.09 ± 1.77 Mg ha^{-1} year^{-1}) to overyielding in years five (1.41 ± 2.77 Mg ha^{-1} year^{-1}) and six (2.60 ± 5.38 Mg ha^{-1} year^{-1}).

Most communities that overyielded did so with half (or fewer) of the constituent species overyielding and the other species underyielding; this was the case in 54, 65 and 73% (across years) of plots that overyielded (Fig. S5). Species that grew more than other species in monoculture also tended to grow more than others within a given mixture; per individual growth of each species in monoculture and mixture was positively associated in 75, 81 and 85% of mixed-species plots (82, 85 and 89% of plots that overyielded). Overyielding had varied relationships with each of light interception, LAI and LIE (Fig. 3d–f), with the slope of these relationships also differing among years ($L_2 \geq 25.66$, $P < 0.001$) (Table S3).

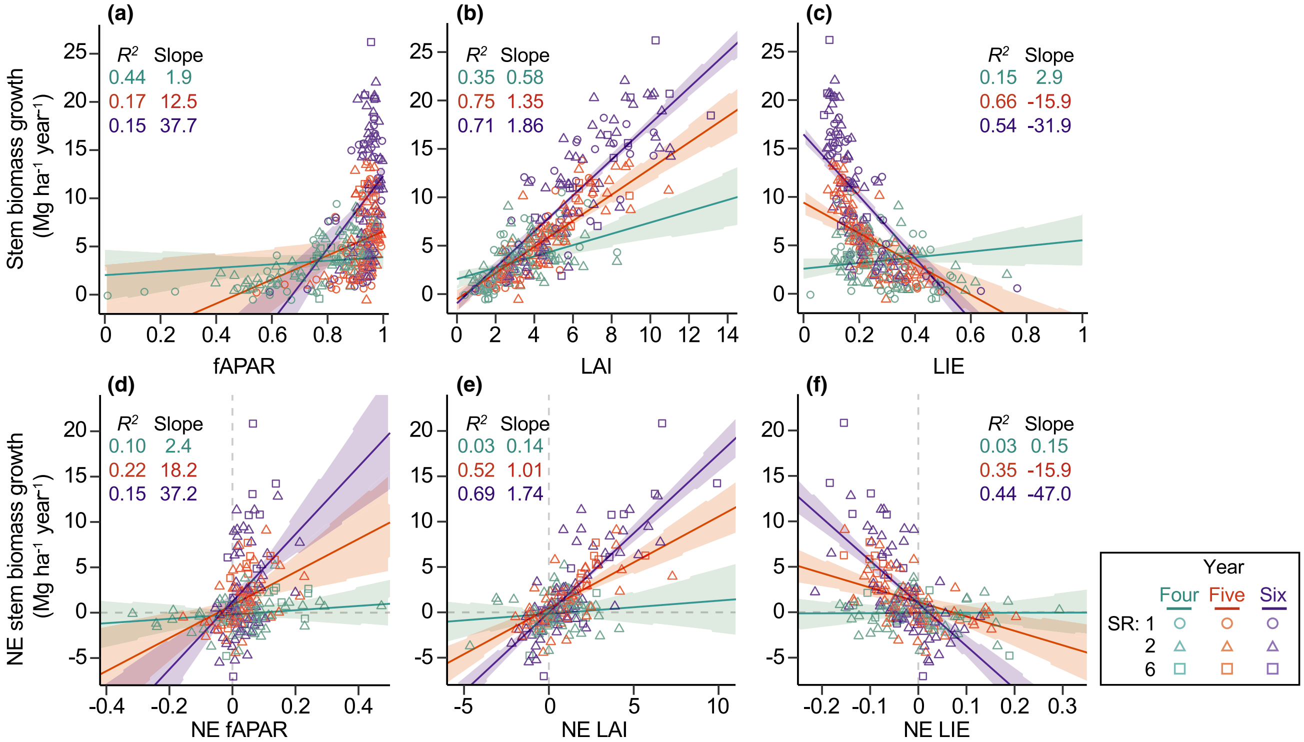

Figure 3 Community-level productivity, light interception, leaf area and light interception efficiency. (a–c) Relationships between productivity (as annual stem biomass growth) and the fraction of light intercepted (fAPAR), leaf area index (LAI) and light interception efficiency (LIE; fAPAR/LAI). (d–f) Relationships between the net effect of diversity (NE) on productivity and NE fAPAR, NE LAI and NE LIE. NEs compare values in mixed-species communities with values in monocultures scaled according to the proportion of trees planted in mixture. fAPAR and LAI were assessed independently with a sensor and line-intercept approach respectively. Relationships are shown across communities for years four, five and six, as colour-coded; symbols indicate the species richness of communities (SR). Relationships significantly differed among years ($L_2 \geq 25.66$, $P < 0.001$); a regression line (shading represents 95% confidence interval), squared Pearson's correlation (R^2) and slope are shown for each year ($n = 108$ communities for each year in panels a–c; $n = 72$ mixed-species communities for each year in panels d–f).

H1 Overyielding is driven by increased light interception

Most mixed-species communities (72, 78 and 83%) intercepted more light than the average of the same set of species in monoculture. Greater light interception in mixed-species communities (compared with monocultures) corresponded with increased overyielding in all years but explained at most 22% of variation in overyielding among communities (Fig. 3d). The slope of the modelled relationship between NE on light interception and overyielding increased from years four to six (Fig. 3d), indicating that increased light interception corresponded with even greater overyielding over time.

H1.1 Overyielding is driven by increased leaf area

Greater LAI in mixtures than monocultures was not related to overyielding in year four but was in years five and six ($R^2 = 0.03$, 0.52, 0.69) (Fig. 3e). Similarly, the slope of the relationship increased through time, indicating that trees grew more in mixtures than monocultures per unit increase in LAI (relative to monocultures) as they became older and larger.

H1.2 Overyielding is driven by increased efficiency of light interception

Overyielding was negatively associated with NE on LIE in years five and six. Over time, NE on LIE explained more variation among communities in overyielding ($R^2 = 0.03$, 0.35, 0.44) (Fig. 3f). Over time, the slope of this relationship became steeper, indicating that increasing NE on LIE more negatively affected overyielding.

H2 Overyielding is driven by increased LUE

NE on light interception explained only a modest portion of variation in overyielding ($R^2 = 0.10$, 0.22, 0.15) (Fig. 3d), which indicates, by definition, that LUE explained a large proportion of variation in overyielding. Most plots that overyielded had a positive NE on LUE (88%, 91%, 100%) (Fig. S5).

H2.1 Overyielding is driven by species with higher inherent LUE intercepting more light

Within mixtures, the fraction of light intercepted by each species tended to positively correspond with their LUE in monoculture. In other words, species with higher LUE in monoculture tended to intercept a greater fraction of light in mixture than the species with lower LUE (positive slopes in Figure S6a–c). A positive relationship between species' LUE in monoculture and species' relative fAPAR in mixture did not always lead to overyielding (Figure S6a–c), but 49%, 65% and 68% of plots with a positive relationship overyielded.

H2.2 Overyielding is driven by species increasing their LUE in mixture

Species' LUE often differed between monocultures and mixed-species communities. Dominant species had greater LUE in mixture than monoculture in less than half of communities (35, 40 and 40%), but almost all of these communities overyielded (68, 83 and 93%) (Fig. S7d-f). Subordinate species had greater LUE in mixture than in monoculture in most communities (61%, 74% and 69%), and most of these communities overyielded (59, 77 and 66%) (Fig. S7g–i).

Drivers of overyielding across species groups

Our experiment's design also enabled us to test whether mixing species from different geographic origins or the major phylogenetic lineages of trees increased community-level light interception and/or LUE, leading to overyielding (see Supplementary Results). The probability and magnitude of overyielding tended to be greater in mixtures of angiosperms than gymnosperms and in mixtures of European species that are non-native to our study site. However, the high productivity of *Betula pendula*, an angiosperm native to Europe, largely drove these trends. The strength of our hypothesised light-related drivers of overyielding did not differ markedly or consistently among these groups of communities.

Relative importance of hypothesised drivers of overyielding

Examining hypothesised drivers of overyielding together (Table S4), mixed-species communities that intercepted more light than the average of the same set of species in monoculture (H1) had a 73–97% chance of overyielding (84% on average across years); this relationship was significant ($\alpha < 0.05$) in years four and five, but not in year six (Fig. 4). Mixtures where species with higher monoculture-based LUE intercepted more light (H2.1) had a 56-83% (average 71%) chance of overyielding (Fig. 4). Mixtures where dominant species plastically increased their LUE relative to monoculture (H2.2a) had an 88-97% (average 94%) chance of overyielding (Fig. 4). Mixtures where subordinate species plastically increased their LUE relative to monoculture (H2.2b) had a 63-93% (average 79%) chance of overyielding (Fig. 4). Communities that overyielded almost always met more than one hypothesised driver, and certain combinations of drivers always led to overyielding such as when a community intercepted more light (H1) and both dominant and subordinate species increased LUE (H2.2a, H2.2b) (Fig. 5).

DISCUSSION

In documenting light interception, LAI and stem biomass growth across monocultures and mixed-species communities, we show that mixing tree species affects species- and community-level light interception, LUE and, in turn, productivity, during early stages of stand development. Interactions among species in mixed-species communities increased community-level LUE in three ways: (1) species partitioned light such that species with inherently higher LUE intercepted more light, (2) dominant species increased their LUE in mixture (compared with monoculture) such that their greater light interception in mixture resulted in more growth than anticipated, and (3) subordinate species increasing their LUE in mixture such that they grew more than expected given their reduced light interception. Enhanced community-level light interception and LUE, via all of these pathways, contributed to overyielding in mixed-species communities.

Enhanced community-level light interception often, but not always, leads to overyielding

Our first hypothesis was that mixed-species communities overyield because they intercept more light than monocultures. Diversity can enhance community-level light interception (Sapijanskas *et al.* 2014; Zhu *et al.* 2015; Forrester *et al.*

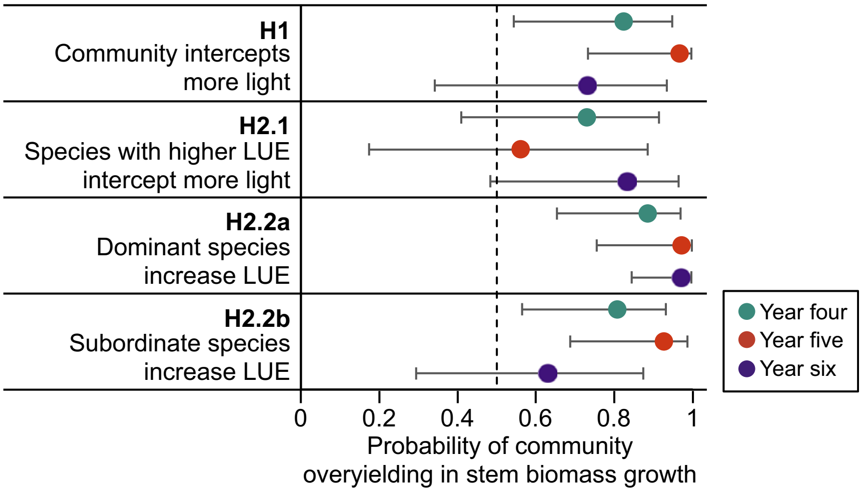

Figure 4 Probability of communities overyielding in stem biomass growth when hypothesised drivers of overyielding were met. Probabilities are based on multiple logistic regression. Error bars show 95% confidence intervals.

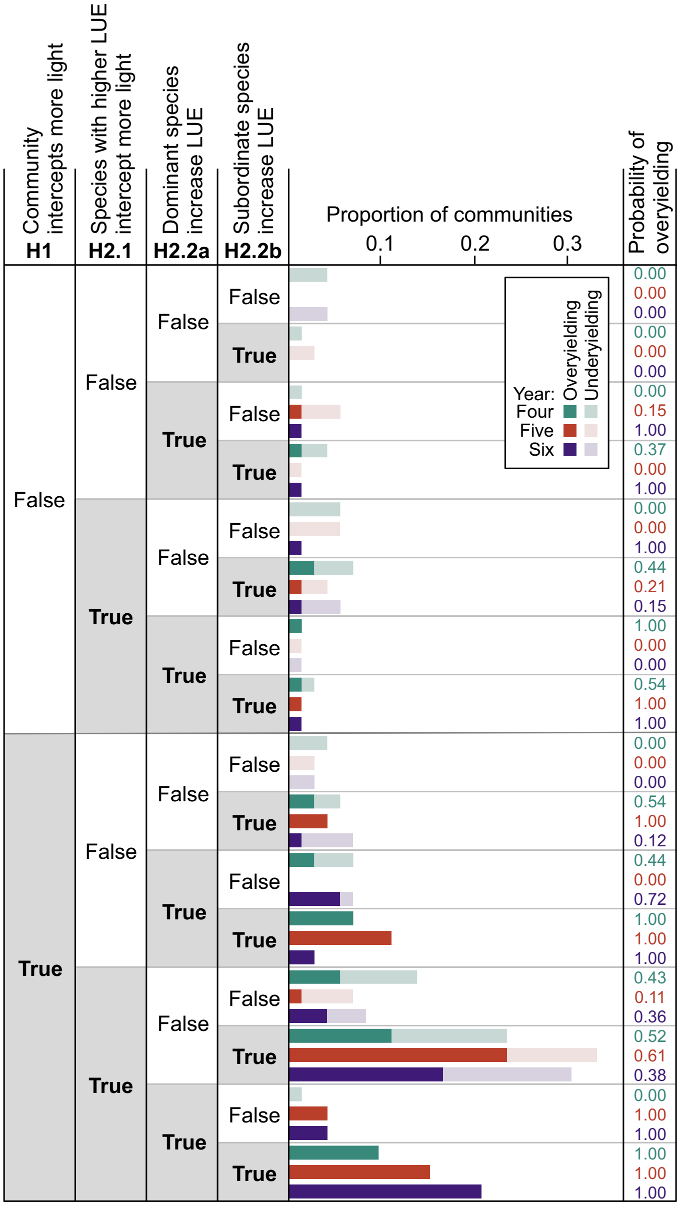

Figure 5 Proportion of communities each year that overyielded or underyielded where hypothesised drivers of overyielding were met (true) or not (false). Numbers to the right show the probability of overyielding, calculated manually, for each combination of hypothesised drivers of overyielding. Note that species-level hypotheses H2.2a and H2.2b were considered 'true' if at least one species within the community had greater LUE in mixture than monoculture.

2019), but increased light interception does not always translate to increased growth (Le Maire *et al.* 2013). We found that light interception was a critical component of productivity but, as canopies closed, many communities intercepted most light despite varying in productivity (Fig. 3a). Increased light interception in mixed-species communities led to a high chance (73–97%) of overyielding in each year (Fig. 4). However, increased light interception in mixed-species communities neither guaranteed (Fig. 5) nor explained the magnitude of overyielding (Fig. 3d).

LAI and leaf display determine community-level light interception but reflect as well as determine overyielding

All else being equal, a canopy with more leaves (i.e. greater LAI) intercepts more light. But, how those leaves are displayed may also matter: a canopy with leaves that are held horizontally and dispersed evenly through canopy space intercepts more light per leaf area (i.e. has greater LIE) (Hirose 2005). Independent measurements of light interception and LAI are rare (see e.g. Forrester *et al.* 2019) but needed to untangle the contributions of LAI and leaf display to light interception.

We found that both LAI and leaf display affected patterns of light interception among communities and over time (Fig. S4). Increasing LAI had diminishing impact on light interception, which we expected as canopies had closed on most stands (cf. Forrester *et al.* 2019). LIE declined over time because increases in LAI surpassed increases in light interception (Fig. S4).

LAI can drive forest productivity (Reich 2012) because it corresponds with light interception – but the direction of causation is bi-directional. If increases in LAI connect to productivity solely through increased light interception, productivity should saturate with increasing LAI alongside saturation in light interception. Instead, we found stem growth increased approximately linearly with LAI (Fig. 3b), suggesting that LAI was both a consequence and determinant of productivity in our young stands. Community-level light interception saturates with increasing LAI, leading to an optimal LAI for community-level productivity, but individuals may continue to increase their leaf area and benefit from greater light interception than their neighbours (Anten & Hirose 2001).

Our recorded values for LAI (maximum of 13.1 m^2 m^{-2}; average of 5.9 ± SD 2.7 m^2 m^{-2} among communities in year six) are modestly high (cf. Reich 2012). These values likely reflect communities being dense, young and not yet affected by self-thinning that will likely reduce LAI (Pinno *et al.* 2001).

Community-level LUE contributes to overyielding and is driven by asymmetry in species' growth

Our second hypothesis was that mixed-species communities overyield because they use light more efficiently. According to the productivity equation, enhanced LUE, by definition, explains differences in overyielding not explained by enhanced light interception (Fig. 3a). Almost all mixed-species communities that overyielded (88-100%) had greater LUE than the same set of species in monocultures (Fig. S6).

Overyielding occurs when all species benefit from mixing or when increased growth in some species overcompensates for decreased growth in others. We found most communities that overyielded had one (or a subset of) species that grew much more in mixture than monoculture while the other(s) grew less (Fig. S5), consistent with Tobner *et al.* (2016) but not Niklaus *et al.* (2017). Species' relative performances in mixtures tended to follow their relative performances in monoculture, as also noted in grasslands (Isbell *et al.* 2018), which indicates that the dominance of productive species (i.e. the selection effect, Loreau & Hector 2001) drove overyielding in our experiment.

Viewed through the lens of light, we found species within mixtures tended to intercept more (or less) light according to their relative ability to use light for growth (i.e. their LUE). In mixtures, species with greater inherent LUE (based on monoculture) tended to intercept more light, and such light partitioning led to 71% chance of overyielding (H2.1). Inherent LUEs positively correlated with shade tolerance (Niinemets & Valladares 2006) (species' mean inherent LUE vs. shade tolerance index: $r^2 = 0.32, 0.36, 0.42$ in years four, five and six respectively) and may broadly correspond with species' locations along the plant economics spectrum (Reich 2014). However, species' LUEs are not fixed.

A species' LUE in mixture may increase if the species grows more and/or intercepts less light – in any combination such that its ratio of growth to light interception increases. Dominant species, which intercept more light per tree than other species in a mixture, may experience less light competition and grow more in a mixed-species community. However, dominant species may not be expected to have higher LUE in mixture than monoculture. Taller trees in mature forests may have lower LUEs due to light saturation (Onoda *et al.* 2014), and size-related increases in respiration costs and carbon allocation to organs other than leaves may further decrease LUE in dominant species (Givnish 1988; Anten & Hirose 1999, 2003; Sendall *et al.* 2016). Indeed, we found the LUE of dominant species in most mixed-species communities decreased relative to monoculture. However, in a substantial portion of cases (35–40% of communities), dominant species had greater LUE in mixture than monoculture (H2.2a), and these mixed-species communities had a 94% chance of overyielding – this was the greatest indicator of overyielding in each year. Increased LUE in dominant species might arise through a plastic shift in species' photosynthetic light-response, leading to a greater photosynthetic rate at high light intensity (Fig. S8), which may follow neighbourhood-driven shifts in leaf functional traits (Williams *et al.* 2020).

Subordinate species' LUE may increase in mixture if they intercept less light without a proportional decrease in growth; a phenomenon anticipated by the photosynthetic light-response curve if the species shifts (to lower irradiance) along a flat part of their curve or if shading reduces photoinhibition (Kothari *et al.* 2020) (Fig. S8). Hence, subordinate species could, in theory, play a role in community productivity disproportional to their resource capture. We found that the LUE of subordinate species increased relative to monoculture in most communities (H2.2b) and these communities had a 79% chance of overyielding. Moreover, this led to overyielding of some communities where dominant species did not increase LUE (Fig. 5).

Future directions

The LUE, or growth-light, relationships we observed in mixed species communities could potentially be explained – at least, in part – by interspecific and community-driven intraspecific differences in photosynthetic light-response curves (Fig. S8). However, our study has limitations to attributing observed patterns to these physiological pathways. First, and most importantly, we examined LUE in terms of net growth rather than carbon assimilation. Thus, diversity effects on LUE captured diversity effects on productivity that operated via light as well as via any other pathway – such as, shifts in herbivory or disease or in the acquisition of other resources (Forrester & Bauhus 2016). Apparent shifts in species' LUE might also arise through diversity-induced shifts in allometries and biomass allocation that influence aboveground growth (Forrester *et al.* 2017; Guillemot *et al.* 2020; Martin-Guay *et al.* 2020). Moreover, enhanced growth may drive enhanced carbon assimilation rather than the reverse (Körner 2015). Second, we considered species' light interception at one point in time each year. Thus, the potential effects of temporal light partitioning over the growing season were not captured. Species intercepting light at different times of the year, via differences in foliar phenology, may enhance growth in mixtures (Sapijanskas *et al.* 2014). A direct evaluation of how light partitioning affects growth in mixtures would require dynamic accounting of carbon assimilation and allocation patterns across the entire growing season.

CONCLUSION

Here we quantified the relative contributions of various hypothesised drivers of overyielding related to light interception and use within many different developing tree communities. We found that greater light interception corresponded to overyielding, but this pathway neither guaranteed nor solely explained overyielding – leaving, by definition, unexplained variation to LUE. Our results show that a single species may dominate resource capture and community-level productivity, but a single species cannot utilise all resources as efficiently as a mixed-species community. Asymmetry among species in their responses to light competition, whereby gains overcompensate for losses, often explains overyielding. These results emphasise the varied pathways by which species' growth-light relationships may shape how species function together in communities.

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AUTHORSHIP

The IDENT experiment was designed and implemented by PBR, CM, AP, AS and KER. This study was conceptualised by LJW, EEB, PBR and JCB. Data were collected by LJW, KER and AS. LJW analysed the data, with assistance from

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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