Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences

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Abstract. Light partitioning is often invoked as a mechanism for positive plant diversity effects on ecosystem functioning. Yet evidence for an improved distribution of foliage in space or time in diverse plant communities remains scarce, and restricted mostly to temperate grasslands. Here we identify the mechanisms through which tree species diversity affects community-level light capture in a biodiversity experiment with tropical trees that displays overyielding, i.e., enhanced biomass production in mixtures. Using a combination of empirical data, mechanistic models, and statistical tools, we develop innovative methods to test for the isolated and combined effects of architectural and temporal niche differences among species as well as plastic changes in crown shape within species. We show that all three mechanisms enhanced light capture in mixtures and that temporal niche differences were the most important driver of this result in our seasonal tropical system. Our study mechanistically demonstrates that niche differences and phenotypic plasticity can generate significant biodiversity effects on ecosystem functioning in tropical forests.

Key words: *biodiversity; crown; ecosystem functioning; intraspecific diversity; light competition; niche differences; overyielding; phenology; phenotypic plasticity; plantation; Sardinilla project, Panama; tree.*

INTRODUCTION

In the face of current biodiversity loss, understanding the relationship between biodiversity and ecosystem functioning (hereafter BEF) has become a major scientific endeavor (Loreau 2010). Hundreds of studies, both experimental and observational, have revealed the strong influence that biological diversity exerts on numerous ecosystem processes and services (Cardinale et al. 2012), and notably on primary production through "overyielding," i.e., an increased biomass production in mixture compared to that expected from monocultures (Schmid et al. 2008). To meet the growing need for a predictive knowledge of the consequences of biodiversity changes, the central issue in BEF research has now moved from establishing whether diversity matters, to identifying the biological mechanisms underlying its effects on ecosystem functioning (Reiss et al. 2009, Mouillot et al. 2011). Yet mechanisms are hardly ever characterized beyond the now classical post hoc statistical distinction between selection and complementarity effects (Loreau and Hector 2001, Hector et al. 2009). In particular, direct demonstrations of niche differences generating biodiversity effects remain scarce (Dimitrakopoulos and Schmid 2004, Cardinale 2011).

This lack of knowledge is of special concern for forest ecosystems, which are among Earth's most important ecosystems. Forests support ~80% of the world's terrestrial biodiversity and provide key services to humanity as they support the livelihoods of ~1.6 billion people, generate well over $300 billion in revenues from annual trade of forest products, and play a key role in carbon sequestration (FAO 2010). Observational studies in natural forests have often been used to compensate for the lack of long-term experimental evidence. They often showed positive effects of tree diversity on forest productivity, but they failed to identify the mechanisms that underlie these effects and that could guide the management of forests and plantations in the face of global changes (Paquette and Messier 2011, Zhang et al. 2012, Gamfeldt et al. 2013, Vilà et al. 2013). Here, our objective is to fill this knowledge gap by identifying and disentangling the detailed mechanisms through which tree species diversity improved light capture in a tropical forest biodiversity experiment.

Through differences in their aboveground growth patterns, different plant species can use different canopy positions in time and space (Anten and Hirose 1999, Ishii et al. 2013), which may allow for a more efficient light capture at the community level. Accordingly,

spatial light partitioning and complementary use of canopy space are frequently invoked to account for overyielding in grasslands (Naeem et al. 1994, Spehn et al. 2005, Yachi and Loreau 2007) and are commonly used in the design of intercropping systems (Vandermeer 1989). Similarly, architectural complementarity among tree crowns and a more complete multi-layered exploitation of light are often proposed to explain growth enhancement in tree mixtures (Erskine et al. 2006, Pretzsch and Schutze 2009). However, quantitative assessments are sparse, restricted to grasslands, and have provided mixed results so far (Fridley 2003, Lorentzen et al. 2008, Vojtech et al. 2008), despite the fact that light competition is widely acknowledged as a major process driving forest dynamics (Oliver and Larson 1996, Purves and Pacala 2008).

Temporal niche complementarity due to differences in phenology has been little explored in the BEF literature, and the few existing studies have provided poor evidence for its contribution to overyielding (Stevens and Carson 2001, Mouillot et al. 2011). This might be due to the fact that most BEF studies have been performed in temperate grasslands, where differences in phenology are limited by unfavorable conditions for plant growth in the winter. Tropical environments, especially seasonal tropical forests, offer excellent opportunities for phenological differences among co-occurring evergreen, brevideciduous, and deciduous tree species, and hence for positive complementarity effects driven by phenological differences.

Besides fixed architectural, ecophysiological, or phenological differences among species, individual phenotypic plasticity may also increase resource capture efficiency in mixed-plant communities. Morphological changes in response to light availability are among the best-studied examples of phenotypic plasticity in plants (Sterck and Bongers 2001, Valladares et al. 2007); they include shifts in biomass allocation between aboveground vs. belowground parts (Bloom et al. 1985, Paquette et al. 2012) and reinforced apical dominance (Ballare 1999). Differences in shading or mechanical constraints caused by neighboring crowns with different species identities could affect a tree species' architecture, which in turn could modify its light capture efficiency and hinder or enhance biodiversity effects due to architectural differences among species. Despite the evidence for phenotypic plasticity in plants, its role has never been examined explicitly in BEF studies so far.

In this study, we investigate the mechanisms through which tree diversity enhances community-level light capture in a tropical forest biodiversity experiment. As in classical BEF experiments, a synthetic gradient of species diversity (48, 24, and 24 subplots with 1, 3, and 6 native Panamanian species, respectively) was established by planting >5000 trees of native species over ~6 ha in Sardinilla, central Panama (Scherer-Lorenzen et al. 2007). Species were chosen to mimic early stages of succession while covering the range or relative growth

rates observed in the nearby natural forest of Barro Colorado Island. Species diversity had little effect on mortality five years after planting, but tree growth was significantly enhanced in mixtures compared to monocultures (Potvin and Gotelli 2008). As a result, overyielding increased in magnitude over time (Sapijanskas et al. 2013). While previous work showed that factors other than light, most likely belowground mechanisms, also contributed to overyielding in this experiment (Sapijanskas et al. 2013), our specific objective here is to disentangle and assess the relative importance of mechanisms leading to aboveground light partitioning, as light competition is widely regarded as a key process in forest ecosystems (Oliver and Larson 1996, Purves and Pacala 2008).

Our approach is as follows (Fig. 1). First, we test whether there is a diversity effect on community-level light capture. Specifically, we test whether, at one point in time, mixtures outperform their "best" monoculture, i.e., the one that reduced light most (Fig. 1A). Light capture, however, is strongly correlated with tree size. Therefore a more complete light capture in mixtures could be a mere consequence, not a cause, of overyielding, and is not enough to demonstrate that light partitioning occurs. We thus develop innovative methods that combine empirical data (light availability and traits related to light capture, including leaf phenology), a spatially explicit light interception model calibrated for the experiment, and bootstrap statistical methods to tease apart the mechanisms contributing to light partitioning. Specifically, we separately test whether, once the confounding diversity effects on tree growth are removed, differences in crown architecture (mechanism M1), plastic changes in crown shape (M2), or temporal niche complementarity (M3, leaf phenology) improve light capture in mixtures (Fig. 1B).

METHODS

Experimental design

The experimental plantation is located in Sardinilla, ~50 km north of Panama City, Panama. Mean annual rainfall at the nearest meteorological station (Buena Vista) is 2351 mm, with 25–50 mm per month during the dry season (January to March) and ~250 mm per month during the rainy season (May to November). Daily and seasonal temperatures are relatively constant, ranging from a daily maximum of 34.3°C to a minimum of 21.1°C in January (STRI 2009). Following the classification of Holdridge and Budowski (1956) the experiment mimics tropical moist lowland forests.

In July 2001, 5566 seedlings of six native species were planted in ~22.5 × 22.5 m subplots to establish a synthetic gradient of species richness (Scherer-Lorenzen et al. 2007). Each species (*Anacardium excelsium*, Ae; *Cordia alliodora*, Ca; *Cedrela odorata*, Co; *Hura crepitans*, Hc; *Luehea seemanii*, Ls; and *Tabebuia rosea*, Tr) was included in eight monoculture subplots, in 12 three-species subplots and in 24 six-species subplots.
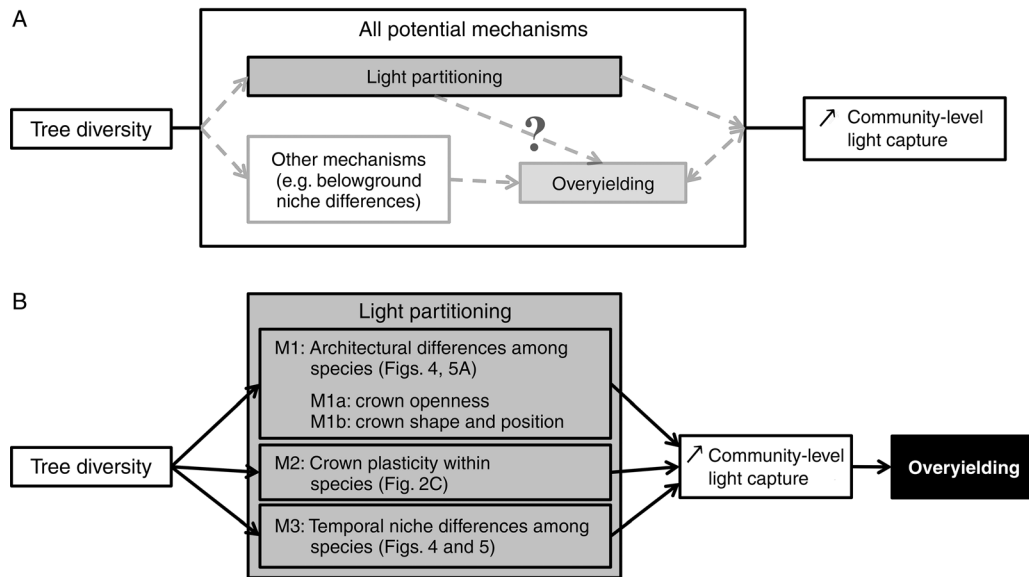
Fig. 1.   Outline of the mechanisms tested. (A) We first tested whether, when all species are fully foliated, mixtures captured more light than their best constituent monoculture. However, a more complete light capture in mixture could be a *consequence*, not a *cause* of overyielding. (B) We then separately tested whether, once diversity effects on tree growth were controlled for, mechanisms M1, M2, or M3 improved light capture in mixtures. Architectural differences among species (M1) were further divided into differences in crown openness (M1a) and differences in crown shape and position (M1b) in our final analysis. Any effect of these mechanisms would indicate that light partitioning occurred and most likely contributed to overyielding.

Composition of the three-species plots was defined by randomly choosing between fast growers (Ca and Ls; RGR of 7.0% and 9.1% per year in BCI [Scherer-Lorenzen et al. 2007]), intermediate species (Ae and Hc; 5.9% and 4.9%), and the two slowest growers (Co and Tr; 2.3% and 3.4%). Consequently, while species composition differed among the three-species subplots, faster- and slower-growing species were equally represented in any given plot. The six-species subplots are, however, perfect replicates. Within each subplot, trees were planted following a multiple Latin-square design, to ensure that systematic environmental variation did not bias the results. *C. alliodora* failed to establish. Of the 900 initially planted, only 51 individuals remained in 2011, all in mixtures. At year 9 after planting, there were thus 88 subplots of interest: 40 monocultures (8 per species), 24 three-species mixtures (T1-1 to T6-4) and 24 six-species mixtures (A1-1 to A6-4). Appendix A provides a complete description of the study site and experimental design.

Observed light availability at ground level

We measured light availability 1 m above ground level at the center of each of the 88 subplots with hemispherical photographs taken in September 2009. Each photograph was analyzed with Gap Light Analyzer (GLA; Frazer et al. 1999) to obtain a gap light index (GLI), which measures the proportion of incident photosynthetically active radiation (PAR) transmitted through the forest canopy to a specific location in the

understory over a certain time period (Canham 1988a). Differences in leaf phenology among species precluded calculations over a whole growing season from our photographs, which captured the quantity and distribution of foliage at one point in time. We therefore adjusted solar and meteorological parameters to estimate GLI for September 2009. Methods followed standard protocols and are further detailed in Appendix B.

Light interception model

We developed a spatially explicit light interception model that predicts light conditions (GLI) as a function of the location, size, and identities of trees in the vicinity, and local solar and meteorological parameters. Our model was adapted from the light module implemented in SORTIE (Canham et al. 1999) to incorporate phenological differences among species and microtopography thanks to a digital elevation model of the Sardinilla experiment (Wolf et al. 2011). The crowns of individual trees were modeled as semiopaque cylinders through which species-specific fractions of incident light (crown openness, CO) are transmitted. The top of the crown was set as the measured height of the tree, while empirical relationships were used to relate tree size to crown base and radius. Species-specific architecture was thus captured through differences in measured height, species-specific CO, and species-specific allometric relationships of crown radius and crown depth. A detailed

description of the model and its calibration using hemispherical photographs are provided in Appendix C.

Predictions of the light interception model were closely related to observed GLI values with a relationship not significantly different from identity (Appendix C: Fig. C2, regression slope 0.95 ± 0.06 and intercept 1.84 ± 2.97). The regression between simulated and observed values was even closer to identity when considering mixture plots only (slope 0.99 ± 0.09 and intercept -1.42 ± 3.89). The absence of bias ensures that systematic deviations between observed and simulated values in bootstrap tests are not due to the light model. Diversity, measured as subplot-level species richness, did not explain deviations from the model (Appendix C). There was no miscalibration that might have produced "false" diversity effects in the subsequent tests, and reciprocally, our light interception model captured the most important aspects that may contribute to diversity effects on community-level light capture, namely, overyielding, differences in architecture among species and/ or plastic changes in crown geometry.

Diversity effects on light capture when trees are fully foliated

We first investigated diversity effects at one point in time, which also allowed us to measure community-level light capture empirically. To do this, we developed a novel, widely applicable method to disentangle causal mechanisms. We designed a set of bootstrap tests that are based on comparisons of empirical measures of community-level performance with null expectations derived from an individual-based mechanistic model (Fig. 2A). All tests share the same basic ingredients: tree assemblages are generated under a specific null hypothesis, percentage of light (GLI) transmitted through these virtual assemblages is computed with the calibrated light model and compared to both direct GLI observations and GLI predicted by the model for each subplot. This double comparison allowed us to check that deviations from null expectations were not due to model bias. Mortality and size of the trees in the direct vicinity of the measurement point are the main factors influencing light availability, and thus they generate biotic and abiotic spatial effects that can be independent of diversity. We therefore used a stratified bootstrapping approach to control for these spatial effects and isolate diversity effects. Basically, these tests compare light measured at one point with what would have been measured at the very same point if the neighboring trees had been different (e.g., in all or certain traits) but similar in relative size classes (see Appendix D for details).

First, we tested whether mixtures outperformed the best monoculture in their ability to capture light (Fig. 1A). For each species i, null assemblages were created by replacing any live tree in mixtures where that species was present with a tree sampled from species i's monoculture and sharing the same relative size class as observed in the mixture (Appendix D). GLI was computed with the light model for 5000 replicate simulations to obtain a bootstrap GLI distribution for every mixture subplot that included species i. In total, we thus computed as many GLI distributions as the number of mixture subplots times their species richness. For each mixture subplot, its observed GLI value was then compared separately, with each GLI distribution obtained from its constituent species. Systematically smaller GLI values in observed mixtures compared to expectations based on all their constituent monocultures, and thus on the best-performing monoculture, are interpreted as evidence that light interception was enhanced thanks to differences in architecture among species, overyielding, and/ or plastic changes in crown geometry.

Second, we tested whether plastic changes in crown shape alone contributed to improve light capture in mixtures (M2, Fig. 1B). We compared GLI in monocultures with GLI in null assemblages constructed by replacing each tree in monocultures with a tree of the same size, height, and species identity, but with a crown depth and crown radius obtained from allometric relationships observed in six-species mixtures. We used a model averaging approach and propagated both model selection uncertainty and uncertainty due to each candidate allometric model to produce 95% confidence intervals of expected GLI. More details on the allometric models are given in Appendix C. Systematically higher GLI values in observed monocultures would indicate that plastic changes in crown shape contributed to diversity effects on light capture.

Differences in leaf phenology

We reconstructed species-specific leaf phenology from four data sources. Three sources spanned a complete year: sap-flux data (grams per square centimeter per day), direct foliage observation and litter trap data (grams per 15 days) (Fig. 3). The fourth consisted of hemispherical photographs taken in December 2007, March and June 2008, and September 2009 (see Appendix B). Granier-type thermal dissipation probes were used to measure sap-flux densities in 12 replicate trees per species, and daily maximum values were estimated (Kunert et al. 2010). The percentage of foliage was estimated on the same individuals on a monthly basis, or more frequently if changes were suspected. Sap flux and percentage of foliage were measured from July 2007 to June 2008 (see Kunert et al. 2010, 2012 for details). Litter collected in 100 traps dispersed over the plantation was weighted to species every two weeks from July 2010 to June 2011 (Potvin et al. 2011).

We modeled leaf dynamics as binary: "foliated" or "leafless" (Fig. 3F). Starting dates of leafless periods were visually identified as fortnights (two weeks) when the percentage of foliage dropped substantially and no longer differed from its minimum observed value, while both litterfall and sap flux were close to their minimum after a peak (Fig. 3). Species were considered to have recovered a fully foliated state when litterfall was close
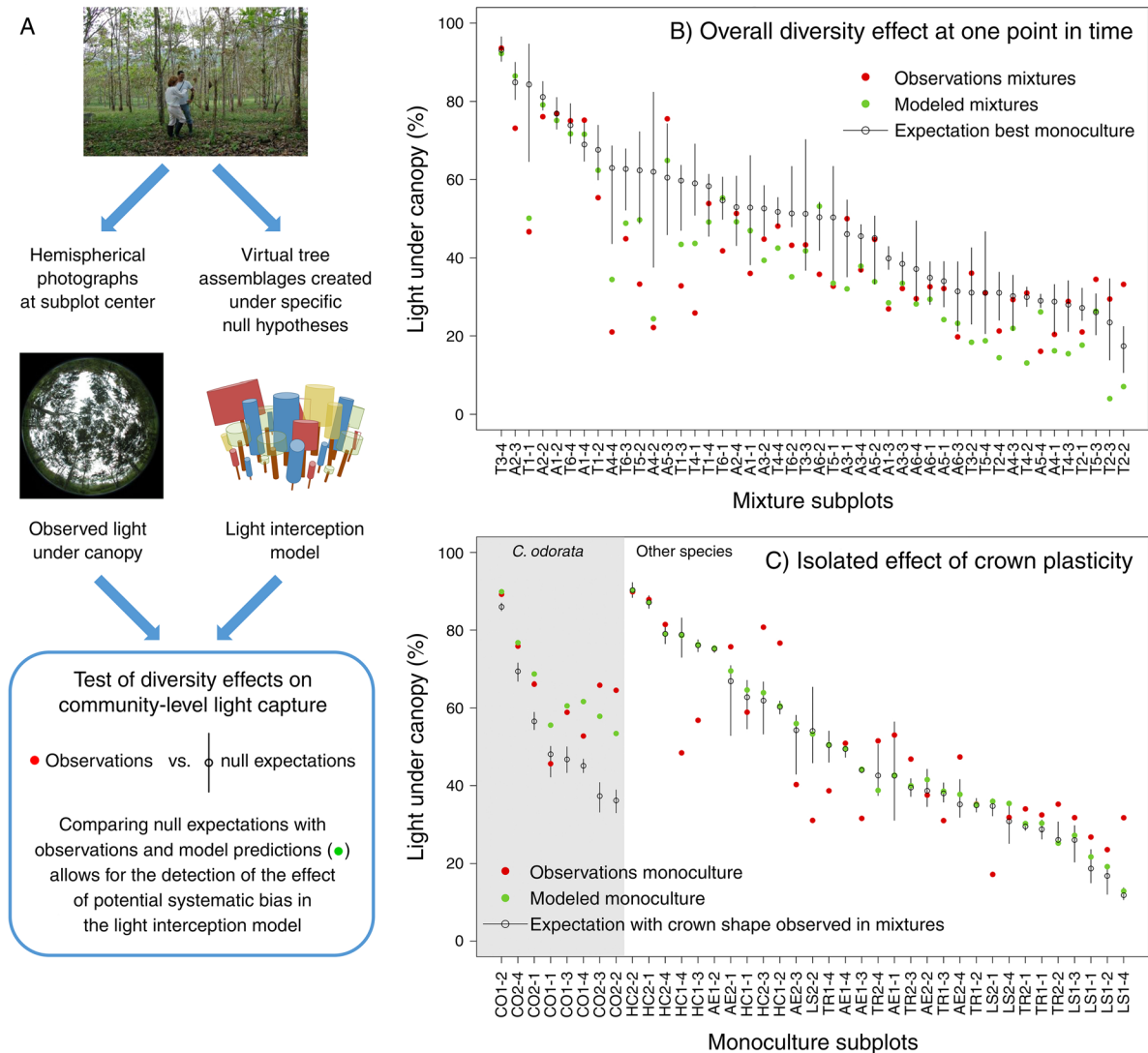
FIG. 2. Diversity effects on light capture at one point in time, when all species are fully foliated (September). Panel (A): overview of the methods. Tree assemblages are generated under a specific null hypothesis. Panel (B): no overall "transgressive" diversity effect; panel (C): no effect of plastic changes in crown allometry within species, percentage of light transmitted through these virtual assemblages is computed with the calibrated light model and compared to observations in each subplot. Panels (B) and (C): Green symbols represent light reaching ground as predicted by the light model; red symbols represent observations. Open symbols and lines: mean and confidence intervals of light capture by the best constituent monoculture controlling for mortality and spatial effects (panel B; Fig. 1A) or by monocultures that would have the same crown allometry as observed in mixtures (panel [C]; Fig. 1B: M2). Panel (B): lines are 99% CI to obtain a 5% type I error at the multiple-comparison level (Bonferroni correction). Panel (C): lines are 95% CI; shaded area shows *C. odorata* monocultures.

to its minimum, and sap flux and foliage were >50% of their maximum simultaneously. Species Hc showed high inter-individual variability and a lack of consistent seasonal pattern in leaf phenology (Fig. 3B). Nevertheless, phenological data (Fig. 3) and hemispherical photographs from phenological periods 1, 2, 3, and 5 allowed us to define two distinct periods corresponding to higher and lower mean foliation, respectively. For Ae and Ls, the only species that had their leaf phenology documented by previous studies, our reconstruction was

consistent with observations in a nearby seasonal tropical forest (Newell et al. 2002, Kitajima et al. 2005).

Diversity effects on light capture over a whole year

While the tests in the previous sections have the advantage of being closely tied to empirical data, they also have the disadvantage of being restricted by the period and location of the light measurements and limited in the mechanistic insights they provide. Therefore we designed four virtual biodiversity experiments that used our light interception model to explore

diversity effects on light capture over a full year while removing the confounding effects of overyielding, i.e., differences in tree growth. These virtual experiments were designed to investigate in turn the combined and independent effects of differences in (M1a) crown openness, (M1b) crown shape and position, and (M3) phenology among species (see Fig. 1).

First, we explored the combined effects of all architectural and phenological differences among species (M1 + M3). We generated a gradient of functional diversity by systematically varying the proportions of the five species included in the virtual experiment. We excluded Ca from the species pool since it failed to establish in the plantation. Virtual stands mimicking our plantation's design were created by sampling trees with replacement from species' respective monocultures to control for overyielding. We numerically integrated over time (a whole year) and space (the whole stand) to calculate the percentage of total PAR captured by the trees as total PAR above the canopy minus PAR reaching the ground. A complete description of the virtual experiment is provided in Appendix E.

Second, we isolated differences in crown openness alone (M1a) because they are bound to generate positive diversity effects due to the functional form of the light interception process (which is nonlinear, see Appendix F) without any real form of complementarity among species. We carried out the same virtual experiment except that we created mixtures by sampling tree diameters and heights from Ls monocultures and applied the leaf phenology and crown allometry of Ls to all trees. We then focused on architectural differences related to crown shape and position (M1b) to detect light partitioning in space. We ran an experiment that removed temporal niche and crown openness differences among species by setting the leaf phenology and the CO of all species to that of Ls. All other differences among species were conserved. Finally, we isolated the effects of (M3) temporal niche differences by setting all species traits except phenology to that of Ls and by sampling tree diameters and heights from the monoculture of Ls. Results were similar with any species used as a reference and are presented with Ls, which is intermediate in its light capture ability.

In all four experiments, we measured the magnitude of the net diversity effect on light capture, Δ, as the surplus yearly PAR captured by a mixture compared to the null expectation based on monoculture performance

$$\Delta = L_{\text{mix}} - \sum_i p_i L_i \qquad (1)$$

where L_i is the average light captured by monocultures of species i, p_i is the proportion of species i in the mixture, and L_{mix} is the total PAR captured by the mixture. If there is no net diversity effect, that is, if mixtures behave like juxtaposed monocultures or, equivalently, if there is no difference in the average amount of light captured per tree, $\Delta = 0$; $\Delta > 0$ and $\Delta <$ 0 correspond respectively to positive and negative net diversity effect. The parameter Δ is similar to Yachi and Loreau's (2007) light complementarity index.

For each simulation, we computed the leaf area index (LAI, ratio of leaf area to ground area, in square meters per square meter), a community-weighted mean crown openness (CWM_{CO}), and a functional diversity index (FD_{pheno}) that increased with the degree of temporal niche complementarity among species. Leaf area was obtained from species-specific allometric relationships of total leaf dry mass (Sapijanskas et al. 2013) and measurements of specific leaf area (Ruiz-Jaen and Potvin 2011). FD_{pheno} was calculated as the functional dispersion (FDis; Laliberte and Legendre 2010) of the following pairwise distances among species

$$d = \frac{\text{Number of days one species only is foliated}}{\text{Number of days both species are foliated}}. \qquad (2)$$

Species were weighted by their leaf area. We computed CWM_{CO}, a proxy of functional identity (Roscher et al. 2012) also referred to as functional dominance (Ruiz-Jaen and Potvin 2011), to capture selection effects on crown openness and foliated period length (Roscher et al. 2012). CWM_{CO} weighted species' yearly average CO by their respective leaf area

$$CWM_{CO} = \frac{\sum LA_i[N_i CO_{\text{leaf},i} + (365 - N_i)CO_{\text{leafless},i}]}{365 \sum LA_i} \qquad (3)$$

where N_i is the number of days species i is foliated, LA is leaf area, and CO is crown openness. The amount of variation in Δ and total amount of light captured explained by LAI, CWM_{CO}, and FD_{pheno} was partitioned by redundancy analysis (RDA) to tease apart the relative contributions of functional trait diversity and functional identity, i.e., complementarity and selection effects (Roscher et al. 2012).

RESULTS

Diversity effects on light capture when trees are fully foliated

Comparing the amount of light observed under the canopy of mixtures with expectations based on their "best" constituent monoculture showed that mixtures captured more light in 63% of the mixture subplots (Fig. 2B). The difference was significant overall (Fisher's combined probability test $\chi^2(92) = -2 \sum \ln P$(bootstrap > obs) = 556.2, $P < 0.001$). Possible model biases cannot explain these results, since all observations of light level under the canopy but one (subplot T2-2) followed the general trend of model predictions (red vs. green symbols in Fig. 2B).

In one species, C. odorata, plastic changes in crown architecture contributed to the more complete light capture in mixtures since all monoculture subplots captured less light than expected if the very same trees
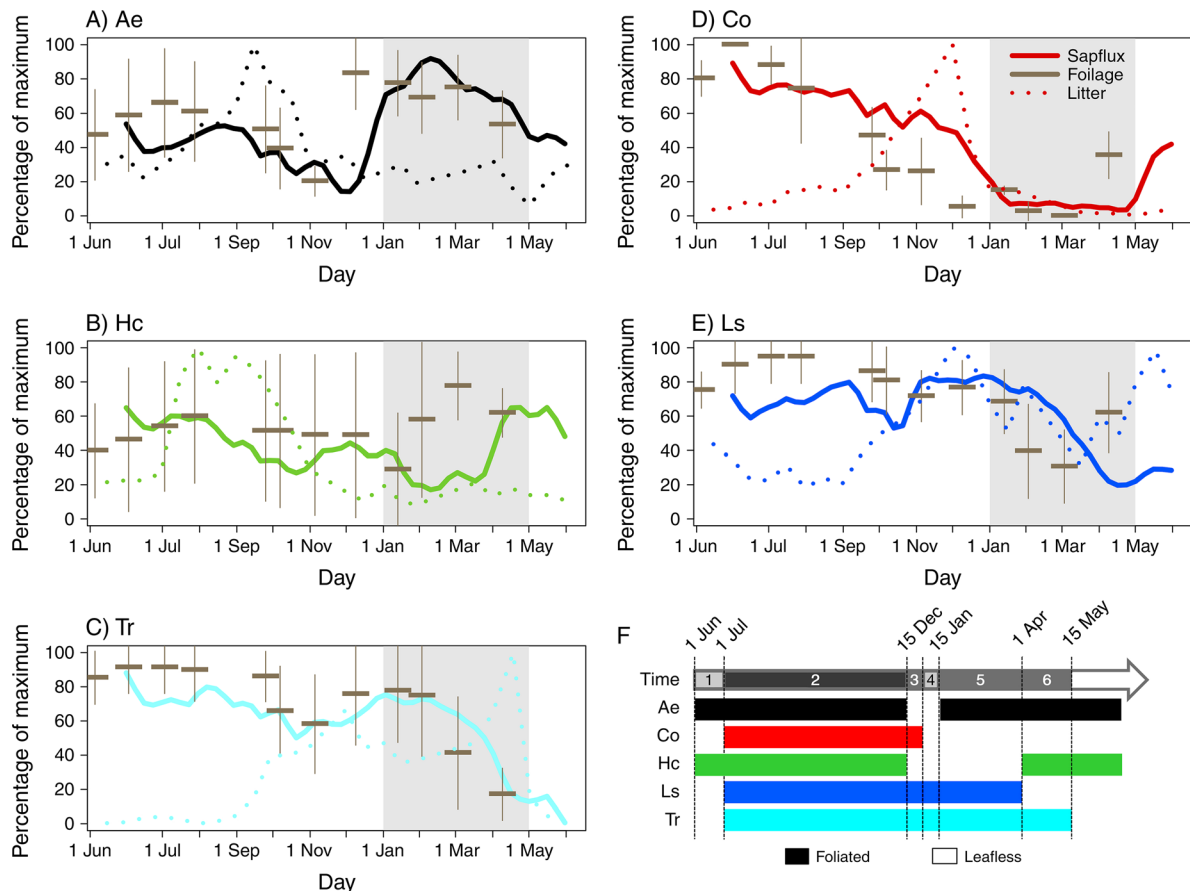
FIG. 3. Observed and modeled leaf phenology in the Sardinilla plantation. Panels (A) to (E): direct foliage observations, litter trap, and sap flux data over a year. (One panel per species: Ae, *Anacardium excelsium*; Hc, *Hura crepitans*; Tr, *Tabebuia rosea*; Co, *Cedrela odorata*; Ls, *Luehea seemanii*; *see Methods: Differences in leaf phenology*). Brown bars and lines are mean and standard deviation of percent foliage (12 replicate trees per species). Thick lines are mean normalized sap flux (maximum daily sap flux relative to yearly maximum, 12 replicate trees). Dotted lines are litter mass accumulation in traps over 15 days relative to yearly maximum. The shaded zone shows the dry season. Panel (F): modeled phenology. In shades of gray, the time line at the top shows six distinct phenological periods with either all (period 2), three (periods 3, 5, and 6), or only two (periods 1 and 4) foliated species.

(same identity, position, height, and diameter) had the crown geometry observed in six-species mixtures (Fig. 2C). Again, possible model biases cannot explain this result, since light measurements in the field were also smaller than expectations in seven out of eight CO subplots. For the other species, with the exception of one subplot (LS2-4), deviations in predicted light under the canopy were smaller than the uncertainty due to allometric models (Fisher's combined probability test $\chi^2(92) = -2 \sum \ln P(\text{bootstrap} < \text{obs}) = 637.9$, $P = 0.32$).

Diversity effects on light capture over a whole year

Over a whole year, the net diversity effect on light capture in virtual stands that included all trait differences among species was positive (mean mixture $\Delta = 5.44$, $t(44.8) = -36$, $P < 0.001$, two-sample t test; Fig. 4B; orange bars). Individual trees in mixtures thus captured more light on average than expected based on their performance in monoculture. Both architectural and temporal niche differences contributed indepen-

dently to these effects (Fig. 4B: gray, white and blue bars) and produced mixtures that captured up to 10% more of total available light than expected (Fig. 4C). The surpluses Δ are to be compared with mean monoculture performances, which ranged from 32% (*C. odorata*) to 74% (*A. excelsium*), with an average of 54% of total available PAR captured. As expected (Appendix F), variation in crown openness had positive effects on light capture (Fig. 4B: gray bars). However, these effects were small compared to those of differences in crown shape and position, indicating that species partitioned light in space in our experiment. The strongest driver of diversity effects was temporal niche differences among species (Fig. 4B).

To further assess the importance of temporal niche complementarity, we partitioned the variation in the surplus light capture Δ into effects explained by the total quantity of leaves (leaf area index LAI) of a stand, the mean crown openness across trees and time (community-weighted mean crown openness, CWM_{CO}) and a

functional diversity index increasing with temporal niche complementarity (FD_{pheno}). In the "combined" virtual experiment that included all trait differences among species, temporal niche complementarity explained 34% (RDA, $P < 0.001$) of the variation in the surplus light capture Δ vs. 7% and 2% for the two controls, LAI and CWM_{CO}, respectively.

However, in this "combined" experiment, the total amount of light captured was strongly associated with CWM_{CO}, which explained 78% of variation on its own (Fig. 5A). FD_{pheno} explained 9% of variation, among which 6% was shared with CWM_{CO} and LAI. The relatively low amount of variation in total light capture explained by FD_{pheno} relative to that for deviations Δ was to be expected, as it would be quite surprising if the degree of temporal niche overlap explained absolute light capture independently of other traits such as crown openness, tree height, or foliated period length. Since CWM_{CO} is a community-level average built from species crown openness and foliated period length, this result shows that mean trait and not variability per se has the strongest explanatory power. Selection effects are thus strong on crown openness or foliated period length. The virtual experiment that considered phenological differences only discarded selection effects on all traits except foliated period length, but yielded similar results (Fig. 5B). FD_{pheno} and CWM_{CO} explained 7% and 48% of variation, respectively, with no overlap, while LAI and CWM_{CO} jointly explained an additional 36%. These results demonstrate that differences in leaf phenology produced both positive selection and complementarity effects on community-level light capture, and that selection effects were dominant.

Diversity effect on growth and light capture in mixtures vs. their best monoculture

Further investigations showed that once diversity effects on tree growth were controlled for, the effects of architectural niche differences and crown plasticity were not strong enough for mixtures to outperform their best monoculture at one point in time (Appendix D). Similarly, the effects of architectural and temporal niche differences were not strong enough on their own for mixtures to outperform their best monoculture over a whole year (Appendix E). Diversity effects on tree growth thus strongly contributed to enhance community-level light capture, and together with architectural and temporal niche differences and crown plasticity, enabled mixtures to outperform their best monoculture (Fig. 2B).

DISCUSSION

Light partitioning is often invoked as a mechanism explaining positive biodiversity and ecosystem functioning (BEF) relationships (Naeem et al. 1994, Yachi and Loreau 2007) but empirical evidence remains scarce, especially in forest ecosystems. Morin et al. (2011) and le Maire et al. (2012) recently attempted to detect light

partitioning in eucalyptus–acacia mixed plantations and European temperate forests, respectively, using a modelling approach. The first study showed a greater light capture in mixed plots. However, this increased light capture did not generate growth enhancement, which was hypothesized to result from other limiting resources. The number of species in this study (2) was also very limited. The second study, solely simulation based, demonstrated that competition for light alone can generate a general and long-term positive effect of tree diversity on forest productivity. Morin et al. (2011) attributed this result to complementarity effects and showed that interspecific differences in shade tolerance, maximum height, and growth rate played a key role in these diversity effects, but they did not formally identify underlying mechanisms.

Teasing apart the causal relationships between overyielding and enhanced light capture

Here we showed that tree diversity effects on tree growth, and hence on foliage density, were sufficiently strong to affect community-level light capture in our tropical forest biodiversity experiment. When all species were fully foliated, mixtures captured more light than their constituent monoculture that reduced light most. Controlling for the confounding effects of diversity effects on tree growth, we still detected positive diversity effects on light capture. Previous biodiversity experiments in grasslands also found that a greater canopy density and leaf area index allowed species-rich plant communities to capture more light (Spehn et al. 2005, Vojtech et al. 2008). Like Morin et al. (2011) and le Maire et al. (2012), however, these studies were unable to rule out the hypothesis that overyielding was caused by some other form of complementarity or selection than light partitioning. Fridley (2003) provided a more direct demonstration of overyielding due to light partitioning in grasslands by adding independent shade and fertility treatments to the classical BEF experimental design. In his study, highly fertilized mixture plots that overyielded when in full sun displayed no diversity effects when shaded at 50%. In Sardinilla, factors other than light, most likely belowground mechanisms, also contributed to overyielding (Sapijanskas et al. 2013). Nevertheless, we found evidence for light partitioning both in space and time after controlling for diversity effects on tree growth. Thus these mechanisms were independent of tree size and added to canopy density effects. Therefore we hypothesize that increased light capture did translate into increased C assimilation and growth in our experiment, thereby contributing to overyielding (dashed line in Fig. 1A).

We did not consider light use efficiency (LUE) because LUE is related more to tree growth than to light capture, and growth enhancement in mixtures has already been documented in our experiment (Potvin and Gotelli 2008, Sapijanskas et al. 2013). Moreover, increased LUE in mixtures would not necessarily
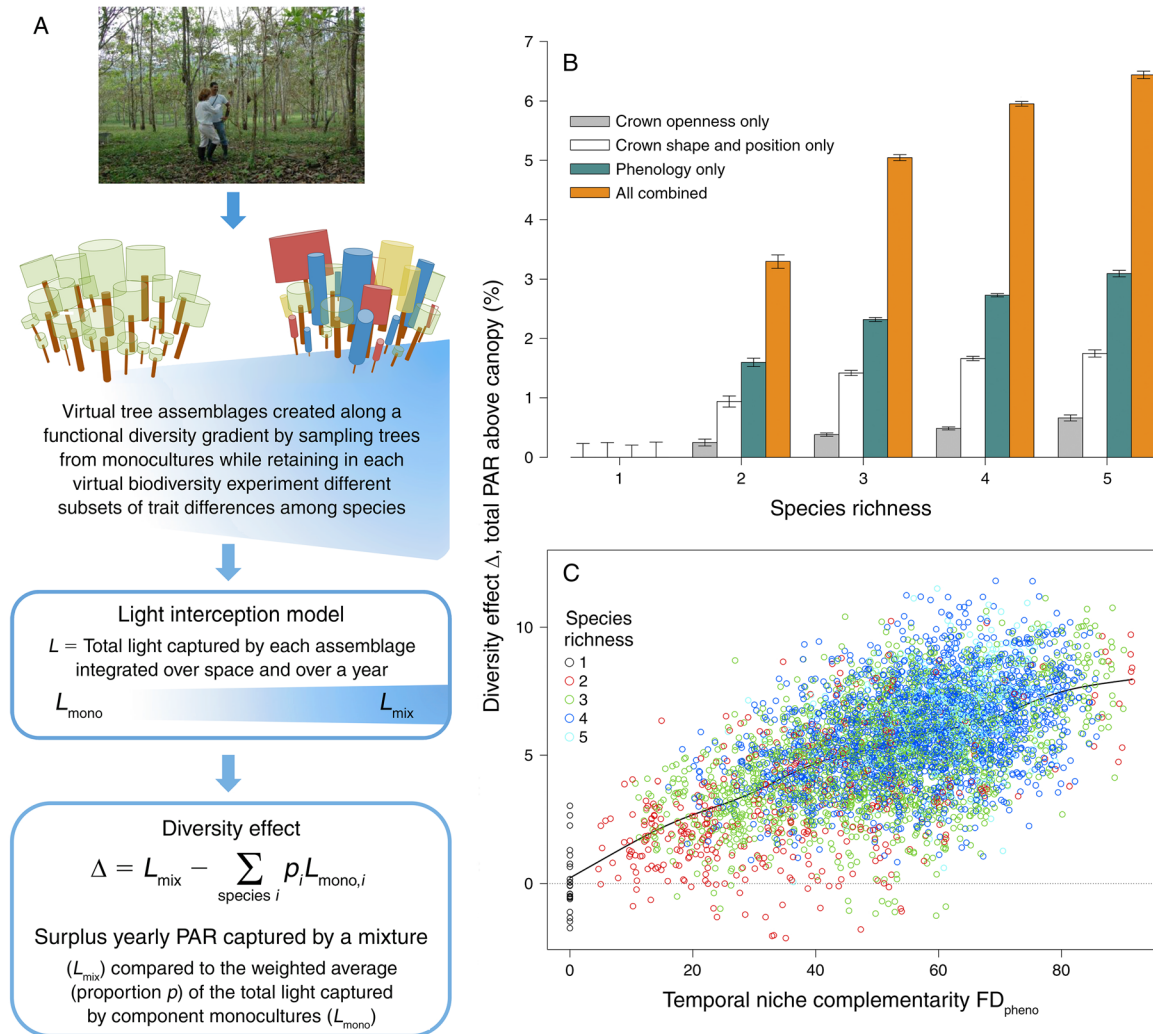
Fig. 4. Combined and independent effects of spatial and temporal light partitioning mechanisms. (A) Overview of the virtual experiments. Tree assemblages mimicking our plantation's design were created along a diversity gradient by sampling trees from monocultures to control for overyielding. Virtual experiments differed in the subset of trait differences retained among species. All (mechanisms M1 + M3 combined, see Fig. 1B); phenology only (M3); crown openness only (M1b); crown shape and position only (M1a). (B) Comparison of the diversity effects on light capture (Δ) in the four virtual experiments: phenological differences only (blue bars; Fig. 1B: M3), architectural differences only (white bars refer to crown shape and position [M1a]; gray bars refer to crown openness [M1b]); and combined differences among species (M1 + M3). Error bars show 95% CI around means. (C) Diversity effects Δ against temporal niche complementarity (FD_{pheno}) in the combined (M1 + M3) experiment. Each point corresponds to a virtual tree assemblage. Color codes for stand-level species richness. The black line shows a generalized additive model (GAM) fit. The net diversity effect Δ is reported as the percentage of total PAR above canopy.

indicate that light use is responsible for overyielding, since other factors, such as release from specialist pathogens and root competition, might be the ultimate causes for this effect. Conversely, light partitioning, provided it is strong enough, could induce overyielding even if LUE were lower in mixtures.

Light partitioning through niche differences and intraspecific crown plasticity

Multi-layering and complementarity among crown shapes are often proposed to explain growth enhancement in tree mixtures (Erskine et al. 2006, Pretzsch and Schutze 2009, le Maire et al. 2012), but to our knowledge these mechanisms have never been tested so far. Here we showed that architectural differences among species did generate positive diversity effects in our experiment. In particular, a virtual diversity experiment isolating the effects of differences in crown shape and position revealed that species partitioned light in space. However, these diversity effects were relatively small, saturated quickly with species richness, and were not sufficient on their own to explain why mixtures outperformed their best monoculture. The relatively minor role played by architectural differences is likely explained by strong
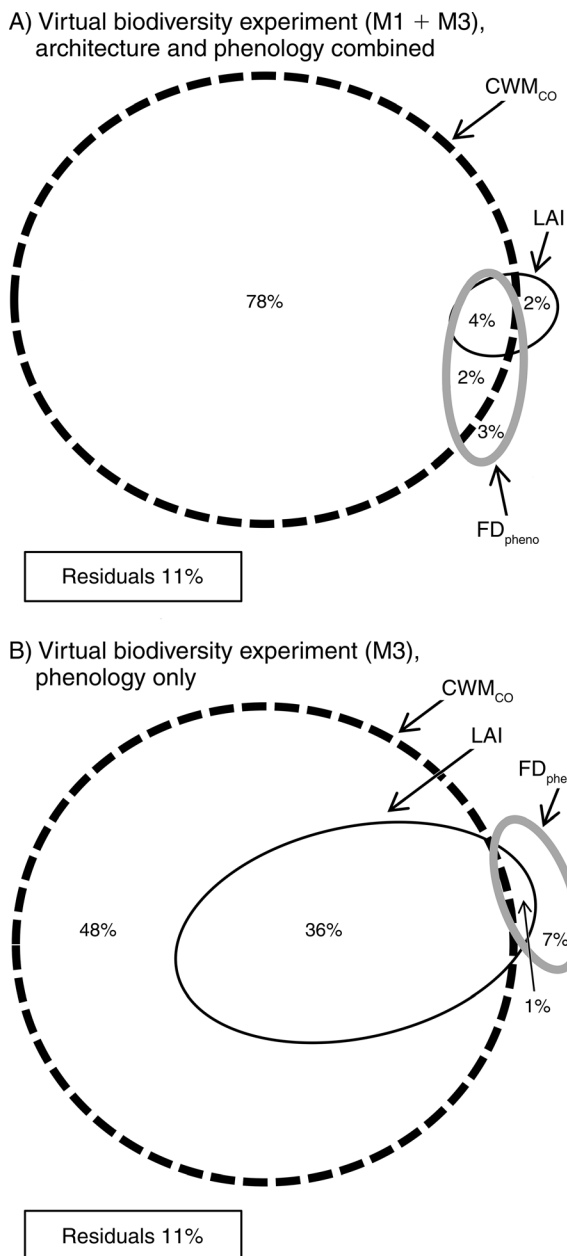
A) Virtual biodiversity experiment (M1 + M3), architecture and phenology combined

Residuals 11%

B) Virtual biodiversity experiment (M3), phenology only

Residuals 11%

Fig. 5. (A) Amount of variation in total light captured over a year explained by leaf area (LAI), community mean crown openness (CWM_{CO}) and temporal niche complementarity (FD_{pheno}) in the virtual biodiversity experiment including either all architectural and phenological differences among species (Fig. 1: M1 + M3); or (B) differences in phenology only (Fig. 1: M3). The area and the position of the circles in the Venn diagram are adjusted to the proportion of the variation explained by each variable. Variance partitioning by partial redundancy analysis (RDA). All testable parts were significant at $\alpha = 0.001$.

trait correlations across species that amplified differences in light capture efficiency among species: species with the most "opaque" crowns also had larger ($\rho = 0.79$) and deeper ($\rho = 0.77$) crowns on average in our study.

Moreover, our experimental plantation is relatively young. As packing constraints build up aboveground, architectural complementarity is likely to increase in more mature forests because of the feedback between crown spatial arrangement and differences in shade tolerance among species, which may allow mixtures to sustain more leaf area than do monocultures (Morin et al. 2011).

There is limited evidence for temporal light partitioning in temperate grasslands (Anten and Hirose 1999), where phenological differences among species can enhance productivity, decomposition, and nitrogen retention (Mouillot et al. 2011). Based on observations in cool-temperate forests in Japan, Ishii et al. (2013) hypothesized that seasonal differentiation and variation in diurnal patterns of photosynthesis among species might provide an explanation for positive BEF relationships in forests. The potential for temporal niche complementarity, however, is probably limited by winter conditions in temperate ecosystems. In our seasonal tropical system, contrasted leaf phenology among species (Fig. 3) held promise for strong complementarity effects on community-level light capture. After controlling for diversity effects on tree growth, we found that differences in leaf phenology were indeed the most important driver of light partitioning and produced both positive selection and complementarity effects on light capture. Selection effects were strong because of correlations among species between foliated period length and average crown radius ($\rho = 0.55$) and crown openness ($\rho = -0.57$). But selection and complementarity effects were partly confounded because the species that had the most distinct phenology also reduced light most. *A. excelsium* was complementary to all other species by having leaves when others are successively leafless, but it is also fully foliated for the longest time, and it grows a large, deep, and opaque crown relatively fast. Thus, overall, our results suggest that seasonal tropical environments offer good opportunities for phenological differences among species to generate positive complementarity effects.

To date, species diversity has been the main level of diversity considered in BEF research, while the effects of intraspecific variation on ecosystem functioning have been largely ignored (Reiss et al. 2009). For a given tree species and diameter, however, crown size and shape may vary substantially among individuals. Tree crowns respond to anisotropic light and space availability (Canham 1988b, Purves et al. 2007) as well as nutrient and water availability (Deleuze et al. 1996), climatic conditions (Geburek et al. 2008), and slope aspect (Ameztegui et al. 2012). Such variability in crown allometry is strong enough to affect light capture in forests (Vieilledent et al. 2010). Accordingly, individual-level plasticity in photosynthesis-related traits might be large enough to explain species coexistence and positive diversity effects in forests (Ishii et al. 2013). In our experiment, *C. odorata* grew larger crowns in mixtures

than in monocultures, most likely as a result of more intense inter- than intraspecific competition for light. These diversity-induced morphological changes improved community-level light capture in mixtures. Plastic changes in plant height are also probably involved in the positive relationship between plant diversity and aboveground biomass production in temperate grasslands (Dimitrakopoulos and Schmid 2004, Spehn et al. 2005, Roscher et al. 2011). Thus, our results add to the scarce but accumulating evidence that a predictive BEF knowledge will require a better understanding of species' plastic responses to changes in biotic interactions as species and functional diversity varies.

From mechanistic model to whole forest

We used a detailed light interception model to tease apart the mechanisms contributing to the effects of tree diversity on light capture. Albeit mechanistic, our model, like any model, has limitations that should be considered when interpreting its results. In particular, tree crowns were represented as semi-opaque cylinders, a simplification that precluded investigation of diversity effects mediated by more subtle architectural differences among species, such as differences in crown geometry, leaf angles, or leaf distribution within crowns (King et al. 1997, Kitajima et al. 2005, Valladares and Niinemets 2007, Duursma et al. 2012). This approximation, however, yielded satisfactory results, since the calibrated model reproduced field observations accurately (Appendix C: Fig. C5). Another potential limitation of our model pertains to the extent to which subtle architectural differences among species might alter community-level light capture. However, the benefit of a better description of leaf angles is doubtful if it is static, as trees can adjust leaf angles to light conditions in a matter of minutes (Posada et al. 2009). Adaptations to shade were not considered here either, because canopy closure is only starting to occur in the Sardinilla experiment. Hence, they were unlikely to play a major role in our results. They may nonetheless be substantial in mature forests where interception of low-intensity light by shade-adapted leaves may contribute to increased light capture by more diverse tree communities. Finally, crown development and its response to light are likely to be size dependent for many species (Sterck and Bongers 2001). Although tree species' rank order in architecture is generally maintained through time, ontogenetic crossovers in architecture have been reported among species (Poorter et al. 2006). Therefore the effects of crown plasticity and architectural differences that we demonstrate in our young plantation should be confirmed in more mature successional stages. But the mechanisms we detected are quite general, and provided similar trait differences are present, our results should be expected to also apply to mature forests.

One burning issue in BEF research is to what extent diversity effects documented in experiments scale up to real ecosystems (Lepš 2004, Srivastava and Vellend 2005). Can results from a tree diversity experiment be relevant to mature or secondary forests? Young plantations differ from mature or secondary forests in many aspects, including structural complexity, soil, and age or trophic structure (Leuschner et al. 2009). But other crucial forest ecosystem properties are less dependent on age. For instance, leaf area index (Messier and Kimmins 1991, Lieffers et al. 2002), fine-root biomass (Berish 1982, Vogt et al. 1987, Lei et al. 2012), soil water retention, and nutrient availability (Martin et al. 2000) are similar in young and mature stands. Ruiz-Jaen and Potvin (2011) compared functional traits of tree species growing in Sardinilla and BCI. Interestingly, the species that reached the largest sizes in Sardinilla all had low leaf mass area ratio and low wood density on BCI. In a recent meta-analysis, Zhang et al. (2012) showed that stand origin (natural vs. plantation) had negligible effects on the positive relationship between tree diversity and productivity. Observational studies in natural forests also suffer from strong methodological limitations, as differences in disturbance regime, stand structure, and environmental factors are likely to confound diversity effects in cross-site comparisons (Loreau 1998, Schmid 2002, Vilà et al. 2007). Thus, despite their limitations, experimental tree plantations are necessary complements to empirical work. Along with theoretical models (Morin et al. 2011), they offer the best way to disentangle causal mechanisms and formulate and test specific hypotheses (Kelty 1989, Scherer-Lorenzen et al. 2005).

Tree plantations are also of interest on their own. The loss of natural forests has been, to a certain extent, offset in many regions by a rapid increase in the amount of land allocated to tree plantations (FAO 2006). Although they account for <5% of forested lands, tree plantations already provide >15% of the world's wood production (Carnus et al. 2006), and will likely meet the global demand for wood in the future (Park and Wilson 2007). The development of well-designed, multi-purposed plantations that can help mitigate climate change by enhancing carbon sequestration or avoiding deforestation is becoming a burning issue in its own right (Paquette and Messier 2010).

CONCLUSION

To understand and predict the effects of biodiversity on ecosystem functioning is essential for assessing the dependence of humans on ecosystems. Nowhere is this need more evident than in forests, which provide critical ecosystem services to humankind. Our study sheds new light on the mechanisms that underlie the effects of biodiversity on ecosystem functioning in plant communities, and in forests in particular. We showed that tree diversity enhanced community-level light capture in our experiment through enhanced tree growth and at least three size-independent mechanisms: architectural differences, temporal niche differences, and morphological

plasticity. These three mechanisms enhanced the average amount of light captured per tree in mixtures, and hence most likely contributed to explain the strong diversity effects on growth observed in our plantation. Our work thus adds to the limited number of studies demonstrating that niche differences and phenotypic plasticity can generate biodiversity effects (Dimitrakopoulos and Schmid 2004, Cardinale 2011). By identifying and disentangling the detailed mechanisms through which diversity affects ecosystem functioning, our work contributes to building a predictive knowledge of the consequences of biodiversity changes.

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SUPPLEMENTAL MATERIAL

Appendix A

Experimental design of the Sardinilla plantation (*Ecological Archives* E095-219-A1).

Appendix B

Supplementary methods for the analysis of hemispherical photographs (*Ecological Archives* E095-219-A2).

Appendix C

Light interception model (*Ecological Archives* E095-219-A3).

Appendix D

Supplementary methods and results for the stratified bootstrap tests (*Ecological Archives* E095-219-A4).

Appendix E

Supplementary methods and results for the virtual biodiversity experiments (*Ecological Archives* E095-219-A5).

Appendix F

Mixtures effects thanks to differences in light extinction abilities (*Ecological Archives* E095-219-A6).