Received: 21 September 2018 | Accepted: 10 May 2019

DOI: 10.1111/1365-2664.13460

RESEARCH ARTICLE

Journal of Applied Ecology
BRITISH ECOLOGICAL SOCIETY

Tree performance in a biodiversity enrichment experiment in an oil palm landscape

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Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: CRC990 and 192626868

Handling Editor: Marney Isaac

Abstract

1. Large-scale conversion of tropical forests into oil palm monocultures has led to dramatic losses of biodiversity and ecosystem functions. While ecological restoration is urgently needed in many oil palm landscapes, there is a lack of scientific knowledge of sustainable management strategies.
2. We established experimental tree islands of varying sizes (25 m^2 to 1,600 m^2) and diversity levels (1, 2, 3 and 6 species) in an oil palm plantation in Sumatra, Indonesia. Six native multi-purpose tree species including *Archidendron pauciflorum* (Jengkol), *Durio zibethinus* (Durian), *Parkia speciosa* (Petai), *Shorea leprosula* (Meranti), *Peronema canescens* (Sungkai) and *Dyera polyphylla* (Jelutung) were planted between living and felled oil palms. Here, we analyse the controlling factors of tree growth and survival during the first 4 years at the level of local neighbourhood and tree island.
3. We found a significant effect of diversity levels on tree productivity, that is, basal area was higher in multi-species than in single-species tree islands. This overyielding was attributed to enhanced tree growth, while mortality had no effect. In the local neighbourhood, tree species richness had a positive effect on tree growth during the first year only, indicating that selection and dominance of well-performing species at high level of diversity are most likely driving overyielding.
4. Trees grew better away from living oil palms, suggesting tree-palm competition. Proximity to felled oil palms increased growth especially during the first years, during which the planted trees might have benefited from the additional available space and resources. Despite positive edge effects from the conventional oil palm management in the surrounding, tree island size had an overall positive effect on tree growth.

Delphine Clara Zemp and Anne Gérard contributed equally to this paper.

5. *Synthesis and applications*. We planted native trees in an oil palm landscape following a tree island pattern. The establishment success differed widely among the six planted species. The selection of particular species is a decisive factor to foster a positive relationship between diversity and tree growth. Planting larger tree islands (e.g. 1,600 square metres) is a better option to enhance tree growth, but tree-palm competition implies a trade-off between tree growth and palm oil production in the tree islands.

KEYWORDS
agroforestry, diversity-productivity relationship, forest landscape restoration, Indonesia, sustainable oil palm, tree diversity experiment, tree growth, tree islands, TreeDivNet

1 | INTRODUCTION

Large-scale conversion of tropical forests into oil palm plantations has occurred in the last decades in particular in South East Asia (Vijay, Pimm, Jenkins, & Smith, 2016) and higher global demand for oil palm products has increased the pressure on remaining forest areas (Koh, Levang, & Ghazoul, 2009). Conventional oil palm plantations host only a minor fraction of the plant and animal species found in rainforests or traditional agroforests (Drescher et al., 2016; Fitzherbert et al., 2008; Foster et al., 2011; Wilcove, Giam, Edwards, Fisher, & Koh, 2013; Rembold et al., 2017). Conversion of forests to oil palm plantations has impaired a wide range of ecosystem functions such as non-harvested primary productivity (Barnes et al., 2014; Clough et al., 2016; Dislich et al., 2016). Planting multiple native tree species in oil palm landscapes might be one option to maintain biodiversity and ecosystem functions (Bhagwat & Willis, 2008; Koh et al., 2009), but trade-offs between the desired goods (e.g. oil palm yield) and ecological services (e.g. biodiversity) are expected (Foster et al., 2011). To alleviate such trade-offs, islands with multipurpose trees have been suggested as potentially area- and cost-effective enrichment planting components in agricultural landscapes (Holl, Zahawi, Cole, Ostertag, & Cordell, 2011; Rey Benayas, Bullock, & Newton, 2008). For example, tree islands were similarly effective in achieving natural vegetation recovery as plantation-like afforestation (Zahawi, Holl, Cole, & Reid, 2013) and allowed to recover a habitat with high tree cover at relatively fast rate (Corbin et al., 2016). However, there are many unknowns regarding the minimum adequate size, species number or composition of tree islands (Corbin & Holl, 2012; Rey Benayas et al., 2008).

The influence of species diversity on ecosystem function, and in particular on plant productivity, has been widely addressed in biodiversity-ecosystem functioning (BEF)-experiments (Cardinale et al., 2012; Quijas, Schmid, & Balvanera, 2010). In contrast to grassland experiments, however, tree-based BEF-experiments are still scarce, particularly in the tropics (Paquette et al., 2018). Results from these tree diversity experiments suggest that tree diversity often positively affects tree growth (Fichtner et al., 2018; Grossman et al., 2018; Huang et al., 2018; Paquette & Messier, 2011; Potvin & Gotelli, 2008; Van der Peer, Verheyen, Ponette, Setiawan, & Muys, 2018), and temporal stability of primary productivity (Hutchison, Gravel, Guichard, & Potvin, 2018; Morin, Fahse, Mazancourt, Scherer-Lorenzen, & Bugmann, 2014). Such BEF-effects have been linked to mechanisms such as niche differentiation, increased resource use efficiency due to interactions between species ("complementarity effects") or selection and dominance of species with particular traits in mixtures ("selection effects"; Loreau & Hector, 2001). Analysing the effects of tree diversity on growth and survival at different levels (tree individual, species, neighbourhood, plot) and over time, accounting for site-specific conditions, is needed to understand mechanisms underlying BEF relationships and thereby advance forest landscape restoration (Ammer, 2019; Paquette et al., 2018).

We investigated tree growth and survival during the first 4 years of trees planted in an oil palm landscape that integrates a BEF-component to test the effectiveness of tree islands as biodiversity enrichment and ecological restoration strategy (Teuscher et al., 2016; Zemp et al., 2019). The tree islands, or experimental plots, varied in size, tree diversity level and species composition. We expected performance to differ between species, as species unsuitable to grow at specific sites or in specific compositions may not survive the initial phase. We anticipated a positive effect of tree diversity on plot-level tree growth, mediated by local tree-tree interactions in mixed-species neighbourhood. Trees might have grown less well near edges, where environmental conditions might have been more stressful (Holl et al., 2011). Consequently, we expected a positive effect of plot size. Finally, we expected competition between trees and neighbouring oil palms. We tested for these effects over time by combining analyses at the level of local neighbourhood and plot, and by accounting for site conditions.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The biodiversity enrichment experiment EFForTS-BEE is located in Jambi province, Sumatra, Indonesia (Teuscher et al., 2016). EFForTS-BEE is part of the collaborative research project "Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems" (EFForTS; Drescher et al., 2016) and of the platform for ecosystem research in tree diversity experiments worldwide (TreeDivNet; Paquette et al., 2018). The climate in our study region is humid tropical, with a mean temperature of 26.7 ± 0.2°C and an annual rainfall of 2,235 ± 381 mm (Drescher et al., 2016). Loamy Acrisol is the dominant soil type in the region (Allen, Corre, Tjoa, & Veldkamp, 2015). The experiment was established in a conventional, mid-sized oil-palm plantation whose management includes regular manual weeding of the understory vegetation, regular application of organic and inorganic fertilizer and occasional application of herbicides and pesticides (for details see Teuscher et al., 2016).

In December 2013, we planted tree islands (or experimental plots) in the oil palm plantation, systematically varying plot size (25 m^2, 100 m^2, 400 m^2 and 1,600 m^2) and tree species diversity (0, equivalent to no tree planting, 1, 2, 3 and 6 species; Figure S1). We planted six native multi-purpose tree species (Table 1): *Archidendron pauciflorum*, Fabaceae, *Parkia speciosa*, Fabaceae; *Durio zibethinus*, Malvaceae; *Dyera polyphylla*, Apocynaceae; *Shorea leprosula*, Dipterocarpaceae and *Peronema canescens*, Lamiaceae. At each diversity level and for each plot size, each species was represented exactly once, following the random partition design by Bell et al. (2009). At diversity level 1 and 6, the species compositions were replicated in four plots of varying sizes. At diversity level 2 and 3, each species was selected randomly without replacement at each plot size, thereby forming unique species compositions. In total, the experiment comprised 24 single -species plots and 24 multi-species plots. The initial design of the experiment included four plots under experimental management at diversity level 0 and four control plots under management-as-usual, which were not incorporated in this study because no trees were planted (for details see Teuscher et al., 2016). The trees were planted in a 2 × 2 m-grid, resulting in six planted trees in the 25 m^2-plots, 25 in the 100 m^2-plots, 100 in the 400 m^2-plots and 400 in the 1,600 m^2-plots. We maximized the distance between trees of the same species (Figure S2). This resulted in a total of 6,354 planted trees (Table 1). The planted tree species differed in their habitat preferences including mid-to late successional species from old-growth (swamp) lowland forests as well as early successional species. The planting material (seeds, seedlings or cuttings) was bought on the local market and collected in the forest and around Jambi city. Therefore, the genetic variability among individuals may have differed among tree species, as well as seedling age at planting (Table 1). Organic and inorganic fertilizers were applied once prior to tree planting (Teuscher et al., 2016). After that, the management in the experimental plots comprised a total stop of fertilizer, herbicide and pesticide application. Manual weeding was done regularly in the plots until May 2016, then restricted to 1-m circles around the planted trees for tree saplings smaller than the surrounding grass layer. We established fences around the plots to protect the saplings from damage by wild boar, livestock, and humans. Photos of the tree species and tree islands are shown in Figures S2 and S3.

We measured a range of variables describing plot-specific site conditions at the beginning of the study period (see supplementary information and Teuscher et al., 2016). The plots were located in undulating terrain; elevation above sea level (ranging from 37–67 m a.s.l.) and slope (ranging from 0–21°) differed between the plots (Table 2). The soil texture and the soil carbon content were variable, whereas pH and bulk density were relatively similar across plots. Oil palm thinning contributed to varying light conditions across plots (Khokthong et al., 2019), and canopy closure did not fully occur at the time of the study (canopy openness ranging from 4%–70%). We determined the position of all planted trees as well as the trunks of felled and living oil palms in the plots, plus all oil palms outside the plots within a distance of 12 m to include the nearest palms in the surrounding plantation (Figure S1).

2.2 | Tree growth measurement and mortality survey

All planted trees were measured once per year between 2014 and 2018 in January and February. For each tree *z* and time *t*, we determined height (H_{z_t}, cm) and basal diameter (D_{z_t}, cm) measured 10 cm above ground, which was then converted to basal area (*BA*, cm^2). Tree survival was monitored by visual inspection and bark scratching and was reported as a binary variable containing "0" (dead) and "1" (survival). During the first year of the experiment, dead trees were replaced every 3 months. To exclude the effect of replanting on tree performance, we included only trees from the final cohort and analysed data starting in January 2015. We calculated relative growth rates (relative height increment *rHi* [$cm\ cm^{-1}\ year^{-1}$] see Equation 1, and equivalent for relative basal diameter increment *rDi* [$cm\ cm^{-1}\ year^{-1}$]) and absolute growth rates (height increment *Hi* [cm/year] see Equation 2, and equivalent for diameter increment *Di* [cm/year]) during the period Δt for each individual z:

$$rHi_{z,\Delta t} = \frac{\ln\left(H_{z_{t+\Delta t}}\right) - \ln\left(H_{z_t}\right)}{\Delta t} \tag{1}$$

$$Hi_{z,\Delta t} = \frac{H_{z_{t+\Delta t}} - H_{z_t}}{\Delta t} \tag{2}$$

The relative growth rates are commonly used because they allow to better account for difference in tree age and size (Ammer, Brang, Knoke, & Wagner, 2004), as it was the case at the time of planting in our experiment (Table 1). Values outside an interval of ±3 absolute standard deviations around the median of relative growth rates were considered outliers (Leys, Ley, Klein, Bernard, & Licata, 2013) and excluded from the analysis, which corresponded to less than 100 individuals in total. Survival rates (survival in %) were calculated as the proportion of planted individuals per unit of interest (e.g. plot, diversity level, overall experiment) that were dead at the time of monitoring. Significant differences in performance between species, and between single- and multi-species plots, were quantified using simple one-way ANOVA followed by a single-step Tukey test using

TABLE 1 Overview of the planted species

Species	Local name	Natural habitat	Main usage	Origin of planting material	Age_{2014} [months]	H_{2015} [cm]	H_{2018} [cm]	BA_{2015} [cm^2]	BA_{2018} [cm^2]	N_{2015}	N_{2018}
Archidendron pauciflorum (Benth.) I.C. Nielsen	Jengkol	Primary and secondary lowland rainforest[1]	Fruit	Seed, bought at the local market	19	163.8 ± 24	530.0 ± 31	0.72 ± 0.8	14.4 ± 21	1,061	910
Durio zibethinus L.	Durian	Lowland rainforests[2]	Fruit (also timber, medicinal)	Seed, bought at the local market	7	85.4 ± 74	274.2 ± 165	0.26 ± 0.3	4.27 ± 6.0	1,057	157
Dyera polyphylla (Miq.) Steenis	Jelutung	Primary lowland swamp rainforest[3]	Latex (also timber)	Seed, collected in the forest	7–8	52.8 ± 19	233.2 ± 105	0.23 ± 0.6	2.79 ± 2.6	1,061	139
Peronema canescens Jack	Sungkai	Profits from forest disturbance, not in primary forests, lowland[4]	Timber (also medicinal)	Cutting, from many trees close to Jambi city	19	224.6 ± 87	602.0 ± 264	3.04 ± 2.2	24.0 ± 22	1,057	1,002
Parkia speciosa Hassk.	Petai	Primary and secondary lowland rainforest[5]	Fruit	Seed, bought at the local market	19	149.0 ± 85	418.3 ± 259	0.79 ± 0.7	7.83 ± 8.4	1,057	824
Shorea leprosula Miq.	Meranti	Mixed dipterocarp lowland forest[6]	Timber	Wildling, collected in the forest	8–9	189.7 ± 193	433.12 ± 232	1.18 ± 0.8	8.67 ± 6.8	1,061	181

Note: Age_{2014} = age of the seedlings in 2014 when planted for the first time. H_{2015} = height measured in 2015, H_{2018} = height measured in 2018, BA_{2015} = basal area measured in 2015, BA_{2018} = basal area measured in 2018, N_{2015} = number of alive individuals in 2015, N_{2018} = number of alive individuals in 2018.

References: [1]Nielsen, 1992; [2]Yap et al., 1993; [3]Rudjiman & Tonanon, 1995; [4]De Graaf et al., 1993; [5]Wiriadinata and Bamroongrugsa, 1994; [6]Ashton, 1982.

TABLE 2 Overview of the environmental variables at the beginning of the study period in the 48 experimental plots used in the analysis, and their effects on tree growth (relative diameter increment *rDi* and relative height increment *rHi*)

	Summary statistics				**Effect on relative diameter increment (*rDi*)**				**Effect on relative height increment (*rHi*)**	
	Mean	***SD***	**Min**	**Max**	**Estimate**	***SE***	***p*-value**	**Estimate**	***SE***	***p*-value**
Elevation (m)	50.6	7.0	37.6	76.1	0.000	0.001	0.734	0.004	0.009	0.672
Slope (°)	8.91	5.9	0.40	21.3	−0.001	−0.002	0.468	−0.001	0.002	0.383
Clay-content	0.29	0.1	0.14	0.47	−0.177	0.072	0.014*	−0.211	0.108	0.051
Silt-content	0.41	0.1	0.18	0.58	0.051	0.072	0.481	0.019	0.063	0.768
Sand-content	0.30	0.1	0.08	0.6	0.015	0.058	0.792	0.036	0.058	0.540
C-content	0.021	0.006	0.0104	0.0394	1.310	0.896	0.144	1.475	2.175	0.498
pH	4.46	0.2	4.04	5.28	−0.063	0.051	0.216	−0.044	0.050	0.371
Bulk density (g/cm^3)	1.08	0.1	0.79	1.43	−0.055	0.039	0.161	−0.005	0.051	0.927
Canopy gap fraction	0.28	0.1	0.04	0.70	0.187	0.060	0.002**	0.287	0.053	$<10^{-7}$ ***

Note: The output of tree growth models are shown using an analysis of deviance (Type II Wald chi-square tests) using the *car* package. In the *rHi* model, the variable “elevation” was Z-transformed due to model convergence failure.
Abbreviations: *SE*, standard error; *SD*, standard deviation.
The environmental variables having a statistical signifiant effect on tree growth are indicated by asterisks (‘***’: *p*-value <0.001; ‘**’: *p*-value 0.01;‘*’:*p*-value <0.05).

'glht' function from 'multcomp' package version 1.4-8 (Hothorn, Bretz, & Westfall, 2008), corrected for heteroscedasticity using the *sandwich* package version 2.5-0 (Zeileis, 2004, 2006). We confirmed the statistical inferences with a Bonferroni-adjusted pairwise Wilcoxon-test.

2.3 | Effect of diversity on tree growth and mortality at plot level

Plot-level basal area (*sBA* in m^2/ha) was calculated as the sum of the basal area of all individual trees per plot divided by the area of the plot and then up-scaled to 1 ha. Plot-level basal area was considered resulting from the combined effects of individual basal area (related to growth) and mortality of the planted trees (Potvin & Gotelli, 2008). We used a bootstrapping approach to quantify the relative contribution of tree growth and mortality to plot-level basal area across diversity levels (Potvin & Gotelli, 2008). We ran three different models: (a) A *tree growth model*, (b) a *mortality model* and (c) a *net model*. In the *tree growth model*, trees in single-species plots were sampled and species-specific mortality probability was based on observations in mixed-species plots. A difference between observed and simulated plot-level basal area indicated an effect of tree diversity on tree growth. In the *mortality model*, trees were sampled in mixed-species plots and species-specific mortality probability was based on observations in single-species plots. A difference between observed and simulated plot-level area indicated an effect of diversity on mortality. In the *net model*, the sampled trees and species-specific mortality probability were based on single-species plots (details in Potvin & Gotelli, 2008). For each model type and diversity level (2, 3 and 6 species-plot), we created 1,000 assemblages and calculated the standardized effect size:

$$\mathrm{SES} = \frac{(\text{Observed sBA} - \text{Mean simulated sBA})}{\text{Standard deviation of simulated sBA}}$$

Following Potvin & Gotelli, 2008, we considered that SES outside the range [−2; 2] indicate significant effect of tree diversity on plot-level basal area after checking the normality assumption.

2.4 | Neighbourhood analysis

We modelled tree growth related to local neighbourhood to investigate tree-tree and tree-palm interactions, and potential plot edge effects. Tree-tree interactions were quantified using individual-based competition indices that accounted for size ratios and distances between the neighbouring trees and the target tree. These indices have been shown to reliably predict tree growth in tropical and temperate forests (von Oheimb et al., 2011; Zhao, Borders, Wilson, & Rathbun, 2006). The competition index *CI* of species s on each target tree *z* at time *t* was calculated as follows:

$$CI_{z,s,t} = \sum_{j \in s} \frac{D_{j,t}}{D_{z,t}(d_{zj} + 1)}$$

with $D_{j,t}$ the basal diameter of neighbour *j* belonging to species *s* at time *t*, $D_{z,t}$ the basal area of target tree *z* at time *t* and d_{zj} the distance between target tree *z* and neighbour *j* (Hegyi, 1974). The overall competition index for target tree *z* ($CI_{z,all,t}$) was the sum of $CI_{z,s,t}$ for all species *s*. The con-specific competition index for target tree *z* ($CI_{z,con,t}$) was $CI_{z,s,t}$ with *s* the species of the target tree, and the hetero-specific competition index ($CI_{z,hetero,t}$) for target tree *z* was the sum of $CI_{z,s,t}$ for all species *s* different from the target tree species (Zhao et al., 2006). Finally, we counted the number of species of the neighbouring trees at time *t* ($R_{z,t}$), considering only species that were different from the target tree species. Trees were considered neighbours if they were located within a certain radius from the target tree. The different radius that were tested (3, 5, 7 and 9 m) did not affect our results, and therefore, we showed results for 5 m, which corresponds to the minimum distance recommended in young subtropical broadleaf forests (von Oheimb et al., 2011).

We fitted linear mixed-effects models using restricted likelihood with relative growth rates (*rDi* and *rHi*) of all tree individuals as dependent variables and plot and species as a random intercepts (dummy-coded variables). The covariates were distances to the nearest living oil palm (in m), to the nearest felled oil palm (in m) and to the plot edge (in m), plot edge length (in m) as well as a tree-tree interaction term that were represented differently in four separate models. In Model 1, we used $CI_{all,t}$ to analyse overall competition. In Model 2, we used the number of tree species (R_t) to analyse local diversity effects. In Model 3, we used $CI_{con,t} + CI_{hetero,t}$. to analyse separately hetero- and con-specific competition. All variables except the number of species were log-transformed, as this improved the model diagnostics (increasing homogeneity of variance of the residuals and reduced bias between residuals and fitted values). To evaluate the

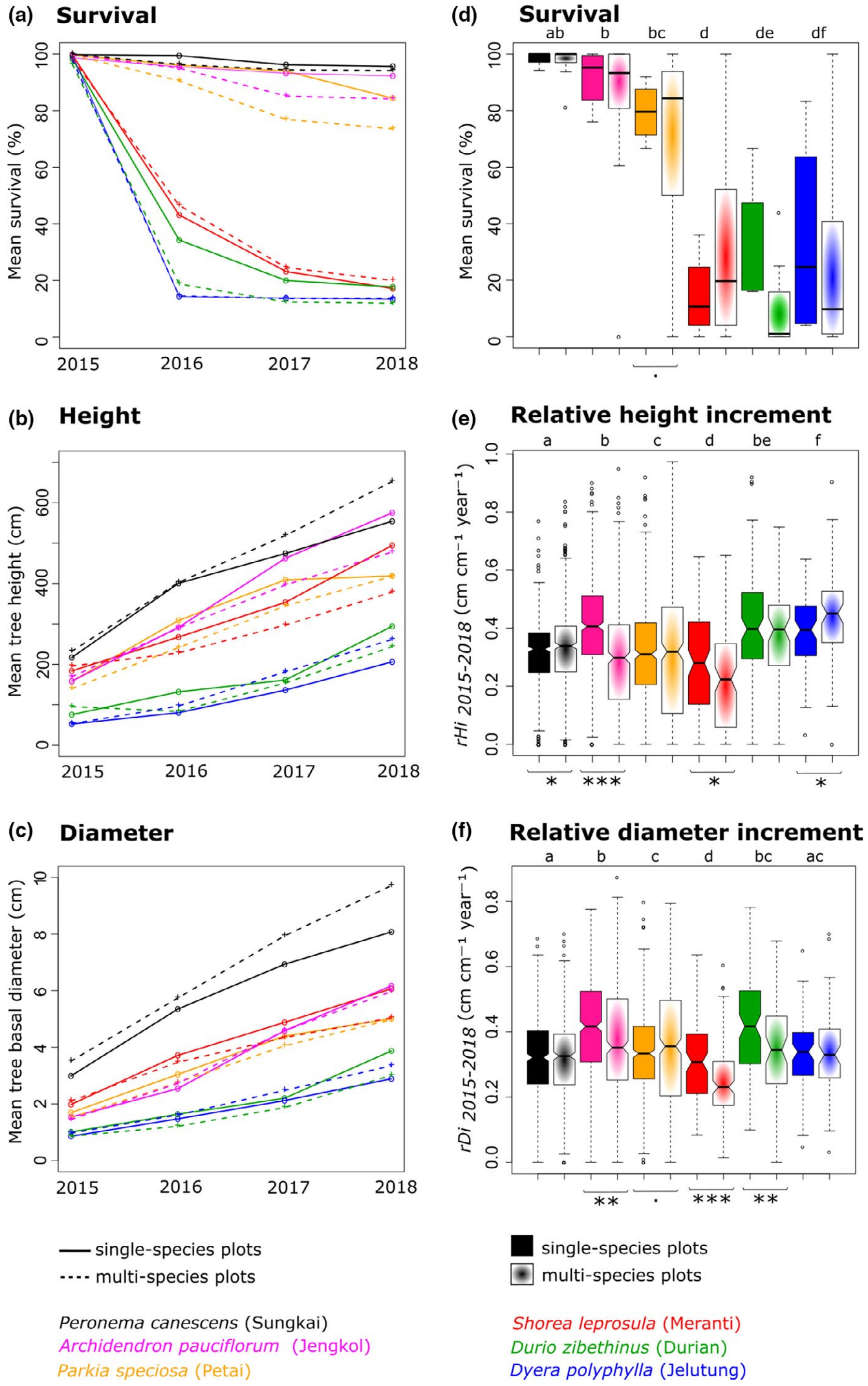

FIGURE 1 Species performances in single- and multi-species plots. For each species, (a) mean survival rate at plot level, (b) mean tree height and (c) mean basal diameter at individual tree level are shown over time. For each species, (d) survival rates in 2018 at plot level, (e) relative height increment (*rHi*) and (f) relative diameter increment (*rDi*) between 2015 and 2018 at individual tree level are shown with boxplots (boxes indicate interquartile ranges and whiskers extend 1.5 times the interquartile range below or above the box). Significant differences ($p < 0.001$) in performance between species are indicated by different letters above the boxplots. Significant differences between single- and multi-species plots are indicated below the boxplots: '.' ($p < 0.1$), '*' ($p < 0.05$), '**' ($p < 0.01$) and '***' ($p < 0.001$). Survival rates were calculated for a similar number of replicates (24 single- and 24 mixed-species plots, each species planted in similar proportion). Tree sizes and relative growth rates were calculated for individuals that survived at the end of the study period

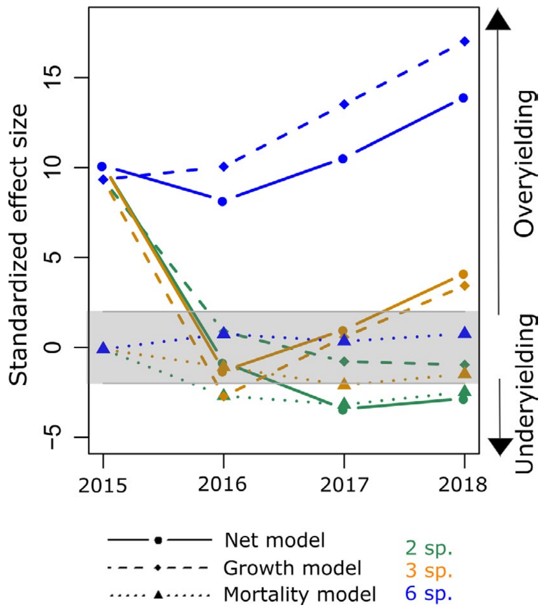

FIGURE 2 Effect of tree diversity on tree growth and mortality quantified from the bootstrapping approach. A standardized effect size above the grey area (SES > 2) means that multi-species plots have a higher plot-level basal area compared to single-species plots. This might be due to the contribution of tree growth (dashed lines), mortality (dotted lines), or both growth and mortality (solid lines)

changes over time, one model was built for each year of the study period ($\Delta t = 1$ year, i.e. 2015–2016, 2016–2017 and 2017–2018). By default, we ran the models using relative growth rates (rDi and rHi). Although relative growth rates are commonly used in tree growth models because they allow to reduce potential effects of varying tree sizes at the beginning of the study period, the effect cannot be completely ruled out for young tree communities (Ammer et al., 2004). Therefore, we also ran the model using absolute growth rates (Di and Hi) and included the basal diameter of the tree individuals at the beginning of the study year as additional covariate in the tree growth models as recommended by Ammer et al. (2004). To reduce the dependency of the model output on the presence or absence of correlated variables, we sequentially dropped covariates in the model according to our research questions. For example, distance to plot edge was entered with and without plot size in order to quantify the impact of plot size for a given edge effect.

2.5 | Influence of site conditions

First, we tested the effect of plot-specific site conditions on plot-level survival rates at the end of the study period (in 2018) and on tree growth during the entire study period (rHi and rDi, with $\Delta t = 3$ years, i.e. 2015–2018). Because we expected species to differ in their response to environmental variables, species identity was introduced as random slope (plot was not introduced to avoid failure of model convergence). In the rHi model, the variable “elevation” was Z-transformed due to model convergence failure. Second, we tested interacting effects between plot-specific site conditions and tree diversity on tree growth (rHi and rDi, with $\Delta t = 3$ years). Plot and species were introduced as random intercepts. We ran one linear mixed effect model for each environmental variable listed in Table 2. The environmental variables were log-transformed. The linear mixed-effects models were fitted and analysed using the packages *lme4* version 1.1-19 (Bates, Mächler, Bolker, & Walker, 2015) and *car* version 3.0-2 (Fox & Weisberg, 2019). All statistical analyses were conducted in R Version 3.5.2.

3 | RESULTS

In February 2018, the overall survival rate was 51% but differed among species (Figure 1). *P. canescens*, *A. pauciflorum* and *P. speciosa* had high survival rates (95%, 86% and 78% of all planted individuals survived respectively), whereas *D. polyphylla*, *D. zibethinus* and *S. leprosula* had low survival rates (13%, 15% and 17% respectively). The survival rate of *D. polyphylla* was lowest shortly after final planting (14% in January 2016), and stabilized in the following years. The survival rates of *S. leprosula and D. zibethinus*, in contrast, were relatively low in January 2016 (41% and 27% respectively) but continued to decrease gradually.

In February 2018, the tallest tree had reached 16.3 m height, and the largest stem had reached 25.8 cm basal diameter (both *A. pauciflorum*). On average, however, *P. canescens* reached higher sizes, followed by *A. pauciflorum*, *S. leprosula* and *P. speciosa* (Table 1). Relative growth rates (rHi and rDi between 2015 and 2018) varied significantly among species (Figure 1). *S. leprosula* was one of the tallest species at the beginning of the study period but had lowest relative growth rates (rHi and rDi). In contrast, *D. polyphylla* and *D. zibethinus* were shortest at the beginning of the study period but had high relative growth rates (highest rHi; Table 1).

Species performances differed between single- and multi-species plots (Figure 1). Compared to single-species plots, relative growth rates in mixed-species plots were higher for *P. canescens* (rHi) and *D. polyphylla* (rHi) but lower for *A. pauciflorum* (rHi and rDi), *S. leprosula* (rHI and rDi) and *D. zibethinus* (rDi). In fact, species growth rates differed depending on the number of planted tree species (Figure S5). Survival rates did not differ significantly between overall multi-species plots and single-species plots. However, the survival rate of *D. zibethinus* was lower in six-species plots compared with single-species plots.

The bootstrapping approach indicates that at the beginning of the study period, plot-level basal area was significantly higher in the multi-species plots compared to the single-species plots (Figure 2). This “overyielding” was attributed to larger basal area of individuals (i.e. tree growth), while mortality had no effect. In January 2016, this effect dropped drastically for two- and three-species plots, where plot-level basal area was no longer significantly different from single-species plots (i.e. no overyielding). In contrast, overyielding remained significant in six-species plots. In the following years (2017 and 2018), overyielding in the three- and six-species plots increased almost linearly, but the effect size was 3.4 times higher for six-species plots. This overyielding was again attributed to enhanced tree

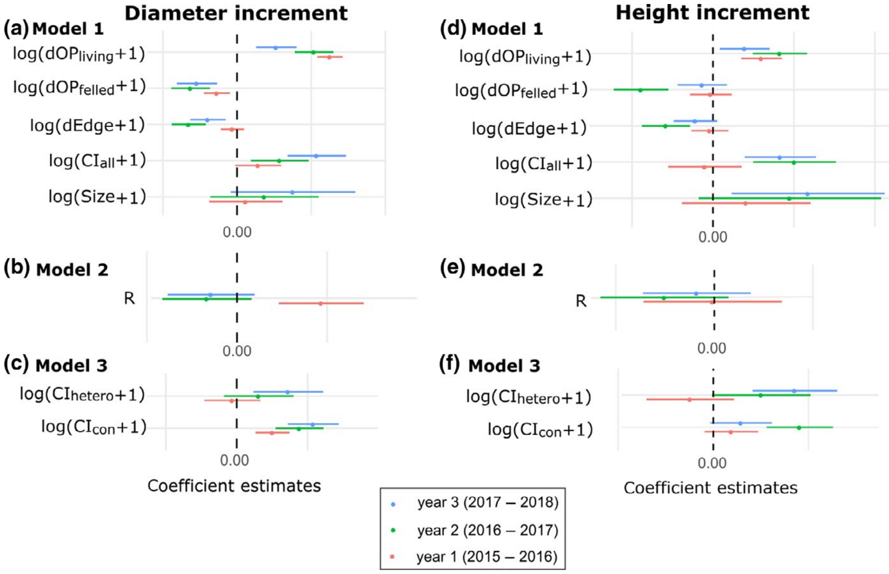

FIGURE 3 Analysis of tree growth at the level of local neighborhood. Effects of distance to the edge (dEdge), distance to living (dOPliving) and felled oil palms (dOPfelled), overall tree competition (CIall) and plot edge length (Size) were quantified in Model 1. Effects of local species richness (R) were quantified in Model 2. All variables except the number of species were log-transformed. Effect of con-specific (CIcon) and heterospecific (CIhetero) competition indices were quantified in Model 3. The x-axis shows coefficient estimates (dots) and 95% confidence intervals (bars) scaled by 2 standard deviations. In agreement with Type II Wald chisquare tests, covariates are considered significant when the error bars intersect zero (dashed lines). The figure was produced using dwplot function from the package dotwhisker version 0.5.0. Results are shown for absolute growth rates, while model results using relative growth rates are shown in the supplementary information

growth. In the two-species plots however, plot-level basal area was lower compared with single-species plots ("underyielding"). The underyielding was attributed to increased tree mortality in two-species plots.

The initial environmental conditions affected tree growth (Table 2). Canopy gap fraction at the time of the establishment positively affected tree growth, in particular for *P. speciosa*; whereas clay content in the soil had a negative effect, in particular for *P. speciosa* and *D. zibethinus* (Figure S6). No significant effect of environmental variables on plot-level tree mortality was detected (Figure S7). There was no interaction between tree diversity and environmental variables in explaining tree growth, except for elevation (p = 0.044 for *rHi*, but p = 0.142 for *rDi*). Neighbourhood analyses (*Model 1*) indicate that trees grew slower close to living oil palms and faster in proximity to felled oil palms, particularly during the second year (Figure 3). From the second year on, trees grew faster close to plot edges. For a given distance to oil palms and plot edges, plot size had a positive effect on tree growth in the third year. The effect of overall tree competition indices on tree growth increased over time and was largely positive. More detailed analyses (*Model 2*) indicated that for a given competitive pressure, the number of species in the local neighbourhood had a positive effect on tree growth during the first year. Separating competition from con-specific and hetero-specific neighbours (*Model 3*) did not indicate a clear difference. These findings remained stable when collinear variables were sequentially dropped from the models. Using relative instead of absolute growth rates did not affect the overall findings (but some variability in the effect of competition indices were found, see Figure S8).

4 | DISCUSSION

4.1 | Overall tree species performances

The overall survival rate of 51% is in line with previous tree planting experiments (see supplementary information). During this early establishment phase, trees are particularly sensitive towards insect and animal damage and other environmental stressors (Burdett, 1990; Evans & Turnbull, 2004), which might explain why mortality was particular high shortly after planting and tended to stabilize in the following years (Figure 1). The three best performing species in our experiment (in terms of survival and size reached in 2018), that is, *P. canescens*, *A. pauciflorum* and *P. speciosa*, are classified as early successional species (De Graaf, Hildebrand, Zwan, & Fundter, 1993; Nielsen, 1992; Wiriadinata & Bamroongrugsa, 1994) and the species that experienced high mortality in our experiment, that is, *S. leprosula*, *D. zibethinus and D. polyphylla*, are more closely associated with primary forest (Ashton, 1982; Rudjiman & Tonanon, 1995; Yap, Martawijaya, Miller, & Lemmens, 1993). This might be explained by the altered ecosystem properties of oil palm plantations in comparison to lowland rainforests, including hotter and dryer conditions (Meijide et al., 2018), more open canopy and reduced litter carbon input (Drescher et al., 2016), and, disregarding fertilizer input, an impoverished nutrient availability in the soil (Allen et al., 2015; Guillaume, Muhammad, & Kuzyakov, 2015). In our study, the effect of site conditions on tree survival was not clear, but it seemed that these two groups of species responded differently to most environmental variables (Figure S7).

4.2 | Effect of diversity on tree performances

Four years after planting, we found evidence for overyielding that was attributed to enhanced tree growth in multi-species plots (Figure 2), which is in line with other experimental and observational studies in forests of different biomes (Grossman et al., 2018; Huang et al., 2018; Liang et al., 2016; Paquette & Messier, 2011; Potvin & Gotelli, 2008). In our experiment, the strength of overyielding varied over time and peaked during the first year after planting. Local neighbourhood analyses (Figure 3) indicated that, for a given competitive pressure from the neighbouring planted trees, local diversity (i.e. the number of heterospecific species around a target tree) had a positive effect on relative growth rates during the first year of study. Hence, the positive effect of diversity on tree growth in the local neighbourhood during the first year of study scaled up and led to community overyielding.

While overyielding dropped in the second year of study in the two- and three-species plots, it remained high in the six-species plots (Figure 2). Because all the six-species plots consisted of the same set of species, the effect of diversity cannot be separated from the particular species chosen in this experiment, and thus the observed high overyielding cannot not be generalized beyond the selected species pool (Huston, 1997). The positive effect of tree diversity was, apart from the six-species plots, not permanent, an indication that the effect was due to a selection rather than a complementarity effect (Loreau & Hector, 2001). Furthermore, inter-specific competition was not lower than con-specific competition, which contrasts previous studies in a Bornean dipterocarp rainforest (Stoll & Newbery, 2005) and in a temperate forest (Zhao et al., 2006) where local neighbourhood diversity reduced competitive pressure in line with classical niche differentiation theory (see review in Ammer, 2019). Here, it is more likely that competitive dominance (Potvin & Dutilleul, 2009; Van der Peer et al., 2018) related to selection effects was the main mechanism at play. Because the planted tree species performed differently under the environmental conditions of the oil palm plantation, fast-growing trees species with high establishment success (*P. canescens*) might have benefited at the expense of species with difficulties to establish (*S. leprosula* and *D. zibethinus*). They are, however, exceptions as less adapted species *D. polyphylla* grew better in multi-species plots and well-performing species *A. pauciflorum* grew better in single-species plots, which might be related to specific traits such as shade tolerance (Van der Peer et al., 2018). The slight interacting effect of tree diversity with elevation on tree growth is in accordance with previous findings stating that BEF relationships may vary with site conditions (Mina, Huber, Forrester, Thürig, & Rohner, 2018; Van der Peer et al., 2018; Zhang, Chen, & Taylor, 2017). However, the mechanisms driving these interactions remain poorly understood (Ammer, 2019). One potential explanation is that complementarity in water resource utilization by different tree species is more pronounced under limited soil water availability (Schwendenmann, Pendall, Sanchez-bragado, Kunert, & Hölscher, 2015). Besides the influence of site conditions, the predominance of selection over complementarity effects is common in young tree plantations (Grossman et al., 2018; Mori, 2018; Potvin & Dutilleul, 2009; Tobner et al., 2016; Van der Peer et al., 2018). The planting density was relatively low in our experimental plots (compared to 1.5 m × 1.5 m in Van der Peer et al., 2018, for example) and canopy closure did not fully occur. Therefore, competition reduction and facilitation driven by above- and below-ground interactions among trees (see review in Ammer, 2019) might take longer to arise.

We found that mortality had either no or only a slightly negative effect on plot-level basal area in multi-species plots . Furthermore, plot-level tree mortality rates did not differ significantly between diversity levels for most species. Hence, our results confirm that tree diversity does not enhance survival-mediated performance of trees in the early plantation development stage (Potvin & Gotelli, 2008; Van de Peer, Verheyen, Baeten, Ponette, & Muys, 2016; but see also Yang et al., 2013). However, because mortality differed between species over time (Figure 1), tree diversity could have stabilized the overall survival probability at plot level. This is particularly relevant as there was a pronounced drought caused by an El-Niño-Southern Oscillation event in August–October 2015 (Meijide et al., 2018). Further research is needed to analyse the potential buffering effects of tree diversity in particular to climate-change driven stresses (Hutchison et al., 2018; Van de Peer et al., 2016) in order to support the establishment success of restoration plantings (Paquette et al., 2018).

4.3 | Methodological considerations

The analyses of the effect of diversity at the level of a plot and the local neighbourhood differed in two fundamental ways. (a) Tree mortality at the two levels was considered differently. The tree growth response to plot-level diversity (in Figures 1 and 2) was based on the initial planting design and hence did not account for tree mortality. Neighbourhood-level diversity (Figure 3), in contrast, was quantified separately for each study period and therefore mortality over time was taken into account. In the former approach, we could not disentangle effects of diversity from the reduced tree density associated with mortality. (b) The methodology to quantify the effect of diversity differed. Accounting for competitive pressure in the spatial-explicit neighbourhood model allowed to detect positive diversity effects despite competition associated with tree performance (i.e. size and survival). The bootstrapping approach (Potvin & Gotelli, 2008), in contrast, ignored the spatial arrangement of trees, as individuals from mixed-species plots were randomly sampled regardless of the density and size of neighbouring trees.

Plot-level analyses are considered useful to assess overyielding (and underyielding), a widely used concept in BEF research to compare productivity across stands (Ammer, 2019). However, local neighbourhoods predominantly drive the response of tree productivity to diversity and can inform about the BEF relationship at plot level (Chen et al., 2016; Fichtner et al., 2018; Potvin & Dutilleul, 2009). Here, we suggest that evaluating the effect of tree diversity over time, accounting for changing competitive pressures in local neighbourhoods, is needed for a comprehensive understanding of BEF relationships in tree diversity experiments.

4.4 | Interactions between trees and oil palms

Competition between the oil palms and the planted trees was indicated by a positive response of growth rates to the distance between the target trees and the living oil palms (Figure 3). This suggests that planted trees competed with oil palms for above or below-ground resources, for example, water that is highly used by medium-aged oil palms (Röll et al., 2015). Besides competition for resources, mechanical abrasion might also have been a limiting factor of tree growth (Hajek, Seidel, & Leuschner, 2015). Furthermore, harvesting of oil palms and leaf pruning led to regular damages of nearby planted trees, mainly due to fallen oil palm leaves. Such management-related factors might have reduced tree performance in the proximity to the oil palms. The planted trees grew better in the proximity to the felled oil palms during the first years, suggesting that the planted trees benefited from the available light, water, space and nutrients not taken up by the oil palms, as well as additional nutrients released from decomposing palm stumps within 12–18 months (Khalid, Zin, & Anderson, 2000) and from potential residual fertilizers around the palm stumps from the management-as-usual plantation phase. For a given competitive pressure from the surrounding trees and palms, the planted trees grew faster close to plot edges (Figure 3) suggesting a benefit from the conventional management of the surrounding oil palm plantation. For a given edge effect, trees grew faster in larger tree islands, an effect that might be attributed to increased soil moisture or more favourable micro-climate (Fischer & Lindenmayer, 2007; Holl et al., 2011) in larger tree islands. In addition, larger tree islands are characterized by lower canopy cover from the oil palms by design (Khokthong et al., 2019), which might partly explain the positive effect of tree island size on tree growth.

Our results suggest an existing trade-off between oil palm productivity and growth of the native trees. During the first 2 years after tree planting, yield losses of felled oil palms were compensated by yield gains of living oil palms, likely due to oil palm thinning (Gérard et al., 2017). In the following years, as some planted trees exceeded the height of oil palms (5.34 m ± 0.9 at meristem in February 2017), competition between trees and palms might have reduced yield of the remaining oil palms. On a longer term, however, alternative economic income from the planted trees, for example, from fruits (*A. pauciflorum* [fruiting in the experiment already after 3 years], *P. speciosa* and *D. zibethinus*), timber (*S. leprosula* and *P. canescens*) or latex (*D. polyphylla*), might partly compensate the yield losses. To determine if planting tree islands is a suitable approach to reconcile agricultural productivity, biodiversity conservation and ecosystem services in oil palm landscapes, comprehensive ecological and socio-economic studies at local and landscape scales are further needed (Rey Benayas et al., 2008).

5 | CONCLUSIONS

Tree performance is an important constraint in ecological restoration and biodiversity enrichment. Our analysis of tree performance in the biodiversity enrichment experiment in an oil palm landscape indicates large species-specific differences in growth and survival rates. During the first year after planting, tree diversity enhanced growth locally that scaled up at the plot level. Temporal analyses of the effect of neighbourhood, however, demonstrate that this effect was transient, suggesting that the initial overyielding was due to selection and dominance of well-performing tree species. Overall, our results reveal tree-palm competition and a positive effect of tree island size, indicating trade-offs between tree growth and oil palm production function that need to be considered for ecological restoration and the establishment of diversified oil palm landscapes.

ACKNOWLEDGEMENTS

We thank PT Humusindo Makmur Sejati and Pak Hasbi and his family for granting us access to and use of their properties. We thank the many field assistants, in particular Juliandi for field work. We are grateful for the logistical support by the EFForTS staff and coordination, as well as for official research permit for D.C.Z, A.G and M.T, by the Indonesia Ministry of Research and Technology. This study was financed by the Deutsche Forschungsgemeinschaft (DFG) German Research Foundation—project number 192626868 – SFB 990 in the framework of the collaborative German—Indonesian research project CRC990 EFForTS (http://www.uni-goettingen.de/crc990). EFForTS-BEE is member of the global network of tree diversity experiments TreeDivNet (http://www.treedivnet.ugent.be).

AUTHORS' CONTRIBUTIONS

The study was designed by D.C.Z., A.G., D.H. and H.K. Data collection and analyses were done by D.C.Z. and A.G. with support from M.T., B.I. and L.S. The manuscript was written by D.C.Z. and A.G., revised by D.H. and H.K., and all authors contributed to improve the manuscript. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and R scripts available via the Dryad Digital Repository https://doi.org/10.5061/dryad.2sf02m1 (Zemp et al., 2019).

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SUPPORTING INFORMATION

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

How to cite this article: Zemp DC, Gérard A, Hölscher D, et al. Tree performance in a biodiversity enrichment experiment in an oil palm landscape. *J Appl Ecol*. 2019;56:2340–2352. https://doi.org/10.1111/1365-2664.13460