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Early indications of success rehabilitating an underperforming teak (*Tectona grandis*) plantation in Panama through enrichment planting

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Abstract

Enrichment planting can be an effective strategy for increasing the ecological and economic value of timber plantations, but success depends on appropriate matching of under- and overstory species and site conditions. This case study in the Panama Canal Watershed explores the viability of enrichment planting for rehabilitating underperforming teak (*Tectonia grandis)* plantations, which are common in the area. Two high-value timber species native to the neotropics, *Dalbergia retusa* and *Terminalia amazonia,* were underplanted in an established teak plantation at the Agua Salud research site in the province of Colon, Panama. Seedling survival, basal diameter, height, total biomass and relative growth rate were assessed for the two years following planting. In contrast with the widespread belief that teak is a poor nurse tree, both species achieved promising early growth with low mortality in plantation understory conditions. Neither understory light availability nor combined above- and below-ground effects of crowding pressure from teak strongly predicted growth of either species. *D. retusa,* thought to be more shade-tolerant, performed equally across a range of intermediate light levels whereas *T. amazonia,* thought to be more heliotropic, performed best at the highest light levels, though light relationships explained little variation in seedling growth. These early findings support the suitability of either species for use in enrichment plantings in established, underperforming teak plantations in the Panama Canal Watershed. Longer-term research is needed to evaluate the potential of enrichment planting to increase profitability and ecosystem services such as carbon sequestration and water resource management in these plantations.

Keywords *Dalbergia retusa* · *Terminalia amazonia* · Tropical plantation management · Native timber trees · Light competition

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Introduction

As natural forests continue to decline worldwide, forest landscape restoration (FLR) and plantation forestry are increasingly important for maintaining tree cover (Paquette et al. 2018; Paquette and Messier 2010; Keenan et al. 2015). This is especially true in tropical forests, which are the most threatened by anthropogenic forest removal and offer the largest potential gains in biodiversity and ecosystem services if restoration is implemented (Benayas et al. 2009). Conservation efforts should directly address the economic pressures driving deforestation, and financial incentive can greatly improve the participation of private landowners in FLR programs (Wunder et al. 2008). To this end, plantation forestry has been heralded as an ecological-economic "win–win" as an opportunity for rural landowners to generate income while preserving the ecosystem services provided by natural forests (Indufor 2012; Kissinger et al. 2012).

However, in practice, the ecological and economic benefits of plantations are equivocal and largely depend on management and species selection. Insecure land rights and long return times on initial financial investments constrain the social and economic benefits of plantations for low-resource producers (Brown et al. 2008). Plantations are often established by large corporations that purchase land from locals and provide minimal long-term benefits to rural communities (Sloan 2008). The majority of tropical plantations, and especially large corporate projects, are planted with exotic species, which may not provide the same ecosystem services as native forests (Davis et al. 2012; Trujillo-Miranda et al. 2020). On a landscape scale, plantations can contribute to a heterogeneous mosaic of land uses and increase per-area productivity to facilitate conservation and minimize over-harvesting of natural forests in other areas (Parrotta et al. 1997; Paquette and Messier 2010), as well as enhancing benefits of natural forests by buffering edges and increasing connectivity amongst forest fragments (Brockerhoff et al. 2008). However, studies of understory plant biodiversity and wildlife habitat within plantations present mixed findings (Cusack and Montagnini 2004; Barlow et al. 2007; Bremer and Farley 2010; McFadden and Dirzo 2018). Plantation establishment and management practices are critical factors in determining ecological benefits (Aubin et al. 2008; Paquette and Messier 2010), and active management of plantation understory may be necessary to encourage a future forest trajectory that is similar to reference plant communities in natural forest (Parrotta et al. 1997). There is increasing interest in incorporating native timber species in FLR and plantations to increase productivity and provision of ecosystem services, but, despite a long history and rich local knowledge of forest stewardship in many areas, a lack of silvicultural information is a major barrier preventing the utilization of a greater diversity of species (Hall et al. 2011; Davis et al. 2012).

There is strong evidence across biomes for Enrichment Planting (EP) as a low-risk strategy for incorporating native species and increasing both ecological and economic value of timber plantations (Paquette et al. 2006; Millet et al. 2013; Ouédraogo et al. 2014). In enrichment planting, valuable species are introduced to the understory of already-established plantations or natural forests, increasing structural complexity and species diversity and providing a more sustained harvest through the incorporation of later-successional trees (Paquette et al. 2006). The partially-shaded conditions of an EP setting can improve seedling survival of later-succession species when compared with full-sun conditions (Ashton et al. 1997; Cole et al. 2011), but light availability can also limit growth of understory seedlings (Rappaport and Montagnini 2014). EP in existing plantations minimizes establishment costs and can increase long-term economic value

through the introduction of slower-growing species (Keefe et al. 2012). However, outcomes of mixed-species plantings are difficult to predict due to unique and understudied light and other site requirements of native tropical species (Redondo-Brenes and Montagnini 2006). Poor performance can greatly reduce or negate financial benefits for land managers (Keefe et al. 2012). EP success is therefore contingent on an appropriate matching of species with both abiotic site conditions such as fertility and the pre-existing biotic neighborhood, which has limited the broad application of this technique (Paquette et al. 2006).

Here, we present a case study of EP in the Panama Canal Watershed (PCW), where the viability of this strategy for enriching the area's exotic timber plantations has not yet been experimentally tested. The vast majority of PCW plantations are monocultures of teak (*Tectona grandis*)—an exotic timber species that is highly valuable but ill-suited to the area's infertile, poor-drainage clay soils (Hall 2013; Stefanski et al. 2015). Panama has the third highest proportion of planted teak coverage of any country worldwide (Kollert and Cherubini 2012), though it accounts for less than 1% of estimated 4.35 to 6.89 million ha of teak plantations worldwide (Kollert and Kleine 2017). In the PCW traditional cattle ranching has been found to provide similar or greater net profitability than teak plantations on an area basis (Stefanski et al. 2015), and the lack of financial gain from teak may be contributing to the slower-than-projected progress of reforestation efforts in the area (Dale et al. 2003).

Additionally, there is evidence that these plantations are not achieving other desired forest functions such as water resource balancing, soil conservation and carbon sequestration (Kraenzel et al. 2003; Fernández-Moya et al. 2014). Critically, teak plantations may not provide the hoped-for "sponge effect" of tree cover: increasing infiltration during periods abundant rainfall, then slowly releasing stored water over drier periods (Peña-Arancibia et al. 2019). Teak's low transpiration efficiency and high water use (Cernusak et al., 2007; Sinacore et al. 2019) may counter the benefits of enhanced groundwater infiltration from planting trees (Hassler et al. 2011; Ogden et al. 2013). The hydrological function of forests can be important for erosion prevention, flood mitigation and year-round fresh water supply in many regions and across spatial scales (Adamowicz et al. 2019; Noordwijk et al. 2017; Zhang et al. 2017), and is especially crucial in the PCW, where seasonal high- and low-flows routinely threaten Canal operations (Ibáñez et al. 2002). One study comparing hydrological services in different forest types of Costa Rica found that topsoil hydraulic conductivity, a key factor in determining peak flow rates and dry-season water availability, was significantly lower in teak plantations versus natural forests, though authors note that plantation age and management were also important sources of variability (Fernández-Moya et al. 2013).

While EP has proven to be a successful strategy for increasing ecological benefits of plantations in many contexts (Lamb et al. 2005; Davis et al. 2012), there is some doubt that teak can serve as an appropriate nurse crop for EP seedlings. A number of studies have put forth both chemical and physiological explanations for the widespread idea and observation that teak overstory impedes understory growth (Healey and Gara 2003). Teak leaf extract was shown to decrease germination and early growth of various annual crops in both greenhouse (Leela and Arumugam 2014; Biswas and Das 2016) and field (Lalmuanpuii 2012) settings, and authors attribute this finding to the presence of allelopathic chemicals in litter rather than soil physical properties or pH (Mensah et al. 2015). In addition to chemical components, teak leaves have a large surface area that may create excessively shaded conditions (Healey and Gara 2003) and increase raindrop size which can ultimately reduce infiltration rates (Calder 2001).

Recent models project smaller gains in planted forest area for Latin America compared with other regions (Korhonen et al. 2020). Maximizing per-area productivity is therefore paramount given the diverse needs of a growing global population. There is a strong need to revitalize teak plantations in the PCW and throughout tropical regions, where inadequate site conditions can cause plantations to underperform (Kumar 2005; Stefanski et al. 2015; Kollert and Kleine 2017). Within this context we reasoned that EP might serve as a silvicultural manipulation that could return poorly-performing teak to some measure of profitability over time, albeit with valuable site-adopted species providing the major revenue stream. As a first step we sought to better understand the early performance of two high-value, native forest species—*Terminalia amazonia* and *Dalbergia retusa*- planted into a recently thinned teak plantation. Our specific study objectives were:

(1) to assess and compare the **establishment and early growth** of *T. amazonia* and *D. retusa* in the novel EP setting of a teak plantation understory.
(2) to assess the combined above- and below-ground **crowding** effects by varying densities of teak overstory on EP seedling early growth.
(3) to partition the above-ground effects of varying **light conditions** from overall crowding effects on the growth of two species thought to differ in their shade tolerance.

Methods

Study site

This study was conducted in a teak plantation within the Smithsonian Tropical Research Institute's Agua Salud Project, an approximately 15-km^2 area near the town of Frijolito, Colon, within the PCW (9°13′N, 79°47′W; Stallard et al. 2010). Agua Salud soils are acidic, highly-weathered Oxisol and Inceptisol clays typical of soils in the surrounding PCW and tropical regions worldwide (further described in publications including: Turner and Engelbrecht 2011; Hassler et al. 2011; van Breugel et al. 2019). Climate is humid tropical; daytime high temperature averages 32 °C year-round, and average annual rainfall is estimated at 2700 mm, typically received almost exclusively during the wet season from May to mid-December (Ogden et al. 2013). During the planting and establishment phase of this study, the strongest El Niño cycle of the last century resulted in historic droughts across Panama; 2014–2016 was the driest period recorded since monitoring began in 1925, and in 2015 Agua Salud only received 1800 mm of precipitation (Bretfeld et al. 2018).

Agua Salud's 30-ha teak plantation was established in 2008, as part of a landscape mosaic consisting of mature and secondary forest, native species plantations and pasture (Weber and Hall 2009). Teak were planted at 3-m spacing, using a triangular design to minimize soil erosion (van Breugel and Hall 2008). Authors note that teak were more expensive and laborious to establish than adjacent native species plantations due to extensive site preparation including liming and fertilization. Chemical fertilizer was incorporated in planting holes and applied selectively to underperforming trees in the initial years of growth, but soil sampling in 2016 did not reveal elevated nutrient levels (author's unpublished data).

A 2013 growth inventory of the plantation indicated that, based on the height growth curve established for Central American teak (Keogh 1982), the Agua Salud site was classified as below average and not projected to be financially profitable within a 20-year rotation (Hall

2013). Prior to this study, overstory heterogeneity and canopy gaps were created as part of a plantation management plan including pre-commercial thinning (typically 30%, but adjusted based on variable growth and survival across the plantation) and pruning. A subsequent inventory in 2016 confirmed that growth remains poor (Table 1).

Study species

Of the many promising timber species native to the neo-tropics, *Dalbergia retusa* (commonly known as "cocobolo") and *Terminalia amazonia* (locally known as "amarillo") were selected for this study for their high-value timber and promising performance in prior growing trials (Hall and Ashton 2016). Despite the long and ongoing tradition of forest stewardship in Panama (Aguilar and Condit 2001) and strong cultural value of these species, little is known about their optimal growing conditions in a plantation or EP setting. Both species perform well on nutrient-poor sites (Mayoral et al. 2017), and *D. retusa* fixes especially high levels of nitrogen through associations with rhizobia bacteria (Batterman et al. 2018). Based on limited previous studies, *T. amazonia* is considered a heliotrophic canopy tree (Redondo-Brenes and Montagnini 2006), whereas *D. retusa* is considered a shade- and small-gap tolerant species (Augspurger 1984). While *T. amazonia* has a generally straight-boled, narrow-crowned growth form that is well-suited to timber production, *D. retusa* tends to have a wide-spreading, multi-stemmed growth form in full sun conditions (Mayoral et al. 2017). In a previous Agua Salud study comparing carbon sequestration, growth and economic viability among teak and native timber species, *D. retusa* far outperformed teak in all measures and *T. amazonia* was also financially competitive (Sinacore 2018). Though this study focuses primarily on aboveground measurements, belowground growth can also influence the provision of ecosystem services such as water management and carbon sequestration. In a previous study of plantation trees in the region, Sinacore et al. (2017) found *T. amazonia* had a greater rooting distance and allocated more biomass to lateral roots compared with *D. retusa;* total belowground biomass fractions and rooting depth were similar for the two species.

Experimental design

In 2015 we initiated the EP trial, planting in two blocks representing different sub-watersheds of the 30-ha Agua Salud teak plantation (Hall 2013). A total of 510 EP seedlings were planted in 21 625 m² (25×25 m) plots established randomly in equal densities and distribution across the two blocks; 221 seedlings across 11 plots in one block and 289 seedlings across 10 plots in the second block. Number of seedlings per plot varied, with an average of 10 seedlings per plot across both blocks. Due to prior thinning and pruning, teak did not fully shade the understory, and it was determined that no additional overstory management was necessary to achieve desired, varied light conditions for EP. Prior to planting, the entire plantation understory was cut with machetes, and a 1-m radius was cleared to bare dirt around each planting

Table 1 Agua Salud Teak Plantation Summary of 2016 Inventory		
Age		8 years
Mean Density (trees/ha)		740 ± 30
Mean Basal Area (m²/ha)		3.2 ± 0.3
Quadratic Mean Diameter (cm)		7.3 ± 0.4

site. Understory regrowth was cut back as necessary (2–3 times annually) for the duration of the study; teak received no additional management.

T. amazonia and *D. retusa* seedlings were grown in tubbettes at the Futuro Forestal nursery in Las Lajas, in the Chiriqui province of Panama, and were less than one-year-old when outplanted. Seedlings were planted at the beginning of the rainy season in 2015, in gaps amongst the established teak, no closer than 1 m to any overstory teak tree. Only seedlings with healthy root systems were planted. *T. amazonia* seedlings were selectively placed in larger gaps to maximize light availability for seedlings thought to be less shade-tolerant than *D. retusa* (Redondo-Brenes and Montagnini 2006). Distance between EP seedlings varied but was at least 4 m to avoid any interaction or competition among seedlings during the early growth period of this study. All seedlings received 90 g of a widely-available chemical fertilizer (12–24-12 NPK) and a large handful of organic material, incorporated with loose dirt at the bottom of the planting hole. Planting sites were marked with painted stakes that indicated both location and species.

Measurements and parameter computation

Objective 1 Native seedling growth and mortality was measured in 2016 and 2017, during the first and second growing (wet) seasons following planting; height (m) and the average of two basal diameter (BD) measurements taken 5 cm above the root collar (mm) were recorded for each seedling. First-year mortality was assessed in 2016 on a per-plot basis by counting stakes with absent or dead seedlings. Second-year mortality was evaluated similarly and compared with 2016 data to assess per-species survival.

BD relative growth rate (RGR) was calculated as:

$$RGR = \frac{\ln\left(BD_2\right) - \ln\left(BD_1\right)}{t_2 - t_1} \tag{1}$$

where t_1 is 2016 and t_2 is 2017, and BD is the average of two measurements taken for each individual seedling for each year, as described above (Fisher 1921).

Total biomass (TB) was estimated for each seedling with species wood-specific gravity (WSG) and individual BD measurements using multi-species equations developed by Sinacore et al. (2017) based on trees of each species growing in plantations in the PCW:

$$TB = -2.586 + (2.456 * BD * \ln(BD)) + (0.915 * BD * \ln(WSG)) \tag{2}$$

Objective 2 Crowding pressure from overstory trees was assessed per plot based on the size and number of teak present, providing an estimate of both below-ground and aboveground interactions (Fichtner et al. 2015). Within each 625 m² plot, the DBH (cm, at 1.3 m height) of all teak was measured in 2016. DBH measurements were used to calculate total plot basal area (BA, m²). Though not spatially-explicit, teak BA provided a localized estimate of crowding pressure that allowed for comparison across plots and sub-watersheds (blocks), thereby optimizing predictive power given sampling constraints (Kuehne et al. 2019). Patchy teak growth and prior thinning provided a range of overstory densities, such that using per-plot measurements captured this gradient. Competition for below-ground resources tends to be more size-symmetric than competition for light (Schwinning and Weiner 1998), but models assumed size-asymmetry given that the relative size of EP seedlings was orders of magnitude smaller than teak overstory during the establishment and initial growth period explored in this study. The single-species (teak only) overstory allowed

for assessment of crowding pressure without the need for a species-specific coefficient used to assess competition in more heterogeneous stands (Canham et al. 2004).

Objective 3 Light availability was directly measured using hemispherical photography and quantified based on a transmission coefficient for each seedling individually, to capture variation on a spatial scale smaller than plot size. Photos were taken 1 m directly above each living seedling in early morning or late afternoon or during overcast weather to avoid direct sunlight. *Hemisfer* software was used to differentiate between leaf and sky components and calculate the transmission coefficient for the ray penetrations (or the fraction of visible sky) reaching the target seedling. Transmission coefficient was strongly correlated with both Leaf Area Index ($R^2 = 0.90$), which was quantified using methods developed with the *Hemisfer* software (Thimonier et al. 2010) and also related to large gap proportion ($R^2 = 0.50$). Of the possible light measurements, transmission coefficient was selected as the best characterization of the forest light environment (Gustafsson et al. 2016) and the only light variable used for analysis to avoid multicollinearity.

Statistical analysis

Objectives 1 and 2 were evaluated similarly using a nested series of Type I (sequential) ANOVA models with different factor ordering. To test among-species differences in response to light availability and crowding it was important to consider second-order interactions among factors prior to main effects, and repeated testing with different ordering accounted for differences in sample size and non-orthogonality of the dataset while preserving the principle of marginality (Hector et al. 2010). This approach was possible given the relatively small number of factors and factor levels. Sequential p-values of factors were compared for different model orderings to assess significance of each factor after accounting for effects of other factors, and complete models were reduced by eliminating insignificant factors and interactions. Diagnostic plots in R were used to check for violations of ANOVA assumptions of normality (Q–Q plot) and homoscedasticity (residuals vs. fitted and scale-location plots); there were no concerning patterns, and all data fell within Cook's distance line (residuals vs. leverage plot).

Plot means were calculated from individual measurements of EP seedling growth to best capture variation across the study area and minimize random effects of individual seedling growth, and plot-level measurements and means were used as predictor and response variables in all models. Variation among plots was confirmed for all growth measures of EP seedlings and teak with one-way ANOVA models. Two-way ANOVA models initially included experimental block and species as factors (*Objective 1*); separate models with each of the 4 measures of EP growth (BD, height, RGR and TB) as response variables were fit with main effects and species x block interactions. The base model of 2017 BD was then expanded to include plot total teak BA, representing crowding pressure, and plot mean transmission coefficient, representing light availability, for each species as potential predictor variables (*Objective 2*). Only second-order interactions among factors were tested, as third- and forth-order interactions were unrelated to experimental objectives and had no biological basis. Pairwise linear regression was used to test multicollinearity among factors. Overall percent mortality was compared among species; statistical analysis was not possible given that species-specific mortality was not distinguished in 2016.

Objective 3 In order to partition the effects of light availability from overall crowding effects, consider more localized variation, and explore potential non-linear relationships, we further explored the relationship between transmission coefficient and 2017 BD for

individual seedlings rather than on a plot level. Candidate variables in the initial multiple linear regression model included transmission coefficient, species and block, and both main effects and higher-order interactions were tested; insignificant factors and interactions were sequentially eliminated. Diagnostic plots confirmed that these data met normality and homoscedasticity assumptions; a Gaussian distribution was an appropriate fit and no transformations were required. Single-species regression models were subsequently used to explore among-species differences in light response and potential non-linear relationships. The effect of transmission coefficient on second-year mortality of *T. amazonia* was assessed using logistic regression.

All data was analyzed using R Studio version 1.1.419 (RStudio Team 2016).

Results

Objective 1 Both *T. amazonia* and *D. retusa* achieved promising early growth with low mortality under conditions provided by a PCW teak plantation (Fig. 1).

In the first year of establishment following planting, both species together had an 8.71% mortality rate. In the second year, mortality for *T. amazonia* was 6.56% and there was no *D. retusa* mortality. The total mortality for all EP seedlings after two years was 12.4%.

D. retusa grew significantly larger than *T. amazonia* by all absolute growth measures in the two years following planting (p-values < 0.001) (Fig. 1a–c). The complete two-way ANOVA models did not indicate a significant species x block interaction for any measure of growth (p-values > 0.4). In reduced models including only main effects, both species and experimental block (p-value = 0.03) were significant predictors of BD for species, but only species predicted significant variation in height and TB (p-value > 0.1 for block). RGR did not differ significantly among species or block (p-values > 0.2) (Fig. 1d).

Objective 2 Crowding pressure from overstory teak had a slight but significant negative effect on growth for both species (Fig. 2).

The initial, complete ANOVA model of plot mean 2017 BD included candidate variables species, block, plot mean transmission coefficient and plot total teak BA. There was a significant difference in transmission coefficient among species (p-value = 0.02), but no significant species x transmission interactive effects on 2017 BD (sequential p-value = 0.63). No other second-order interactions among factors were significant (p-values > 0.3) so model was reduced to include only main effects. There was no significant effect of block after accounting for other factors (sequential p-value = 0.25), likely due to significant among-block differences in teak BA (p-value = 0.038). Transmission coefficient and teak BA were negatively correlated ($R^2_{adj.}$ = 0.52, p-value < 0.001), and the inclusion of transmission coefficient did not improve model fit (sequential p-value > 0.09). In contrast, the effects of teak BA were significant even after accounting for transmission coefficient (sequential p-value = 0.049). A nested model F-test comparing the complete model with all 4 candidate variables to a reduced model with only species and teak BA confirmed that elimination of transmission coefficient and block did not significantly affect model fit (Partial F-statistic = 1.21, p-value = 0.31). In the final model the combined main effects of both species (sequential p-value < 0.001) and teak BA (sequential p-value = 0.01) explained 55% of variation in 2017 EP seedling BD (F-statistic = 23.2 on 2,35 df, p-value < 0.001). A further reduced model with species as the only explanatory variable had significantly less predictive power than when the effects of teak BA were considered (F-statistic = 7.24, p-value = 0.01).

Fig. 1 From upper left to lower right: Second-year growth measures of **a** basal diameter **b** height **c** total biomass and **d** relative growth rate of basal diameter for both *D. retusa* (white boxes) and *T. amazonia* (grey boxes). *D. retusa* grew significantly larger in all growth measures except for relative growth rate (from first to second year after planting)
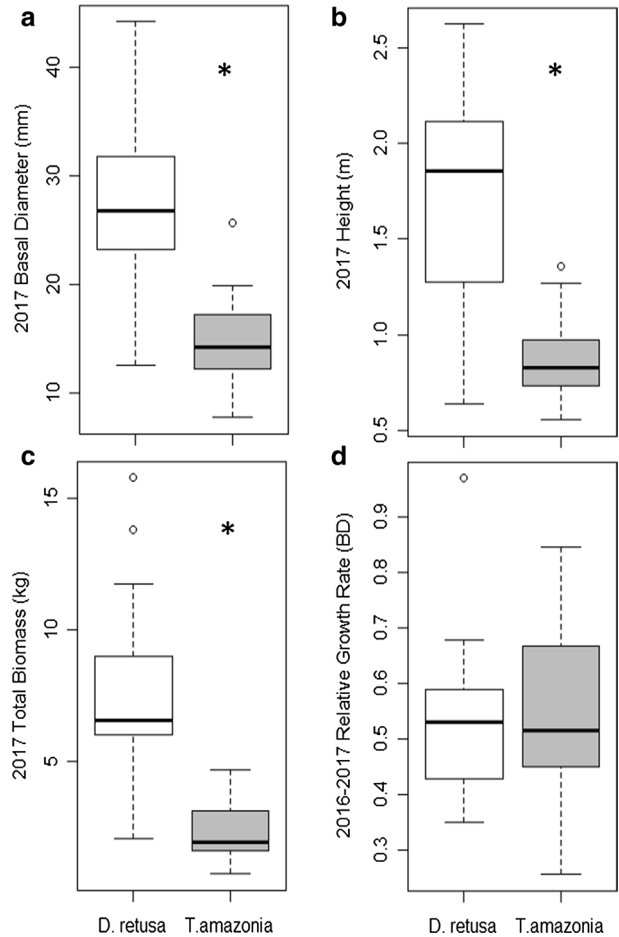
Objective 3 Even when assessed on the individual seedling level, light availability was a weak predictor of EP growth overall but patterns in responses differed among species (Fig. 3).

For all EP seedlings, the mean transmission coefficient, the measurement selected to represent light availability, was 58.75% and values ranged from 12.8 to 96.7%, representing a light availability spectrum from partial shade to nearly full sun. Though *T. amazonia* seedlings had a higher mean transmission coefficient ($63.3 \pm 16.2\%$) compared with *D. retusa* ($46.3 \pm 15.4\%$), as expected per planting protocol, the range for both species almost completely overlapped, allowing for comparison of overall response curves and growth at different light levels between the two species.

Similar to findings from plot-level data in *Objective 2,* transmission coefficient had little effect on individual EP seedling growth. The complete ANOVA model including all higher-order interactions explained a low proportion of variation in individual EP seedling 2017 BD (($R^2_{adj.} = 0.31$), and only the species coefficient was significant (sequential p-value < 0.0001, all other p-values > 0.2). All possible factor orderings were considered and third-order, species x light and light x block interactions were sequentially dropped
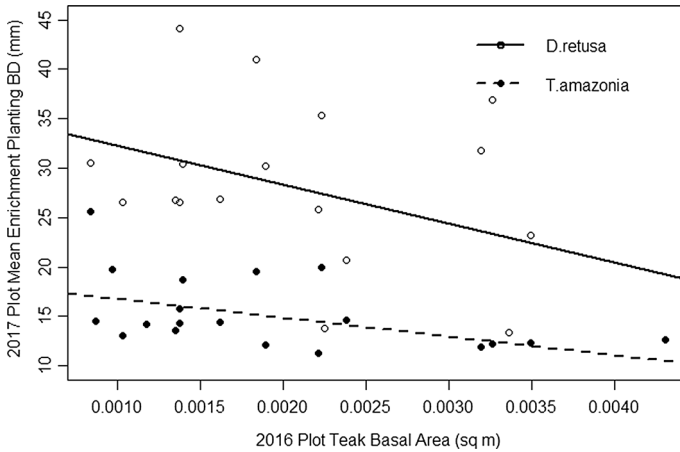
Fig. 2 Total plot teak basal area (m²), a distant-independent crowding metric, was weakly but significantly negatively related to second-year growth (basal diameter, mm) of both *D. retusa* (open points, black line) and *T. amazonia* (filled points, dashed line)
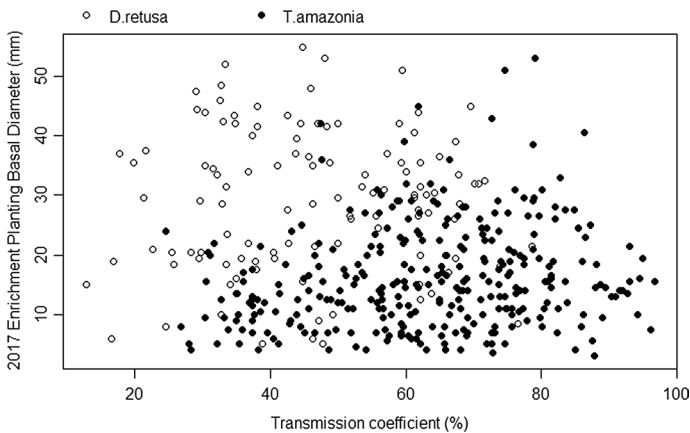

Fig. 3 Second-year growth (2017 basal diameter, mm) of *D. retusa* (open points) and *T. amazonia* (filled points) across a continuum of light availability (transmission coefficient, %). There was a significant, positive, linear correlation between *T. amazonia* growth and light availability but this relationship explained very little of the variability in seedling growth ($R^2_{adj.} = 0.029$, p-value = 0.0016); no light-growth relationship was discernable for *D. retusa* seedlings for either linear or quadratic models (p-value > 0.05)

(sequential p-values > 0.05) while the significant species x block interaction (sequential p-value = 0.01) was retained, though inclusion of this interaction improved model predictive power by less than 1% ($R^2_{adj.} = 0.29$ for both models). A nested model F-test indicated that the inclusion of light as a factor improved model fit in comparison with only species and block (Partial F-statistic = 4.9, p-value = 0.03), but there was no meaningful increase in model predictive power ($R^2_{adj.} = 0.28$ without light).

   Scatterplots display the weak correlation between light availability and EP seedling growth but also suggest some among-species differences in response to light availability:

whereas the largest *T.amazonia* seedlings were found in higher light conditions, *D. retusa* growth was maximized at intermediate transmission coefficient values (Fig. 3). Separate regression models were fit for each species to explore these differences. A linear model for *T. amazonia* was significant but had almost no predictive power ($R^2_{adj.} = 0.029$, p-value = 0.0016), whereas no light-growth relationship was discernable for *D. retusa* seedlings for either linear or quadratic models (p-value = 0.12).

There was not a significant relationship between transmission coefficient and other measures of seedling growth (height, TB, RGR) in either single-species or second-order models (p-values > 0.05).

Mortality in the second year of growth (2017) for *T. amazonia* was unrelated to light availability (p-value = 0.26), and *D. retusa* achieved 100% survival across the full spectrum of light availability. Though not formally assessed, no strong trends were observed in light conditions of dead seedlings in the first year (2016).

Discussion

The results of this study suggest that, contrary to popular belief and findings from previous studies, teak plantations can provide suitable conditions for EP establishment and early growth. *D. retusa* and *T. amazonia* responded similarly to crowding pressure from teak overstory, and these effects appear to be driven primarily by competition for resources other than light. When light conditions were considered on an individual seedling rather than plot level, there were slight among-species differences in growth response.

The high survival of EP seedlings in this study provides no evidence that teak overstory impedes early survival of either *T. amazonia* or *D. retusa*. The low mortality we observed for both species is consistent with findings in full-sun plantation conditions; Mayoral et al (2017) recorded < 2% mortality after 5 years in Agua Salud's native species plantations, and Hall and Ashton (2016) found < 10% mortality in a wet, infertile site for both study species. These longer-duration studies give no indication that the high survival we observed should be expected to decrease significantly in future years. Past studies attribute findings of an inhibitory effect of teak on understory establishment to the species' heavy water usage, large leaf size and alleliopathic chemicals (e.g., Biswas and Das 2016; Healey and Gara 2003; Leela and Arumugam 2014). The transplanted seedlings in our study were already past the germination and early growth stages evaluated in other studies so may have been better able to overcome the possible presence of inhibitory chemicals. Our study species are also known to perform well on acidic, low-fertility soils (Mayoral et al. 2017), so may not be affected by lower pH due to acidic teak leaf litter in the same way as annual crop species used in other experiments. Furthermore, native species from areas of wet/dry climate cycling may be adapted to periodic water stress and therefore resilient to amplified dry season water shortages due to plantation uptake. While *D. retusa* is known to be drought-tolerant, *T. amazonia* is associated with wetter areas (Craven et al. 2011); historic drought conditions over the duration of this study (Bretfeld et al. 2018) may have contributed to the slightly higher, though still low, mortality observed in *T. amazonia* seedlings (Sinacore et al. 2019).

Without direct evaluation, it is important not to over-generalize plantation effects on water availability, fertility and other soil characteristics; this depends on many factors including age, species, level of diversity, and management (Delagrange et al. 2004; Fernández-Moya et al. 2013). In contrast to common assertions, Fernández-Moya et al. (2014)

found no evidence that teak plantation establishment lowers pH and increases soil erosion; the authors suggest that management is more important in determining plantation effects on soil than any intrinsic quality of teak. These findings align with a recent Agua Salud study comparing decomposition and below-ground microbial activity among plantations of teak, *D. retusa* and *T. amazonia* (Kerdraon et al. 2019). These authors found similar nutrient content and pH in *T. amazonia* and teak plantations (though higher for *D. retusa*, which is expected given its nitrogen-fixing activity). Dry-season soil water content was similar in *D. retusa* and teak plantations (though higher for *T. amazonia*, which forms a denser canopy and is not deciduous in the dry season).

The potential effect of overstory trees on EP seedling performance ranges from facilitation, by amelioration of harsh growing conditions, to suppression, through competition for resources such as light, water and nutrients. The slight, negative relationship between the growth of both EP species in this study and localized (plot) teak BA, a distant-independent metric of crowding pressure (Kuehne et al. 2019), does not suggest any facilitative effects and indicates slight suppression of EP growth with increasing teak density. This finding aligns with past EP studies of different target species that have identified a trade-off between growth and survival at varying overstory densities; survival is higher in more shaded conditions, but growth is slower (Millet et al. 2013). In a similar EP study of native seedlings in an exotic timber plantation in Sri Lanka, the greatest EP seedling growth was achieved with the highest levels of overstory removal (Ashton et al. 1997). A meta-analysis of EP studies across biomes found that in tropical systems growth was much greater in intermediate- versus high-density overstory, while further thinning reducing overstory from intermediate- to light-density had only slight growth benefits (Paquette et al. 2006). The weak relationship between crowding pressure and EP performance in our study could be due to a low to intermediate overstory density in Agua Salud; these data do not allow for the evaluation of high-density overstory. Though teak in the Agua Salud plantation were planted in a triangular format with 3-by-3 m spacing, thinning and pruning combined with poor growth provide less-crowded conditions than in similarly-spaced but better-performing or differently managed plantations. Studies in older and more densely-growing plantations could provide further insight into how crowding by teak affects EP performance.

Our sequential (Type I) ANOVA approach allowed us to partition the effects of light availability (transmission coefficient) from overall crowding pressure (teak BA), which includes competition for belowground as well as aboveground resources. Though only slightly over half of the variation in light availability was explained by crowding pressure, crowding pressure accounted for all of the effects of light availability on seedling growth. The significant negative effect of crowding pressure not explained by the effects of light availability suggest that belowground dynamics may be important in understanding and predicting EP performance. Further partitioning of crowding pressure to assess nutrient and water availability as separate factors could provide additional insight into the observed suppression of EP growth at increasing overstory densities. From a management perspective, our findings support the usefulness of distant-independent crowding metrics, which are far less labor-intensive to obtain than spatially explicit measures, in predicting EP performance.

While not a significant predictor of seedling growth on a plot level, among-species differences in response to light emerged when assessed on a finer spatial scale. *T. amazonia* achieved maximum growth near the highest light levels (96% transmission coefficient) tested in this study, and growth decreased slightly but significantly at lower levels. *D. retusa* achieved equivalent growth across the broad range of intermediate light levels this species was exposed to (12–78% transmission coefficient). *T. amazonia* is categorized

as a long-lived pioneer species that performs well in typical full-sun plantation establishment conditions (Nichols 1994), and a previous study found that first-year growth and survival were lower in understory light conditions versus small-gap conditions of higher light availability (Augspurger 1984). In contrast, Craven et al. (2011) found that *T. amazonia* maintained constant growth with decreased spacing, suggesting that early performance is not affected at low levels of light competition. In our study system seedlings tolerated light availability lower than 25% transmission with only a minor decrease in growth relative to higher-light seedlings, supporting the Craven et al. (2011) observations. Some prior studies noted an increase in *T. amazonia* aboveground growth rates after the first 2 years (e.g. Mayoral et al. 2017), suggesting that initial growth may not be indicative of longer-term trends. Continued monitoring in this study system will provide insight into whether light availability affects height or BD growth beyond the early seedling stage. The lack of any significant relationship between light availability and *D. retusa* performance, even when non-linear (quadratic) models were explored, aligns with *D. retusa*'s classification as more shade-tolerant relative to *T. amazonia*. Future EP studies involving denser overstory would be useful in assessing whether *D. retusa* growth is related to light availability at lower ends of the spectrum. It should be noted that even the lowest light levels in this study are still substantially higher than typical tropical rainforest understory conditions. Measurements of relative irradiance, comparable to this study's transmission coefficient, in the understory of tropical moist forest on Panama's Barro Colorado Island and in Agua Salud primary forest averaged less than 2% (Wirth et al. 2001; van Breugel et al. 2013), which aligns with other past studies (e.g. Baraloto et al. 2006; Gustafsson et al. 2016).

Given that planting year and specific site conditions can greatly influence seedling growth, directly comparing growth rates across different studies does not provide an accurate assessment of performance in full-sun versus EP. However, considering results and patterns from past trials involving our study species can provide potentially important insights. In Agua Salud's native species plantations adjacent to this study site (established in 2008 in full-sun but otherwise nearly identical site conditions), Mayoral et al. (2017) found that *D. retusa* seedlings were taller and thicker in the initial 2 years, but in subsequent years *T. amazonia* growth rates increased significantly. Seven years after planting, *T. amazonia* had far surpassed *D. retusa* and all other study species by every measure of growth. This is consistent with the current study's finding that, while *D. retusa* seedlings outperformed *T. amazonia* in all absolute growth measures after the second year, the RGR of seedlings calculated between year 1 (2016) and two (2017) was not significantly different. Craven et al. (2011) and van Breugel et al. (2011) also evaluated the first two years of *D. retusa* and *T. amazonia* growth planted in full-sun in Panama. Craven et al. (2011) observed similar trends as the present study in a study site near Agua Salud with similar climate but more fertile soils: *D. retusa* seedlings had lower mortality and more rapid growth (height, BD and RGR) than *T. amazonia.* In contrast, van Breugel et al. (2011) found that in 2 years *T. amazonia* grew taller on-average than *D. retusa* in a wetter site characterized as infertile, though with much higher nutrient availability than Agua Salud soils. A study in the Darien region of Panama evaluated teak*, T. amazonia* and *D. retusa*, among other species, for use in the "taungya" system of cultivating annual crops within timber plantations (Paul 2014). Here, seedlings were planted in full-sun conditions in a similar climate but with different and more fertile soil characteristics than our study site. In the Darien site two-year growth (height and DBH) was higher for *T. amazonia* than *D. retusa,* though teak outperformed both native species.

In three of the four aforementioned studies, average heights were taller for both species than in our EP study. In contrast, on soils very similar to our study, Mayoral et al. (2017)

found that *D. retusa* grown in full-sun at Agua Salud were shorter and thinner on-average than EP seedlings in our study while full-sun *T. amazonia* grew larger on-average than the EP seedlings. The superior relative performance of *D. retusa* in a partially-shaded EP setting versus full-sun is consistent with the species' greater shade tolerance compared with *T. amazonia,* though there was not a significant interaction between light availability and species in either our plot-level or individual seedling EP growth models. Overall lower seedling growth in our study compared with prior results is not surprising given the historic drought conditions of 2015 and 2016 and more productive soils of the other study sites. However, Sinacore et al. (2019) found *D. retusa* to be largely unaffected by the drought in terms of water stress. Drought tolerance may additionally explain this species' achievement of stronger growth in drought conditions compared with the earlier Agua Salud study during wetter years (Mayoral et al. 2017). A controlled experiment with treatment groups for both full-sun and EP would allow for a more accurate comparison of growth rates between the different establishment and early growth conditions.

The Agua Salud teak that provide the overstory for this study were first measured 4 years post-planting, so data is not available for a direct comparison with early growth rates of the native species in this study. However, even with considerable post-planting fertilization and liming to raise soil pH, Agua Salud teak is underperforming and economic projections suggest that this plantation will not be financially profitable within the planned 20-year rotation (Hall 2013; also see Stefanski et al. 2015). In contrast, the EP of native species in the same site achieved promising early growth despite historic drought conditions and without the extensive investment in site preparation for teak establishment. Our findings support past studies suggesting that selected native species may outperform exotic species such as teak, which continue to dominate timber plantations in the PCW and across Latin America (Lam Bent et al. 2011; Davis et al. 2012; Sinacore 2018).

Conclusion

Forest cover is critical for wildlife connectivity and hydrologic function in the PCW, and there is clear evidence that the predominant reforestation strategy, single-cohort monocultures of teak, is not meeting all desired objectives. EP is one potentially low-risk option for increasing ecological and economic value of plantations but is not successful in all applications worldwide. This study critically examines the efficacy of EP at one site in the PCW, and initial findings are highly encouraging. When established in EP, both *T. amazonia* and *D. retusa* achieved early growth and low mortality consistent with performance in full-sun plantation conditions. The slight negative relationship between teak BA and EP growth supports the consideration of potential trade-offs between overstory density versus EP performance in managing plantations for maximum productivity and profitability. The weak relationships between seedling growth and light availability do not support specific management guidelines for optimal light levels but rather attest to the suitability of either species as an EP in low- to mid-density overstory conditions.

These initial results suggest that EP with *D. retusa* and *T. amazonia* may be a viable silvicultural intervention in underperforming teak plantations, though longer-term monitoring is needed to confirm predictions. Increasing plantation diversity in Central America to include species that are drought-resistant and support other ecosystem services such as soil conservation is paramount given climate change projections of decreased water availability and increased frequency of extreme weather events throughout the region (Imbach et al.

2018). In addition to adapting to climate change, plantations can also play a critical mitigating role through carbon sequestration (Paquette and Messier 2010); EP as a strategy for increasing carbon sequestration and other ecosystem services such as wildlife habitat and drought resistance should be further investigated in the context of teak plantations. More long-term results and trials with other native species are needed to appropriately determine the viability of EP in the PCW. Given conflicting findings in the literature and reports from land managers, further research on soil factors and microbial symbionts could provide valuable insight into what drives EP project success or failure.

Data availability Full data set is available upon request in electronic tabular form from corresponding author, email requests to Jefferson Scott Hall at hallje@si.edu.

Code availability Full data set is available upon request from corresponding author (see above).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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