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TAILORED RESTORATION RESPONSE: PREDICTIONS AND GUIDELINES FOR WETLAND RENEWAL

RESEARCH ARTICLE

Accounting for seedling performance from nursery to outplanting when reforesting degraded tropical peatlands

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Reforestation is promoted to address the dual global climate and biodiversity crises. This is particularly relevant for carbon-rich, biodiverse tropical peatlands, for which active reforestation typically involves two post-germination stages: nursery rearing of seedlings, then outplanting. Yet, linkages between these stages and cumulative seedling performance are rarely quantified during tropical peatland reforestation. By monitoring tree seedling survival and growth, we investigate factors influencing seedling performance (species identity, seedling source, treatments, and climate), whether nursery performance predicts outplanting performance, and calculate cumulative survival (nursery plus outplanting) in Sebangau National Park, Indonesian Borneo. Standardized survival at 2 years was higher in the nursery (mean 67% across 40 species) than outplanting (44% across 24 species). For nursery and outplanting, species identity was the main source of variation in survival and height growth. Seedling source, treatments, site condition, and precipitation had no significant impact on survival but did influence growth in some cases. Nursery survival did not predict outplanting survival, but nursery height did predict outplanting height. Across species, around a quarter of seedlings survived from nursery to outplanting over 4 years. Cumulative survival represents a more realistic basis for assessing the genetic and other resource costs of tropical peatland reforestation. Our two-phase approach identified outplanting as the greater bottleneck to cumulative seedling survivability. We argue that the nursery stage may be used to harden seedlings for degraded peatland conditions by selecting more relevant treatments (e.g. flooding) and screening for resilience to common disturbances (e.g. fire) to enhance outplanted, and thus cumulative, seedling survival.

Key words: field planting, Indonesia, relative growth rate, Southeast Asia, survival, tropical peat-swamp forest

Implications for Practice

- Tree planting projects in tropical peatlands should account for seedling survival across the nursery and outplanting phases to provide a truer assessment of their costs.
- Because outplanting represented the largest seedling survival bottleneck, the potential may exist to improve cumulative survival through nursery interventions designed to improve outplanting performance, such as hardening to flooding or screening for fire resilience.
- As seedling survival and growth were unrelated across species, practitioners should consider these species performance metrics separately when selecting species to suit project needs.
- Despite the higher cost, the use of organic baskets made from sedge grass in outplanting may be preferred by practitioners, as these did not diminish seedling performance, but reduced plastic consumption and provide alternative local incomes.

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Introduction

The global climate and biodiversity crises have generated unprecedented international scientific and political focus on ecosystem restoration (Griscom et al. 2017; Pörtner et al. 2021). This has resulted in international and national commitments toward ecosystem restoration (UNEP 2010; UN 2015), culminating in 2021–2030 being designated the UN Decade on Ecosystem Restoration (UNEP & FAO 2020). Globally, ambitious goals have been set to plant billions or trillions of trees (Holl & Brancalion 2020). This requiresng vast tree seedling/wildling stocks, which are commonly sourced from wild populations, creating over-exploitation risks (Pedrini et al. 2020). Consequently, it is important to understand the survivability of seeds and seedlings/wildlings harvested from forests for reforestation planting, as a measure of its genetic resource cost.

Tropical peatlands are important in relation to restoration commitments: they store vast amounts of carbon that cause high emissions upon degradation (Page & Baird 2016), house rich biodiversity (Posa et al. 2011; Husson et al. 2018), are of public health relevance (Koplitz et al. 2016; Harrison et al. 2020), and provide livelihood options and other benefits to local communities (Dommain et al. 2016). Whereas tropical peatlands in Africa and South America remain generally less altered (Roucoux et al. 2017; Dargie et al. 2019), those in Southeast Asia have experienced widespread degradation and loss (Miettinen et al. 2016). Numerous reforestation projects have thus been initiated in the region over the last three decades (Dohong et al. 2018; Smith et al. 2022). Tropical peatland reforestation includes both supporting "passive" natural regeneration and "active" tree planting, is considered important for reducing fire risk and conserving biodiversity, and presents local livelihood opportunities (Graham et al. 2017; Dohong et al. 2018; Yuwati et al. 2021).

Many tropical tree species' seeds are recalcitrant, so cannot be dried and stored (Corlett 2009; Li & Pritchard 2009), and no known tropical peatland tree species display seed dormancy (Graham et al. 2017). Unless seed/wildlings can be sown or transplanted directly from nearby forest (e.g. Saito et al. 2010; Maimunah et al. 2014), active reforestation typically involves two post-germination phases: nursery rearing of seedlings and subsequent outplanting. Selecting optimum species and approaches is important at both stages to maximize revegetation success, with numerous factors likely influencing seedling performance (e.g. species, fertilization, shading: Graham et al. 2017; Wibisono & Dohong 2017; Smith et al. 2022). In a recent meta-analysis, outplanting treatments produced weak effects on tropical peatland seedling survival and growth compared to species identity (Smith et al. 2022), yet it is unclear whether treatments are more important at the younger nursery stage.

Numerous studies have documented tropical peatland seed species performance under both nursery conditions (e.g. Ismail & Shamsudin 2003; Graham 2013*a*; Banjarbaru Forestry Research Unit et al. 2014) and upon outplanting (see recent review in Smith et al. 2022). While tropical peatland revegetation guidelines do consider both stages (Graham et al. 2017; Wibisono & Dohong 2017), few published quantitative studies consider how these stages are linked across the "seedling lifetime" (though see Graham et al. 2013 and Turjaman et al. 2011 for specific tests involving two species). This information gap is important, given findings from tropical peatlands (Turjaman et al. 2011; Graham et al. 2013) and other ecosystems (South et al. 2001; Pardos et al. 2003; Puértolas et al. 2009) that high nursery seedling performance does not necessarily equate to high outplanting performance, the main effects of each stage may not be additive and nursery treatment choices may influence outplanted seedling performance. For tropical peatland reforestation, this limits the ability to predict the number of seedlings and length of time required, and allocate the financial and other resources necessary, to achieve planting targets.

We investigate the linkages between nursery and outplanted tropical peatland tree seedling performance to:

(1) Quantify sources of performance variation in nursery and outplanting, specifically asking:
   (a) Which factor(s) are associated with the greatest performance variation (survival and growth) in the nursery (species, seedling source, treatment) and upon outplanting (species, site conditions, treatments)?
   (b) Are survival and growth rates related across species?
(2) Determine whether nursery seedling performance predicts outplanting performance.
(3) Calculate cumulative seedling survival from nursery to outplanting, to obtain a truer estimate of the number of seedlings required to meet reforestation targets.

Methods

Study Site

Data were collected from the Natural Laboratory of Peat-swamp Forest special research zone in Sebangau National Park, Central Kalimantan, Indonesia (Fig. 1). This is an ombrogenous, non-masting peat-swamp forest, with peat depth ranging from 1 m in riverine areas to ≥10 m in the dome center (Page et al. 1999). At least 215 tree and 92 non-tree flora occur here, plus a diverse fauna (Husson et al. 2018), including important seed dispersers (e.g. *Pongo pygmaeus wurmbii*: Tarszisz et al. 2018). See Page et al. (1999) and Husson et al. (2018) for detailed descriptions of habitat characteristics and biodiversity. The mean annual rainfall is 2,978 mm, with mean daily temperature ranges of 22.0–28.5°C (Harrison et al. 2016). Water pH in the forest and nearby Sebangau River range from around 3.4 to 4.3 and 3.2 to 4.8, respectively (Thornton et al. 2018), and mean humidity (in dry months) in the area ranges from 54.9 to 73.6% (Ishikura et al. 2017).

The forest experienced selective logging over an approximately 40-year period by timber concessions until 1997 and illegal hand-loggers until 2004, following which only low-level, sporadic small-pole exploitation occurred. Past illegal logging was associated with the creation of numerous small canals, causing peat drainage, subsidence, and heightened dry season fire risk (Wösten et al. 2008). Consequently, the riverine forest has been lost since the 1950s, with sporadic fires and frequent

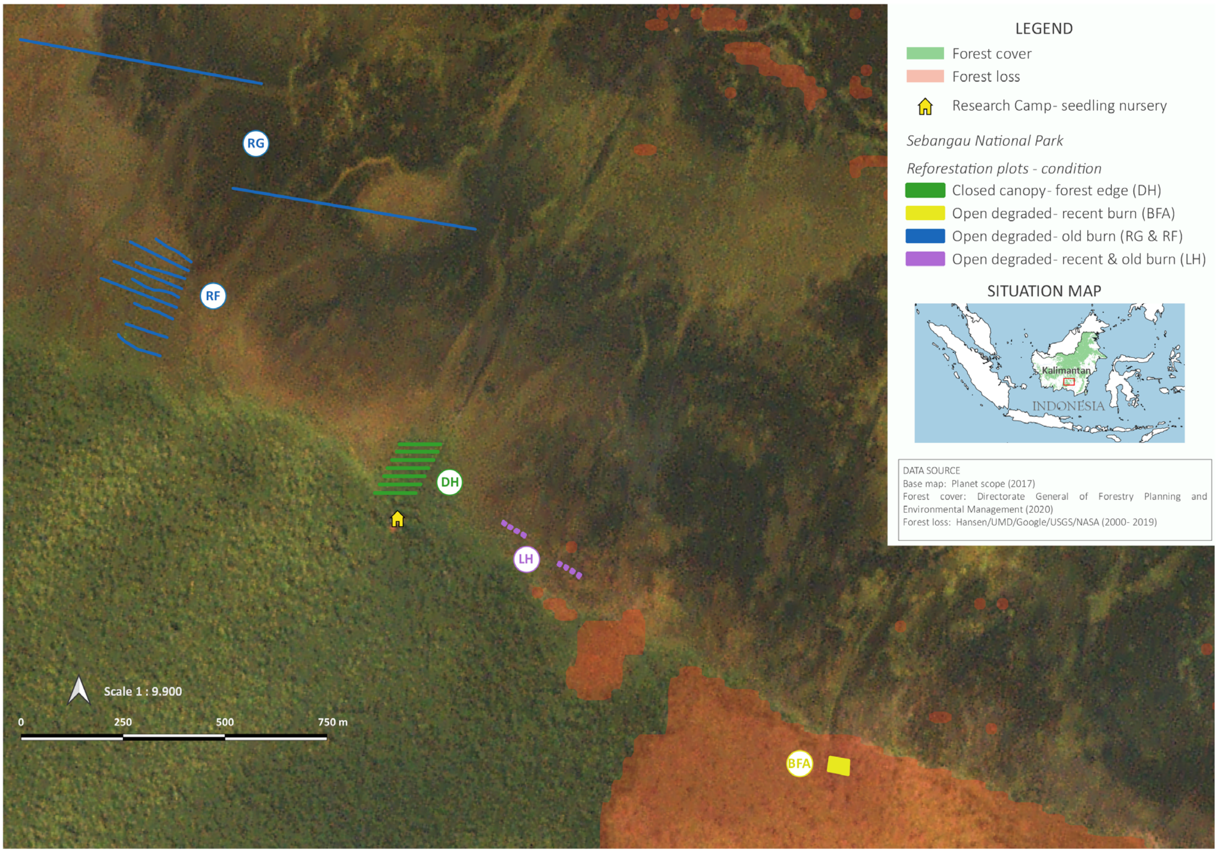

Figure 1. Map showing seedling nursery and outplanting locations in the border area of Sebangau National Park, and (inset) location of this in Kalimantan, Indonesia. The blackish area on this map to the north east of the forest edge up to the Sebangau River (visible in the top-right corner) has experienced various burns and is dominated by low-growing sedge swamp with small shrubs. The pink areas of forest loss indicated result from fires in 2006 (smaller patch) and 2015 (larger patch including outplanting site). Outplanting dataset abbreviations: RG = RG-2009; RF = RF-2012 and RF-2013 (distinct transects used in each of these trials); DH = DH-2014; LH = LH-2016; BFA = BFA-2016. Coordinates for these outplanting locations are provided in Table S1.3.

flooding occurring, and the area is now dominated by low-growing sedge swamps with small shrubs (Page et al. 1999; Morrogh-Bernard 2011). Since the designation of Sebangau National Park and locally-led patrols stopped illegal logging in 2004, canal blocking and forest patrols have helped restore swamp hydrology and reduce fire risk, allowing some forest and wildlife recovery (Husson et al. 2015; Harrison et al. 2021; Setyawati et al. 2021). Harsh environmental conditions (fire, flooding, dense sedge growth) in heavily degraded areas have, however, slowed natural regeneration (Graham & Page 2011; Graham 2013*b*; Setyawati et al. 2021). Tree planting has thus been trialed to accelerate reforestation (Morrogh-Bernard 2011; Graham 2013*b*; Ottay et al. 2021).

Nursery

A seedling nursery was constructed in October 2005 (2°19′00.46″S, 113°54′28.23″E; Fig. S1.1), positioned within the forest to replicate forest light, humidity, and rainfall (described in detail by Graham et al. 2007). In September 2010, the nursery was moved gradually to a semi-open area near the forest edge (2°18′58.56″S, 113°54′29.40″E; Fig. S1.2), to replicate better the environmental conditions that seedlings experience upon outplanting and to allow nursery expansion. At different times, the nursery consisted of either individual netted tables or was entirely netted with fine, black netting, providing permeable roofing to reduce insect herbivore damage, give 50% shade and natural rainfall exposure.

Seeds and wildlings were sourced from adjacent relatively undisturbed forests (Fig. 1). Seeds were collected from the ground, with damaged seeds discarded, and germinated in peat trays. Soil pH, nitrogen, and phosphorus concentrations of peat used were comparable to those from adjacent forests (Table S1.1). Seedlings typically germinated after 15–30 days, depending on the species. Upon reaching 0.5–1 cm height, seeds were transferred to plastic, peat-filled polybags and given a unique numbered tag to facilitate monitoring. During dry periods, seedlings were watered with local rainwater and, when necessary, water was pumped up from the peat. Seedlings were generally grouped into species cohorts on entry into the nursery. Weeds were removed regularly by hand, taking care not to disturb seedling roots. Fertilizer was added for some seedling batches (typically 6–9 g of Dekastar Plus: 13% N, 13% P_2O_5, and 13% K_2O, plus micro-elements B, Cu, Mn, Mo, and Zn).

As details on the quantity, frequency and application method were not typically recorded, fertilizer use is categorized as non-fertilized (30 cohorts), fertilized (16 cohorts), or unknown (51 cohorts). No chemical or biological pest control agents were used.

Nursery data were collected between December 2009 and February 2014 for 40 native tropical peat-swamp forest species from 29 genera (Table S1.2). Monitoring involved recording whether a seeding was alive and measuring the height from the main stem base to the top of the highest leaf/branch. Seedlings were considered dead when all leaves were lost and the stem wood was dry; and ready for outplanting when a sufficient height was reached based on expected flood conditions at the planting site (initial outplanting height: mean 45 ± SD 24 cm; median 40 cm), with the caveat that stems and leaves appeared healthy (no withering).

Outplanting

Outplanting occurred under six distinct small-scale trials implemented between 2009 and 2016, to address applied questions relevant to the reforestation team's current knowledge (gaps) and goals. This produced a combination of species mixes (total 24 species; mean 7, range 2–11 species per trial), use of seedlings versus wildlings, treatments, and site conditions across trials. For details of planting trials and their environmental conditions see Table S1.3. Most outplantings occurred along a 1- to 2-km-wide strip of deforested and (recent/old) burned sedge swamp between the forest edge and Sebangau River, though some also occurred near the forest edge and as supplementary planting within the relatively undisturbed forest (Fig. 1). All species used were native to tropical peat-swamp forests in the region. Outplanted seedlings were sourced mainly from our seedling nursery, but there was no continuous monitoring of tagged nursery seedlings for outplanting. No root pruning was conducted.

Seedlings were transported to outplanting locations in their plastic polybags, which were removed upon planting, taking care to minimize root disturbance. Seedlings were typically planted immediately following transport to outplanting sites. Two trials included planting in weaved organic baskets (referred to by the local name "*bakul*" herein), typically measuring 20 cm in height and 15 cm in diameter (Table S1.3). These were made by local women's cooperative groups from sustainably sourced "*purun*" sedge (*Lepironia articulata* Domin.), to increase benefits to community members that are less commonly engaged in restoration projects and reduce plastic waste from polybags. Bakuls were not removed before outplanting.

Climate: Precipitation

To investigate potential climate impacts, we used PERSIANN-CDR daily precipitation data for our location, which is generated from the PERSIANN algorithm using GridSat-B1 infrared data at a spatial resolution of 0.25° (Sorooshian et al. 2014; Ashouri et al. 2015). Using this, we calculated total precipitation for seedlings up to 2 years to match the standardized survival and growth calculations.

Data Processing and Analysis

Species Identification. Species identification follows Husson et al. (2018), with nomenclature following the Angiosperm Phylogeny Group (2016) and Taxonomic Name Resolution Service (Boyle et al. 2013). Species were classed as pioneers based on the list in Wibisono & Dohong (2017, table 7) and if not listed were considered non-pioneers.

Seedling Cohorts: Year, Project, Seedling Source, Treatments, and Site Conditions. To calculate survival rates and ensure consistency in analyses, individually monitored seedling data were grouped by seedling cohorts. For nursery studies, cohorts were defined as groups of the same species, seedling source (seedling or wildling), and treatment (fertilized, non-fertilized, or unknown) entering the nursery in a given month. For outplanting trials, seedling cohorts were defined as the same species, site condition ("open old burn," burned before 1999; "open recent burnt," burned in either 2006 or 2015; "forest edge" near the forest-sedge boundary; or "relatively undisturbed forest," for which there was no historical evidence of fire), treatment (control, bakul, roof, bakul plus roof, or—in cases where no bakuls or roofs were used and there was thus no control group—no treatment), and plot or transect (see Table S1.3 for full details). Seedling cohorts were used to calculate survival through time and averaged for growth measurements. In total, the nursery dataset consisted of 97, and outplanting 156, seedling cohorts.

Seedling Survival and Growth. To derive comparative survival and height growth measures across nursery studies of different monitoring durations we adopted a line-fitting approach (details below) using time-series monitoring data (Smith et al. 2022). Total nursery monitoring duration averaged 318 days (median 310, range 225–509 days), whereas outplanting monitoring averaged 1,570 days (median 1,802, range 638–1,810 days). To bridge these differences, we standardized survival and height growth at 2 years (730 days), but these were compared to final survival and height, and other derived measurements (below). Our main survival and growth measures analyzed were:

(1) *Survival at 2 years*: Predicted using linear, exponential, power-law, asymptotic, and logistic models of mortality (inverse of survival) as a function of time. Models were run separately for nursery and outplanted cohorts. The best model fits were selected based on the lowest Akaike Information Criteria score and models with $r^2 < 0.5$ were removed, as these represented the lowest fifth percentile. Based on the best model, survival was estimated at 2 years. Line-fitting could not predict cohorts with 0% mortality that did not change throughout monitoring, thus these were manually included as 100% survival if monitoring extended beyond 2 years. Using a similar line-fitting approach, we predicted half-life, duration of time until 50% mortality, and final survival for

each nursery and outplanting seedling cohort. Predicted survival at 2 years, half-life and final survival for both stages were all strongly correlated (Fig. S1.3). For simplicity, hereafter survival at 2 years is referred to as "survival."

(2) *Height at 2 years*: Calculated following the above method, but with seedling height fitted as a function of time. Heights recorded in the nursery ranged from 1 to 150 cm (mean 20 ± SD 13; median 16 cm) and for outplanting from 3 to 290 cm (61 ± 32; 55 cm). Negatively predicted heights at 2 years and heights exceeding 10 m were removed. The predicted height at 2 years and final height in both stages were strongly correlated (Fig. S1.3). Predicted height at 2 years is hereafter referred to as "height."

(3) *Relative growth rates* (*RGR*): Calculated using a similar line-fitting approach. RGR as a linear form is seedling height per time unit, divided by the initial height of the monitoring time interval. For non-linear model types, we used RGR calculation adjustments derived by Paine et al. (2012). Like height, RGR was determined at a standard time of 2 years. RGR and height at 2 years were poorly correlated, especially for outplanting (Fig. S1.3H), and, thus, we ran separate analyses for these. RGR was expressed as cm cm^{-1} day^{-1}.

(4) Cumulative survival: Calculated sequentially at a species level, first using the predicted mean survival at 2 years in the nursery and then, of those surviving individuals, the predicted outplanting survival at 2 years, thus providing cumulative estimates over 4 years.

Statistical Analysis. To analyze survival, height, and RGR we applied a meta-analytical approach using multilevel linear models with covariates through the "rma" function in the R package "metafor" (Viechtbauer 2010). We viewed our outplanting trials as separate studies, thus meta-analyses allowed us to account for heterogeneity across trials, and, by extension, meta-analysis was applied to the nursery study to standardize analytical approaches. For meta-analyses, survival, height, and RGR were weighted by sample size; e.g. for seedling cohort survival, sample variance was calculated as the proportion of individuals surviving minus the proportion dying, divided by the total number of individuals planted (Viechtbauer 2010). For height and RGR, we used mean raw differences between variables, including standard deviation across seedling measurements (Viechtbauer 2010). Model tests and confidence intervals were computed using the Hartung-Knapp-Sidik-Jonkman method (Pappalardo et al. 2020). Analyses were split into nursery and outplanting, and three metrics (survival, height, and RGR), totaling six models.

In multilevel linear nursery models, covariates were species identity, seedling origin, fertilization, and total precipitation. In outplanting models, covariates were species identity, site condition, site treatment, and total precipitation. In the outplanting survival model, the original planting height was included as an additional covariate, but this was not included in height and RGR models as the original height is integrated into these predictions (see above). All multilevel linear models assumed normal data distribution, yet survival should be bounded between 0 and 100% (Douma & Weedon 2019). Following survival analysis, three nursery and three outplanting species deviated by 0 and 100%, yet most predicted species-level survivals followed observed species-level averages (Fig. S1.4). Furthermore, we carried out additional tree-level generalized linear models assuming binomial distribution (Supporting Information S2). The

Table 1. Summary of five top and poorest survivors in the nursery and outplanting identified from species contrasts of survival modeling. Shown for each species are mean survival at 2 years, final survival, and number of significant ($p < 0.05$) contrasts. Nursery species model contrasts included 36 species and outplanting species contrasts included 23 species. All errors are presented as ±1 SD. Local and family names for each species are provided in Table S1.2.

Reforestation stage	*Performance*	*Species*	*Survival (%) at 2 years*	*Final survival (%)*	*Significant survival contrasts*
Nursery	Top survivors	*Calophyllum hosei*	84 ± 11	94 ± 3	7
		Memecylon sp. 1	95 ± 8	76 ± 40	6
		Shorea balangeran	92 ± 3	92 ± 3	6
		Diospyros areolata (bantamensis)	88 ± 6	91 ± 4	6
		Lophopetalum cf. *rigidum*	83 ± 9	91 ± 8	6
	Poor survivors	*Sandoricum beccarianum*	0	0	21
		Syzygium sp. 6 cf. *myrtifolium (campanulatum)*	2	41	20
		Syzygium sp. 15	19 ± 18	27 ± 35	20
		Melaleuca cajuputi	27 ± 32	45 ± 26	15
		Combretocarpus rotundatus	34 ± 39	37 ± 33	14
Outplanting	Top survivors	*Lophopetalum* cf. *rigidum*	89 ± 13	79 ± 20	5
		Elaeocarpus acmocarpus	83 ± 1	82 ± 2	5
		Syzygium sp. 6 cf. *myrtifolium (campanulatum)*	83 ± 11	62 ± 10	5
		Shorea balangeran	50 ± 20	42 ± 20	5
		Calophyllum sclerophyllum	49 ± 39	34 ± 40	5
	Poor survivors	*Palaquium leiocarpum*	9 ± 9	4 ± 9	23
		Palaquium pseudorostratum	13 ± 14	6 ± 12	23
		Horsfieldia crassifolia	21 ± 25	11 ± 17	23
		Licania splendens	23 ± 12	10 ± 7	23
		Calophyllum hosei	31 ± 34	20 ± 29	23

advantage of binomial models was avoiding erroneous predictions of survival outside the natural bounds of 0 and 100%, but the disadvantage was the inability to standardize the time interval of analysis due to highly heterogeneous tree census intervals. The major findings of the multilevel linear models and generalized linear models were similar (see Supporting Information S2) and, given the advantages and disadvantages associated with both approaches, we have opted to be consistent in the type of statistical approach used across survival, height, and RGR analyses.

To further investigate species differences in our multilevel linear models, we generated species contrasts by releveling the dataset and running multiple models with different species as the initial comparator (Viechtbauer 2010). The ability of nursery species seedling performance to predict outplanting performance was determined using linear models averaging survival, height, and RGR across other factors (e.g. treatments, site conditions, etc.) per species.

All analyses were performed in R v4.2.0 (R Core Team 2022), using the packages "tidyverse" (Wickham et al. 2019) and "readxl" (Wickham & Bryan 2022) for data processing. Model diagnostics such as residual versus fitted values, publication bias using funnel plots, and sensitivity analysis of study-site outliers were checked using "metafor" (Viechtbauer 2010). GLMM residuals and diagnostics were checked using the "DHARMa" package (Hartig 2020).

Results

A total of 5,311 nursery seedlings were monitored, representing 21,478 data points from 40 species, with 2–757 individuals per species; whereas across outplanting, a total of 5,517 seedlings were monitored, yielding 87,485 data points from 24 species, with 2–1,176 seedlings per species (Table S1.2). In total, survival, height, or RGR measurements were shared across the two stages for 21 species. However, the inability of line fitting to predict survival, height, and RGR in all cases, for instance due to stochastic changes through time, means the number of species in specific analyses varied.

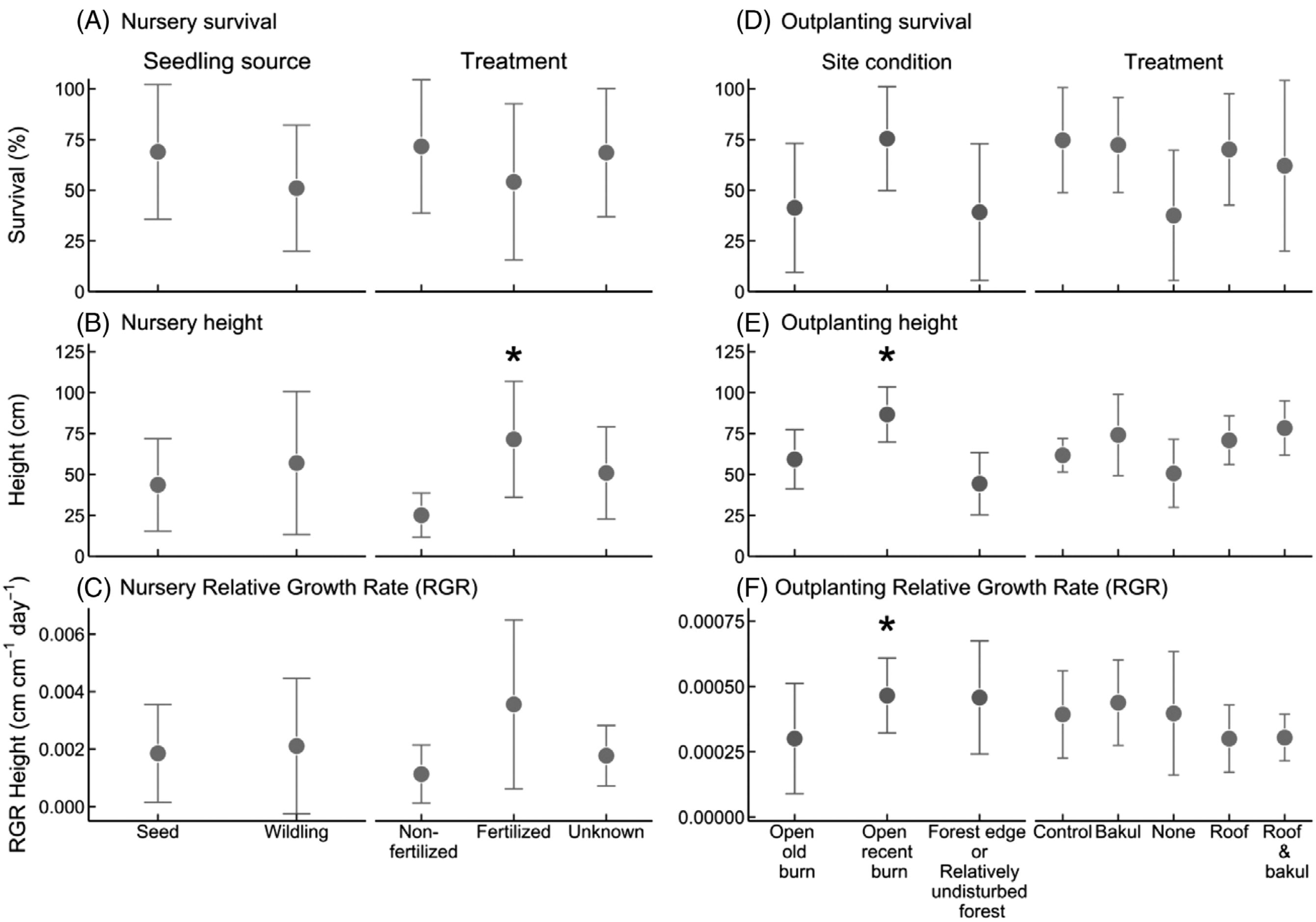

Figure 2. Tree seedling survival and growth averages in relation to seedling source and treatments in the nursery, and outplanting site condition and treatment. Nursery (A) survival and (B) height at 2 years and (C) relative growth rate are averaged across seedling source (seed vs. wildling) and treatment (fertilized, non-fertilized, or unknown). Outplanting seedling performance is averaged across site condition (forest edge or relatively undisturbed forest, open recent burned or open old burn) and treatments (roofed and weaved rattan bakset [*bakul*], roof only, bakul only, none, and control). Asterisks above nursery treatment represent significant differences to non-fertilized controls (Table S1.5) and for outplanting site conditions represents significant difference to open old burn (Table S1.6). Each bar represents averages across species for the factor and error bars are ±1 SD.

Sources of Variation in Seedling Performance in Nursery and Field

Seedling survival averaged 67% (confidence interval [CI] 60–74%) in the nursery and 44% (38–49%) for outplanting. For the species shared across both stages, nursery survival was still higher (mean 70%; outplanting 44%). In both stages, there were significant species differences in survival (Tables S1.2, S1.4, & S1.5). The best-performing nursery species in terms of survival were *Calophyllum hosei*, *Memecylon* sp.1, and *Shorea balangeran* (means ≥ 89% at 2 years) (Table 1). For outplanting, all species outperformed five poor survivors, namely *Palaquium leiocarpum*, *Palaquium pseudorostratum*, *Horsfieldia crassifolia*, *Licania splendens*, and *C. hosei* (means ≤33% at 2 years); nevertheless, we list top-performing species with highest survival in Table 1. While the mean survival of pioneer species was lower than for non-pioneers in the nursery and higher on outplanting, these differences were not significant (Table S1.4). Nursery and outplanted seedling survival were not significantly influenced by any other factors. There were no significant differences in survival due to nursery seedling source, original planting height and site conditions for outplantings, and treatments or precipitation for both stages (Tables S1.4 & S1.5; Fig. 2). Survival and height were not significantly correlated across species in the nursery ($r_s = 0.09$, degrees of freedom [df] = 30, $p = 0.606$) or in outplantings ($r_s = 0.38$, $df = 17$, $p = 0.109$).

Nursery (mean 45; CI 38–51 cm) and outplanting (55; 51–59 cm) seedling heights were similar. There were significant species height differences in both stages (Tables S1.2, S1.4, & S1.5). Across all trials, the fasting growing nursery species were *Memecylon* sp. 2 and *Combretocarpus rotundatus* (means >0.005 cm cm^{-1} day^{-1}); and upon outplanting were *C. hosei* and *Nephelium lappaceum* (>0.0007 cm cm^{-1} day^{-1}). Seedling height and RGR were significantly influenced by some factors other than species identity. In the nursery, fertilization increased seedling height by almost 185%, from an average 25 cm without to 71 cm with fertilizers (Fig. 2B). Although unknown fertilized seedlings were taller, these were not significantly different from controls, suggesting this group contained a mixture of fertilized and unfertilized seedlings (Table S1.4; Fig. 2B). RGR was higher for fertilized compared to non-fertilized seedlings, but this was not significant (Table S1.5; Fig. 2C). Nursery wildlings did not significantly differ in heights or RGR compared to seedlings reared from seeds (Table S1.5). Outplanting treatments of bakuls, roofs and their combination did not significantly influence seedling height or RGR (Table S1.6).

Site conditions significantly affected outplanted seedling height and RGR (Table S1.6; Fig. 2). Seedlings outplanted in open recent burn were 46% taller than in open old burn conditions and showed higher RGR, though there were no differences in height or RGR between relatively undisturbed forest and open old burn conditions (Fig. 2E). Nursery seedling height showed a declining trend ($p = 0.05$) with higher precipitation (Table S1.5; Fig. S1.4), with lower heights experiencing above 8,700 mm precipitation over 2 years. Similarly, nursery RGR was lower with higher precipitation, but not significantly (Table S1.5; Fig. S1.4). Outplanted

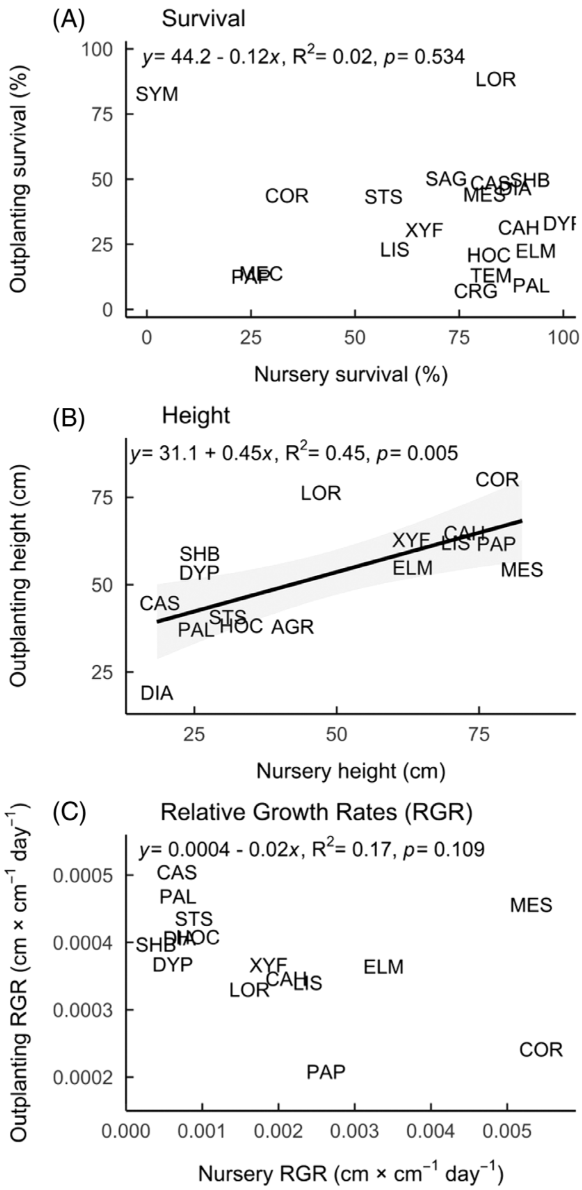

Figure 3. Nursery seedling performance used to predict outplanted seedling (A) survival, (B) height, and (C) relative growth rates (RGR) for 21 tropical peat-swamp forest species from Sebangau National Park, Indonesia. Species abbreviations: AGR, *Aglaia rubiginosa*; CAH, *Calophyllum hosei*; CAS, *Calophyllum sclerophyllum*; COR, *Combretocarpus rotundatus*; CRG, *Cratoxylon glaucum*; DIA, *Diospyros areolata (bantamensis)*; DYP, *Dyera polyphylla (lowii)*; ELM, *Elaeocarpus mastersii*; HOC, *Horsfieldia crassifolia*; LIS, *Licania splendens*; LOR, *Lophopetalum* cf. *rigidum*; MEC, *Melaleuca cajuputi*; MES, *Memecylon* sp. 2 (local name: milas); PAL, *Palaquium leiocarpum*; PAP, *Palaquium pseudorostratum*; SAG, *Santiria* cf. *griffithi*; SHB, *Shorea balangeran*; STS, *Stemonurus* cf. *scorpiodes*; SYM, *Syzygium* sp. 6 cf. *myrtifolium (campanulatum)*; TEM, *Ternstroemia magnifica*; and XYF, *Xylopia fusca*. Only significant linear model line of best for is shown with 95% error margins.

seedling height and RGR showed no significant relationship with precipitation (Table S1.6; Fig. S1.4.). However, we note that outplanting occurred during drier conditions than in the

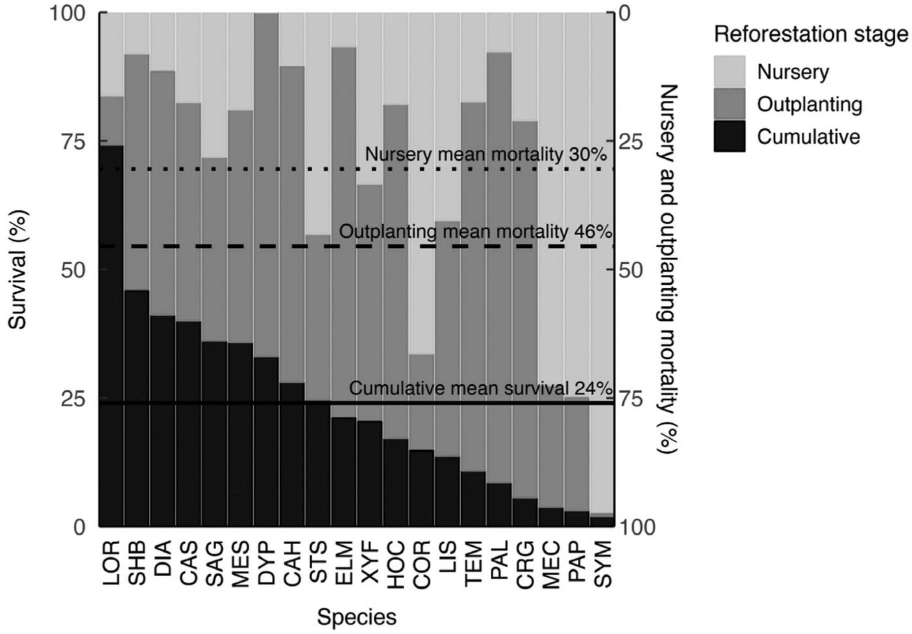

Figure 4. Cumulative seedling survival from rearing in the nursery to outplanting in degraded peatlands for 20 tropical peat-swamp forest species from Sebangau National Park, Indonesia. Bars represent sequential survival from nursery to outplanting, each for a standard 2-year period calculated separately for each stage (see Methods). Species abbreviations follow those in Figure 3.

nursery and outplanting did not occur during exceptionally wet periods (highest total precipitation, 6,500 mm; Fig. S1.5).

Does Species Seedling Nursery Performance Predict Outplanting Performance?

Following species model contrasts, 14 top surviving species were shared across the two stages, out of 19 species. Only outplanted seedling height was predicted by nursery height, and not survival or RGR (Fig. 3). Species survival from our nursery was not significantly correlated with the frequency of species use in tropical peatland outplanting projects in Central Kalimantan identified by Smith et al. (2022) (Fig. S1.6).

Cumulative Survival from Nursery to Outplanting

Mean cumulative seedling survival from nursery to outplanting was 24 ± SD 18% (median 21%) (Fig. 4). In other words, if rearing 1,000 seedlings, we would expect on average 240 to survive after 4 years (2 years each in nursery and outplanting). For most species, nursery survival rates were higher than outplanting (Fig. 4). *Lophopetalum* cf. *rigidum* was the only species exceeding 50% cumulative survival, surviving well in both the nursery and outplanting (Fig. 4).

Discussion

Our study represents a rare, detailed analysis of tree seedling survival and growth across the two common active reforestation stages: nursery and outplanting. This addresses a growing need to understand how nursery seedling quality influences outplanting success in tropical ecosystems (Grossnickle & MacDonald 2018) and especially in tropical peatlands, for which studies of cumulative seedling performance are rare (though see Turjaman et al. 2011; Graham et al. 2013). In so doing, we identify sources of variation in seedling performance, including in relation to both species and treatments (Q1a); relationships between survival and growth rates across species (Q1b), and between nursery and outplanting (Q2). Such information is important to help practitioners consider how cumulative seedling performance under differing nursery and outplanting conditions may interact to influence a project's ability to meet its reforestation targets, and the genetic and other resources that may be required to meet these targets (Q3).

We found that the most consistent source of variation in seedling performance in both stages was species identity, which was indeed the only significant source of variation for survival. We also observed no significant difference in survival between pioneer and non-pioneer species in both stages. Together, these findings illustrate the importance of species selection and point toward the challenge of effectively screening diverse tropical peatland tree flora for reforestation (Smith et al. 2022). This is complicated further by our observation that nursery seedling survival and growth did not consistently predict outplanting performance, except for height. Thus, it may be impossible to screen for nursery traits as a predictor of outplanting performance, especially as others have found generally weak traits relationships from seedlings to mature trees (Cornelissen et al. 2003). This implies that species selection may need to be considered separately for survival and growth, depending on a planting project's targets. Furthermore, the observation that species survival from our nursery was not significantly correlated with the frequency of species use in tropical peatland outplanting projects in Central Kalimantan identified by Smith et al. (2022), indicates that factors other than nursery survival govern outplanting species selection.

Available nutrients in tropical peat soils are usually low (Page et al. 1999; Yule & Gomez 2009) and, unsurprisingly, despite the potentially higher phosphorus levels in commercially sourced peat used in the nursery, we detected a large positive influence of fertilizer application on nursery seedling growth. Similar growth responses have been reported in other nursery studies, though effects vary greatly between species (Yuwati et al. 2015; Mawazin 2017). Nursery seedling height and RGR did not differ for wildlings compared to seedlings reared from seed.

Site condition did not significantly influence outplanted seedling survival across our datasets, but seedlings planted in recently burnt open sites were taller with a higher RGR than those in open degraded and relatively undisturbed forests, possibly owing to (short-term) provision of nutrients from ash (Agus et al. 2020). While the use of bakuls, roofs, and their combination did lead to greater height across all species, the absolute height increase was marginal and there were no significant influences on RGR or survival. Overall, this indicates a limited impact of bakul use on seedling performance. Furthermore, despite the higher cost, bakuls have the advantage of potential provision of alternative income benefits (e.g. USD 800 income across two groups involving 19 local women, from producing 3,000 bakul for Borneo Nature Foundation-related planting in 2019: BNF, unpublished data), plus avoiding the plastic waste costs associated with polybags (Haase et al. 2021).

Our tests revealed no influence of precipitation on survival in either stage and inconsistent growth responses. There was a negative trend for precipitation and seedling height but not RGR in the nursery, and for outplanted seedlings there was no significant influence of precipitation on either variable. This may be because outplanting typically occurred in relatively drier periods than those experienced in the nursery and that nursery (but not outplanted) seedlings were watered during dry periods.

We found that seedling survival across species was substantially higher in the nursery compared to outplanting, and only a mean of 24% of seedlings would be expected to survive 4 years from nursery to the field. On this basis, obtaining and allocating genetic and financial resources totaling around four times an intended cumulative target would be required to meet that target. This is particularly important for planning sustainable seedling sourcing involving wild harvesting and where target species may be (locally) rare (e.g. *Nephelium lappaceum* is relatively rare at our site; Harrison et al. 2010). While this may be less problematic for seeds in tropical peatlands than other forest systems, owing to the former's lack of seed bank (Graham & Page 2018), it may create a larger issue for wildlings by limiting the ecosystem's ability to replace these. Given the billions to trillions of trees aimed to be planted worldwide (Holl & Brancalion 2020), and ambitious aims to restore tropical peatlands in countries such as Indonesia (BRGM 2018), this is of both global and national policy relevance. It also highlights the relatively limited usefulness of (tropical peatland) revegetation projects employing solely the nursery seedling stock or a number of seedlings planted as their restoration target, or using these as sole indicators of success (as discussed in Fleischman et al. 2020; Di Sacco et al. 2021).

Our analyses across nursery and outplanting offer an approach to leverage interventions to maximize cumulative survival for tropical peatland reforestation. Seedling survival was much lower in outplanting than in the nursery, thus perhaps generating opportunity to target interventions and screening in the nursery to positively influence outplanting survival. Similar to other forestry sectors, hardening is used in tropical peatlands to acclimatize nursey seedlings to, e.g., higher light and reduced watering before planting (Dommain et al. 2016; Graham et al. 2017). Given our weak nursery and outplanting treatment results, and those identified in Smith et al.'s (2022) wider systematic review, we propose such hardening should be tailored more specifically toward conditions common in degraded peatlands; e.g. flooding seedlings. While tropical peatland nursery studies have investigated tree species flooding tolerance (Santosa et al. 2014; Tata et al. 2022), to our knowledge these do not outplant survivors versus unflooded control seedlings to determine whether nursery flooding treatments influence outplanted seedling survival. Other relevant treatments may include mycorrhiza inoculation to avoid/reduce fertilizer use (Turjaman et al. 2011; Graham et al. 2013), full leaf scorching to stimulate post-fire resprouting and identify species' fire regeneration adaptations (Hadi et al. 2019), and seedling flammability (Rahman et al. 2023). Research to address these questions using rigorous controlled experimental designs could thus be highly beneficial to revegetation efforts in tropical peatlands and more widely.

Our study exhibits some limitations that would be beneficial to address in the future. First, as detailed in the Methods, we did not track performance for individually identified seedlings from nursery to field, thus preventing direct assessment of interactions between nursery and field conditions and treatments. Second, as also noted by Smith et al. (2022), we had no data on "natural" seedling survival and growth rates in intact peatswamp forests as a reference for comparison to nursery and outplanting performance. Finally, we did not monitor seedling germination, which may also vary within and between species in tropical peatlands (Graham et al. 2007; Tarszisz et al. 2018), potentially further influencing the genetic and financial resources required to reach active revegetation targets. Future studies could also benefit from incorporating data on seed sizes and numbers produced as additional resource cost parameters and extending the monitoring period.

In summary, we illustrate the value of combining seedling performance data from the two key post-germination stages typical of replanting projects—nursery and outplanting—to understand the sources of variation in performance, potential survival bottlenecks and intervention points, and estimate cumulative seedling survival and growth. Based on this, we highlight the need to: (1) screen more species for planting in tropical peatland reforestation, especially for traits enhancing resilience to degraded peat conditions (e.g. flooding tolerance, resprouting post-fire, mycorrhizal colonization); (2) trial interventions in nurseries with the aim of improving outplanting performance (e.g. hardening to flooding); and (3) generate alternative incomes through developing nursery-outplanting cycles that enhance or have no detrimental impact on outplanting performance (e.g. bakuls in our study). We encourage wetland reforestation, in particular tropical peatland revegetation, projects to account for cumulative survival across the nursery and outplanting in their analyses to provide truer estimates of the genetic and financial cost of wetland reforestation.

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Supporting Information

The following information may be found in the online version of this article:

Table S1.1. pH and chemical composition of peat from the Sebangau study site compared to illustrative peat ordered from Jakarta and used in the nursery ("Nursery peat").
Table S1.4. Descriptive statistics and results of unpaired *t*-test comparing differences in seedling survival between pioneer and non-pioneer species in both nursery and outplanting.
Table S1.5. Statistical output for three models for nursery seedling survival and height at 2 years, and relative growth rate (RGR).
Table S1.6. Statistical output for three models for outplanting seedling survival and height at 2 years, and relative growth rate (RGR).
Figure S1.1. Exterior (a) and interior (b) images of the original seedling nursery used in this study, prior to 2010. Photos by Laura Graham.
Figure S1.2. Images of the "new" seedling nursery used in this study from 2010 onwards, showing (a) subsection of nursery table layout and (b) seedlings pictured from inside table netting.
Figure S1.3. Correlations between survival and height growth measures for peat-swamp forest seedlings in the nursery and field planting.
Figure S1.4. Fitted vs. predicted survival for nursery and outplanting multilevel linear models as part of a meta-analysis of tree seedling survival.
Figure S1.5. Relationships between total precipitation and nursery and outplanting survival, height and relative growth rate (RGR).
Figure S1.6. Relationship between species performance in our nursery and number of outplanting studies recorded by Smith et al. (2022) as using the species in Central Kalimantan province, Indonesian.
Table S1.2. List of tree species used, number of seedlings monitored and performance metrics for both nursery and outplanting.
Table S1.3. Details of outplanting monitoring datasets included in this study.
Data S2. Supporting Information.
Table S2.1. Statistical output from three models analyzing tree seedling survival using binomial error distributions in the nursery at 1 year, and outplanting at 1 and 2 years.
Table S2.2. Statistical significance of individual terms used in models analyzing tree seedling survival using binomial error distributions in the nursery at 1 year, outplanting at 1 year and outplanting at 2 years.

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