Received: 28 August 2021 | Accepted: 22 April 2022
DOI: 10.1111/1365-2664.14232

Journal of Applied Ecology
BRITISH ECOLOGICAL SOCIETY

REVIEW

Tree species that 'live slow, die older' enhance tropical peat swamp restoration: Evidence from a systematic review

Stuart W. Smith[1,2] | Nur Estya Binte Rahman[1] | Mark E. Harrison[3,4] | Satomi Shiodera[5,6,7] | Wim Giesen[8,9] | Maija Lampela[10,11] | David A. Wardle[1] | Kwek Yan Chong[12,13] | Agusti Randi[10,14] | Lahiru S. Wijedasa[10,15,16] | Pei Yun Teo[17,1] | Yuti A. Fatimah[1] | Nam Thian Teng[18] | Joanne K. Q. Yeo[1] | Md Jahangir Alam[19] | Pau Brugues Sintes[20] | Taryono Darusman[21] | Laura L. B. Graham[22,23] | Daniel Refly Katoppo[24] | Katsumi Kojima[25] | Kitso Kusin[26] | Dwi Puji Lestari[21] | Faizah Metali[27] | Helen C. Morrogh-Bernard[3] | Marlide B. Nahor[8] | Richard R. P. Napitupulu[28] | Darmae Nasir[26] | Tapan Kumar Nath[19] | Reuben Nilus[29] | Mariko Norisada[25] | Dony Rachmanadi[30] | Henti H. Rachmat[30] | Bernat Ripoll Capilla[20] | Salahuddin[24,26] | Purwanto B. Santosa[31] | Rahayu S. Sukri[32] | Benjamin Tay[33] | Wardah Tuah[32] | Béatrice M. M. Wedeux[34] | Takashi Yamanoshita[25] | Elisa Yukie Yokoyama[33] | Tri Wira Yuwati[30] | Janice S. H. Lee[1]

[1]Asian School of Environment, Nanyang Technological University, Singapore, Singapore; [2]Department of Physical Geography, Stockholm University, Stockholm, Sweden; [3]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Exeter, UK; [4]School of Geography, Geology and the Environment, University of Leicester, Leicester, UK; [5]Department of Global Liberal Studies, Faculty of Global Liberal Studies, Nanzan University, Nagoya, Japan; [6]Centre for Southeast Asian Studies, Kyoto University, Kyoto, Japan; [7]Research Institute for Humanity and Nature, Kyoto, Japan; [8]Euroconsult Mott MacDonald, Arnhem, The Netherlands; [9]Naturalis Biodiversity Centre, Leiden, The Netherlands; [10]Environmental Research Institute, National University of Singapore, Singapore, Singapore; [11]Department of Forest Sciences, University of Helsinki, Helsinki, Finland; [12]Singapore Botanic Gardens, National Parks Board, Singapore, Singapore; [13]Department of Biological Sciences, National University of Singapore, Singapore, Singapore; [14]Natural Kapital Indonesia, Pontianak, Indonesia; [15]BirdLife International, Cambridge, UK; [16]ConservationLinks Pvt Ltd, Singapore, Singapore; [17]Future Cities Lab Global, Singapore-ETH Centre, Singapore, Singapore; [18]Department of Earth Sciences, University of Oxford, Oxford, UK; [19]School of Environmental and Geographical Sciences, University of Nottingham Malaysia, Semenyih, Malaysia; [20]Borneo Nature Foundation International, Penryn, UK; [21]PT Rimba Makmur Utama, Jakarta, Indonesia; [22]Borneo Orangutan Survival Foundation, Bogor, Indonesia; [23]Tropical Forests and People Research Centre, University of the Sunshine Coast, Maroochydore DC, Queensland, Australia; [24]Yayasan Borneo Nature Indonesia, Palangka Raya, Indonesia; [25]Asian Research Center for Bioresource and Environmental Sciences, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan; [26]Centre for the International Cooperation in Sustainable Management of Tropical Peatlands, University of Palangka Raya, Palangka Raya, Indonesia; [27]Faculty of Science, Universiti Brunei Darussalam, Jalan Tungku Link, Brunei Darussalam; [28]Faculty of Forestry, University of Jambi, Jambi, Indonesia; [29]Sabah Forestry Department, Sandakan, Sabah, Malaysia; [30]Research Center for Ecology and Ethnobiology, National Research and Innovation Agency (BRIN), Cibinong, Indonesia; [31]Research Center for Plant Conservation, Botanical Garden and Forestry, National Research and Innovation Agency (BRIN), Bogor, Indonesia; [32]Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Jalan Tungku Link, Brunei Darussalam; [33]PM.Haze, Singapore, Singapore and [34]Department of Plant Sciences, University of Cambridge Conservation Research Institute, Cambridge, UK

Correspondence
Stuart W. Smith
Email: another.swsmith@googlemail.com

Stuart W. Smith and Nur Estya Binte Rahman contributed equally to the development of the study.

Funding information
Arcus Foundation; Darwin Initiative; European Association of Zoos and Aquaria; European Outdoor Conservation Association; Fundacion Bioparc; JSPS KAKENHI, Grant/Award Number: JP20K12266; National Research Foundation Singapore, Grant/Award Number: NRF2019-ITC001-001; NERC-GCRF, Grant/Award Number: NE/T010401/1; Ocean Parks Conservation Foundation Hong Kong; Orangutan Land Trust; Research Institute for Humanity and Nature, Grant/Award Number: 14200117; Save the Orangutan; Singapore Ministry of Education Research Fund, Grant/Award Number: MOE2018-T2-2-156; Taronga Zoo; The National Conservation Trust Fund for Natural Resources, The National Conservation Trust Fund for Natural Resources, Government of Malaysia, Grant/Award Number: NRE(S) 600-2/1/48/2Jld.2 (9); The Orangutan Project; Ministry of Environment & Forestry; PT Rimba Makmur Utama

Handling Editor: Sharif Mukul

Abstract

1. Degraded tropical peatlands lack tree cover and are often subject to seasonal flooding and repeated burning. These harsh environments for tree seedlings to survive and grow are therefore challenging to revegetate. Knowledge on species performance from previous plantings represents an important evidence base to help guide future tropical peat swamp forest (TPSF) restoration efforts.
2. We conducted a systematic review of the survival and growth of tree species planted in degraded peatlands across Southeast Asia to examine (1) species differences, (2) the impact of seedling and site treatments on survival and growth and (3) the potential use of plant functional traits to predict seedling survival and growth rates.
3. Planted seedling monitoring data were compiled through a systematic review of journal articles, conference proceedings, reports, theses and unpublished datasets. In total, 94 study-sites were included, spanning three decades from 1988 to 2019, and including 141 indigenous peatland tree and palm species. Accounting for variable planting numbers and monitoring durations, we analysed three measures of survival and growth: (1) final survival weighted by the number of seedlings planted, (2) half-life, that is, duration until 50% mortality and (3) relative growth rates (RGR) corrected for initial planting height of seedlings.
4. Average final survival was 62% and half-life was 33 months across all species, sites and treatments. Species differed significantly in survival and half-life. Seedling and site treatments had small effects with the strongest being higher survival of mycorrhizal fungi inoculated seedlings; lower survival, half-life and RGR when shading seedlings; and lower RGR and higher survival when fertilising seedlings. Leaf nutrient and wood density traits predicted TPSF species survival, but not half-life and RGR. RGR and half-life were negatively correlated, meaning that slower growing species survived for longer.
5. *Synthesis and applications*. To advance tropical peat swamp reforestation requires expanding the number and replication of species planted and testing treatments by adopting control vs. treatment experimental designs. Species selection should involve slower growing species (e.g. *Lophopetalum rigidum*, *Alstonia spatulata*, *Madhuca motleyana*) that survive for longer and explore screening species based on functional traits associated with nutrient acquisition, flooding tolerance and recovery from fire.

KEYWORDS
drainage, fires, *kerapah*, mounding, native species, oceanic Niño index, palms, revegetation, tropical peatland, weeding

1 | INTRODUCTION

The restoration of degraded forested lands is a global priority incentivised by international commitments to counteract decades of rapid deforestation (United Nations Framework Convention on Climate Change, 2019). For some types of less degraded forests, passive restoration (including assisted natural regeneration) without planting trees can be a resilient and cost-effective form of reforestation (Chazdon & Guariguata, 2016; Crouzeilles et al., 2017; Molin et al., 2018). However, many degraded forests may require active reforestation, specifically the planting of trees. Ensuring that planted trees survive is not a simple task, and entails multiple ecological, economic and social considerations (Di Sacco et al., 2021; Meli et al., 2014). Selecting which tree species to plant represents a central consideration and depends upon the goal of the restoration project, while being constrained by logistical issues such as seed availability (Chechina & Hamann, 2015; Meli et al., 2014). Trial and error through pilot trials, local knowledge and accumulated past experience helps guide species selection (Chechina & Hamann, 2015; Graham et al., 2017). Syntheses using seedling monitoring data from past reforestation projects remain rare, particularly in the tropics (Dimson & Gillespie, 2020; Suding, 2011). This dearth of syntheses may be due to the perception that species performance is too site specific, the physical and linguistic difficulties in accessing 'grey literature' (e.g. government reports, conference proceedings, working papers), and a legitimate lack of monitoring which is dropped during projects following budget cuts (Corlett, 2011; Graham et al., 2017; Holl, 2017; Suding, 2011). Nevertheless, evidence-based syntheses on species performance are valuable tools that can aid future species selection and improve reforestation outcomes.

Tropical peat swamp forests (TPSF) are wetland forest ecosystems globally valued for carbon storage, centres of species endemism, floral and faunal diversity, and regional for water cycling, livelihoods for local communities, public health and cultural landscapes (Harrison, Ottay, et al., 2020; Harrison, Wijedasa, et al., 2020; Page et al., 2011; Posa et al., 2011). Globally tropical peatlands cover 185 to 470 million km^2, equivalent to ~3% of the global land surface area, with large expanses of TPSF found across Southeast Asia, South America and equatorial Africa (Dargie et al., 2017; Gumbricht et al., 2017; Xu et al., 2018). However, TPSF have experienced rapid degradation in recent decades through timber logging, land conversion for agricultural purposes, associated drainage and fire, with particularly widespread loss and degradation of TPSF across Southeast Asia (Harrison, Ottay, et al., 2020; Miettinen et al., 2016; Page et al., 2009). Between 1990 and 2015, the area of 'intact' TPSF in Southeast Asia declined from 76% to 29% (11–4.6 Mha) of its original 25 million ha cover (Miettinen et al., 2016). Intact TPSF have poor drainage, permanent waterlogging and anaerobic conditions that slow decomposition and lead to the formation of peat, that is, partially decomposed organic matter. Conversion and drainage cause peat oxidation and elevated CO_2 emissions, subsidence (lowering of the peat surface) and flooding, increased risk of fires (particularly during drier El Niño conditions), and a surface vegetation primarily comprised of a dense thicket of sedges and ferns that competes with naturally recolonising trees and planted seedlings (Blackham et al., 2014; Miettinen et al., 2017; Mishra et al., 2021; Page et al., 2009).

The highest levels of degradation can impede natural regeneration of tree cover for over several decades, thus necessitating tree planting (Giesen & Sari, 2018; Graham et al., 2017; Graham & Page, 2018; Page et al., 2009). While substantive efforts have been made to reforest degraded peatlands, the ecological knowledge needed to reliably inform TPSF reforestation decision-making remains limited. There have been literature reviews detailing species planted in past projects and their survival rates (see (Dohong et al., 2018; Giesen & Sari, 2018; Giesen & van der Meer, 2009; Graham, 2009; Taylor et al., 2019). Although useful, such reviews lack the strength of a systematic review and quantitative meta-analysis that provides a more robust approach to inform restoration (Andivia et al., 2019; Romanelli et al., 2021), for instance, by accounting for the variations in numbers of seedlings planted and duration of monitoring in assessing the variability of species survival.

Harsh environmental conditions in degraded TPSF, stemming from draining, burning, periodic flooding and lack of canopy cover are known to threaten the survival of establishing tree species (Giesen & van der Meer, 2009; Lampela et al., 2018; van Eijk et al., 2009). In an attempt to improve survival and growth of planted species on degraded peatlands, a plethora of seedling and site treatments have been applied. Several of these treatments are generic to forest restoration, for example fertilisation, shading and weeding (Graham, 2013; Lampela et al., 2018; Taylor et al., 2019) and inoculating seedlings with mycorrhizal fungi (Graham et al., 2013; Turjaman et al., 2011; Yuwati et al., 2008). Other treatments are largely specific to peatlands, particularly rewetting for preventing further peat oxidation and reducing fire risk (Giesen & Sari, 2018; Page et al., 2009; Wösten et al., 2006), and the control of water levels and mounding to prevent seedling submergence and reduce seedling mortality (Giesen, 2004; Lampela et al., 2018; Rotinsulu et al., 2016). While most, if not all, native TPSF species are tolerant to flooding, severe flooding above the height of tree seedlings can increase seedling mortality (Giesen, 2004; Rotinsulu et al., 2016; van Eijk et al., 2009). Flooding risk is exacerbated by the loss of naturally occurring micro-topography found in intact TPSF; that is, local highs—'hummocks'—and lows—'hollows'—caused by tree fall, tree buttresses, root pneumatophores and deposits of organic matter (Freund et al., 2018; Lampela et al., 2016). Constructing artificial mounds to raise seedling heights above the flood line is designed to mimic these naturally occurring TPSF hummocks. Yet, mounding has been shown to have both positive (Nuyim, 2000; Santosa et al., 2011; Wibisono et al., 2005) and neutral effects (Lampela et al., 2018) on tree seedling survival.

Knowledge about plant functional traits is increasingly being applied to predict how tree species respond to site-specific barriers in restoration (Wainwright et al., 2018). Broadly, plant functional traits are biochemical, morphological, phenological and physiological properties of individuals that enable them to survive, grow, and thereby have higher fitness within a given environment (Violle et al., 2007). The ideal tree species for reforestation would be fast growing to reforest a degraded site quickly, have a high enough survival rate to maintain the site for other species to recruit naturally under them, and be inexpensive to rear and plant to meet planting targets. To maximise photosynthesis and growth, faster growing tree species generally have larger and thinner leaves, higher nutrient contents and lower wood densities, but at a cost of higher mortality rates due to vulnerability to disturbance damage and natural enemies (Philipson et al., 2014; Russo et al., 2021; Wright et al., 2010). In the context of tropical forest restoration, plant functional traits have been successfully applied to identify species across the growth-mortality spectrum (Charles, 2018; Charles et al., 2018; Martínez-Garza et al., 2013). For example, species with higher wood densities have higher probability of survival when planted to restore degraded wet tropical forests (Charles, 2018). Despite some research on leaf and wood functional traits in pristine TPSF (Tuah et al., 2003;

Wedeux, 2015; Yanbuaban et al., 2007), to our knowledge, there has been no formal consideration of plant functional traits to guide species selection in TPSF reforestation.

In this study, we undertake a systematic review of TPSF reforestation across Southeast Asia. The focus of the review is on active restoration, namely tree planting on degraded peatlands to facilitate ecological restoration, and tree planting in agroforestry systems, for example by planting fruit trees (Giesen & Sari, 2018). The aim of the review is to generate a comprehensive assessment of the factors influencing planted TPSF tree species survival and growth that can ultimately help improve reforestation outcomes. Using species-specific monitoring data compiled through a systematic literature review, we carried out a meta-analysis to address the following questions: (1) Which TPSF species survive and grow best when planted in degraded tropical peatlands? (2) Which seedling and site treatments, and environmental conditions (notably drained vs. rewetted) have the strongest impact on tree seedling survival and growth? and (3) Can plant functional traits be used to predict planted TPSF seedling survival and growth rates?

2 | MATERIALS AND METHODS

2.1 | Searches

A literature search of tropical peat swamp reforestation across Southeast Asia was conducted between May and October 2020. Bibliometric searches followed guidelines outlined by the Collaboration for Environmental Evidence (Collaboration for Environmental Evidence, 2018), and targeted scholarly and grey literature, with the latter including government and non-government reports, guidelines, conference proceedings, theses and unpublished datasets (Haddaway et al., 2020; Haddaway & Bayliss, 2015). A total of 15 search engines, 94 journal archives, 32 full conference proceedings (conferences spanning 1995–2018) and 28 institute and regional forestry department repositories were searched (Tables S1–S5, Appendix 1 in Supporting Information). Online search engines were explored using a combination of 64 keywords optimised by text-mining and keyword co-occurrence networks using the R package 'LitSearchR' (Grames et al., 2019) (Table S6, Appendix 1 in Supporting Information). All searches were carried out in English, Indonesian and Malay languages. Potentially relevant articles with English titles or abstracts but main text in Japanese or German were also included. Collectively, these searches resulted in 605 potentially relevant articles that were screened for eligibility (Figure S1, Appendix 1 in Supporting Information).

2.2 | Article screening and study inclusion criteria

Screening and cross-checking among screeners were carried out by nine authors (SWS, NEBR, MEH, SS, AR, ML, NTT, JKQY and PYT). To be eligible for further review, full texts were required to detail the following:

1. Tree planting located in Southeast Asia;
2. Planting in degraded TPSF and/or on peat (histosol) soil. Nursery, greenhouse or laboratory studies were excluded. *Kerapah* (waterlogged heath forests) on shallow peat was considered as forested tropical peatland (Giesen et al., 2018). Our definition of degraded TPSF encompassed open peatlands with limited or no tree cover, and enrichment plantings in logged over secondary TPSF or crop plantations, for example, oil palm (Ismail et al., 2006);
3. Planting of at least one native TPSF tree species. Monitoring data for native palms, native non-peat forest species and non-natives were included as long as the study planted at least one native TPSF tree species;
4. Planting tree seedlings or palm suckers reared in a nursery or directly planting tree wildlings. We excluded studies that directly sowed seeds due to life-stage differences in survival and growth rates, and because we found only two studies with monitoring data sowing seeds (Maimunah et al., 2014; Saito et al., 2010);
5. Monitoring of species-specific survival and/or growth. Studies presenting averaged monitoring data for sites or treatments were excluded, albeit after contacting authors for species-specific data (see below). Monitoring needed to start within the first 2 months of planting to measure initial survival and growth parameters (see below). This criterion served to exclude studies that surveyed mature plantings only.

Results from the same reforestation site were sometimes reported across multiple studies and publication formats (e.g. journals, conference proceedings, reports). Therefore, duplicate site information was consolidated into a single *study-site* for the systematic review and analysis. A study-site was defined as an identifiable site location (i.e. georeferenced location or site name) and planting period. Studies were split into multiple study-sites based on different locations and habitat types (e.g. open peatlands vs. forest enrichment) or timing of planting, for instance replanting at the same site following (near-) complete mortality of the original planting. Experimental units of larger sites, for example, blocks, transects or plots, were not considered as separate study-sites. Conversely, separate articles presenting results for different treatments at the same site and planting period were grouped into a single study-site.

The full texts of articles fulfilling the eligibility criteria were read in-depth to gather information on study location, species planted, seedling and site treatments, site condition and disturbance history including peat hydrological condition, applied treatments, monitoring duration, and seedling survival and growth monitoring data. Almost all articles lacked some information necessary for the systematic review and none provided raw data. We contacted 46 authors to request missing or additional data for one or more study-site and 16 authors provided partial or full datasets of studies. Several authors provided additional reports and 15 unpublished study-site datasets of which four have since been published (Table S7, Appendix 1 in Supporting Information). In total from bibliometric searches and author datasets, our review contained a total of 94 TPSF reforestation study-sites (Table S7; Figure S1, Appendix 1 in Supporting Information).

Searches for TPSF plant functional traits were conducted, following the same approach outlined above. Criteria for inclusion of plant trait data included:

1. Field measurements of traits, that is, trait data from nursery, greenhouse and laboratory studies were excluded. The underlying soil substrate for woody trait literature could not usually be ascertained; thus, woody traits may have been measured on either peat or mineral soils for species found across substrates. We recognise that this could potentially influence wood properties measured such as wood density (Luostarinen et al., 2017);
2. Leaf traits collected from mature, fully expanded, living and sun facing leaves. Trait measurements from newly emerging leaves and leaf litter were excluded;
3. Trait measurements from seedlings to mature trees were included.

All leaf traits used in this review were collected from the literature (Table S8, Appendix 1 in Supporting Information), but wood densities were supplemented by those reported in three regional and global online databases: PROSEA (https://www.prota4u.org/prosea/search.aspx), ICRAF (http://db.worldagroforestry.org//) and DRYAD Global Wood Density (https://datadryad.org/stash/dataset/doi:10.5061/dryad.234). In total, 27 functional traits found for species in the literature-matched species identified in the review. A subset of seven traits were included in our analyses due to sufficient corresponding species survival and growth monitoring data (Table S9, Appendix 1 in Supporting Information) (see below).

2.3 | Critical appraisal of screened articles

Species taxonomic names were verified against taxonomic records for TPSF and Southeast Asia (Giesen et al., 2018; Posa et al., 2011). Species were assigned to one of three categories: (1) native to Southeast Asian TPSF, (2) those that occur on non-peat (mineral soil) habitats only, but native to Southeast Asia, or (3) exotic species. Species were excluded if they had an unknown taxonomic name, if they were believed to be mis-identified, if they were known only from a specific region distant from the reforestation site, or if they had been identified to genus only. Taxonomic names were checked against a global database of known vascular plant species (The Plant List, 2013) and synonyms unified with most up-to-date records. Our dataset mainly comprises tree species, but also includes tree-like palms (e.g. *Areca* and *Metroxylon* species). We generally refer to 'seedlings' for simplicity.

There was a large variety of seedling and site treatments used across studies, which would have been impossible to fully incorporate into the analyses. We therefore grouped seedling and site treatments into broad categories (Table S10, Appendix 1 in Supporting Information). For example, treatments inoculating seedlings of different mycorrhiza fungal types (AM and ECM) and fungal species were grouped as 'mycorrhizal-inoculated'. Studies using a combination of treatments (e.g. mounding, weeding and fertilisation) were kept as treatment combinations rather than as single treatments. Treatments of different intensities (e.g. 50% shade vs. 100% shade) were grouped into a single 'shading' treatment category (Table S10, Appendix 1 in Supporting Information).

Across studies, there was little consistent reporting of site environmental conditions. Given the importance of hydrological recovery to TPSF restoration and its impacts on tree seedling survival, we concentrated our efforts on determining whether study-sites were drained or rewetted. This categorical variable was based upon water table measurements, descriptions of hydrological management and interventions (e.g. active or blocked peat drainage canals) provided in the articles, and where necessary author's responses to questions. We also tried to determine the post-fire monitoring period (i.e. for seedlings that had been planted before a fire and then monitored post-fire) of the studies but this was later excluded, because only one study undertook such monitoring (Lampela et al., 2017).

2.4 | Data extraction and effect modifiers

Where possible, time-series monitoring of seedlings over multiple intervals was collected from each study. Data were either shared by authors or extracted from text, tables and visualisations, the latter using WebPlotDigitizer (Rohatgi, 2020). Seedling growth was measured variously as height, diameter, number of leaves and biomass. Height was the most commonly monitored growth metric and was therefore the focus of our analysis. Studies varied substantially in numbers of planted individuals and duration of monitoring, and to address these issues we used three metrics of tree species survival and growth:

1. *Survival*, which we define as final survival at the end of the study, was analysed using a meta-analytical approach that weighted survival by the number of individuals planted. The sample variance was calculated as the proportion of individuals surviving minus the proportion dying, divided by the total number of individuals planted (Viechtbauer, 2010). Only studies with known numbers of individuals planted were included in this analysis;
2. *Half-life* as the duration in months until 50% mortality of the original planted cohort occurred. This was determined by fitting mortality (inverse of survival) as a function of time using linear, exponential, power-law, asymptotic and logistic models for each species, study-site and seedling and site treatment combination separately (Paine et al., 2012). The best models were selected based on the lowest Akaike information criteria (AIC) score and models with $R^2 < 0.5$ were removed as these models represented the lowest 5th percentile. The longest monitoring duration in the review was 180 months, so longer half-life estimates were excluded from our analysis.

3. *Relative Growth Rate (RGR)* as the height increase per original height planted was calculated first by fitting tree height as a function of time using linear, exponential, power-law, asymptotic and logistic models (Paine et al., 2012). Similar to the above, the best models were then selected based on the lowest AIC score and models with an $R^2 < 0.5$ were removed. Assuming a linear relationship, RGR was calculated as change in seedling height per unit time divided by the initial height for each monitoring time interval. For nonlinear model types, we used RGR calculation adjustments derived by Paine et al. (2012). Monitored seedling heights used to calculate RGR ranged from 8 to 990 cm with a mean height of 123 ± 165 cm (mean $\pm$ standard deviation, median 65 cm). RGR was determined at a standard height of 300 cm to enable comparison across species, study-sites and treatments. This higher-than-average height used to standardise RGR was selected to accommodate the tallest initial planted height in our dataset of 268 cm and its early growth trajectory.

All three measures of survival and growth considered an individual datapoint as a unique combination of species planted at a specific study-site and seedling and site treatments. Half-life and RGR required time-series data with a minimum of three measurements for line-fitting. Asymptotic model fits could generate negative RGR estimates, presumably due to exceptionally low RGR, and these predictions have been omitted. Study-sites were only included in the survival analysis if there were at least 14 individuals planted, because the sampling variances were exceptionally high (three times higher than the average) when the numbers of planted individuals were lower than 14. For the half-life and RGR calculations, we averaged all survival or height monitoring data over the first 2 months, because some studies replaced dead seedlings within the first few months and larger reforestation plantings took over 1 month to complete initial monitoring.

2.5 | Data analysis

Given the patchiness of the survival and growth data in relation to seedling and site treatments and site conditions, the analysis was split into multiple models to maximise data inclusion for addressing specific questions (Figure S1, Appendix 1 in Supporting Information; Hector et al., 2010). Survival, half-life and RGR were each analysed separately in five separate models, totalling 15 models. The five models tested for differences among the following: (1) species, (2) seedling treatments, (3) site treatments and planting densities, (4) rewetting (drained vs. rewetted), and (5) plant functional traits including RGR (Figure S1, Appendix 1 in Supporting Information). Treatments were only included in our treatment analyses if the study applied a treatment vs. control experimental design (Andivia et al., 2019). This experimental design was not applied to site-level rewetting; instead only species found in both rewetted and drained sites were included in the rewetting analyses. Furthermore, species and treatments were only included in the analyses if they were replicated across more than one study-site. In the functional trait analyses, a species could be represented by a single study-site due to a lack of paired species and trait data (see below) (Violle et al., 2015).

Survival models were analysed using the final proportion of surviving individuals. To investigate species differences and effects of seedling and site treatment and rewetting on survival, we applied multilevel linear mixed models with covariates (moderators) using the 'rma.mv' function in the meta-analysis R package METAFOR (Viechtbauer, 2010). Model tests and confidence intervals were computed using the Hartung–Knapp–Sidik–Jonkman method (Pappalardo et al., 2020). All multilevel linear mixed models for survival contained species as a covariate. Seedling and site treatment models had treatment as covariate, and the site treatment model also included planting density as a separate covariate. Seedling and site treatment models contrasted control vs. treatments and the rewetting model contrasted drained vs. rewetted. Random factors in survival models were species as the inner random factor and study-site as outer random factor, scaled using an identity matrix. This random structure assumes survival between species is independent and survival within study-sites is correlated. A second random factor of study duration as categorical intervals was used for survival models, because the survival data did not account for variable study durations. For the functional trait model, survival was averaged per species across study-sites and treatments and analysed in relation to seven functional traits selected due to sufficient species coverage (leaf calcium, nitrogen, magnesium, phosphorus, potassium, wood density and RGR), all averaged at the species level (Table S8, Appendix 1 in Supporting Information). The only random component in the survival functional trait model was a phylogenetic correlation matrix. The phylogenetic tree for the model was constructed using the 'phylo.maker' function in the R package V.PHYLOMAKER (Jin & Qian, 2019; Figure S2, Appendix 1 in Supporting Information).

Half-life and RGR were analysed using generalised linear mixed models using the function 'glmmTMB' in R package GLMMTMB (Brooks et al., 2017). Half-life was log transformed and RGR was square root transformed in species and rewetting models to meet model homoscedasticity requirements. All models were fitted assuming a Gaussian distribution and fixed factors were species, seedling treatment, site treatment and planting density and drainage, in respective models (the same covariates as outlined above). Study-site was a random effect in all models, except for the functional trait model that used a phylogenetic correlation structure (outlined above) as part of a phylogenetic generalised linear mixed model using the function 'glmmTMBphylo' in R package PHYLOGLMM (https://github.com/wzmli/phyloglmm).

To further investigate the species differences in survival, half-life and RGR, we generated species contrasts by releveling the dataset and running multiple models with a different species as the initial comparator (Viechtbauer, 2010). For the two most commonly planted species (*Shorea balangeran* and *Dyera polyphylla*), we explored temporal trends in survival, half-life and RGR using the same model outlined above, but with only El Niño-Southern Oscillation (ENSO) (El Niño, La Niña or neutral) climatic conditions dominating the first

6 months of planting for each project as the moderator or fixed term (National Oceanic and Atmospheric Administration, 2021).

All analyses were performed in R statistical software v4.0.2 (R Core Team, 2020). Model diagnostics such as residual vs fitted values, publication bias using funnel plots and sensitivity analysis of study-site outliers were all checked using 'metafor' (Viechtbauer, 2010). Residuals and diagnostics of generalised linear mixed models were checked using the DHARMA package (Hartig, 2020).

3 | RESULTS

3.1 | Reforestation across Southeast Asia

Of the 94 study-sites identified in this review, the majority were located in Indonesia (83%), principally in the Central Kalimantan province (50%) (Figure 1a). The year of planting spanned over three decades from 1988 to 2019 with the number of studies increasing substantially after 1997/1998 (Figure 1b). The duration of monitoring averaged 30 ± 34 months (mean ± standard deviation, median 18 months, range 2.5–180 months) (Figure 1c). The diversity of TPSF species planted was generally low, with one-third of study-sites planting a single species, an average of 4 species and a maximum of 23 species (Figure 1d). The number of seedlings planted ranged from 14 to almost 56,000 per species (Figure 1e). Overall, there were 141 tree and palm species planted in degraded TPSF across Southeast Asia, comprising: 113 species native to TPSF, 16 species from non-peat forests native to Southeast Asia and 12 exotic species (Figure 2). The two species most commonly planted were *Shorea balangeran* (39 study-sites) and *Dyera polyphylla* (34), followed by *Gonystylus bancanus* (17), *Melaleuca cajuputi* (11) and *Alstonia pneumatophora* (10), all of which are native to TPSF (Figure 2).

3.2 | Species differences in survival and growth

A total 62 species across 64 study-sites were included in the modelling for survival, 43 species for half-life, and 24 species for RGR (Figure S1; Table S11, Appendix 1 in Supporting Information). Across these models, all except eight species were native to Indonesian TPSF. The overall mean seedling survival was 62% (95% CI: 6 to 118%) across all 439 study-site, species and seedling and site treatment combinations (Figure 2). Average half-life across study-sites and treatments was 33 months, ranging from 0.6 to 174 months. Species differed significantly in survival and half-life, but not RGR, likely due to the lower number of species in the RGR analysis. Validating our half-life measure, time until 45%–55% mortality was significantly positively correlated with half-life (Spearman's correlation; r_s = 0.97, *df* = 82, p = <0.001; Figure S3, Appendix 1 in Supporting Information).

Species with a significantly higher survival and longer half-life compared to other species included *Lophopetalum* cf. *rigidum*, *Cratoxylum arborescens*, *Shorea balangeran*, *Alstonia spatulata* and *Madhuca motleyana* (Table 1; Table S11, Appendix 1 in Supporting

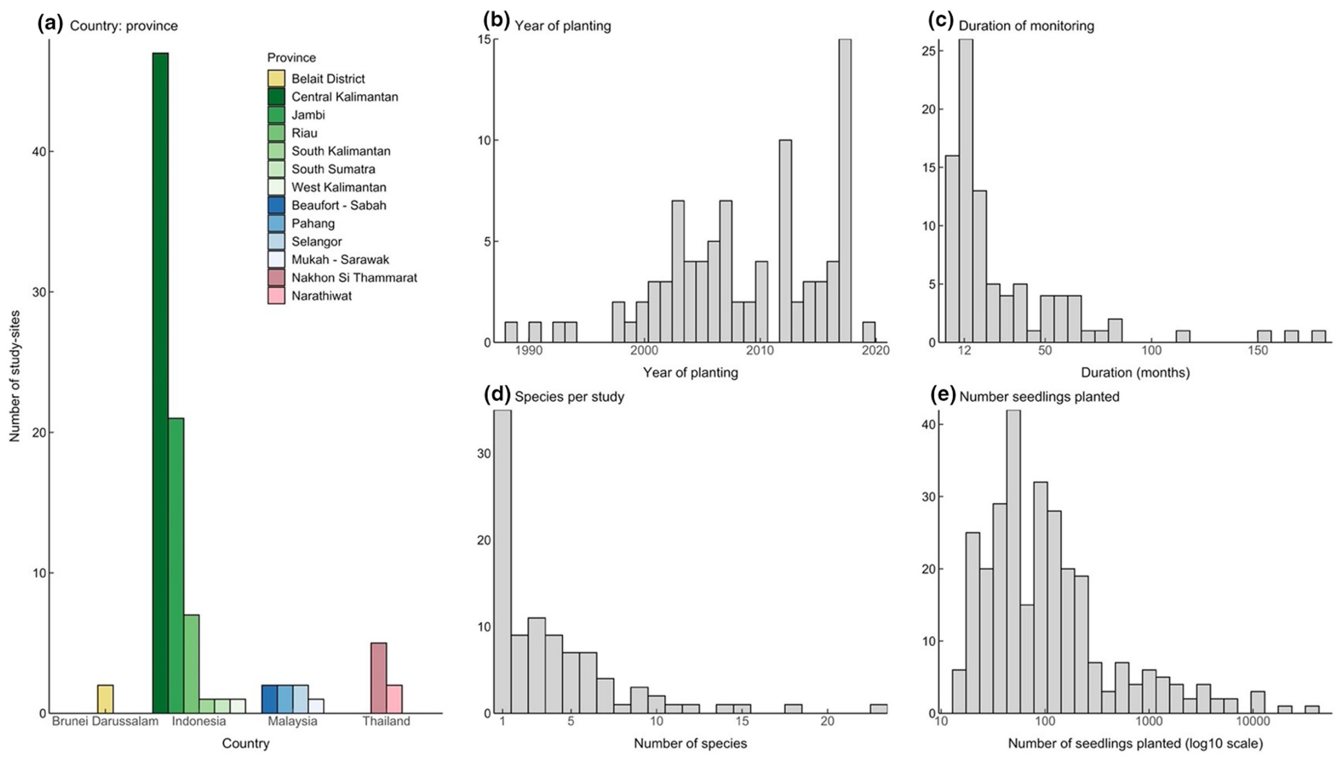

FIGURE 1 Number of study-sites in relation to (a) location of tropical peat swamp reforestation site, (b) year of planting, (c) duration of monitoring, (d) number of species planted and (e) number of seedlings planted per study-site species, averaged across species and treatments. Number of species are only those verified following taxonomic checks in the systematic review.

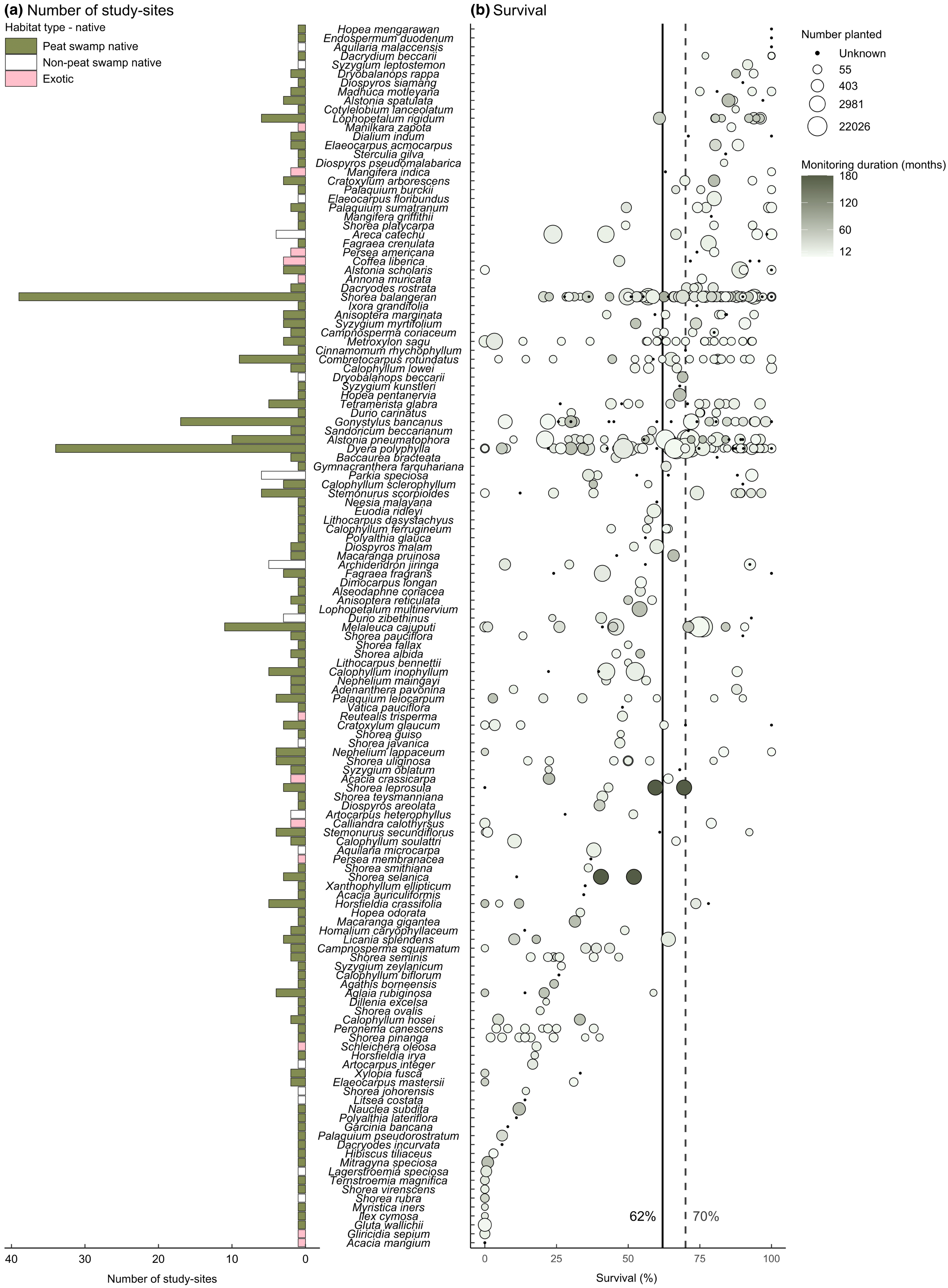

FIGURE 2 Tree species planted to restore degraded tropical peat swamp forests across Southeast Asia, (a) abundance of species across study-sites and (b) survival across study-site, species and seedling, and site treatments ordered by average species survival. The solid line represents mean survival and dashed line median survival across all 141 species.

TABLE 1 Summary of 10 top and poorest survivors identified from species contrasts of survival and half-life (months until 50% mortality) modelling. Shown for each species are average final survival, half-life and relative growth rate (RGR), and number of significant ($p < 0.05$) contrasts to other species out of a total of 62 species in survival and 43 species in half-life models. All measures of error are presented as ±1 *SD*

Species	Tropical peat swamp species	Survival (%)	Half-life (months)	RGR (cm × cm^{-1} month^{-1})	Significant survival contrasts	Significant half-life contrasts
(a) Top survivors						
Lophopetalum cf. *rigidum*	TPSF native	82.4 ± 12.6	75.4 ± 30.3	0.007 ± 0.011	27	37
Cratoxylum arborescens	TPSF native	86.7 ± 9.4	41.5 ± 40.2	0.035	11	21
Shorea balangeran	TPSF native	68.6 ± 22.4	35.2 ± 38.1	0.026 ± 0.027	14	8
Syzygium myrtifolium	TPSF native	71.7 ± 26.9	31.4 ± 12.7	0.001	9	13
Alstonia spatulata	TPSF native	85.8 ± 1.2	34.3 ± 40.5	0.014 ± 0.006	12	6
Madhuca motleyana	TPSF native	87.1 ± 8.7	92.5 ± 58.1	0.012	11	6
Alstonia scholaris	TPSF native	89.7 ± 0.9	41.8 ± 30.7	-	1	11
Combretocarpus rotundatus	TPSF native	60.5 ± 26.8	12.8 ± 9.7	0.029 ± 0.055	8	2
Tetramerista glabra	TPSF native	74.3 ± 12	31.6 ± 12.9	0.013 ± 0.018	7	2
Dyera polyphylla[a]	TPSF native	59.3 ± 29.4	28.3 ± 33.9	0.05 ± 0.047	1	4
(b) Poor survivors						
Shorea seminis	TPSF native	27.6 ± 9.2	5.4 ± 2.5	-	3	23
Aglaia rubiginosa	TPSF native	23.4 ± 25.2	21.6 ± 17	0.000001 ± 0.000002	12	12
Horsfieldia crassifolia	TPSF native	28.5 ± 39.5	19.6 ± 12.9	0.014 ± 0.014	12	4
Palaquium leiocarpum	TPSF native	48.2 ± 31.5	16.1 ± 12.4	0.019 ± 0.002	8	7
Stemonurus secundiflorus	TPSF native	20.7 ± 34.9	59 ± 97.1	0.014 ± 0.003	11	4
Shorea uliginosa	TPSF native	38 ± 18.3	7.5 ± 4.1	0.029	1	10
Xylopia fusca	TPSF native	16.7 ± 23.5	15.5 ± 0.5	0.034 ± 0.032	10	1
Licania splendens	TPSF native	30.7 ± 29.1	14.4 ± 10.2	0.007 ± 0.002	5	3
Durio zibethinus	Non-peat swamp	32 ± 12	12.5 ± 4	0.079	2	4
Archidendron jiringa	Non-peat swamp	18.2 ± 15.9	11 ± 3.5	0.061 ± 0.025	1	4

[a]*Dyera polyphylla* was also identified as top poor survivor surpassed by other species in two significant species survival and three half-life contrasts.

Information). In contrast, species with a lower survival and shorter half-life compared to other species included: *Calophyllum hosei*, *Aglaia rubiginosa*, *Horsfieldia crassifolia*, *Licania splendens* and *Xylopia fusca* (Table 1; Table S11, Appendix 1 in Supporting Information). Additional analyses for the two most commonly planted species, *S. balangeran* and *D. polyphylla*, showed ENSO conditions in the initial 6 months of planting significantly influenced survival, half-life and RGR (Table S12, Appendix 1 in Supporting Information). Compared to neutral years *S. balangeran* survival, half-life and RGR were significantly lower for La Niña (wetter) conditions, but only RGR was significantly lower for El Niño (drier) conditions. Meanwhile, *D. polyphylla* survival was only significantly lower during El Niño (drier) conditions (Table S12; Figure S4, Appendix 1 in Supporting Information).

3.3 | Seedling treatments

Mycorrhizal fungal inoculation was the only sufficiently replicated seedling treatment to be included in the statistical analyses, with seven species across 10 study-sites with subsets of this dataset included in modelling half-life and RGR (Figure S1, Appendix 1 in Supporting Information). Seedlings inoculated with mycorrhizal fungi had a small but statistically significantly greater survival, increasing from 78% to 86% across species (Figure 3a–c; Table S13, Appendix 1 in Supporting Information). However, there were no significant differences in half-life or RGR between mycorrhizal-inoculated and control seedlings (Table S13, Appendix 1 in Supporting Information). Six tree species were inoculated with arbuscular mycorrhizal fungi (AM), but only one (*S. balangeran*) with

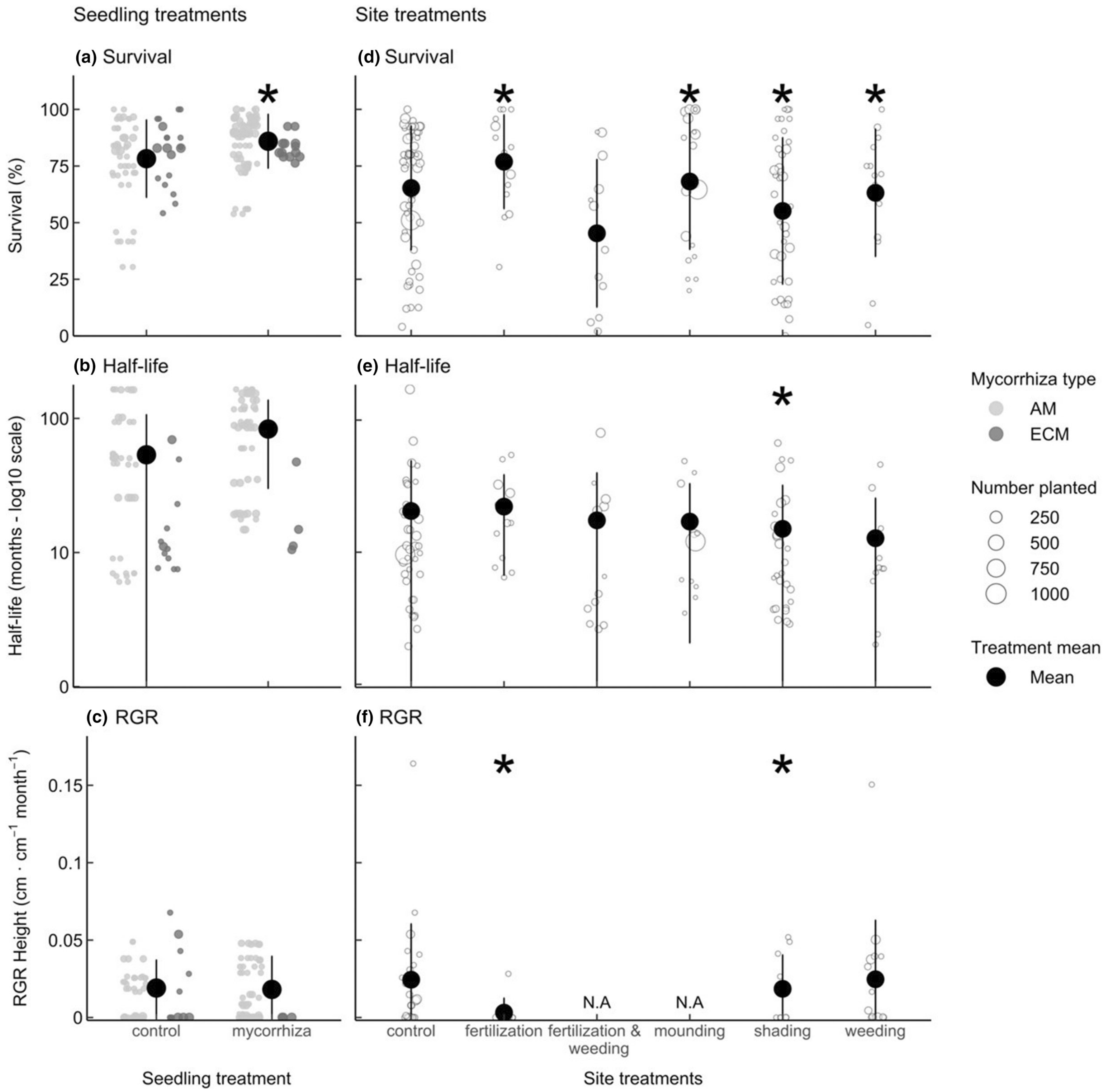

FIGURE 3 Seedling treatment differences in (a) survival, (b) half-life, and (c) relative growth rates (RGR) and site treatment differences in (d) survival, (e) half-life, and (f) RGR for seedlings planted to reforest degraded tropical peat swamp forests. Individual data points are shown as either grey (seedling treatment) or white (site treatment) filled symbols representing separate species, treatments and study-sites. Significant differences ($p < 0.05$) in the seedling treatments compared to the control are indicated by *. Error bars represent ±1 *SD*.

ectomycorrhizal fungi (ECM). Due to this imbalance, mycorrhiza type was not included in our analysis, although it is shown separately in Figure 3.

3.4 | Site treatments and rewetting

In total, 18 species across 11 study-sites were included in site treatment modelling of survival, with subsets of this dataset included in modelling half-life and RGR (Figure S1, Appendix 1 in Supporting Information). Although several site treatments had statistically significant effects, overall treatment differences in survival, half-life and RGR were small (Figure 3d–f; Table S14, Appendix 1 in Supporting Information). A significant negative effect of shading was corroborated across survival, half-life and RGR; for instance, 50% mortality occurred on average 12 months sooner when shaded compared to controls (Figure 3; Table S14, Appendix 1 in Supporting Information). Fertilisation significantly reduced seedling growth rates but increased survival, although with no significant difference in half-life (Figure 3; Table S14, Appendix 1 in Supporting Information). On average, RGR was reduced by 87% when fertilised and survival was on average 5% higher. All other significant differences between control and treatments were small (i.e. <3%) and only observed for a single metric of survival or growth, specifically: the positive effect of mounding and negative effect of weeding on survival, and the positive effect of planting densities on RGR (Figure 3; Table S14, Appendix 1 in Supporting Information). Across species and other treatments, survival was significantly higher in drained versus rewetted sites, averaging 69% versus 59%, respectively (Table S14, Appendix 1 in Supporting Information). However, rewetting did not significantly affect half-life or RGR (Table S14, Appendix 1 in Supporting Information).

3.5 | Plant functional traits

Only native TPSF tree species were included in the functional trait modelling due to sufficient trait coverage (Table S9, Appendix 1 in Supporting Information). TPSF species exhibited generally low leaf nutrient contents with ranges across 33 species (included across the trait analyses; Figure S1, Appendix 1 in Supporting Information) of between 1.1 and 24.6 mg/g for calcium; 7.5 and 18.5 mg/g for nitrogen; 0.6 and 6.6 mg/g for magnesium; 0.1 and 1.8 mg/g for phosphorus, and 1.6 and 10.6 mg/g for potassium. Average wood densities were variable and ranged from 0.28 to 0.9 g/cm^3 across species. Only seedling survival was significantly predicted by some plant functional traits, specifically survival was higher for species with lower leaf magnesium contents and wood densities, but higher leaf potassium contents (Table S15, Appendix 1 in Supporting Information).

Seedling RGR was significantly negatively related to half-life (Figure 4). In other words, seedling cohorts of slower growing species last longer before reaching 50% mortality. When the analysis was expanded to include our full dataset of 66 species for both RGR and half-life, this negative relationship was statistically significant (Table S4, Appendix 1 in Supporting Information; Figure 4). Although survival and RGR showed a similar trend, this was not statistically significant in the trait analysis or across the larger dataset of 45 species with survival and RGR data (Table S4, Appendix 1 in Supporting Information).

4 | DISCUSSION

This systematic review provides the first quantitative synthesis on the survival and growth rates of tree species planted to reforest TPSF. On an average, survival rates were 62% and planted cohorts lasted 2.5 years until 50% mortality across species, treatments, and study-sites. Intact tropical forest ecosystems have many tree species that are slow growing and long lived (Russo et al., 2021; Wright et al., 2010), and our review finds these slower growing species last longer when planted to reforest TPSF. Our results give promise that tree planting can assist TPSF reforestation, but also provides a sense of realism of the remaining challenges. One major challenge identified in this review is the seemingly marginal and inconsistent effects of treatments on seedling survival, half-life, and growth. Another challenge is the chronic underutilisation of the TPSF flora in reforestation: only one-tenth of the 1173 known native TPSF tree species of Southeast Asia (Giesen et al., 2018; Posa et al., 2011) have been reported in the literature as planted. A final challenge is how best to select species given the tremendous variation in survival and half-life. We find that screening plant functional traits offers an approach to help predict species survival though not half-life and RGR. To improve trait-based predictions, further research is required to collect traits as part of TPSF reforestation projects incorporating site-specific environment and climatic variability.

4.1 | Rewetting and treatments

Rewetting tropical peatlands is pivotal to prevent further peat oxidation and emissions, and for reducing the risk of fires. In our review, seedling survival was lower in rewetted than in drained peatlands, but seedling half-life and RGR were unaffected. While native TPSF species are anatomically and physiologically adapted to waterlogging especially to root hypoxia (Tanaka et al., 2011; Yamanoshita et al., 2005), seedlings can still die when full submergence leads to stomatal closure and reduced photosynthesis (Rotinsulu et al., 2016). Rewetted peatlands are still subject to water-level fluctuations and flooding, leading to high seedling mortality as seen in rewetted study-sites in this review (Giesen, 2004; van Eijk et al., 2009; Wibisono et al., 2005). Mounding is a treatment that can in theory reduce the risk of flooding related mortality, yet we found only a small (<3%) increase in survival across species. Given the high costs of mounding, especially when upscaled over large target areas, it is questionable as to whether this treatment justifies the expense (Lampela et al., 2018). In degraded peatlands retaining natural peat micro-topography, a cheaper solution to mounding is to allocate flood-intolerant species to drier hummocks (Nahor, 2019; Rachmanadi et al., 2021). Such innovative solutions that use knowledge of species flooding tolerance are required to balance revegetation, rewetting and restoration costs.

Treatments that demonstrated the most consistent effects were shading having lower survival, half-life and RGR; and fertilisation having higher survival, but lower RGR. Negative effects of shading align with nursery manipulations using TPSF species, where shading reduces photosynthetic, growth and survival rates (Jans et al., 2004; Rusmana et al., 2014; Tanaka et al., 2011). Positive effects of fertilisation on survival fit with some of our leaf trait findings, such as higher survival rates for species with higher potassium (discussed below). A greenhouse experiment using TPSF species found fast growing species were not significantly affected by fertilisation, and only slower growing species had increased growth (Yuwati et al., 2015). Fertilisation could negatively influence growth rates due to the response of the soil fungal community: in boreal forests, a fertilisation experiment found lower ericaceous species growth rates due to negative effects on the soil fungal community (Wardle et al., 2016), while the opposite was observed in Peruvian rainforests when fertilisation increased tree seedling growth

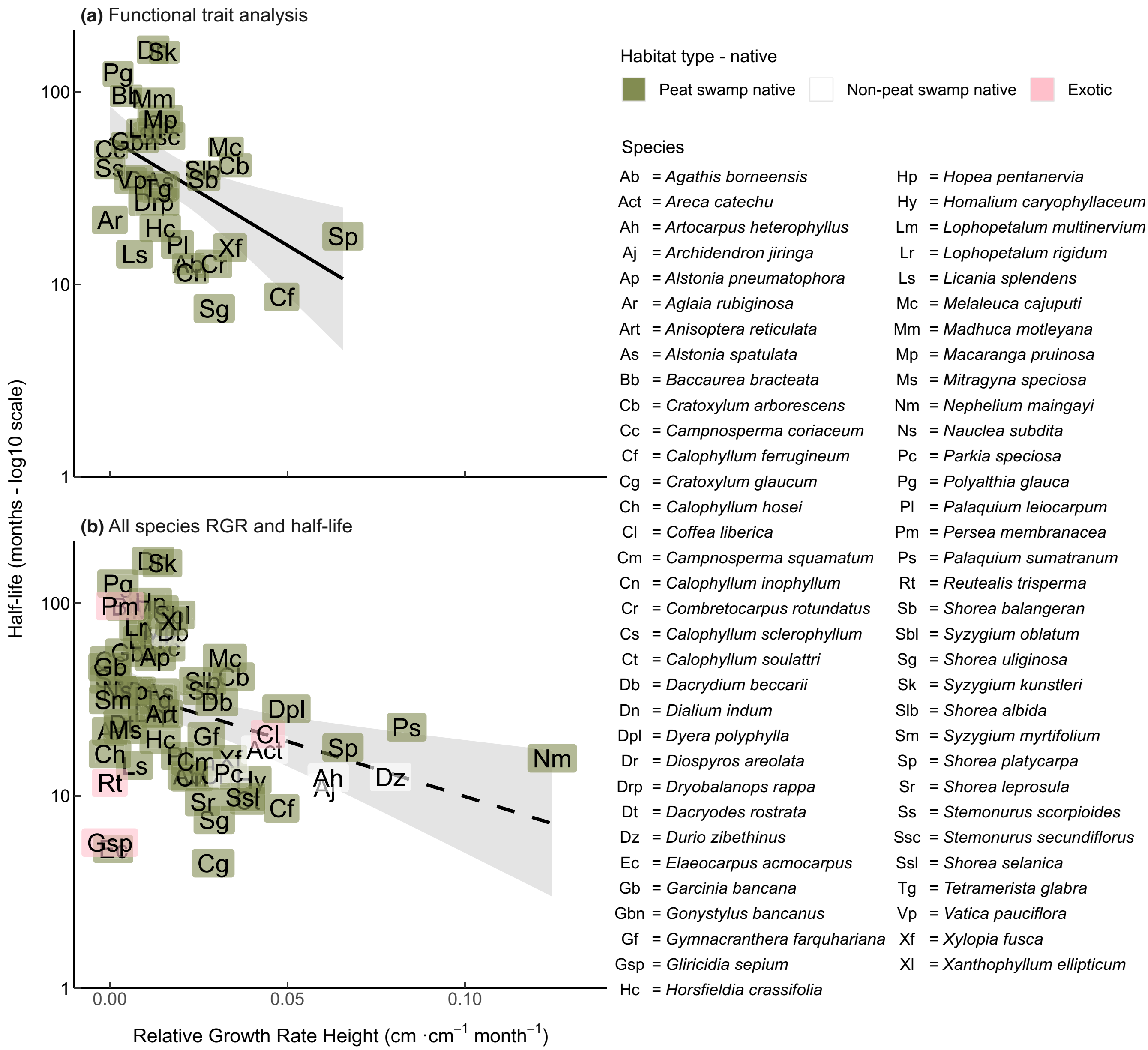

FIGURE 4 Relative growth rate (RGR) based on seedling height vs half-life (months until 50% seedling mortality) for tree and palm species planted to reforest degraded tropical peat swamps. Two sets of analyses were conducted on RGR vs half-life: (a) functional trait analysis using 32 species with predicted line of best fit as a solid line; (b) full dataset of 66 species with predicted line of best fit as a dashed line. Each symbol is the average RGR and half-life for a given species in the review. Grey shading around predictions line represent ±1 *SD*.

and mycorrhizal colonisation (Fisher et al., 2013). In our review, mycorrhizal inoculation enhanced TPSF seedling survival, but not half-life or RGR. A promising avenue for further research would be investigations into the nutrient acquisition strategies of TPSF species, for example, mycorrhizal symbiosis (Mishra et al., 2021) to develop alternative strategies to the application of artificial fertilisers.

4.2 | Underutilisation and replication of TPSF species

The pool of potential species that could be planted in TPSF reforestation is underutilised and poorly replicated across study-sites. In this review, most species were planted in a single study-site and five of the top 10 surviving species were planted in fewer than five study-sites (Figure 2; Table 1). This apparent underutilisation of the TPSF flora may stem from ecological and technical constraints on species availability, for example low seed availability of mast fruiting species during non-masting years (Din et al., 2018; Graham et al., 2017). Socio-economic values also govern species selection, for example, the two most commonly planted species, *S. balangeran* and *D. polyphylla*, are commercially valued for timber and latex, respectively (Giesen & Sari, 2018; Sundawati et al., 2020). Interestingly, *S. balangeran* and *D. polyphylla* exhibited above-average survival rates also suggesting a degree of knowledge sharing of successful species among project proponents, but this does not extend to other species with high survival rates. Based on these findings, we strongly encourage more native TPSF species to be planted in a replicated manner across multiple reforestation sites, particularly trialling the 500 native TPSF species that can provide food, medicine or other non-timber forest products benefits for local communities (Giesen, 2021).

4.3 | Plant functional traits

The application of plant functional traits as predictors of survival and growth in restoration ecology remains a developing research area (Charles, 2018; Wainwright et al., 2018). Native TPSF tree species with higher leaf potassium and lower magnesium contents had higher survival, yet otherwise leaf traits were weak predictors of half-life and RGR. Potassium is involved in osmotic regulation, and higher leaf potassium contents have been linked to flood tolerance (Wang et al., 2013). Exchangeable magnesium can be depleted in drained peatlands compared to other peat available nutrients (Westman & Laiho, 2003) and low leaf magnesium contents could therefore be reflective of species tolerant of nutrient poor conditions. TPSF species with lower wood densities also had higher survival rates, which may signify species with porous wood structures (e.g. vessel diameters and densities) needed for withstanding hydrological variation (Martínez-Cabrera et al., 2011). Whereas for reforestation on mineral soils, tropical tree species with higher wood densities have higher survival rates (Charles, 2018; Charles et al., 2018). The mechanistic underpinnings of these trait relationships in TPSF require further investigation, though our review results support the judicious use of functional traits as a tool to advance species selection in TPSF reforestation.

Planted TPSF species exhibited a growth-mortality trade-off, which has not been documented previously. The growth-mortality trade-off is common for tropical tree species found in less-disturbed ecosystems (Philipson et al., 2014; Russo et al., 2021; Wright et al., 2010). Despite the importance of TPSF species growth rates, no traits significantly predicted growth in our analysis. This may have arisen for several reasons; common growth-related morphological traits (e.g. specific leaf area) (Martínez-Garza et al., 2013; Paine et al., 2015; Wright et al., 2010) were not included in the analysis due to insufficient data (Table S9, Appendix 1 in Supporting Information); predicting tropical tree growth rates may require scaling leaf-organ traits to the size of individuals (Liu et al., 2016; Yang et al., 2018), and lastly, there is also considerable noise and variability to our survival- and growth–trait relationships, because trait information was not collected at specific reforestation sites to reflect site-specific environmental and climatic conditions.

4.4 | Spatially and temporally heterogeneous TPSFs

All findings from this systematic review should be interpreted from the perspective that TPSF are highly temporally and spatially variable ecosystems. Survival rates, half-life and growth rates of the most commonly planted species *S. balangeran* were significantly lower when planted during wetter La Niña conditions and survival of *D. polyphylla* was lower during El Niño. High seedling mortality rates in intact TPSF have been observed during El Niño droughts compared to neutral years (Nishimua et al., 2007), yet we are unaware of similar observation studies during wetter La Niña conditions. In addition to climatic conditions, there are several sources of variability unaccounted for in our main analyses. Land-use history, such as fire and drainage history, can shape the environmental conditions at a specific degraded TSPF study-site (Giesen & van der Meer, 2009; Graham et al., 2017). High site-specific variation in environmental conditions and land-use history will govern the effectiveness of site treatments. Adequately testing treatments by adopting rigorous control vs. treatment experimental designs (Andivia et al., 2019) and measuring site-specific environmental conditions alongside seedling survival and growth monitoring will aid future syntheses of TPSF reforestation.

5 | CONCLUSIONS

Knowledge of planted tree species survival and growth, natural regeneration potential (i.e. animal-dispersal) and socio-economic value have enabled the development of species selection frameworks that guide restoration of tropical forests (Chechina & Hamann, 2015; Elliot et al., 2013; Meli et al., 2014). In addition to survival and growth rates addressed in this review, developing a species framework to reforest degraded TPSF in Southeast Asia requires knowledge on species' flooding tolerance (and/or microtopographic preference), nutrient acquisition strategies (e.g. mycorrhiza) and recovery from fire, with the last being the most significant knowledge gap. Fires have the potential to kill almost all planted seedlings, although this is difficult to confirm based on monitoring data from one study (Lampela et al., 2017). While seedling survival rates tend to be higher in drained sites, we expect damage due to fire occurrence to be higher in drained compared to rewetted peatlands. Taken together, our analysis highlights the value of post-planting monitoring to underpin evidence-based syntheses for guiding future TPSF reforestation, which as more data emerge can hopefully be transferred to other tropical peatland regions. Continued long-term monitoring of TPSF reforestation will enable proximate measures of restoration success—tree survival and growth—to better connect to ultimate measures of biodiversity recovery, climate goals and community benefits.

AUTHORS' CONTRIBUTIONS

S.W.S. and N.E.B.R. conceived the review with input on the scope and design from the expert team of M.E.H., S.S., W.G., M.L., D.A.W., K.Y.C., A.R., L.S.W., Y.A.F., J.S.H.L.; bibliometric searching, screening and data collation was performed by S.W.S., N.E.B.R., M.E.H., S.S., A.R., M.L., N.T.T., J.K.Q.Y. and P.Y.T.; the majority of other authors contributed partial or full datasets from reforestation projects;

S.W.S. undertook the statistical analysis and led the writing of the manuscript with all other authors providing critical feedback and final approval for publication.

ACKNOWLEDGEMENTS

We are grateful for the assistance rendered by Yoyok Wibisono, Mitsuru Osaki, Jyrki Jauhiainen, Susan Page, Kunihide Takahashi and Marinus Harun in obtaining grey literature and many more authors for answering queries regarding specific study-sites. We thank Alex Cobb, Xingli Giam and Lindsay Banin for constructive inputs on an earlier version of the manuscript. S.W.S., N.E.B.R., D.A.W., K.Y.C., Y.A.F. and J.S.H.L. were supported by the Singapore Ministry of Education Research Fund (MOE2018-T2-2-156) and D.A.W. by National Research Foundation Singapore (NRF2019-ITC001-001). M.E.H., P.B.S., D.R.K., H.C.M.-B., B.R.C. and S. were supported by UKRI GCRF (grant no. NE/T010401/1), The Orangutan Project, Arcus Foundation, Darwin Initiative, Save the Orangutan, Orangutan Land Trust, Indonesia Climate Change Trust Fund, Ocean Parks Conservation Foundation Hong Kong, European Outdoor Conservation Association, Taronga Zoo, European Association of Zoos and Aquaria, Fundacion Bioparc. S.S. was supported by JSPS KAKENHI (grant no. JP20K12266), Research Institute for Humanity and Nature (RIHN: a constituent member of NIHU) (project no. 14200117). T.D. and D.P.L. were supported by PT Rimba Makmur Utama. T.K.N. was supported by The National Conservation Trust Fund for Natural Resources, Government of Malaysia ((NRE(S) 600-2/1/48/2Jld.2 (9)). D.R., P.B.S. and T.W.Y. were supported by the Ministry of Environment & Forestry, Indonesia. R.S.S., F.M. and W.T. were supported by the ASEAN-Korea Environmental Cooperation Project (AKECOP) Grant (2014–2016), Universiti Brunei Darussalam (UBD/RSCH/1.13/FICBF(b)/2018/003 and UBD/RSCH/1.13/FICBF(b)/2020/019). M.E.H., P.B.S. and H.C.M.-B. thank the Indonesian Ministry of Research and Technology/National Research and Innovation Agency (RISTEK-BRIN), and these authors plus D.R.K., S., D.N. and K.K. also thank UPT LLG CIMTROP-UPR, Sebangau National Park (BTNS), Suwido Limin, Ici Kulu, Hendri, Frank van Veen, Nicholas Marchant and Simon Husson. In particular, we thank Yunsiska Ermiasi, an exceptional, dedicated local conservationist who contributed towards data collection for the BNF/CIMTROP datasets included in this review, who sadly passed away as this manuscript was in preparation and to whom we dedicate this paper.

DATA AVAILABILITY STATEMENT

Data used to derive findings from this systematic review are either freely available or available on request from corresponding project authors, via https://zenodo.org/record/6535087 (Smith et al., 2022).

ORCID

Stuart W. Smith https://orcid.org/0000-0001-9396-6610
Nur Estya Binte Rahman https://orcid.org/0000-0002-6274-1205
Mark E. Harrison https://orcid.org/0000-0002-0729-8407
Satomi Shiodera https://orcid.org/0000-0002-6849-8568
Wim Giesen https://orcid.org/0000-0003-2579-6706
Maija Lampela https://orcid.org/0000-0002-6635-1394
David A. Wardle https://orcid.org/0000-0002-0476-7335
Kwek Yan Chong https://orcid.org/0000-0003-4754-8957
Agusti Randi https://orcid.org/0000-0002-4262-2604
Lahiru S. Wijedasa https://orcid.org/0000-0001-5030-6962
Yuti A. Fatimah https://orcid.org/0000-0002-6807-8184
Nam Thian Teng https://orcid.org/0000-0003-3958-1108
Faizah Metali https://orcid.org/0000-0002-2508-1535
Tapan Kumar Nath https://orcid.org/0000-0001-6436-1778
Dony Rachmanadi https://orcid.org/0000-0002-9456-5357
Henti H. Rachmat https://orcid.org/0000-0003-4586-6820
Purwanto B. Santosa https://orcid.org/0000-0002-9347-9991
Rahayu S. Sukri https://orcid.org/0000-0002-2662-399X
Béatrice M. M. Wedeux https://orcid.org/0000-0003-1890-6778
Tri Wira Yuwati https://orcid.org/0000-0002-8477-0795
Janice S. H. Lee https://orcid.org/0000-0001-6368-6212

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SUPPORTING INFORMATION

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

How to cite this article: Smith, S. W., Rahman, N. E. B., Harrison, M. E., Shiodera, S., Giesen, W., Lampela, M., Wardle, D. A., Chong, K. Y., Randi, A., Wijedasa, L. S., Teo, P. Y., Fatimah, Y. A., Teng, N. T., Yeo, J. K. Q., Alam, M. J., Brugues Sintes, P., Darusman, T., Graham, L. L. B., Katoppo, D. R. … Lee, J. S. H. (2022). Tree species that 'live slow, die older' enhance tropical peat swamp restoration: Evidence from a systematic review. *Journal of Applied Ecology*, *00*, 1–17. https://doi.org/10.1111/1365-2664.14232