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RESEARCH ARTICLE

Bornean tropical forests recovering from logging at risk of regeneration failure

David C. Bartholomew[1,2,3] | **Robin Hayward**[4,5] | **David F. R. P. Burslem**[6] | **Paulo R. L. Bittencourt**[1] | **Daniel Chapman**[4] | **Mohd. Aminur Faiz Bin Suis**[7] | **Reuben Nilus**[7] | **Michael J. O'Brien**[8] | **Glen Reynolds**[9] | **Lucy Rowland**[1] | **Lindsay F. Banin**[10] | **Daisy Dent**[11,12]

[1]School of Geography, University of Exeter, Exeter, UK
[2]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
[3]Botanic Gardens Conservation International, Richmond, UK
[4]Biological and Environmental Sciences, University of Stirling, Stirling, UK
[5]School of Earth and Environment, University of Leeds, Leeds, UK
[6]School of Biological Sciences, University of Aberdeen, Aberdeen, UK
[7]Forest Research Centre Sepilok, Sandakan, Malaysia
[8]Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Almería, Spain
[9]SE Asia Rainforest Research Partnership, Kota Kinabalu, Sabah, Malaysia
[10]UK Centre for Ecology & Hydrology, Edinburgh, UK
[11]Smithsonian Tropical Research Institute, Balboa, Panama
[12]Department of Environmental Systems Science, ETH, Zürich, Switzerland

Correspondence
David C. Bartholomew, School of Geography, University of Exeter, Laver Building, 23 North Park Road, Exeter EX4 4QE, UK.
Email: davidclivebartholomew@gmail.com

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Abstract

Active restoration through silvicultural treatments (enrichment planting, cutting climbers and liberation thinning) is considered an important intervention in logged forests. However, its ability to enhance regeneration is key for long-term recovery of logged forests, which remains poorly understood, particularly for the production and survival of seedlings in subsequent generations. To understand the long-term impacts of logging and restoration we tracked the diversity, survival and traits of seedlings that germinated immediately after a mast fruiting in North Borneo in unlogged and logged forests 30–35 years after logging. We monitored 5119 seedlings from germination for ~1.5 years across a mixed landscape of unlogged forests (ULs), naturally regenerating logged forests (NR) and actively restored logged forests via rehabilitative silvicultural treatments (AR), 15–27 years after restoration. We measured 14 leaf, root and biomass allocation traits on 399 seedlings from 15 species. Soon after fruiting, UL and AR forests had higher seedling densities than NR forest, but survival was the lowest in AR

David C. Bartholomew and Robin Hayward should be considered joint first author.

Lindsay F. Banin and Daisy Dent should be considered joint senior author.

forests in the first 6 months. Community composition differed among forest types; AR and NR forests had lower species richness and lower evenness than UL forests by 5–6 months post-mast but did not differ between them. Differences in community composition altered community-weighted mean trait values across forest types, with higher root biomass allocation in NR relative to UL forest. Traits influenced mortality ~3 months post-mast, with more acquisitive traits and relative aboveground investment favoured in AR forests relative to UL forests. Our findings of reduced seedling survival and diversity suggest long time lags in post-logging recruitment, particularly for some taxa. Active restoration of logged forests recovers initial seedling production, but elevated mortality in AR forests lowers the efficacy of active restoration to enhance recruitment or diversity of seedling communities. This suggests current active restoration practices may fail to overcome barriers to regeneration in logged forests, which may drive long-term changes in future forest plant communities.

KEYWORDS
demography, disturbance, diversity, fruiting, functional traits, general masting, lowland tropical forests, mortality, restoration, selective logging

1 | INTRODUCTION

The spatial extent of human-modified forests now exceeds that of primary forests across most of the tropics (Laurance et al., 2014). The long-term recovery of forest communities after logging is dependent on the successful recruitment of future generations of seedlings (Bagchi et al., 2011; Chazdon, 2003). Despite this, the long-term effects of logging on forest tree communities remain poorly understood, especially with regard to the complex processes affecting tree regeneration dynamics (Brown & Gurevitch, 2004; Baraloto et al., 2012; Cazzolla Gatti et al., 2015; Ewers et al., 2015; Shima et al., 2018). Restorative practices including rehabilitation and ecological restoration (Gann et al., 2019) have the potential to help the recovery of logged forests and may vary widely across the intervention continuum (Chazdon et al., 2021). Understanding the capacity of logged forests to regenerate under both natural regeneration and active rehabilitative restoration management strategies that include enrichment tree planting, cutting of climbers and bamboo and liberation thinning is critical for optimising the ecosystem restoration and sustainable resource use of logged forests.

Regeneration of forest plant communities is dependent on both the ability to produce sufficient seedlings and their ability to survive to maturity. In lowland Southeast Asian forests, the production of large seedling populations via general masting is important to promote seed predator satiation (Janzen, 1974; O'Brien et al., 2022; Sun et al., 2007; Visser et al., 2011). Removal of large, reproductively mature individuals through logging may reduce the strength of masting and seed production and thus the capacity to satiate seed predators. This inability to satiate seed predators may be exacerbated in logged forests, where larger populations of ungulate seed predators are supported (Malhi et al., 2022), because of greater ground-level vegetation that grows in the more open environment, and because these species are more likely to travel in groups (Brodie et al., 2015; Davison et al., 2019).

Logging of tropical forests not only changes seed predator populations but may also induce other changes to the biotic and abiotic environment that inhibit natural regeneration. Logging practices typically remove the largest trees (Slik et al., 2013), reduce total forest basal area (Riutta et al., 2018) and change vertical forest structure (Cazzolla Gatti et al., 2015; Milodowski et al., 2021), leading to greater understorey light availability and reduced microclimatic buffering (Blonder et al., 2018; De Frenne et al., 2021; Hardwick et al., 2015; Jucker et al., 2018). Meanwhile, nutrient and water availability are reduced in logged forests following the removal of large nutrient stores in timber and leaf canopies, particularly if timber is not debarked prior to removal (Inagawa et al., 2023; Swinfield et al., 2020). Soil erosion (Baharuddin et al., 1995; Brooks & Spencer, 1997; Sidle et al., 2004), soil compaction (Ziegler et al., 2006) and shifts in microbial communities (McGuire et al., 2015), may also alter ecosystem functioning in logged forests, although these effects may be highly localised (e.g. because of skid trails) and depend on logging intensity. These novel environmental conditions created by logging may inhibit the regeneration of forest plant communities if seedlings have higher mortality risk under these conditions.

Logging is unlikely to affect all plant species equally. Some species are better adapted to degraded environments, particularly those with acquisitive traits, such as low leaf mass per area, that can maximise the use of increased light availability, but still thrive under reduced nutrient and water availability. Differences in conditions between logged and unlogged forests (ULs) affect species and functional groups differently, resulting in distinct patterns of survival across species and functional groups. In logged forests, this will lead to shifts in the functional composition of communities and may act to reduce species richness and diversity compared to ULs. If the relative importance of abiotic conditions in determining seedling mortality is higher in logged than ULs, we may expect mortality rates to differ between functional groups and be more tightly coupled to species traits (Qie et al., 2019). Some species may, however, have the capacity to respond to environmental shifts by modifying traits and thus allowing successful recruitment in logged environments. The high degree of specialisation in Bornean forests (Bartholomew et al., 2022; Bittencourt et al., 2022) may, however, reduce the capacity for intraspecific adjustment of traits and therefore limit the ability to respond to environmental shifts in logged forests.

Active restoration techniques, including silvicultural rehabilitative treatments, are often used to accelerate the recovery of forest biomass, canopy closure and abundance of stems from species targeted during selective logging (Gourlet-Fleury et al., 2013; Mills et al., 2019; Osuri et al., 2019; Philipson et al., 2020). Techniques include enrichment planting of tree seedlings and cutting and liberation thinning of early successional stems and lianas to reduce competition with late-successional species (Finegan, 2014). Planting seedlings after logging may enhance forest structure and ultimately increase seed production, but the impacts of rehabilitative restoration on seed production may have long lag periods as trees grow to reproductive age. Increasing tree cover after logging may enhance seedling survival, via greater microclimatic buffering, reduced competition from shrubs and lianas and greater cross-pollination, if the density of flowering conspecifics is increased (Maycock et al., 2005). If seed production and survival rates are enhanced in actively restored logged forests, active restoration may alleviate the long-term effects of logging in tropical forests, although this mechanistic link has not yet been established.

In this study, we present data on the diversity, demography and functional traits of seedlings after a masting event spanning unlogged (UL), naturally regenerating (NR) and actively restored via silvicultural treatments (AR) logged forests in Northern Borneo, 30–35 years after logging and 15–27 years after restoration interventions. We analyse the effects of selective logging and subsequent restoration on the diversity, demography and functional composition of seedling communities over the first 1.5 years post-germination across 174 seedling plots (86 UL, 40 NR and 48 AR). We aim to provide mechanistic explanations for differences in seedling survival following germination to contribute new insights into the potential long-term effects of logging on forest communities. Specifically, we address the following predictions:

1. NR logged forests have lower seedling production and survival rates than UL and AR forests.
2. Species composition of seedlings differs between UL, NR and AR logged forests. Seedling communities of NR and AR forests have lower species diversity than UL forests, with active restoration of logged forests promoting a partial recovery of the species diversity of UL forests.
3. NR logged forests have seedling communities with more acquisitive functional strategies that can maximise use of greater light availability, while AR logged forests have more conservative traits because of greater light and belowground resource limitation and seed production from planted late successional species. These shifts in community function are driven by changes in species composition rather than intraspecific adjustment of traits.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in the Danum Valley Conservation Area (DVCA) and adjacent Ulu Segama Forest Reserve (USFR), where a mast fruiting event occurred from July to August 2019, enabling the comparison of seedling community responses in UL forests (DVCA) and forests selectively logged from 1981 to 1993 (USFR). Selective logging practices prioritised the extraction of the largest and most valuable trees and retention of non-target trees in the forest landscape.

The DVCA and USFR contain lowland dipterocarp forests in a 10,000 km^2 concession in East Sabah, Malaysian Borneo, that is currently designated for conservation (Reynolds et al., 2011). DVCA (438 km^2) has remained unlogged while the USFR (1268 km^2) was divided into multiple logging coupes (~27 km^2 each) that were harvested annually between 1981 and 1993 (Figure 1; Reynolds et al., 2011; Sabah Forestry Department, 2019). Harvesting was carried out once per coupe by a mixture of tractor and high-lead logging with a mean timber extraction rate of 118 m^3 ha^{-1} (42.5–128.2 m^3 ha^{-1}), where all commercially viable stems >60 cm DBH were removed (Foody & Cutler, 2003; Pinard et al., 2000). Mean annual rainfall at this site is 2305 mm and the mean daily temperature is 25.8°C (Fick & Hijmans, 2017).

Rehabilitative silvicultural treatments were applied to a subset of the logged coupes (logged 1981–1989; Figure 1) between 1992 and 2004 (15–27 years prior to this study and an average of 9 years post-logging) as part of the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO; Face the Future, 2011; Moura Costa, 1996). The purpose of these interventions was to offset carbon dioxide emissions. These active restoration strategies comprised a combination of liberation cutting, girdling of early successional tree species and planting of seedlings every 3 m along parallel lines (cut 2 m wide and 10 m apart) throughout the targeted areas (Face the Future, 2011; Moura Costa, 1996). Seedlings were grown in nurseries to a height of ~50 cm and with at least 10 leaves (4–8 months growth), before being planted in logged forests, and were a mix of 52 dipterocarp species, five non-dipterocarp canopy species and 16 non-dipterocarp native fruit tree species (Table S1; Face the Future, 2011; Moura Costa, 1996). After the initial restoration effort, sites were maintained by clearing competing vegetation every 3 months for 3 years, with no subsequent management implemented (Face the Future, 2011; Moura Costa, 1996).

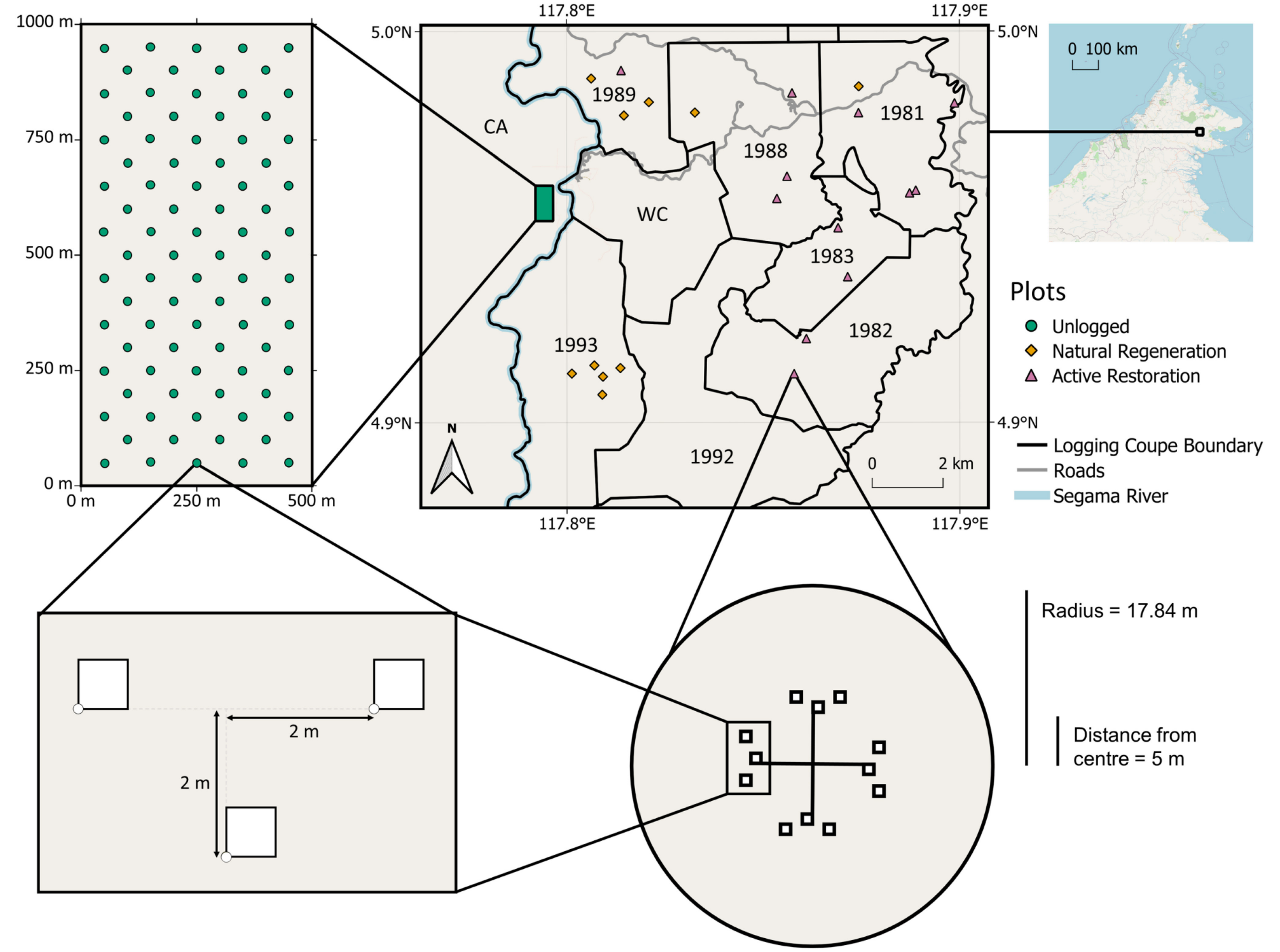

FIGURE 1 Location of seedling plots in the Danum Valley Conservation Area and Ulu Segama Forest Reserve. Colours indicate logging and regeneration method (consistent throughout this paper). Coupes are labelled by logging year, WC (water catchment) or CA (conservation area). Access roads are shown in grey and the Segama River in blue. Locations of unlogged seedling stations are shown within the Forest Global Earth Observatory (ForestGEO) study area (rectangular inset). Arrangement of seedling stations, clustered in groups of four at logged forest plots, is shown within the radius of the mature tree census area (circular inset). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

2.2 | Seedling censuses

Following the mast fruiting in July and August 2019, seedling communities were censused four times between September 2019 and March 2021 (1–2 months, 3–4 months, 5–6 months and 18–19 months post-mast; Burslem et al., 2022a). Censuses were carried out across 174 stations (86 UL, 40 NR and 48 AR; Figure 1). Each station consisted of three 1 × 1 m quadrats, located 2 m from a central point in a T-shaped configuration at 5 m from the centre of the tree plot (Figure 1). Since tree plots were randomly located, the locations of seedling plots also represent a randomised sampling design. At each census, all recently germinated seedlings were counted and identified with reference to collections held at the Danum Valley Herbarium, seedling mortality was assessed and census date was recorded. Where seedlings could not be identified to species, they were assigned to genera or to distinct morphospecies which were kept consistent among plots, censuses and with adult tree identification. In logged forests, stations were clustered in groups of four to maximise census efficiency in remote forest plots (Figure 1).

Established trees (>20 cm DBH) were censused in plots surrounding each seedling station centroid (radius = 17.26 m, area = 1000 m^2) in 2016, as part of the Forest Global Earth Observatory 50 ha plot (Davies et al., 2021) and Indicators of Forest Sustainability projects (INDFORSUS; Foody & Cutler, 2003). Smaller trees were not included here because of their low contribution to fruit production.

To quantify exposure of seedlings to sunlight, canopy gap fractions immediately above each seedling station (Figure 1) were recorded between July and November 2018 by taking an upwards-facing hemispherical photograph at 1.3 m height using a Nikon D-7000 DSLR, equipped with a Jintu 180° fish-eye lens (8 mm, F 3.0; Origo et al., 2017). Canopy photos were processed to determine percentage gap fractions using Can-Eye version 6.495 (INRA, 2017).

2.3 | Trait sampling

We measured traits of 399 seedlings from 15 species in January–February 2020 (6 months post-mast) across the UL ($n=195$ seedlings), AR ($n=147$ seedlings) and NR ($n=41$ seedlings) forests (Table S2; Burslem et al., 2022b). Seedlings were sampled from 76 seedling stations (46 UL, 20 AR and 10 NR), 30–35 years after logging and 15–27 years after restoration interventions. It was not possible to sample seedlings from many of the logged forest stations because of high mortality in the 6 months between masting and our sampling campaign, and because of difficult plot access. Species selection followed a mixed approach to ensure that species representing >80% of seedlings on the plots were sampled and to allow intraspecific comparisons between seedlings growing in logged and UL forests. Six species (*Agelaea* sp., *Koompassia excelsa*, *Parashorea malaanonan*, *Shorea johorensis*, *Shorea leprosula* and *Shorea parvifolia*) were found in more than one seedling plot and were sampled in both UL and logged forests. We used the *multipatt* function in R package *indicspecies* to determine the indicator species of UL forests (Cáceres & Legendre, 2009). This function identifies species that are associated to the forest type in which they have been found through a variance minimisation approach with a likelihood of 95% (Cáceres & Legendre, 2009). Three additional species were sampled only from UL forests (*Parashorea tomentella*, *Shorea seminis* and *Spatholobus* sp.) and four additional species only from AR forests (*Dryobalanops lanceolata*, *Intsia bijuga*, *Pterospermum javanicum* and *Shorea fallax*). *Buchanania sessifolia* was collected in AR and NR forests only and *Shorea macrophylla* was collected only from NR forests. For each species at each station, three seedlings were collected just outside the permanent seedling station to avoid disruption to continued monitoring of seedling demography. To obtain sufficient material for foliar nutrient analyses, an additional 10 seedlings were collected and combined with the three seedlings used for trait measurements prior to analysis. Where seedlings were unavailable in the immediate vicinity because of low initial abundance or high mortality, additional samples were taken ~20–40 m from the seedling plot to allow for replication and improved estimates of the species' mean trait values.

We measured 14 traits on each seedling that relate to resource acquisition and use: leaf mass fraction (LMF—relative C investment in leaves), root mass fraction (RMF—relative C investment in roots), leaf mass per area (LMA—investment in leaf photosynthetic strategy), leaf thickness (investment in leaf photosynthetic strategy), leaf force to punch (LFP—leaf toughness, associated with defence against insectivorous herbivory), leaf area to shoot area ratio (LA: SA—water transport and use strategy), root length to shoot length ratio (RL: SL—relative investment in above- and belowground resources), specific maximum root length (SMRL—relative investment in deep versus lateral roots), leaf calcium ($[Ca]_{leaf}$—Ca acquisition strategy), magnesium ($[Mg]_{leaf}$—Mg acquisition strategy), nitrogen ($[N]_{leaf}$—N acquisition strategy), phosphorus ($[P]_{leaf}$—P acquisition strategy) and potassium ($[K]_{leaf}$—K acquisition strategy) concentrations per unit mass, and leaf nitrogen to phosphorus ratio ($[N]_{leaf}$: $[P]_{leaf}$—relative nitrogen versus phosphorus limitation). Seedlings were collected in the morning before being transferred to the Danum Valley Field Centre for trait measurements. Seedlings were cut in the field immediately after harvest at the base of the stem to separate above- and belowground organs before being sealed in moist ziplock bags to minimise water loss during transfer. For each seedling, the length of the longest root (RL) and shoot length (SL) were measured using a ruler and shoot diameter was measured just below the first branch using precision callipers. Shoot diameter was converted into shoot cross-sectional area (SA) based on the assumption that all shoots were circular. To calculate leaf area (LA), all leaves were scanned using a flatbed scanner (CanoScan LiDE 120, Canon Inc., Tokyo, Japan) and analysed using ImageJ software in the R package LeafArea (Katabuchi, 2015). Leaf thickness was measured on three leaves, where available, using precision callipers avoiding any major veins, and a mean was calculated. LFP was measured at three points on the leaf using a Chantillon DFXII Digital Force Gauge with a 1-mm^2-flat head rod (AMETEK Sensors, New York, USA) and the mean was calculated. Leaves, shoots and roots were air-dried before being transferred to the Forest Research Centre, Sepilok, where they were dried to constant weight in an oven at 50°C before being weighed. LMF and RMF were calculated by dividing dry leaf and dry root mass by total dry mass, respectively. LMA was calculated by dividing dry leaf mass by leaf area. LA: SA was calculated by dividing leaf area by the cross-sectional area of the shoot, RL: SL by dividing root length by shoot length and SMRL by dividing maximum root length by dry root mass.

The leaves of the sampled seedlings were combined with the additional sample material from the same plot before being analysed for foliar nutrient concentrations at the Forest Research Centre, Sepilok. Leaves were ground using a SM2000 Heavy-duty Cutting Mill (Retsch, Haan, Germany) to pass through a 100-mesh (212 µm) sieve. The ground material was digested using a hydrogen peroxide–sulphuric acid digestion (Allen, 1989). $[N]_{leaf}$ and $[P]_{leaf}$ were measured colorimetrically using an Astoria-Pacific Flow Analyzer (Astoria-Pacific, OR, USA). $[Ca]_{leaf}$, $[K]_{leaf}$ and $[Mg]_{leaf}$ were measured spectrometrically using a SpectroArcos FHX22 (Spectro Analytical Instruments, Kleve, Germany). A subsample of the leaves was dried at 105°C to constant weight to calculate the percentage moisture content and to correct laboratory analyses to an oven dry basis. $[N]_{leaf}$: $[P]_{leaf}$ was calculated by dividing $[N]_{leaf}$ by $[P]_{leaf}$.

2.4 | Data analysis

2.4.1 | Seedling demography

For prediction 1, we tested for effects of logging/restoration treatment on seedling counts per 1 × 1 m seedling plot between UL, NR and AR forests over the initial 1.5 years post-mast using generalised linear mixed models (GLMMs) for plots where one or more seedlings were observed at any census using the R package *glmmTMB* (Brooks et al., 2017). We modelled seedling counts using a generalised Poisson error family with a log link function to account for under-dispersion of residuals (Consul & Famoye, 1992). The generalised Poisson distribution is a discrete probability distribution that enhances the classic Poisson distribution with an extra parameter for over- or under-dispersion and is used for modelling count data where mean and variance differ (Thomas, 2015). Census date was included as a continuous variable, and restoration/logging treatment (UL vs. NR vs. AR), established community basal area (stems >20 cm DBH within a 17.84-m radius, equivalent to 1000 m^2) and canopy gap fraction were all included as fixed effects. We fitted additional models to compare restoration treatments only with logging intensity and time since logging as additional fixed effects. Interactions between all fixed effects and census date were included in all models to test for variation in effects over time. We included seedling station nested in location as a random intercept effect to account for spatial clustering of stations within the logged forest plots. Census date was measured in days since the start of census 1 and was natural log transformed where comparison of models with and without transformation suggested this would have a better fit based on the Akaike information criterion (AIC; Sakamoto, 1994). Canopy gap fraction was natural log transformed and basal area of mature trees was square root transformed to ensure normality of residuals, and all continuous numeric variables were centred and scaled to zero mean and unit variance prior to modelling. Model simplification was performed using the *dredge* function in R package *MuMin* (Barton, 2009) to find the model with the lowest AIC or the fewest terms if ΔAIC <2.

We additionally modelled seedling survival rates using mixed effect Cox models (Lee & Wang, 2003) with survival rates between logging/restoration treatments compared using log-rank tests (Lee & Wang, 2003). Analyses were done at the whole community level and on community subsets (indicator vs. non-indicator species of UL) to understand whether species that dominate UL seedling communities are more vulnerable to the effects of logging and restoration. All survival analyses were conducted using the *survival* R package (Therneau, 2022a), except for mixed effect Cox models that were conducted using the *coxme* R package (Therneau, 2022b).

2.4.2 | Diversity

To test prediction 2, differences in community composition of seedlings between forest types (UL, NR and AR) over the first 6 months post-mast (censuses 1–3) were analysed by permutational analysis of variance (PERMANOVA; 10,000 permutations) accounting for effects of date, time since logging and logging intensity. Interactions were modelled between date and all other variables to test for differing trajectories of community change over time. The Bray–Curtis dissimilarity based on seedling counts was used as the metric for these analyses (Bray & Curtis, 1957) and all PERMANOVA tests were performed in the *vegan* R package (Oksanen et al., 2019). We additionally calculated species richness and Shannon's diversity index for each seedling plot using the R package *SYNCSA* (Debastiani & Pillar, 2012). Differences between logging/restoration treatments were compared using linear mixed models with location included as a random intercept effect for each diversity index.

2.4.3 | Functional traits

To test prediction 3, we calculated and compared community-weighted mean (CWM) trait values across logging/restoration treatments. CWMs are calculated by weighting measured species mean trait values in each forest type by the abundance of that species in each plot (Pla et al., 2012). For species where traits were not measured, the mean value for all species in that forest type was used. Differences in CWM traits were compared using linear mixed models with location included as a random intercept effect in the R *stats* package (R Core Team, 2020).

To test for intraspecific adjustment of traits between UL and AR forests for the subset of species sampled in both forest types, we fitted linear mixed effects models using the R package *lme4* (Bates et al., 2014). Low sampling effort and low availability of seedlings in NR resulted in the exclusion of seedlings in this forest type for this analysis. Each trait was modelled with forest type (UL vs. AR) as a fixed effect and seedling plot nested within location nested within species as a random intercept to account for our sampling design. For foliar nutrients, species was included as the random intercept. To capture trait plasticity and/or genetic differentiation among populations, we additionally compared traits between UL and AR forests using linear models, analysing each species separately, while accepting the limitations of the sample size and statistical power.

We additionally tested the effects of plot-level conspecific and total seedling density, basal area of all trees >200 mm within a 10-m radius, canopy gap fraction and functional traits on survival rates using mixed effects Cox models (Cox, 1972; Therneau & Grambsch, 2000). Standardised hazard scores were calculated to represent how fixed effects affect risk of seedling mortality. All effects and their interaction with logging treatment were included as fixed effects, with seedling station nested in location included as a random intercept. The optimal model was selected using backwards stepwise selection based on the lowest AIC score (Sakamoto, 1994). To test for time-dependent effects of the explanatory variables on survival, we subsequently fitted an Aalen's additive regression models using the formula for the optimal Cox model (Aalen, 1989). All data analysis was undertaken in R statistical software v.3.6.3 (R Core Team, 2020).

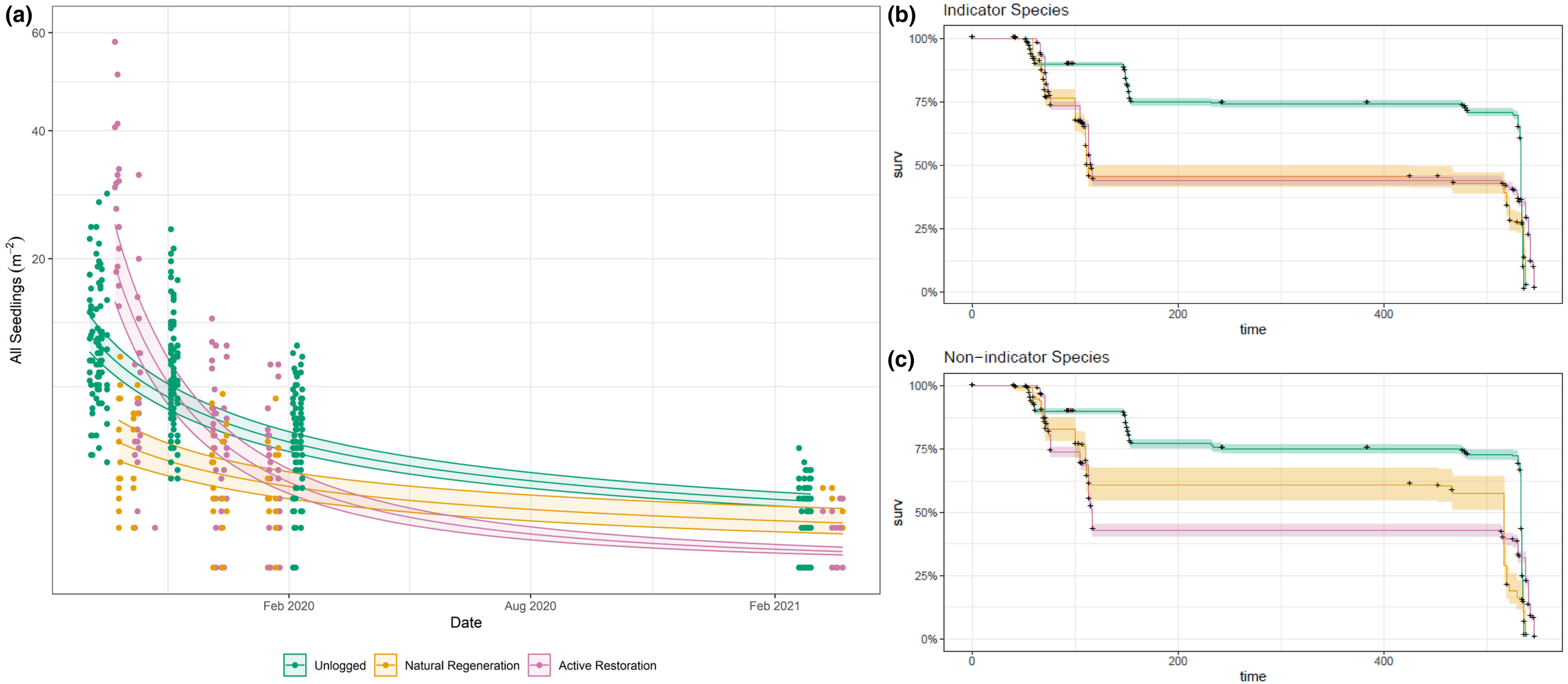

FIGURE 2 Seedling survival rates in unlogged (UL; green), naturally regenerating logged (NR; yellow) and actively restored logged (AR; pink) forests during the first 1.5 years post-mast. Seedling density across time is presented in (a) with lines representing median predictions from generalised linear mixed models. Survival rates fitted using the Kaplan–Meier method are presented for (b) indicator and (c) non-indicator species of unlogged forests. Shading around the lines represent the 95% confidence interval around the predicted values.

3 | RESULTS

3.1 | Seedling density and survival

A total of 5119 seedlings were monitored across 174 quadrats of 1m^2 for ~1.5 years after a masting event with 1272 surviving at the end of the study. All six species sampled in both UL and logged forests, except *Agelaea* sp., were identified as seedling indicator species of UL forests.

TABLE 1 GLMM model summary for the effects of logging and restoration treatment (naturally regenerating—NR/actively restored—AR, relative to unlogged forest—intercept) and time since masting as predictors of seedling density following the 2019 masting event at Danum Valley. All numeric independent variables are centred and scaled. The best model was selected using the R MuMIn dredge function (Barton, 2009). Station variance (a nested random intercept effect of different seedling stations at each plot location) was .344 and model R^2 values were .900 (conditional) and .707 (marginal).

Variable	Estimate	SE	*p*-value
(intercept)	2.548	0.079	<.001
NR	−0.898	0.177	<.001
AR	−0.405	0.151	.007
Log$_{10}$ (census date)	−0.754	0.027	<.001
Log$_{10}$ (canopy gap fraction)	−0.079	0.059	.183
Sqrt (established tree basal area)	0.047	0.063	.453
Date: NR	0.076	0.101	.454
Date: AR	−1.148	0.082	<.001

Plots in NR and AR logged forests had fewer seedlings present than those in UL forest for most of the first 1.5 years after masting (Figure 2, Table 1). At 1–2 months post-mast, median germinated seedling counts were higher in UL (median = 9.66 ind. m^{-2}; Figure 2) and AR forests (median = 8.33 ind. m^{-2}) than in NR forests (median = 1.33 ind. m^{-2}). Seedling counts in AR logged forests declined at a faster rate than in UL forest (Table 1) such that AR forests had lower average seedling counts than either UL or NR forests by 1.5 years post-masting, despite having the highest density of germinated seedlings immediately post-mast (Figure 2). In contrast, seedling densities in UL and NR forests declined at similar rates (Table 1). Seedling density was lower in plots with high canopy gap fraction and higher in plots with higher tree basal area (Table 1).

Seedling mortality was the greatest within the first 100 days within the census interval (Figure 2a; Figure S2). Over the entire census, seedlings in UL forest had higher survival rates than seedlings in AR and NR logged forests (Figure 2b,c; Figure S2). When comparing among community subsets, seedling survival of first-census indicator species of UL forest (4 dipterocarp and 1 legume species positively associated with UL forest) was greater in UL forest than either of the logged forests but did not differ among restoration treatments during the first 500 days post-mast (Figure 2b). In contrast, survival rates of seedlings of non-indicator species of UL forest were greater in NR logged forests than AR forests but were lower than in UL forest during the first 500 days post-mast (Figure 2c).

In logged forests, seedling density of indicator species of UL decreased with logging intensity but increased with logging intensity for non-indicator species of UL (Table S3). Median canopy gap fraction was 3.03% (interquartile range = 2.00%–4.94%) in UL, 3.76% (IQR = 2.31%–7.20%) in NR and 2.71% (IQR = 1.62%–3.51%) in AR. Seedling density increased with basal area of mature tree individuals (>20 cm DBH) for non-indicator but not for indicator species of UL

TABLE 2 Results of PERMANOVA tests (10,000 permutations) showing the effect of forest type (unlogged forest, naturally regenerating logged forest or actively restored logged forest) and the date of census on seedling community composition over the first 6 months post-mast.

	R^2	*F*	*df*	*p*
Unlogged versus natural regeneration				
Date	.018	6.635	1	<.001
Forest type	.084	30.369	1	<.001
Date: forest type	.005	1.845	1	.043
Unlogged versus active restoration				
Date	.026	9.945	1	<.001
Forest type	.051	19.548	1	<.001
Date: forest type	.005	1.903	1	.040
Natural regeneration versus active restoration				
Date	.016	3.188	1	<.001
Forest type	.050	10.034	1	<.001
Logging year	.034	6.855	1	<.001
Logging intensity	.028	5.566	1	<.001
Date: forest type	.010	2.056	1	.003
Date: logging year	.006	1.138	1	.284
Date: logging intensity	.006	1.133	1	.286

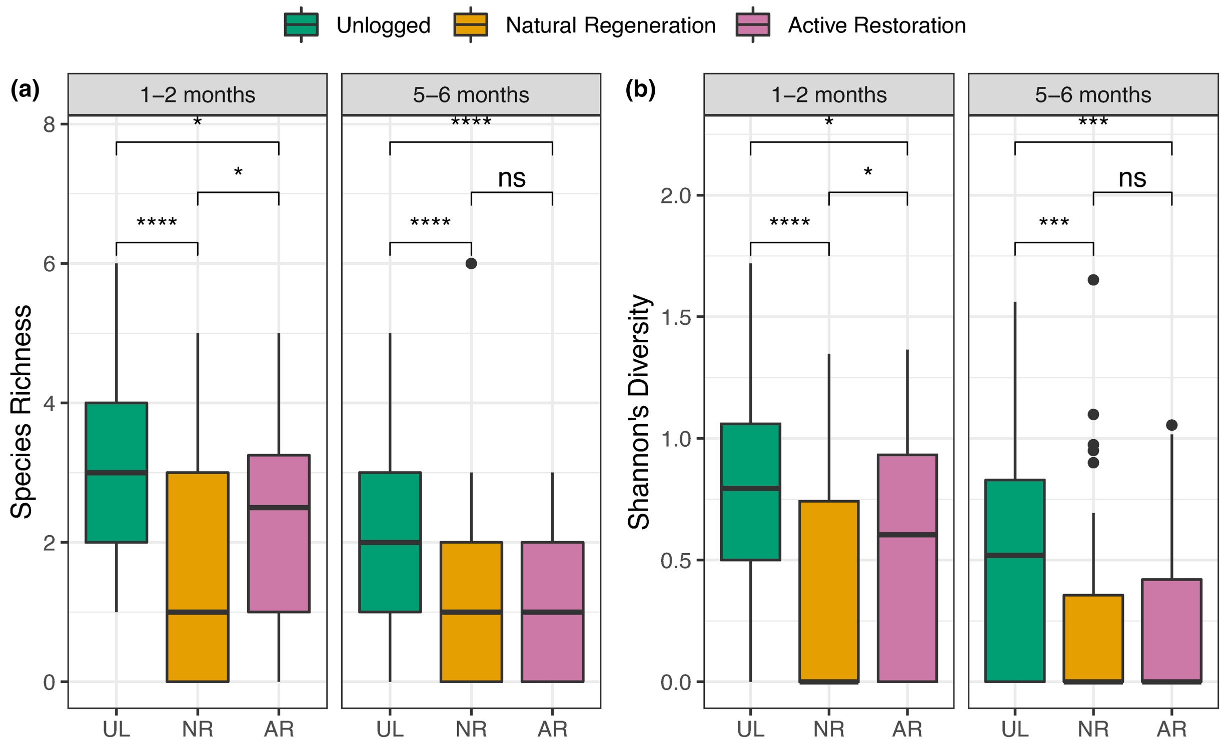

FIGURE 3 Species richness (a) and Shannon's diversity index (b) over the first 6 months after masting in unlogged (UL), naturally regenerating logged (NR) and actively restored logged (AR) forests. Significant differences between logging/restoration treatments are presented: ns—$p > .05$; *$p < .05$; ***$p < .001$; ****$p < .0001$.

(Table S3). The time since logging did not affect the abundance of either indicator or non-indicator species of UL (Table S3).

3.2 | Community composition and diversity

Seedling community composition differed among UL, NR and AR forests (PERMANOVA; Table 2) and changed over time across all treatments (Table 2). In comparisons of seedling communities, there was an interaction between census date and forest type (Table 2), indicating that the similarity of these communities changed over time due to processes that occurred post-germination. Community differences between 1–2 months and 5–6 months are illustrated in the NMDS (Figure S1). At 1–2 months, most plots in UL forest contained relatively similar seedling communities that were distinct from those in logged forests. The PERMANOVA analysis indicates that seedling communities in logged forests (both NR and AR) show high inter-plot dissimilarity.

In AR and NR, PERMANOVA results showed the effects of logging year (time since logging) and logging intensity (Table 2) on seedling community composition across censuses. These variables had no interaction with seedling census date (Table S3) and therefore had no effect on seedling community trajectory after germination.

Mean species richness and Shannon's diversity were the highest in UL forest plots at both 1–2 months (richness = 3.06 ± 0.13; Shannon's diversity = 0.75 ± 0.02) and 5–6 months (richness: 1.99 ± 0.12; Shannon's diversity = 0.75 ± 0.03; Figure 3). At 1–2 months, AR forests had higher species richness (AR: 2.42 ± 0.23; NR: 1.58 ± 0.23) and Shannon's diversity (AR: 0.56 ± 0.05; NR: 0.49 ± 0.07) than NR forests, but they did not differ after 5–6 months (richness—AR: 1.00 ± 0.15, NR: 1.00 ± 0.21; Shannon's diversity—AR: 0.34 ± 0.06, NR: 0.31 ± 0.06).

3.3 | CWM traits

There were differences in the CWM for 9 of 14 measured seedling traits across logging/restoration types, with a tendency for the greatest dissimilarity in mean traits between NR and AR forests (Table S4; Figure 4). CWMs of LA:SA ($\Delta = 2.73 \pm 1.02\,\text{cm}^2\,\text{mm}^{-2}$, $p = .009$) were higher in UL forest than AR forests (Figure 4). Logged NR forests had higher CWM RMF ($\Delta = -0.064 \pm 0.025\,\text{g}\,\text{g}^{-1}$) than UL forest, but these forest types did not differ in any other traits (Figure 4). CWM of 10 traits did not differ between AR and NR forests, but there was higher $[\text{N}]_{\text{leaf}}$ ($\Delta = -8.30 \pm 2.65\,\text{mg}\,\text{g}^{-1}$), $[\text{N}]_{\text{leaf}}$: $[\text{P}]_{\text{leaf}}$ ($\Delta = -3.88 \pm 1.85\,\text{g}\,\text{g}^{-1}$), RMF ($\Delta = -0.063 \pm 0.01\,\text{g}\,\text{g}^{-1}$) and RL: SL ($\Delta = -0.165 \pm 0.04\,\text{mm}\,\text{mm}^{-1}$) in NR than in AR forests (Figure 4).

3.4 | Intraspecific adjustment of traits

We tested for intraspecific adjustment of traits for the five indicator species of UL forest between UL and AR forests using mixed effect models. Overall, intraspecific differences were observed for 5 of 14 measured traits, with lower LMF ($\Delta = -0.033 \pm 0.014\,\mathrm{g\,g^{-1}}$), $[N]_{leaf}$ ($\Delta = -1.123 \pm 0.406\,\mathrm{mg\,g^{-1}}$), $[P]_{leaf}$ ($\Delta = -0.095 \pm 0.041\,\mathrm{mg\,g^{-1}}$), $[Ca]_{leaf}$ ($\Delta = -0.975 \pm 0.289\,\mathrm{mg\,g^{-1}}$) and higher LMA ($\Delta = 1.815 \pm 0.809\,\mathrm{g\,m^{-2}}$) for seedlings growing in AR logged forests than in UL forest (Table 3). Of these

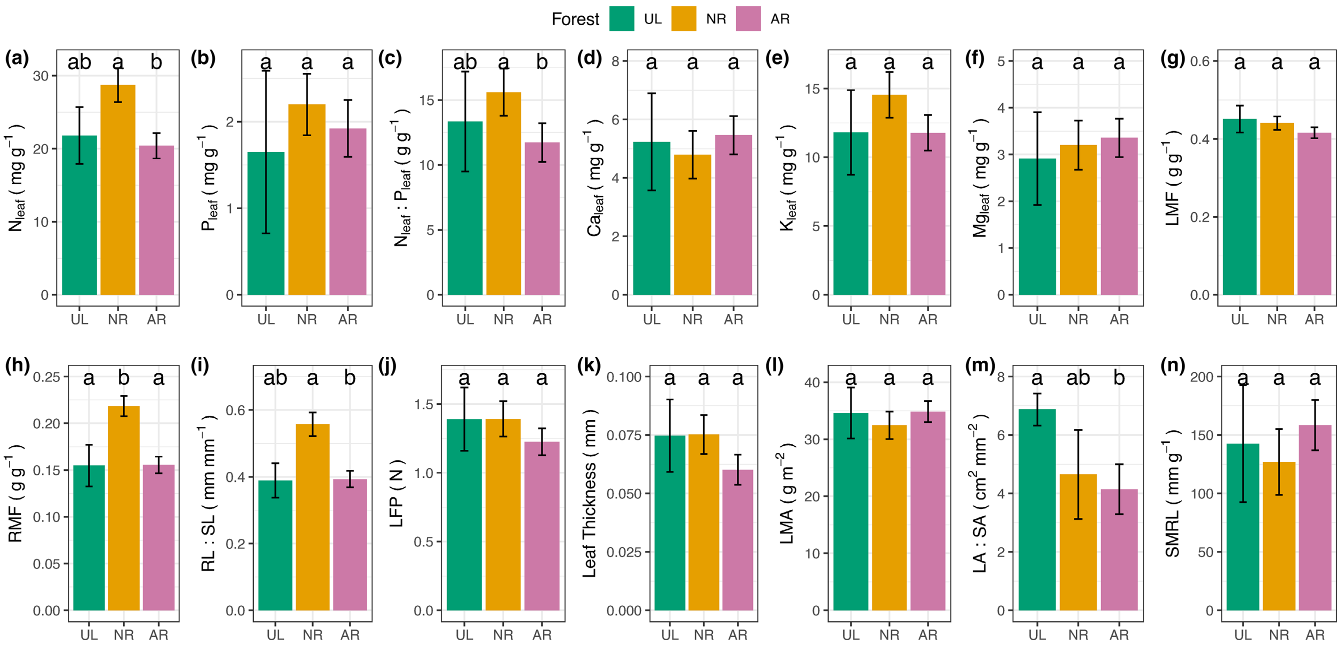

FIGURE 4 Community-weighted mean trait values in unlogged (UL; *n* = 46), naturally regenerating (NR; *n* = 6) and actively restored (AR; *n* = 19) logged forests for (a) $[N]_{leaf}$, (b) $[P]_{leaf}$, (c) $[N]_{leaf}$: $[P]_{leaf}$, (d) $[Ca]_{leaf}$, (e) $[K]_{leaf}$, (f) $[Mg]_{leaf}$, (g) leaf mass fraction (LMF), (h) root mass fraction (RMF), (i) root length to shoot length ratio (RL:SL), (j) leaf force to punch (LFP), (k) leaf thickness, (l) leaf mass per area (LMA), (m) leaf area to shoot area (LA: SA) and (n) specific maximum root length (SMRL). Bars represent the mean, and error bars are one standard error of the mean. Different letters represent significantly different groups ($p < .05$) detected from linear mixed models (see Section 2 for details).

TABLE 3 Summary of results comparing mean trait values between unlogged (UL) and actively restored (AR) logged forests for the five indicator species of UL forest. Traits were modelled using linear mixed models with forest as a fixed effect and seedling plot nested in species as a random intercept effect, except for foliar nutrients where only a species-level random intercept was used because of bulking of samples. Mean and standard error (SE) values are presented for the UL forest and the difference (Δ) for AR forests. The difference in mean trait value in AR compared to UL forest is presented for each species from models on subsets of the data, with asterisks representing the significance level (*<.05, **<.01, ***<.001). Species mean trait values are presented in Table S5. Significant effects are presented in bold.

			UL		Δ AR	
Trait	**Units**	**Function**	**Mean**	**SE**	**Mean**	**SE**
LMF	$\mathrm{g\,g^{-1}}$	Light acquisition	0.438	0.02	**−0.034**	**0.01**
LMA	$\mathrm{g\,m^{-2}}$	Leaf longevity	31.960	3.26	**1.817**	**0.65**
Leaf thickness	mm		0.069	0.01	−0.007	0.01
LFP	N	Herbivory resistance	1.328	0.13	0.050	0.12
LA:SA	$\mathrm{cm^2\,mm^{-2}}$	Hydraulic supply capacity	5.706	2.01	1.804	1.44
RMF	$\mathrm{g\,g^{-1}}$	Water and nutrient acquisition	0.161	0.01	0.013	0.01
RL:SL	$\mathrm{mm\,mm^{-1}}$	Light foraging versus nutrient foraging	0.382	0.03	0.006	0.03
SMRL	$\mathrm{mm\,g^{-1}}$	Nutrient and water acquisition	153.432	21.60	−23.870	12.48
$[N]_{leaf}$	$\mathrm{mg\,g^{-1}}$	Macro-nutrient availability	23.161	2.82	**−1.123**	**0.41**
$[P]_{leaf}$	$\mathrm{mg\,g^{-1}}$	Macro-nutrient availability	1.634	0.08	**−0.095**	**0.04**
$[Ca]_{leaf}$	$\mathrm{mg\,g^{-1}}$	Macro-nutrient availability	5.697	0.54	**−0.975**	**0.29**
$[K]_{leaf}$	$\mathrm{mg\,g^{-1}}$	Macro-nutrient availability	12.474	1.572	−0.369	0.27
$[Mg]_{leaf}$	$\mathrm{mg\,g^{-1}}$	Macro-nutrient availability	3.121	0.40	−0.108	0.101
$[N]_{leaf}$:$[P]_{leaf}$	$\mathrm{g\,g^{-1}}$	Nitrogen versus phosphorus limitation	14.293	1.74	0.257	0.28

Abbreviations: LA:SA, leaf area to shoot area; LFP, leaf force to punch; LMA, leaf mass per area; LMF, leaf mass fraction; RL: SL, root length to shoot length; RMF, root mass fraction; SMRL, specific maximum root length.

intraspecific differences, only differences in LMF and $[P]_{leaf}$ had the same directionality as shifts in CWM trait values, indicating that differences in CWMs are driven by differences in species composition rather than intraspecific trait adjustment. The magnitude of intraspecific trait shifts was highly variable across species and was inconsistent when compared with the magnitude of change in CWMs (Table 3). Of the five species, *P. malaanonan* and *S. leprosula* had six traits, and *K. excelsa* had five traits that were different between UL and AR forests (Figure S3; Table 3), while *S. johorensis* had only one trait and *S. parvifolia* had no traits that differed between UL and AR forests. A low abundance of UL indicator species in NR forests meant that intraspecific comparisons could not be made.

3.5 | Drivers of seedling mortality

Over the initial 100 days post-germination, functional traits were largely unable to predict mortality of seedlings, indicating that initial mortality is unrelated to plant traits. However, beyond 100 days seedling mortality rates could be explained by functional traits and forest type (Figure 5; Table S6). Across all forest types, greater LMA was associated with increased mortality risk of seedlings. In UL forests, greater LFP increased seedling mortality risk. In AR forests, lower LFP, RMF and SMRL and greater RL: SL were associated with increased mortality risk of seedlings as indicated by a interaction between these functional traits and forest type in our Cox models (Figure 5; Table S6).

4 | DISCUSSION

Our study indicates that the active restoration of logged forests appears to have successfully recovered seed production such that the initial production of seeds and the number of germinating seedlings in AR forests are similar to UL forest in terms of quantity and more similar than NR forest in terms of composition. However, the subsequent phase of seedling recruitment suggests that seedlings of UL forest indicator species have disproportionately high mortality rates in AR forests. Our study shows distinct differences in the taxonomic composition, dynamics and functional traits of the seedling community in response to logging and restoration history. This variation in the seedling communities indicates that current active restoration via rehabilitative silvicultural treatments are insufficient to reduce the risk of regeneration failure in logged forests and may drive long-term changes in future forest plant communities if the differences continue to persist and reflect consistent patterns across masting events. Long-term observations of recovering forests are crucially needed to understand community dynamics during forest recovery.

4.1 | Community composition and diversity of logged forests

Existing data indicate selectively logged forests maintain high species richness in adult tree and sapling communities, including after active restoration (Berry et al., 2010; Hayward et al., 2021; Putz

	Intraspecific differences in mean trait value				
p	*Koompassia excelsa*	*Parashorea malaanonan*	*Shorea johorensis*	*Shorea leprosula*	*Shorea parvifolia*
.003	−0.038	**−0.102*****	0.009	−0.025	−0.035
.007	2.004	2.316	1.044	1.429	**2.257***
.209	0.017	−0.003	−0.007	−0.021	−0.004
.676	0.057	0.139	−0.228	0.209	−0.013
.214	0.328	8.576	0.351	−0.129	0.210
.211	**0.089***	**0.060****	0.006	−0.033	0.018
.824	0.070	0.038	0.041	−0.106	0.028
.060	−77.681	−20.388	−14.222	−12.938	−28.189
.007	**−4.702****	−0.933	−0.579	−0.118	**−1.682*****
.024	**−0.427*****	−0.167	−0.018	0.001	**−0.138*****
.001	−0.968	**−1.221****	−0.602***	−0.639	**−0.944*****
.180	−0.132	**−1.073***	0.034	0.137	**−0.662****
.292	**0.768***	**−0.384*****	0.007	0.057	**−0.238***
.364	**3.273*****	0.690*	−0.212	−0.064	0.280

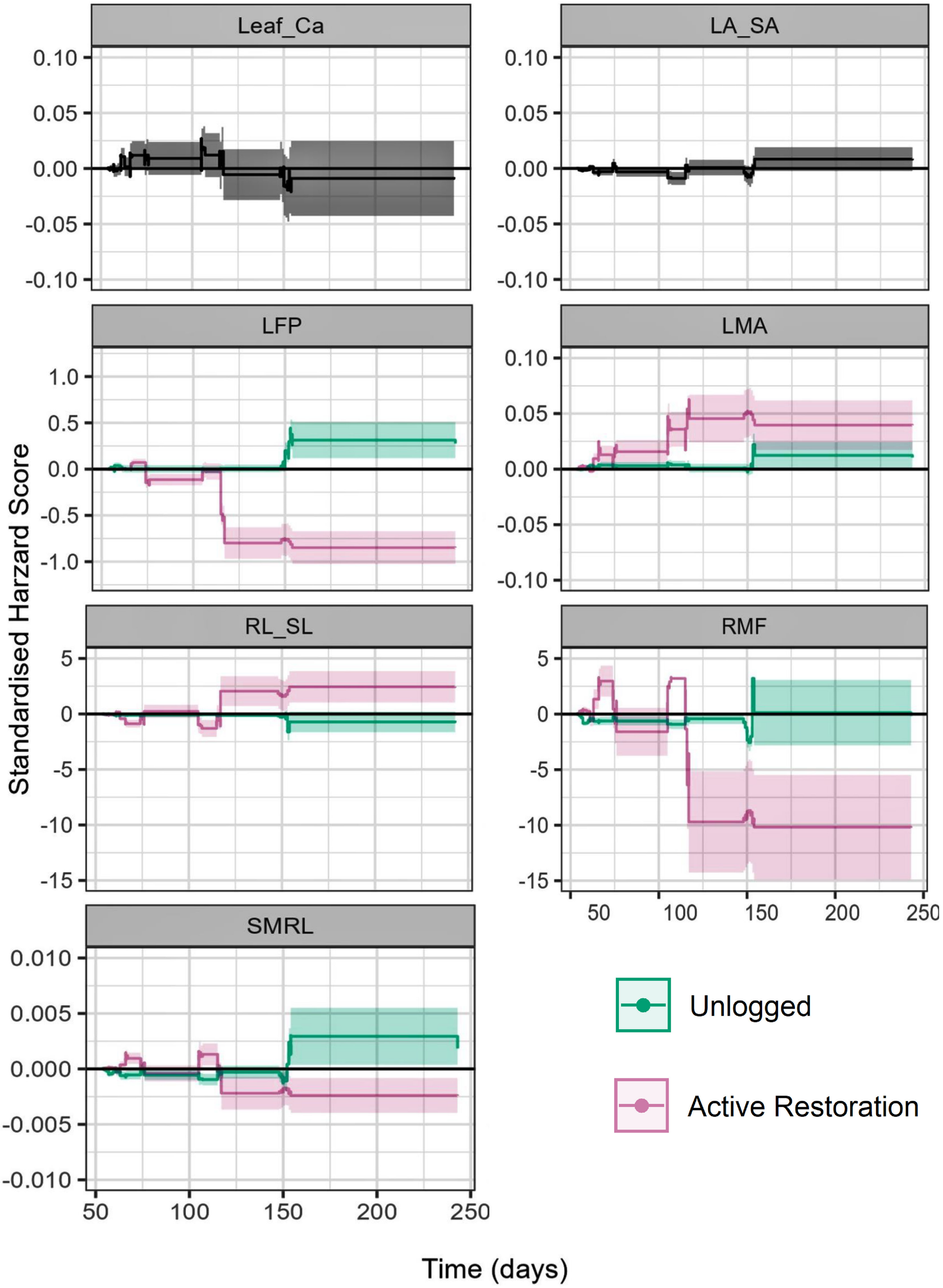

FIGURE 5 Standardised hazard scores for functional traits over time for unlogged forests (green) and logged forests with active restoration (pink). Functional traits were tested as predictors using Cox mixed effect models (Table S6). The optimal model formula was subsequently used to fit an Aalen's additive regression model to test how hazard scores for functional traits change with time since germination, where values greater than zero indicate greater mortality hazard (i.e. higher trait values increase probability of seedling mortality) and conversely for values less than zero. Panels in black represent hazard scores for traits that affected mortality equivalently in UL and AR forests. For model coefficients, see Table S7. Shading shows the 95% CIs of estimated hazard scores, showing significant positive/negative effects on hazard/departures from zero over time. Leaf_Ca, leaf calcium concentration; LA_SA, Leaf area: shoot area ratio; LFP, leaf force to punch; LMA, leaf mass per area; RL_SL, root length: Shoot length ratio; RMF, root mass fraction; SMRL, specific maximum root length.

et al., 2012), but we found this did not hold for regenerating seedling communities. We found that local-scale ($1\,m^2$) species richness of NR logged forests was approximately half of that found in UL forest by 5–6 months post-mast. Seedling communities in NR forests also had distinct species compositions from UL forest and higher species evenness, indicating that logging may have long-term effects on community composition within these forests. Selective logging in lowland dipterocarp forests predominantly targets dipterocarps and other tall species (Milodowski et al., 2021). Indicator species of UL forest (i.e. species abundant in UL forest) were largely missing from seedling communities in NR forests, likely driven by the removal of reproductively mature individuals of these species. Without intervention, our results suggest that the disruption of regeneration processes linked to logging could drive a long-term shift in the species composition of these forests.

Selective logging practices can vary considerably in intensity, with timber yields of $42–310\,m^3\,ha^{-1}$ declared at USFR (Foody & Cutler, 2003). Our results show that logging intensity is an important determinant of seedling community composition that persists throughout the first 1.5 years post-mast. Logging at lower intensity may reduce the loss of diversity in logged forests and reduce the extent of community composition shifts (Marsh et al., 2022; Rivett et al., 2016). Despite causing shifts in species composition, logging intensity did not affect seedling density. Instead, greater tree basal area and more closed canopies were associated with increased seedling density, indicating that the maintenance of large canopy trees is critical in maintaining fruit production and germination rates.

While the co-benefits of biodiversity recovery during silvicultural approaches for biomass recovery are often presumed (Crouzeilles et al., 2017; Hariharan & Shankar Raman, 2022; Osuri et al., 2022), it remains unknown whether active restoration through these means delivers recovery of the reference community assemblage. Our study shows that 15–27 years after implementation of active restoration via rehabilitative silvicultural treatments in the logged forests, the richness and evenness of seedling communities were higher than those in adjacent NR forests and more closely resembled those of the seedling communities in UL forest, while nonetheless remaining distinct from these, in the initial 2 months after masting. However, these patterns did not persist beyond 1–2 months, and by 5–6 months no difference in seedling diversity between AR and NR logged forests could be found. Active restoration via rehabilitative silvicultural treatments can therefore enhance seed production and the recovery of canopy structure and carbon density (Gourlet-Fleury et al., 2013; Mills et al., 2019; Osuri et al., 2019; Philipson et al., 2020), but these patterns were not reflected in seedling survival, which may have implications for the long-term recovery of restored logged forests.

4.2 | Seedling demography in logged forests

In NR forests, seedling density was lower than in UL forest at the census 1–2 months after mast fruiting. Selective logging systematically removes large, reproductively mature trees (Sist et al., 2003) and their removal likely reduces the number of seeds produced, especially of timber species (Pillay et al., 2018). Within the Danum Valley landscape, stem density and basal area of established trees (>20 cm DBH) were the greatest in UL forest and the lowest in NR logged forests (Hayward et al., 2021), supporting the hypothesis that seed production is related to the biomass and density of parent trees. Shifts in allocation of NPP to woody production in logged forests (Riutta et al., 2018) may also reduce resource availability for seed production and/or reduce germination success (Pillay et al., 2018). Active restoration via rehabilitative silvicultural treatments that include enrichment planting and cutting of climbers and bamboo and liberation thinning can increase stem abundance in logged forests (Gourlet-Fleury et al., 2013; Mills et al., 2019; Osuri et al., 2019; Philipson et al., 2020). Mast fruiting may have been enhanced in AR relative to NR logged forests, as median seedling density 1–2 months post-mast was four times greater in AR than in NR forests. Since lianas reduce reproduction of host trees (Estrada-Villegas et al., 2022; Estrada-Villegas & Schnitzer, 2018; Wright et al., 2015), greater fruit production in AR forests may be related to reduced liana loads relative to NR forests. Our findings suggest that active restoration via rehabilitative silvicultural treatments can effectively restore the strength of general masting in lowland dipterocarp forests.

High rates of seedling mortality in the months immediately following general masting are typical in Bornean lowland dipterocarp forests (Itoh et al., 1995; Oshima et al., 2014). Within the first 6 months, we observed high mortality rates across all forests including 66% mortality in UL forest. Despite initially having the highest seedling density, AR forests showed the highest rates of mortality, resulting in a similar seedling density to NR forests by 5–6 months and lower values in NR forest by 18–19 months post-mast. In contrast, seedling declines did not differ between UL and NR forests, following patterns reported elsewhere in Borneo (Curran & Webb, 2000). These results suggest that the seedling mortality rates are not just driven by the historic impacts of logging but there are likely to be ecological processes in the actively restored forest areas driving enhanced seedling declines, as we discuss further below.

Intense seed and seedling predation immediately after mast fruiting drives early mass mortality of seedlings (Curran & Webb, 2000). The steep decline in seedling density in AR forests suggests that predator satiation may not have occurred, despite greater seed production and germination than in either UL or NR forests. The inclusion of fruit trees in the planted species mix likely increases the abundance of bearded pigs and other seed eating wildlife in AR forests with rehabilitative silvicultural treatments, contributing to reduced seed predator satiation. This reduction in predator satiation may enhance mortality that may already be elevated in logged forests because of greater abiotic stress that may persist for decades in areas that have experienced intensive logging. Logged forests can support greater abundance of herbivorous mammals (Malhi et al., 2022) that may prevent predator satiation, even in the presence of high seedling production. The restored forests at our study site are contiguous with a large expanse of NR logged forest

(Reynolds et al., 2011). AR forests, particularly if they were overstocked with fruit trees, may represent islands of high food availability for large mobile seed predators, such as bearded pigs, embedded within a matrix of low-quality habitat in terms of food availability. It is possible that this patchiness in the availability of an abundant food source may have attracted mobile seed predators to areas of high seedling density (Hautier et al., 2010), although a greater understanding of the movement patterns of seed predators would be needed to confirm this hypothesis. Seed predators may thus choose to remain in restored areas, which retain higher food availability than the surrounding NR forests, instead of moving on to new areas as they do when foraging in UL forest (Curran & Leighton, 2000). The presence of AR forests may have reduced the pressure on the matrix of NR forests if seed predators were concentrated in AR forests, allowing seedlings to maintain higher survival rates in NR forests despite their lower abundance.

High seedling mortality in AR forests could also result from a low genetic diversity of parent trees (de Morais et al., 2020; Nutt et al., 2016). Seedlings planted during active restoration are often collected from a small number of parent trees (Nef et al., 2021). In this study, planted stems were grown in nurseries from seeds and cuttings, likely collected from a relatively small and accessible group of parent trees (Face the Future, 2011). If the seedlings planted during restoration interventions in 1992–2004 are now reproductively mature, and their progeny have contributed substantially to the high initial densities of seedlings in the AR forests, then the seedling cohort may possess low heterozygosity resulting from a high frequency of sib–sib mating among closely related adults. Low genetic diversity may also arise in logged forests if the density of reproductive trees is not recovered through restorative treatments. Previous studies from Sabah show that low genetic diversity can reduce seedling survival, possibly due to the shared vulnerability of closely related seedlings to pathogens (de Morais et al., 2020; Nutt et al., 2016). Dipterocarp seedlings would be especially vulnerable to these effects because pollen dispersal distances are short and even natural populations possess strong fine-scale genetic structure (Kettle et al., 2011). Lower genetic diversity among seedlings is also likely to reduce adaptive capacity of populations by reducing functional trait diversity (Jump et al., 2009). Shifts in restoration practices towards planting with more diverse mixtures within and between species could enhance adaptive capacity and help overcome high mortality rates and accelerate the recovery of logged ecosystems (Veryard et al., 2023).

4.3 | Functional traits

Functional traits of seedling communities varied across forests with different logging and restoration histories. For seedlings growing in NR logged forests, a shift towards greater biomass investment in deeper roots compared with those in UL forest was observed. Greater investment in belowground biomass in seedlings is indicative of reduced light limitation relative to water and nutrient limitation (Boonman et al., 2020; Kramer-Walter & Laughlin, 2017; Umaña et al., 2020, 2021; Waring & Powers, 2017; Wurzburger & Wright, 2015). Logging of the largest trees in tropical forests reduced canopy leaf cover by >50% and increased understorey light availability at our study site 23–28 years after logging (7 years before this study; Milodowski et al., 2021). Logging may also reduce nutrient availability through export of nutrients in timber and soil erosion (Baharuddin et al., 1995; Swinfield et al., 2020), particularly if timber is not debarked prior to removal as at our study site since bark can store 2.9–13.7 times the concentration of nutrients as heartwood (Inagawa et al., 2023). At our study site, the high intensity of logging indicates that large quantities of nutrients will have been removed from biogeochemical cycles in this ecosystem and these will not have been replaced within 35 years after logging. Meanwhile, logging may exacerbate water shortage via changes to both the microclimate and soil physical properties (Baharuddin et al., 1995; De Frenne et al., 2021; Hardwick et al., 2015; Ziegler et al., 2006), resulting in enhanced drought stress for seedlings (Qie et al., 2019), and disrupt soil microbiota. These impacts, however, may be affected by the presence of skid trails that we have not fully studied here. These concomitant increases in light and reductions in nutrient and water availability may drive greater investment in belowground biomass.

Functional composition also differed between AR and UL forests, but this difference did not follow an equivalent trajectory to NR forests. In AR forests, rather than exhibiting greater belowground investment, seedlings invested in stem biomass in the first 6 months after the masting event. Active restoration via rehabilitative silvicultural treatments can accelerate canopy closure (Gourlet-Fleury et al., 2013; Mills et al., 2019; Osuri et al., 2019; Philipson et al., 2020) and reduce understorey light availability, mirrored by our own finding of lower median canopy gap fractions in AR than in NR or UL forest. Greater competition for light may accelerate investment in shoots to gain access to light in the more shaded understorey environments of AR forests (Umaña et al., 2020, 2021). Seedlings in AR forests also had more acquisitive traits (lower leaf thickness, lower LFP, higher SMRL and higher leaf P, K and Mg concentrations) than those in UL forest, which likely reflects the functional composition of species planted in AR forests. Disturbance by logging likely favours species with more acquisitive traits because of intense competition for both above and belowground resources (Carreño-Rocabado et al., 2012). Survival rates of species that are not indicators of UL (i.e. species with more acquisitive traits) were lower in AR forest than in NR forest. In contrast, species that are indicators of UL (i.e. species with less acquisitive traits) did not have different survival rates in AR compared with NR, indicating that it is species with acquisitive traits have poorer survival outcomes in forests that had undergone restorative treatments. Functional traits are related to life history traits, with acquisitive traits associated with shorter life history strategies (Adler et al., 2014). A shift towards a community with acquisitive traits, and thus short life histories in AR forests may contribute to the higher rates of seedling mortality at the community scale in this habitat.

Differences in CWM between AR and UL forests were driven by changes in species abundance, rather than by intraspecific plasticity or population-level genetic shifts, with individual species either failing to adjust their traits, expressing a low magnitude of intraspecific trait variation or changing traits in the opposite direction to the CWM trait values. Low plasticity in species that are indicators of UL forest may prevent these species from adapting to logged environments. While a lack of intraspecific variation was detected in most indicator species for most traits, it should be noted that low sample sizes may have reduced our statistical power. Shifts towards communities with more acquisitive traits may represent a change in functional composition with fewer late successional species, such as dipterocarps, which may result in future reductions in the carbon storage, economic value and biodiversity of AR logged forests as they mature (Philipson et al., 2020). The restoration activities implemented within logged forest here may therefore fail to facilitate long-term recovery of these ecosystem services if recruitment of new seedling communities repeatedly fails.

Functional traits had low capacity to predict mortality within the first 100 days after masting, but increased in importance with time since masting, particularly in AR forests. Individuals with higher RL:SL had a higher hazard risk in AR forests, indicating that access to light is likely key to survival after the period when many species are reliant on cotyledons for photosynthesis, nutrients and carbon (Itoh et al., 1995). Higher hazard scores for individuals with lower leaf force to punch in AR forests also indicate that insect herbivory may be a risk factor for mortality in AR forests. High density of conspecific seedlings in AR forests may intensify herbivore pressure (Forrister et al., 2019) and increase mortality of individuals without the ability to resist herbivory. Acquisitive functional strategies increased in importance over time in AR forests as individuals with higher LMA and lower SMRL had greater mortality risk after 3 months. Facilitating the transition of functional composition of logged forests towards that of UL forest may require manipulations that induce equivalent environmental filtering after early (<3 months) seedling development but prior to establishment (Baldeck et al., 2013).

5 | CONCLUSIONS

Overall, our results highlight the complexity and challenge of restoring long-term regeneration dynamics in logged forests. Active restoration via rehabilitative silvicultural treatments can promote recovery of carbon stocks (Philipson et al., 2020), faunal populations (Malhi et al., 2022) and seed production (this study) of logged forests. However, current restoration and management practices fail to reduce the risk of regeneration failure in logged forests and thus the long-term recovery of their biodiversity if these patterns repeat in the long term. The exact drivers of regeneration failure are not completely clear, but low genetic diversity of planted trees, over-predation by seedling predators and failure to restore soil conditions may all contribute. The recovery of all ecosystem attributes is likely to be critical to ensure that active restoration effectively recovers biodiversity (Gann et al., 2019). The field of restoration ecology remains relatively young, with restoration only included in official targets of the Convention on Biological Diversity since 2010 (Convention on Biological Diversity, 2010). We highlight the ongoing need to continue research and monitoring to ensure active restoration practices effectively recover biodiversity of degraded environments over longer time frames.

AUTHOR CONTRIBUTIONS

David C. Bartholomew: Conceptualization; formal analysis; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **Robin Hayward:** Formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **David F. R. P. Burslem:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Paulo R. L. Bittencourt:** Conceptualization; investigation; methodology; writing – review and editing. **Daniel Chapman:** Formal analysis; writing – review and editing. **Mohd. Aminur Faiz Bin Suis:** Project administration. **Reuben Nilus:** Project administration. **Michael J. O'Brien:** Conceptualization; investigation; methodology; project administration; writing – review and editing. **Glen Reynolds:** Project administration. **Lucy Rowland:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Lindsay F. Banin:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Daisy Dent:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings are available at: Burslem et al. (2022a, 2022b).

ORCID

David C. Bartholomew https://orcid.org/0000-0002-8123-1817
Robin Hayward https://orcid.org/0000-0002-9653-225X
David F. R. P. Burslem https://orcid.org/0000-0001-6033-0990
Paulo R. L. Bittencourt https://orcid.org/0000-0002-1618-9077
Daniel Chapman https://orcid.org/0000-0003-1836-4112
Mohd. Aminur Faiz Bin Suis https://orcid.org/0009-0005-5151-599X
Michael J. O'Brien https://orcid.org/0000-0003-0943-8423
Glen Reynolds https://orcid.org/0000-0002-6792-8589
Lucy Rowland https://orcid.org/0000-0002-0774-3216
Lindsay F. Banin https://orcid.org/0000-0002-1168-3914
Daisy Dent https://orcid.org/0000-0002-1219-7344

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SUPPORTING INFORMATION

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

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