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RESEARCH ARTICLE

Persistent declines in forest-dependent birds following active restoration of logged tropical forest in Borneo

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Abstract

1. Tropical forest restoration is critical for mitigating biodiversity loss and climate change, including in forests impacted by selective logging. Active restoration through liana cutting and enrichment tree planting can substantially accelerate carbon recovery, potentially reducing economic pressures to convert logged forests. But its long-term biodiversity impacts remain unknown.
2. Using over two decades of bird surveys from Borneo's largest logged forest restoration project, we quantified occupancy patterns for 171 species across primary, naturally regenerating and actively restored logged forests spanning a 30+ year post-logging chronosequence.
3. Forest-dependent, threatened and near-threatened species generally declined through time in actively restored areas, whereas many species in naturally regenerating forests progressively recovered towards primary forest levels. Between 14% and 39% (9–25 of 64) of threatened or near-threatened species had consistently lower occupancies in actively restored than in naturally regenerating forest. Across species of global conservation concern, median occupancies in restored areas remained ~23% below primary forest even 50 years after harvests (versus ~3% higher with natural regeneration).
4. Arboreal insectivores, frugivores and predatory species appeared most negatively affected by active restoration, with 27%–49% (17–30 of 62) arboreal gleaning insectivores, 13%–31% (5–12 of 39) arboreal frugivores and 20%–33% (3–5 of 15) predatory species having higher occupancy in naturally regenerating than actively restored forests. Sallying insectivores also showed a possible but uncertain

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response (6%–41%; 1–7 of 17 species), whereas ground-associated frugivores and insectivores were largely unaffected by restoration treatment.
5. Concerningly, even 50 years post-logging, 28%–64% (14–32 of 50) of species highly dependent on forests remained below primary forest occupancy in actively restored forest (versus 0%–6%; 0–3 of 50 with natural regeneration), suggesting persistent negative impacts of vine-cutting and/or tree planting activities on avian populations.
6. *Synthesis and applications*. Despite substantial carbon benefits, active restoration within selectively logged forests may impede the recovery of forest-dependent biodiversity. This challenges the common assumption embedded within nature-based climate solutions that carbon and biodiversity outcomes will necessarily align. Nonetheless, despite the persistent declines in bird communities, actively restored forests continued to provide key habitat for many species. Active interventions may thus still contribute to broader biodiversity conservation objectives if they protect logged areas from conversion, potentially via carbon payments.

KEYWORDS
biodiversity, Bonn Challenge, forest management, forestry, restoration, selective logging, silviculture, sustainable forest management

1 | INTRODUCTION

Tropical forest restoration is accelerating globally, driven by major commitments to mitigate climate change and biodiversity loss (Edwards et al., 2021; Strassburg et al., 2020). The Bonn Challenge aims to restore 350 million hectares by 2030, while the Kunming-Montreal Global Biodiversity Framework commits to conserving and recovering 30% of the world's lands (Pillay et al., 2024). To date, most political and scientific attention has focused on the potential ecological and climate gains from enabling secondary forest regeneration on former or current agricultural lands (Cook-Patton et al., 2020; Strassburg et al., 2020; Williams et al., 2024), showing that forest regrowth in priority regions can cost-effectively reduce extinctions and sequester ~23 Gt C over the next three decades (Strassburg et al., 2020; Williams et al., 2024). In contrast, relatively little research has explored the long-term ecological impacts of restoring degraded tropical forests that have had persistent forest cover (Cerullo & Edwards, 2019). This is despite growing evidence that a substantial portion of global forest restoration potential lies within existing degraded forestlands (Mo et al., 2023; Robinson et al., 2025), where interventions also carry notably lower risks of agricultural displacement. More than 400 million hectares of tropical forest are designated for timber production and have been or soon will be selectively logged, involving the removal of large merchantable trees while maintaining partial canopy cover (Blaser & International Tropical Timber Organization, 2011), with a large additional area also affected by illegal harvests. Selective logging alters tropical forest structure, causes the reduction of forest specialist biodiversity and drives short-term losses of carbon storage and other ecosystem services (Bourgoin et al., 2024; Maxwell et al., 2019; Pearson et al., 2017). Yet logged forests represent a critical land base that could contribute to ambitious national restoration commitments (Cerullo & Edwards, 2019; Ewers et al., 2024; Lim et al., 2026; Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020; Sagang et al., 2026).

Several restoration approaches exist within logged landscapes. Passive natural regeneration involves removing additional pressures following logging to enable forests to recover without assistance, and is the most common approach pantropically (Mo et al., 2023). However, forest managers are increasingly using active interventions, especially in heavily degraded areas where natural regeneration potential is impaired or where accelerating above-ground biomass or merchantable timber stock recovery is a primary goal (Finlayson et al., 2022; Putz et al., 2022). Key active interventions include the cutting of lianas and other climbers which proliferate in the brighter post-harvest understorey, as well as the enrichment planting of overexploited tree species (Cerullo & Edwards, 2019; Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020). Both restoration actions have relatively well-evidenced climate and timber recovery benefits compared to passive regeneration (Finlayson et al., 2022; Jackson et al., 2026; Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020; Ruslandi et al., 2017; Veryard et al., 2023). For example, one pantropical meta-analysis found that liana cutting was associated with an 88% increase in carbon accumulation relative to untreated forests (Finlayson et al., 2022), while enrichment planting more than doubled the recovery rate of merchantable timber in lowland dipterocarp forests in Indonesia (Ruslandi et al., 2017). Where intensive logging has left vast areas of degraded forest with overexploited timber resources and high

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agricultural conversion pressures (e.g. especially in SE Asia), active restoration of logged forests is increasingly promoted as a nature-based climate solution (Cerullo et al., 2019; Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020).

As restoration agendas gather momentum, there is growing expectation that forest restoration should deliver biodiversity co-benefits alongside any climate gains (Griscom et al., 2020; Soto-Navarro et al., 2020). Yet the long-term, species-level impacts of restoration in selectively logged tropical forests remain largely unknown. Unlike reforestation on former agricultural land, where biodiversity recovery typically follows predictable increases in recolonization by forest-using species and eventual community convergence towards reference compositions (Metz et al., 2026), selective logging leaves behind a complex mosaic of mostly closed-canopy patches harvested at different intensities and times and interspersed with unlogged patches (Putz et al., 2019), resulting in highly variable regeneration impacts. Within this context, active restoration via liana cutting and enrichment planting may accelerate the recovery of old-growth structures and resources, thereby benefiting forest specialist species (e.g. by increasing coverage of large trees, Jackson et al., 2026). However, such interventions could also reduce resource availability and heterogeneity of recovering forests, especially because lianas are ecologically important as nesting and foraging substrates, and because planting often emphasizes a narrow range of merchantable timber species (Cerullo & Edwards, 2019). Detecting whether active restoration confers biodiversity benefits beyond passive regeneration in logged forests is therefore important but also challenging because it requires field data tracking species-level responses across a wide range of post-harvest recovery times and restoration types, plus unlogged reference sites. Yet all studies exploring the biodiversity impacts of logged forest restoration to date have focused on short-term impacts (Ansell et al., 2011; Cerullo et al., 2019; Cerullo & Edwards, 2019; Cosset & Edwards, 2017; Hayward et al., 2021), overlooking the temporal and species-specific dynamics critical for designing effective, lasting restoration strategies.

Here, we overcome these challenges using more than two decades of systematically collected avian data from Malaysian Borneo, the site of the tropics' largest and longest-running logged forest restoration project. Our sampling effort includes 10,368 detections of 171 bird species across 200 survey points spanning old-growth, naturally regenerating, and actively restored once-logged forests (subject to liana cutting and enrichment planting), surveyed along a >30-year post-logging chronosequence. Research in our study landscape has previously shown that compared to natural regeneration, active restoration increased annual above-ground biomass accumulation by 50% in the three decades following logging (Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020), and that short-term outcomes for birds following active restoration included the retention of insectivorous species but losses in frugivores and phylogenetic diversity (Ansell et al., 2011; Cosset & Edwards, 2017). We ask two key unresolved questions: (i) how do long-term restoration outcomes vary with species' ecology and conservation status; and (ii) does active restoration enhance biodiversity recovery in logged forests over time compared with natural regeneration?

2 | METHODS

2.1 | Study landscape

Avian surveys were carried out in the 1Mha Yayasan Sabah concession, among the largest remaining contiguous blocks of lowland dipterocarp rainforest in Southeast Asia, encompassing a mixture of primary and selectively logged forests (Figure 1; Reynolds et al., 2011). Primary forest areas were located within the Danum Valley Conservation Area (DVCA; 43,800 ha), and the nearby Tawau Hills Park (28,000 ha), both of which support the same forest type and bird communities (Edwards et al., 2011). Logged forest areas were within the Ulu Segama Forest Reserve (USFR; 238,000), adjacent to Danum Valley. The USFR was selectively logged once between 1972 and 1993, extracting an average of 113 m^3 ha^{-1} of timber, with some remnant patches of unlogged forest remaining in steep or riparian zones (Fisher et al., 2014; Reynolds et al., 2011). A further section of once-logged forest was logged at the same time and intensities as naturally regenerating once-logged forests but was then actively managed under the INFRAPRO Forest Rehabilitation Project (Ansell et al., 2011; Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020), undergoing liana cutting and enrichment planting. We refer to these areas as 'actively restored'. This large-scale restoration project began in the early 1990s with the goal of accelerating the recovery of forest structure and carbon. Active restoration treatments were applied to once-logged areas averaging 9 years post-harvest, using remaining logging infrastructure for planting and cutting access. Restoration proceeded as follows (see Philipson, Cutler, Brodrick, Asner, Boyd, Costa, et al., 2020 for details): 6 months before planting all climbers and lianas were cut across the entire area, then prior to planting, all vegetation within 2 m wide parallel lines (spaced 10 m apart) were cut through the logged forest understorey. Seedlings of over 50 native dipterocarp and fruit tree species were then planted every 3 m along these cleared lines, with repeated liana cutting up 3 years after planting to reduce competition with growing seedlings. In total, between 1993 and 2004, INFRAPRO restored patches ranging from 83 to 1745 ha (Figure 1).

2.2 | Bird surveys

Avian point counts were conducted following Edwards et al. (2011) and Mitchell et al. (2018), covering 200 point locations and 10,368 detections of 171 species, excluding flyovers. Briefly, sites were established at least 500 m apart and 200 metres from roads or edges, with sites consisting of transects of 9–12 point locations separated by >200 m to maintain independence. We returned to survey 90% ($n = 180$) of points over 3 consecutive days, while 10% of points were surveyed for an additional day (i.e. over 4 days). Points were stratified across primary forest (8 sites, 92 points), naturally regenerating forest (5 sites, 60 points; post-harvest range = 19–62 years) and actively restored forests (4 sites, 48 points; post-harvest range = 21–41 years). At each point, all birds seen or heard within

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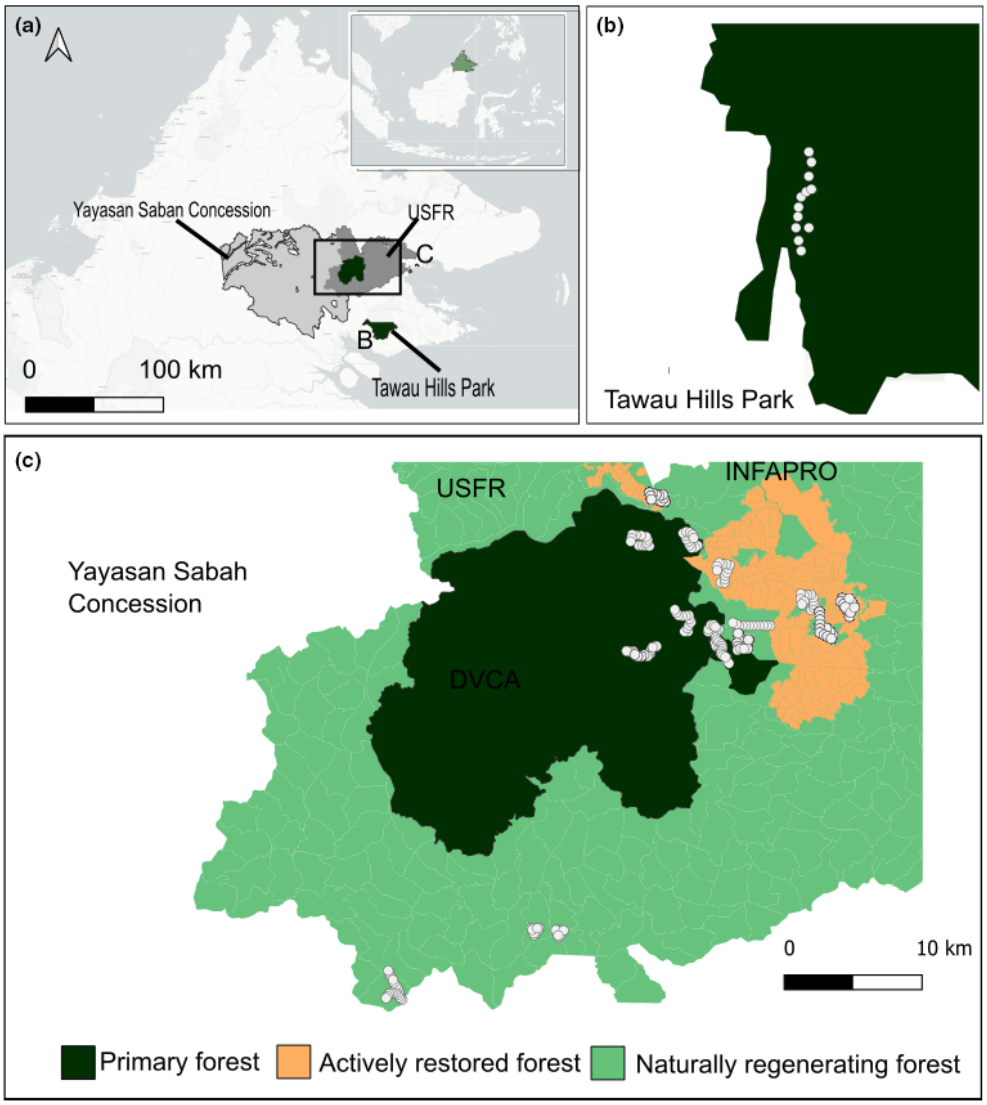


FIGURE 1 Location of sample points in Sabah Malaysia. Avian point counts were located in the Yayasan Sabah logging concessions, predominantly within the Ulu Segama Forest Reserve (a), with a small number of primary forest points located in Tawau Hills Park (b). Points within the Danum Valley Conservation Area (Dark Green) were primary forest, and all points within the USFR and wider Yayasan Sabah area were once-logged. A section of this once-logged landscape forest was actively restored as part of the INFAPRO restoration area (yellow), with remaining forest left naturally regenerating (light green).

100 m of the point locations were identified, with surveys conducted on mornings with no rain between 05:50 and 11:00 between May and Aug in 2008, 2009, 2011, 2017 and 2022 by three expert ornithologists (DE, SM, DK). Every forest type was surveyed across multiple sampling years (Primary: 2008, 2009, 2011, 2017, 2022; naturally regenerating: 2008, 2009, 2011, 2022; actively restored: 2008, 2009, 2022) and by at least two independent observers (primary by three: DE, SM, and DK; naturally regenerating and actively restored each by DE and DK), with observer included as a random effect in the occupancy model to absorb any residual observer-level variation in detection probability (see below). Point locations between forest treatments were similar in terms of distance to nearest road and town, although actively restored sites were at moderately lower elevations (median 184 m, range 124–283 m) than both naturally regenerating(258 m, 174–451 m) and primary points (248 m, 150–516 m; see Figure S1 and Methods S1), likely due to enrichment planting being more likely in flatter more logistically accessible terrain (Runting et al., 2019).

2.3 | Occupancy detection modelling

2.3.1 | Occupancy

To examine how alternative restoration approaches affected bird species occupancy through time, while accounting for imperfect detection, we fitted a hierarchical Bayesian multispecies detection-occupancy model (Socolar et al., 2022; Socolar & Mills, 2023). This allowed us to estimate species-specific responses to restoration treatments, plus primary forest reference conditions, while

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accounting for variables influencing detection. A priori, we expected that species occupancy would vary according to the management treatments ('primary', 'naturally regenerating', 'actively restored'), as well as the time since logging (Burivalova et al., 2014), and that these changes would interact with species' habitat preferences (particularly their degree of forest dependency). To capture these sources of variation, we classified each bird species detected in field surveys as having either 'high', 'medium' or 'low', forest dependency (50, 106, 15 species, respectively), following BirdLife International's classifications, but merging 'low' and 'not normally found in forest' categories, due to low sample sizes for these categories (Mills et al., 2023). We then pooled variance within these categories, assuming that species in the same category responded on average more similarly to forest treatment. Such pooling improves occupancy estimates for rarely detected species, which we expected to be most sensitive to forest structural change (Banks-Leite et al., 2014).

Specifically, we structured the occupancy component of our models as:

$$\begin{aligned}\text{logit}(\psi_{i,s}) = {} & \alpha_{\text{year}[i]} + \gamma_{\text{site}[i]} + \beta_{0,\text{dep}[s],s}\,\text{Primary}_i \\ & + \beta_{1,\text{dep}[s],s}\,\text{NatRegen}_i + \beta_{2,\text{dep}[s],s}\,\text{ActivelyRestored}_i \\ & + \beta_{3,\text{dep}[s],s}\,\text{NatRegen}_i \cdot \text{time}_i \\ & + \beta_{4,\text{dep}[s],s}\,\text{ActivelyRestored}_i \cdot \text{time}_i\end{aligned}$$

Here, ψ_i, is the probability that species, *s*, is present at point *i*. Any community-wide annual variation in occupancy is accommodated by a random intercept on year, $\alpha_{year[i]}$, where $year[i]$ refers to the sampling year of point *i*; and spatial variation by a random intercept for site, $\gamma_{\text{site}[i]}$. Treatment-effects were captured using a series of mutually exclusive habitat dummy variables (i.e. a point could only belong to one management treatment, 'primary', 'naturally regenerating', 'actively restored'). The subscripting on each parameter indicates species-specific random slopes for treatment and time-since-logging effects (denoted by dep[s], which identifies the forest dependency class of species *s*, within which the species-specific effects were partially pooled). In addition, *time[i]* represented the time since logging at point *i*, included in interaction terms to capture temporal dynamics in occupancy recovery within naturally regenerating and actively restored forests. Thus, this structure allowed each species to have its own effect for each forest treatment and its interaction with time since logging, while borrowing strength from other species within the same hierarchical dependency class.

2.3.2 | Detection

The detection component was modelled as a function of management treatment, forest structure, time of day and point-count observer identity, while also capturing species-level variation in detectability. Fixed effects included the management treatment, time of day, and observer. To account for potential variation in visibility within forests of different structures, we also calculated the mean above-ground carbon density within 50 m radius buffers surrounding point-count locations, using a carbon-density LiDAR product covering the state of Sabah for the year of 2016 (ABD50; Asner et al., 2018). This year falls approximately equidistantly between our earliest and latest sampling year (2008 and 2022). To account for variation in detection across observers and species, we included a random intercept for each observer–species combination. We also allowed detection to vary across species as a function of time of day by including a species-specific random effect.

Specifically, detection was modelled as:

$$\begin{aligned}\theta_{i,s} = {} & \text{Primary}_i + \delta_1\,\text{NatRegen}_i + \delta_2\,\text{ActivelyRestored}_i + \delta_3\,\text{ABD50}_i \\ & + \delta_4\,\text{time_of_day}_{i,j} + \delta_5\,\text{observer}_i + b_{s1}\,\text{time_of_day}_i + b_{\text{obs}[i],s}\end{aligned}$$

Here, $\theta_{i,s}$ represents the probability of detecting species *s* during visit *j* at point *i*. The term $observer_i$ refers to the observer (DE, SM, DK) conducting the survey at point *i*, and $b_s time_of_day_i$, captures the specific time of the *j*th visit at point *i*. The random effect b_{s1} modelled species-specific variation in how detectability changes across the day, while $b_{ob[i],s}$ accounted for variation in detection across observer–species pairings. To capture differences in vegetation structure that might have affected visibility at point-count locations, we included ABD50, calculated as the mean above-ground density within a 50 m-radius buffer of each survey point (see above). We fitted the occupancy detection model in Stan (v2.26.1) via cmdstanr (v0.5.3), using the flocker package (Socolar & Mills, 2023). All models were run with four chains of 2000 warm-up and 4000 post-warm-up iterations. We applied weakly informative priors on all parameters and monitored convergence through standard diagnostics with model adequacy evaluated via posterior predictive checks (see Materials S1).

2.4 | Threat status and guild data

We examined species-level responses as a function of (i) threat status, derived from the IUCN Red List (Critically Endangered [CR], Endangered [EN], Vulnerable [VU], Near Threatened [NT] and Least Concern [LC]); (ii) species forest dependency (described above); and (iii) foraging–feeding guilds. Species were assigned into separate foraging guilds (i.e. arboreal, sallying and terrestrial foragers, the latter including undergrowth foragers) and feeding guilds (i.e. frugivores, insectivores, predators, nectarivores or piscivores), following Edwards et al. (2012). These guilds capture differences in resource and forest strata use and may therefore influence responses to restoration; however, we pooled variance by forest dependency to impose a weakly informative hierarchical structure, reflecting prior expectations that species would respond coherently to forest structure and disturbance intensity (Burivalova et al., 2014, 2015; França et al., 2024). To assess uncertainty in the differences in species occupancy between actively restored and naturally regenerating forests, we calculated the *Probability of Direction* (or pd), which is defined as the proportion of posterior samples that share the same sign as the median estimate (either positive or negative, Makowski et al., 2019).

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Thus, a pd of 0.5 indicates no consistent directional effect (i.e. equal support for higher occupancy in either treatment), whereas a pd of 1 indicates complete agreement among posterior draws in the direction of the effect (e.g. consistently higher occupancy in naturally regenerating than actively restored forests or vice versa). We applied probability of direction (pd) thresholds of 0.75 and 0.9 to represent less and more conservative evidence cut-offs, respectively, reflecting the need in conservation practice to balance sensitivity to potential forest management interventions with caution against over-interpreting uncertain trends. We used these same thresholds to evaluate temporal consistency in species' responses by assessing whether changes in occupancy between different time points (e.g. early vs. late recovery stages) showed a consistent direction across posterior draws. This allowed us to identify which species had robust directional trends through time and how these compared to primary reference occupancies.

2.5 | Ethical approval

Site access across years was enabled through research permits and agreed site access with Yayasan Sabah, Danum Valley Management Committee and the Sabah Biodiversity Council.

3 | RESULTS

3.1 | Impacts by forest dependency and species global conservation status

Among species with a high forest dependency, 28%–52% (14–26 of 50 species, depending on the pd threshold) showed higher occupancy in naturally regenerating forest, while medium-dependency species exhibited similar but weaker patterns, with 12%–32% (13–34 of 106 species) favouring naturally regenerating over actively restored forests (Figure 2a; Figures S2 and S3 shows species-level estimates with associated uncertainties). In total, across all species, we detected 64 globally threatened or near-threatened species (CR, EN, VU, NT) across the landscape. Of these birds of conservation concern, over 42% (27 species) showed consistent differences in occupancy between actively restored and naturally regenerating forests (at pd > 0.75), decreasing to ~14% of species ($n = 9$ species) when using a more stringent cutoff of $pd > 0.9$ (Figure 2b). Of these potentially affected species of conservation concern, 93%–100% (25 of 27 species where pd > 0.75 and 9 of 9 where pd > 0.9) had higher occupancy in naturally regenerating than actively restored forest, including species like Rufous-crowned Babbler (NT; $pd = 0.91$), Yellow-crowned Barbet (NT; $pd = 0.91$) and Scarlet-rumped Trogon (NT; $pd = 0.94$). Only two species of conservation concern, Greater Green Leafbird (EN; $pd = 0.80$) and Sabah Partridge (VU; $pd = 0.80$), showed a consistently higher predicted occupancy in actively restored forests (Figure S4). For all birds of conservation concern, median occupancies in actively restored forest were ~23% below primary forest even after 50 years of recovery, whereas in naturally regenerating forests occupancies were slightly higher (~3%) than in primary forest.

Among the 107 least concern species (Figure S5), 13%–31% (14–33 species depending on pd) showed higher occupancy in naturally regenerating forest than primary forest, whereas only 6% (6 species) did so in actively restored stands at pd > 0.75, and just one species at pd > 0.9. Despite this, least concern species showed virtually indistinguishable differences in median occupancy compared to primary forest, with median occupancies only ~1% below primary forest levels in actively restored, compared with ~11% higher in naturally regenerating forest. All results were robust to the moderately lower elevation of restored sites (see Figure S1) compared to primary and naturally regenerating sites; if anything, occupancy was weakly higher at lower elevations, the opposite of the active restoration deficit we report, making our findings of the higher value of naturally regenerating forests conservative (see Material S1 for full details).

3.2 | Impacts across feeding-foraging guilds and forest dependency

While species from most foraging–feeding guilds showed some response to restoration treatment, impacts were particularly evident for arboreal and predatory species (Figure 3). Nearly half of arboreal gleaning insectivores had higher occupancies in naturally regenerating than in actively restored forest (30/62 species at pd > 0.75, declining to 17/62 at pd > 0.9; Figure 3), with median occupancies in actively restored forest ~12% lower than in primary forest baselines (versus ~17% higher under natural regeneration). Arboreal frugivores and mixed frugivore–insectivores showed similar patterns: 31% (12/39 species) favoured naturally regenerating forest at pd > 0.75, falling to ~13% (5/39) at pd > 0.9. This group included several species with apparent preferences for naturally regenerating forest, including Green Broadbill (pd = 0.86) and Blue-rumped Parrot (pd = 0.80). Indeed, arboreal frugivores' median occupancies were ~11% higher than primary forest in naturally regenerating stands but moderately (~5%) lower in actively restored forest. The minority of frugivores which were more common in restored forest included Olive-winged Bulbul (pd = 0.76), Yellow-vented Bulbul (pd = 0.77) and Yellow-breasted Flowerpecker (pd = 0.83). Predators also showed clear impacts from restoration treatments, with 33% (5/15 species) having higher occupancy in naturally regenerating than actively restored forest at pd > 0.75, falling to 20% (3/15) at pd > 0.9. These included large-bodied species such as Bushy-crested Hornbill (pd = 0.85) and Rhinoceros Hornbill (pd = 0.86), and there was a general tendency for larger-bodied birds to prefer naturally regenerating forest (Figure S6). Median predator occupancies were ~20% lower in actively restored compared to primary forest (cf. ~4% higher with natural regeneration).

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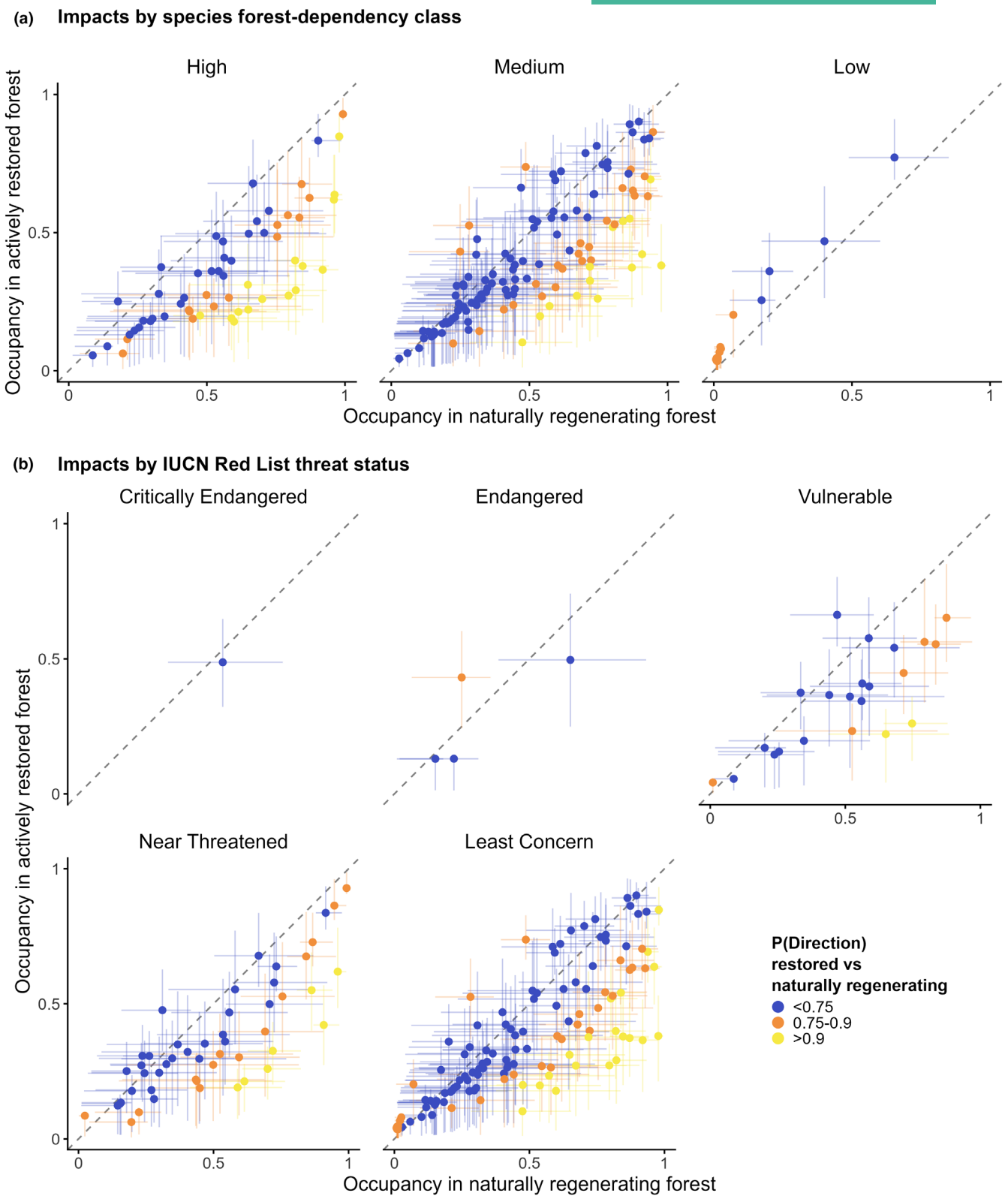


FIGURE 2 Relationship between estimated avian occupancy in naturally regenerating and actively restored once-logged forests across a lowland dipterocarp-dominated rainforest landscape in Sabah, Borneo. Each point represents the mean occupancy for a species, with horizontal and vertical bars representing 50% credible intervals for occupancy estimates calculated across 500 posterior draws per year between 19 and 50 years post-logging. Species are faceted by (a) BirdLife forest dependency class and (b) IUCN threat status. The 1:1 line (dashed) indicates equal occupancy between forest types. Points above the line reflect species with higher mean occupancy in restored than once-logged forests and vice versa. Points are coloured by the *probability of direction* (PD), which reflects the consistency in the direction of the restoration effect across posterior draws. Brighter colours (orange and yellow) indicate greater certainty that occupancy differs between restoration treatments.

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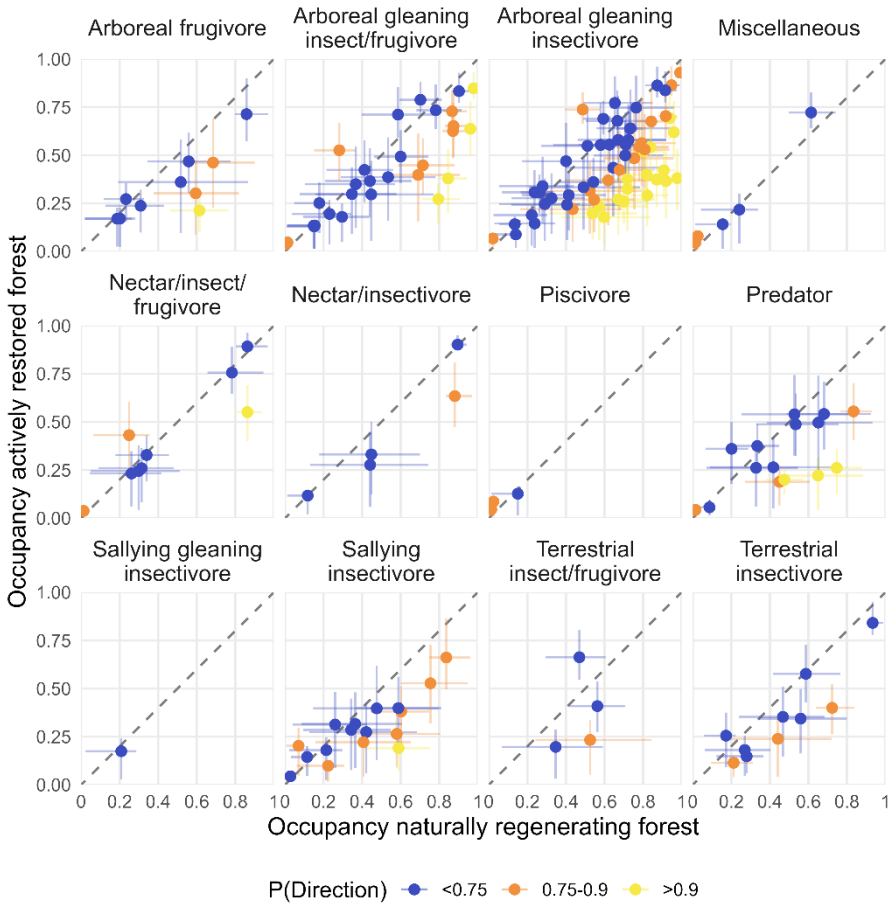


FIGURE 3 Relationship between species' estimated occupancy in actively restored and naturally regenerating once-logged forests, grouped by foraging–feeding guild. As in Figure 2, each point represents the mean occupancy for a species in actively restored (*y*-axis) and naturally regenerating (*x*-axis) forests, with credible intervals showing 50% credible intervals calculated across 500 posterior draws per year between 19 and 50 years post-logging. Colours indicate greater certainty that occupancy differs between restoration treatments.

Sallying insectivores also appeared sensitive to restoration actions, but this was more uncertain. At a lower evidence threshold (pd > 0.75), 41% of species (7/17) had higher occupancy in naturally regenerating forest, but this dropped to just one species—the Scarlet-rumped Trogon (pd = 0.9)—under a stricter cut-off (pd > 0.9). Across the guild, median occupancies were ~ 13% lower than primary forest in actively restored stands, compared to ~5% higher with natural regeneration. By contrast, more ground-associated birds, including terrestrial insectivores and mixed terrestrial insectivore–frugivores, showed limited and uncertain responses. Only 29% of species belonging to these guilds (4/14) crossed pd > 0.75, and 7% (1/14) met pd > 0.9. The few species showing consistent differences at lower thresholds included Black-crowned Pitta (pd = 0.86) and Western Hooded Pitta (pd = 0.83), both favouring natural regeneration. Yet even though effects were uncertain for terrestrial species, median occupancies in actively restored forest were still ~28% lower than primary forest, compared to only ~4% lower with natural regeneration, reinforcing the overall pattern of reduced recovery in actively restored stands.

3.3 | Temporal recovery within restoration treatments

Species' post-logging recovery trajectories towards primary forest levels differed between restoration treatments and was influenced by forest dependency, threat status and foraging–feeding guild (Figure 4, Figures S7 and S8). High forest dependency species showed the clearest long-term gains under natural regeneration: after ~50 years, median occupancy in naturally regenerating forest averaged 5% higher than in primary forest (median ~ 11% higher), and 96% (48/50) of species increased between 20- and 50-years post-logging. When considering different uncertainty cut-offs, these positive trends were consistent for 56% (28 species at pd > 0.75) and 22% (11 species at pd > 0.9), with nearly half of these showing no detectable difference from primary forest occupancy, indicating recovery to pre-logging levels. Recovering species included Golden-whiskered and Yellow-crowned Barbets and Red-naped and Scarlet-rumped Trogons. In contrast, only 4% (2/50) of species with high forest dependency increased through time in actively restored stands. Median occupancy in actively

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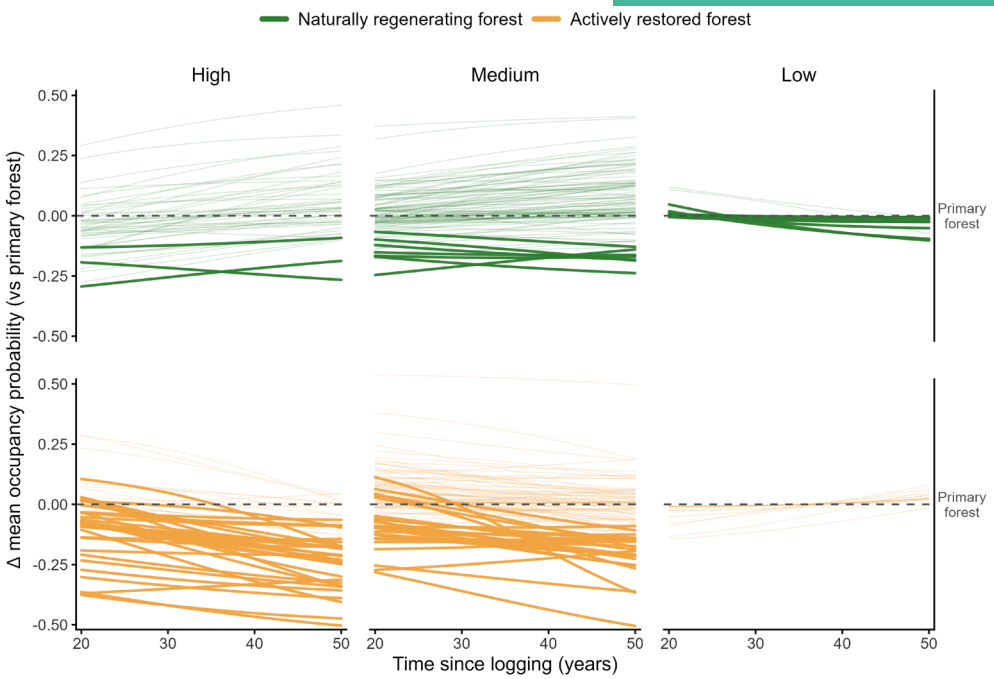


FIGURE 4 Recovery of species' occupancy relative to primary forest in naturally regenerating and actively restored forest across a lowland dipterocarp rainforest landscape in Sabah, Borneo. Each line shows the difference between a species' mean occupancy probability in a given management treatment, naturally regenerating (top row, green) or actively restored (bottom row, orange), and its mean occupancy in primary forest (Δ occupancy), calculated across 500 posterior draws per year between 20 and 50 years post-logging. The dashed horizontal line at zero denotes parity with primary forest. Lines above the horizontal dashed line indicate species occurring at higher occupancy than in primary forest, and lines below indicate species that remain below primary forest levels. Columns group species by overall forest dependency (high, medium, low), as defined by BirdLife International. Bold lines highlight species that remain consistently below primary forest at 50 years post-logging (probability of direction, $P(\Delta < 0) > 0.75$). Equivalent temporal outcomes grouped by foraging–feeding guild and IUCN threat status are shown in Figures S7 and S8.

restored forest harvested 50 years post-logging remained 31% below primary forest levels, and 64% (32 species, pd > 0.75) ended the period still below primary forest (the bold trajectories in Figure 4). This fell to 28% (14 species; pd > 0.9) under a more conservative threshold, highlighting both the uncertainty around recovery trajectories in actively restored forest and the potential for these forests to continue supporting avifaunal communities. Meanwhile, only 0%–6% (0–3 of 50 depending on pd) of species with a high forest dependency remained below primary forest occupancy levels within naturally regenerating forest.

Overall, these temporal patterns were similar for medium forest-dependent species (Figure 4; Figure S3). Of 106 species, 85% (90 species) increased in median predicted occupancy in naturally regenerating forests, with trends consistent for 34% (36 species at pd >0.75) and 7% (8 species at pd >0.9) and with median occupancies on average ~15% higher in naturally regenerating versus primary forest. In actively restored forest, ~24% (25 species) of medium forest-dependent species remained below primary forest occupancy 50-years post-logging (falling to 8%, 8 species, at pd > 0.9), although absolute occupancies differences were small and more similar to primary forest (~5% below primary). Patterns for the small number of low forest dependency species detected were reversed, with median occupancy declining under natural regeneration but increasing in actively restored stands (Figure 4).

Threatened species also recovered primarily in naturally regenerating forest (Figure S7). Of 64 globally threatened or near-threatened species, 89% (57 species) increased between 20 and 50 years after logging, with consistent increases for 7%–45% (5–29 species across pd thresholds). By contrast, only 11% (7 species) increased in actively restored forest, with just a single species—the Lesser Fish Eagle (NT; pd = 0.85)—showing a consistent increase, and none reaching pd > 0.9. In total, 45% (29 species) of species of conservation concern remained below primary forest occupancy 50 years post-logging in actively restored forest (the bold trajectories in Figure S7; ~23% below primary on average), falling to 16% (10 species) at pd > 0.9, whereas only 6% (4 species) did so under natural regeneration, where median occupancy was instead ~3% above primary.

Recovery trajectories also varied across foraging–feeding guilds (Figure S8). Arboreal guilds showed the clearest recovery with natural regeneration, with 18%–43% (16–39 of 91 arboreal insectivores and insectivore–frugivores) increasing through time across pd thresholds. Terrestrial insectivores (10%–40%; 1–4 of 10 species) and predators (7%–40%; 1–6 of 15 species) showed similar but slightly weaker positive trends, while sallying insectivores showed uncertain recovery trajectories: 41% (7 of 17 species) increased at pd > 0.75, but none at pd > 0.9. In contrast, recovery in actively restored forest was limited across all guilds, with only 3% (2 of 62

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species) of arboreal gleaning insectivores, 6% (1 of 7 species) of sallying insectivores, 6% (1 of 17 species) of sallying insectivores, 13% (2 of 15 species) of predators and 10% (1 of 10 species) of terrestrial insectivores increasing at pd > 0.75; no species in any guild met pd > 0.9.

4 | DISCUSSION

Our multi-decade, species-level analysis provides the first broad-scale, long-term evaluation of how the biodiversity consequences of active restoration in selectively logged tropical forests compare with those of natural regeneration (Cerullo & Edwards, 2019). Although research in our study landscape previously revealed that enrichment planting and vine-cutting increased rates of annual carbon recovery by ~50%, offering potentially cost-effective carbon drawdowns (Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020), we found little evidence that these benefits have been complemented by increases in avian occupancy. Instead, species with a high forest dependency and threatened species have generally failed to recover in actively restored areas, whereas many species in naturally regenerating logged forests have returned to primary forest occupancy levels. Despite uncertainty around species-level responses in our estimates—likely driven by high spatial and temporal variability in forest structure and resource availability within selectively logged forests (Asner et al., 2018; Burivalova et al., 2014; Ewers et al., 2024; Putz et al., 2019)—our findings challenge the common assumption embedded within nature-based climate solutions that carbon and biodiversity benefits will necessarily align (Matos et al., 2020; Seddon et al., 2021; Soto-Navarro et al., 2020).

The apparently persistent lack of recovery we observed in threatened and high forest dependency species following active restoration likely results from the long-term effects of silvicultural interventions on forest structure and composition. Liana removal is designed to release regrowing trees from competition and accelerate canopy recovery (Finlayson et al., 2022; Putz et al., 2023; Ruslandi et al., 2017), and repeat-LiDAR surveys in our wider landscape indicate that vine-cutting enhances growth, reduces mortality of large trees and accelerates post-logging canopy gap closure (Jackson et al., 2026). However, vine cutting also removes important nesting and foraging substrates, fruit resources and movement pathways for wildlife, with these features being more likely to persist or recover in naturally regenerating forest (Ansell et al., 2011; Campbell et al., 2015; Cerullo & Edwards, 2019). This may explain the more pronounced declines we observed in arboreal insectivores and frugivores, as well as large-bodied predatory species in actively restored forests: species in these guilds rely on more heterogeneous canopy structures, fruits or invertebrate or vertebrate prey resources hosted within vine tangles, that may be lost after vine cutting or in the denser or darker canopies recovering in actively restored forests (Jackson et al., 2026; Velho et al., 2012). By contrast, sallying and particularly more terrestrial species showed less clearcut differences in their responses to active and natural restoration, potentially because these species' prey base (ground leaf-litter prey or aerial insects) is less associated with forest structural attributes. Enrichment planting in our study also incorporated a high diversity of timber species (up to 50 species), so it is possible that understorey microclimates and ground-level conditions were relatively comparable in naturally regenerating and actively restored forests (Hayward et al., 2021; Philipson, Cutler, Brodrick, Asner, Boyd, Moura Costa, et al., 2020).

The sustained apparent occupancy losses among a large proportion of large-bodied frugivores and threatened or near-threatened species are particularly concerning because it implies erosion of key ecosystem functions and potentially reduced population persistence following repeated liana cutting and enrichment planting in logged forests (Fricke et al., 2025; Velho et al., 2012). This aligns with previous findings that actively restored logged forests support avian communities with reduced functional and phylogenetic diversity (Cosset & Edwards, 2017). Our results extend these insights by revealing the temporal dynamics of species' responses, showing that many forest-dependent species continue to decline or remain below primary occupancies many decades after logging and restoration interventions have ceased, whereas naturally regenerating forests tend to recover gradually towards primary forest levels. Although the relatively high uncertainty around these contrasting trajectories underscores the value of additional future sampling campaigns within recovering logged forests, these patterns could be explained by short-term demographic bottlenecks in the aftermath of multiple rounds of liana cutting leading to long-term declines and extinction debts or else be driven by active interventions leaving lasting structural and prey-based legacies that constrain bird recovery (Johnson et al., 2023). Our findings thus highlight the need for greater investment in long-term biodiversity monitoring as well as future studies that track abundance and demography directly (Cosset et al., 2019), ideally including immediate post-cutting surveys and before–after control–impact designs to overcome the limits of space-for-time approaches, which cannot fully control for the effects of prior forest structure within sites (França et al., 2016). Future studies should also explore restoration impacts on other taxa and in more heavily degraded forests than those in our study landscape, since active interventions could still provide benefits not detected here, particularly where repeated logging has more seriously impaired natural regeneration potential via intensified liana infestation (Marshall et al., 2020; Ngute et al., 2024).

Although it was not possible to disentangle the effects of liana cutting from enrichment planting in our study landscape, the financial costs of enrichment planting alone are substantial (≈$1500–$2500 USD ha^{-1}) in the project area (Philipson, Cutler, Brodrick, Asner, Boyd, Costa, et al., 2020). These high costs, combined with the stronger recovery of forest-dependent and threatened species in naturally regenerating forests, suggest that when biodiversity recovery is the primary goal of restoration,

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investments may be better directed towards supporting natural regeneration in areas of high recovery potential, such as through targeted purchases of logged forest land or community stewardship programmes (Fisher et al., 2011; Harrison et al., 2020). Modifying the active restoration treatment within logged forests (e.g. via one-time or more targeted liana cutting, or else a reduced emphasis on strip-planting) could further reduce active restoration costs and presumably also the apparent trade-off between carbon and biodiversity outcomes we observe here. However, given rampant avian trapping and hunting pressures across Southeast Asia, funding community-led patrols and anti-hunting initiatives in logged-over areas may ultimately provide more cost-effective and reliable returns for biodiversity than expensive silvicultural interventions focused primarily on timber or carbon recovery (Morton et al., 2021; Nishijima et al., 2016; Sagar et al., 2023; Symes et al., 2018).

Future studies that directly quantify the cost-effectiveness of alternative interventions in increasing species' population persistence—including actions spanning avoided deforestation, reduced hunting and degradation, as well as contrasting active and passive restoration strategies—would help decision-makers contextualize the benefits and trade-offs of contrasting investments within logged forest landscapes (Deere et al., 2020; Ewers et al., 2024). Nevertheless, the reality in much of Southeast Asia is that many logged-over forests lie within inactive concessions, have been stripped of much of their commercial timber, and now face an increased risk of forest conversion to industrial plantations, with disastrous consequences for biodiversity (Burivalova et al., 2020; Malhi et al., 2022; Marsh et al., 2025; Milodowski et al., 2021). Where active restoration can prevent such conversion by extending forest protection across restored logged forests, potentially supported by carbon finance, it may still deliver substantial biodiversity benefits relative to conversion. Indeed, we show that actively restored logged forests do appear to continue to provide habitat for many species, including threatened ones. Yet where the realistic counterfactual to active restoration of logged forests is natural regeneration, our findings indicate that passive recovery of logged forests may offer superior outcomes for biodiversity, even if not for carbon sequestration.

AUTHOR CONTRIBUTIONS

Cerullo, Gianluca: conceptualization, methodology, investigation, formal analysis, writing—original draft, visualizations, funding acquisition. Balmford, Andrew: methodology, writing—review and editing. Benedick, Suzan: writing—review and editing. Finlayson, Catherine: writing—review and editing. Jackson, Toby: writing—review and editing, conceptualization. Jucker, Tommaso: writing—review and editing, conceptualization. Kong, Daniel: writing—review and editing, investigation. Mills, Simon: methodology, writing—review and editing. Mitchell, Simon: writing—review and editing, investigation. Morton, Oscar: methodology, writing—review and editing. Edwards, David: methodology, writing—review and editing, investigation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code to needed to replicate the analyses and findings of this study are available on Zenodo: https://doi.org/10.5281/zenodo.22800815 (Cerullo, 2026).

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SUPPORTING INFORMATION

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

Figure S1. Point-level physical characteristics of bird sampling points across the three treatments. Shown are the distributions of (a) mean elevation within a 50-m buffer (b) straight-line distance to the nearest road, and (c) straight-line distance to the nearest town, for the $n = 200$ unique sampling points used in the bird occupancy analysis (Primary $n = 92$, naturally regenerating $n = 60$, Actively restored $n = 48$). Boxes show the inter-quartile range with a horizontal line at the median; whiskers extend to the most extreme value within 1.5 × IQR; individual points are jittered behind each box.

Figure S2. High forest dependency species responses to restoration treatment. Each point represents the mean difference in occupancy (Δ occupancy = habitat−primary) for a species in naturally regenerating (green) and actively restored (orange) forests, estimated at 40 years post-logging. Thick lines indicate 50% credible intervals and thin lines indicate 90% credible intervals, calculated from 500 posterior draws per species. Species are ordered by mean Δ occupancy in restored forests. The vertical dashed line at zero indicates no difference in occupancy between disturbed and primary forest. Positive values reflect higher occupancy in once-logged or restored forest than in primary forest, and negative values reflect lower occupancy. Points shown in bold have a probability of direction (pd) > 0.75, suggesting that the estimated difference from primary forest is relatively consistent across posterior draws and therefore likely reflects a genuine directional effect rather than random variation.

Figure S3. Medium forest dependency species responses to restoration treatment. Same as S2, but for medium forest dependency species.

Figure S4. Threatened and near-threatened species-level changes in occupancy in naturally regenerating and actively restored forests relative to primary forest, across a lowland dipterocarp rainforest landscape in Sabah, Borneo. Same as S2 but for species of conservation concern.

Figure S5. Responses across species of Least Concern. Same as Figure S2 but for species listed by the IUCN as of global 'Least concern'.

Figure S6. Species responses to restoration interventions across foraging-feeding guilds, with species body mass (log10) showing the relative masses of different species.

Figure S7. Temporal responses by IUCN threat status. Same as Figure 4 but by IUCN threat category.

Figure S8. Same as Figure 4 but for species foraging-feeding guild.

Figure S9. Posterior predictive checks of the multispecies occupancy model.

Table S1. Bird species detected during point-count surveys across primary, once-logged and restored forest in Sabah, Borneo ($n = 171$ species).

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