Biological Conservation 279 (2023) 109901

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Avifauna recovers faster in areas less accessible to trapping in regenerating tropical forests

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ARTICLE INFO

Keywords:
Birds
Conservation
Ecosystem restoration
Nature-based climate solutions
Pet trade
Reforestation

ABSTRACT

Tropical forest restoration stands to deliver important conservation gains, particularly in lowland Southeast Asia, which has suffered some of the world's highest rates of recent forest loss and degradation. This promise, however, depends on the extent to which biodiversity at forest restoration sites continues to be exposed to threats. A key knowledge gap concerns the extent to which biodiversity recovery in naturally regenerating tropical forests is impacted by trapping for the multi-million-dollar wildlife trade. Here, we use a repeated survey dataset to quantify rates of avian community recovery under forest regeneration, at a flagship restoration site in the lowland rainforests of Sumatra, Indonesia. We show that over a decade, forest regeneration was associated with significant abundance increases for 43.8 % of bird species. However, the apparent negative impacts of trade-driven trapping on avian populations also intensified: the proportion of species dependent on very remote forests increased from 5.4 % to 16.2 %. Moreover, the overall accessibility of the forest increased. We found that 14 % of species did not recover as fast as predicted based on the observed forest regeneration over the study period. We found trapping to disproportionately impact species targeted for trade: compared to opportunistically trapped species, twice more species showed increased abundance only in very remote forests. Our results highlight the potential for rapid avifaunal recovery in regenerating tropical forests, but also emphasize the urgency of tackling the serious threat of wildlife trade to Southeast Asia's biodiversity.

1. Introduction

Tropical forests worldwide have undergone widespread loss and degradation with severe consequences for biodiversity, people, and critical ecosystem services (Barlow et al., 2018; Edwards et al., 2019; Gibson et al., 2011; Watson et al., 2018). While the protection of existing

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https://doi.org/10.1016/j.biocon.2023.109901
Received 22 July 2022; Received in revised form 21 December 2022; Accepted 5 January 2023

old-growth forests is paramount, restoration of degraded lands can also deliver important conservation gains (Chazdon and Brancalion, 2019; Lewis et al., 2019; Strassburg et al., 2020; Watson et al., 2018). This is particularly true for Southeast Asia, where only 8.4 % of the historical old-growth forest remains intact (Potapov et al., 2017; Sodhi et al., 2010; Wilcove et al., 2013). The future of biodiversity in this region, among the richest in the world, depends to a large extent on the effective and timely restoration of its forest habitats (Cosset and Edwards, 2017; Edwards et al., 2014, 2009; Senior et al., 2019). While the increasing momentum of forest restoration in Southeast Asia is encouraging (Chazdon et al., 2017; FAO and UNEP, 2020), the realization of its conservation success hinges on tackling the negative biodiversity impacts of other threats in forests undergoing restoration, especially wildlife trapping.

Across Southeast Asia, wild bird trapping driven by the pet trade poses a severe conservation threat (J. A. Eaton et al., 2015a; Harris et al., 2017; Symes et al., 2018). The pet bird trade in the region, part of a global issue, is estimated to be worth hundreds of millions of dollars annually (Hughes, 2021; Marshall et al., 2019; Morton et al., 2021). It affects thousands of species, particularly those targeted for singing competitions and pet-keeping (Jepson, 2010; Scheffers et al., 2019; Shepherd, 2006). Market and household surveys in Indonesia suggest that the pet bird trade is ubiquitous across the country and that most traded birds are sourced illegally from the wild (Burivalova et al., 2017; Chng et al., 2015, 2018a; Shepherd et al., 2004). There is evidence that the scale of trade has increased over the past decade driven in part by increased accessibility due to forest loss and degradation (Marshall et al., 2019). Limited field evidence has linked increase in trapping to decrease in bird populations in the wild (Harris et al., 2017). Together, this suggests that trade-driven trapping could dampen the recovery of bird populations in forests undergoing restoration in Southeast Asia.

In this study, we evaluated the recovery of avian diversity over 10 years of forest restoration in a region increasingly impacted by trade-driven trapping, at a flagship ecosystem restoration site in the now heavily modified lowlands of Sumatra, Indonesia. We conducted repeated bird surveys at the community level, sampling across gradients of forest condition and trapping pressure. We examined how species abundance changed over time, its relationship with forest conditions and trapping pressure, and the extent to which its recovery had been affected by intensifying trapping pressure. We also assessed how species recovery related to the market demand, habitat association, and IUCN Red List status of each species.

2. Methods

2.1. Study site

We conducted our study in the Harapan Rainforest (‘Harapan’ hereafter), which straddles the provinces of Jambi and South Sumatra in Sumatra, Indonesia (2°08′ S, 103°22′ E, 50–80 m a.s.l.; Fig. 1). Harapan was established as Indonesia’s first ecosystem restoration concession in 2007. It was jointly managed by a consortium of conservation

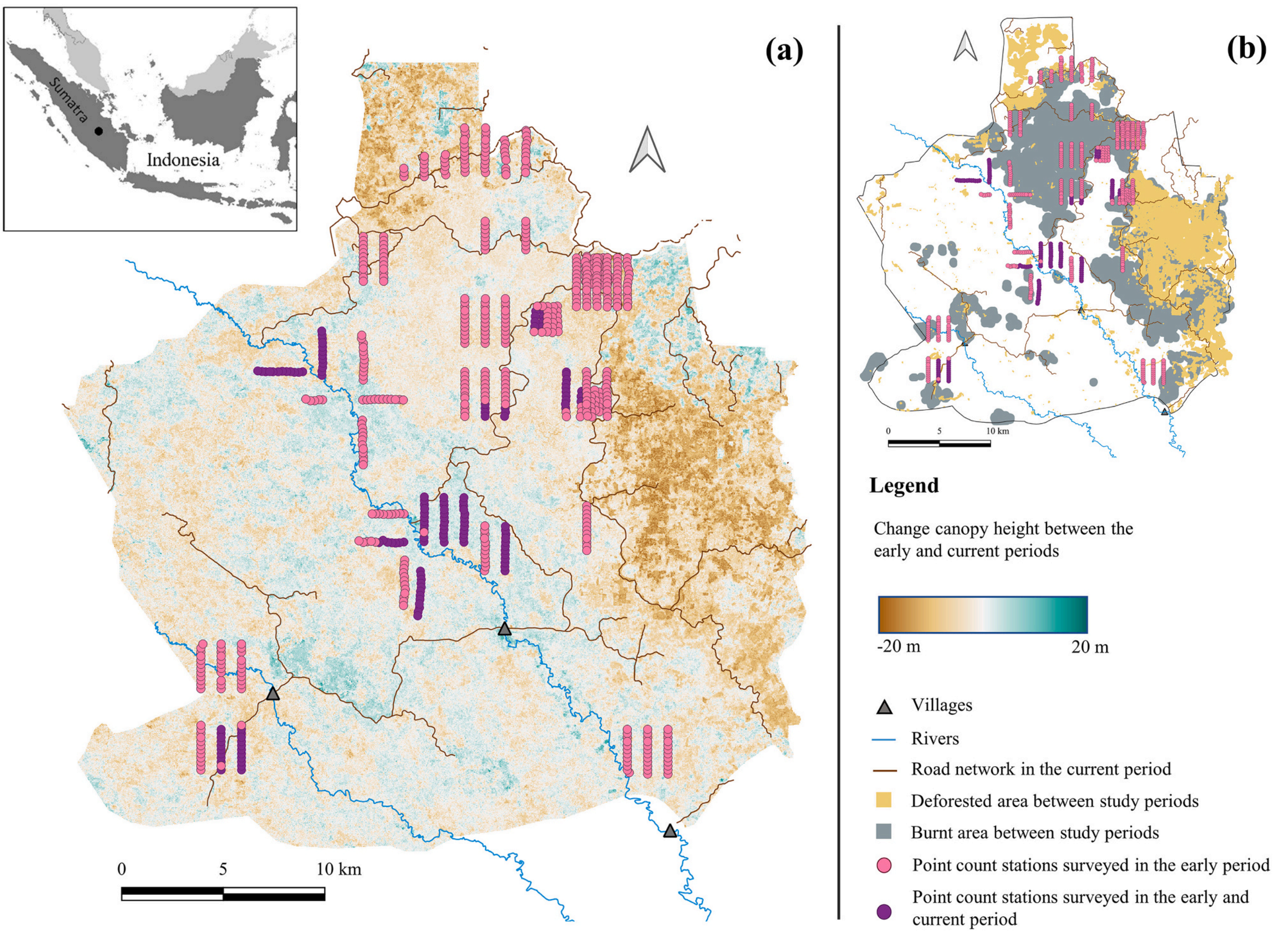

Fig. 1. 1a - Location of point count stations and changes in canopy height (i.e., the metric of top-of-canopy height) over time at Harapan Rainforest. Point count stations were surveyed either during the early period (2009–2011, pink) or during both the early and current periods (2009–2011 and 2018, purple). Change in canopy height was estimated from Landsat imagery using a LiDAR training dataset. 1b - Location of anthropogenically degraded areas in Harapan between the early and current periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

organizations with heavy financial investment and on-the-ground presence since 2008, with the main goal of recovering biodiversity in forests after logging (Harrison and Swinfield, 2015; Hua et al., 2016; Lee et al., 2014, 2019). As of 2018, it covered 98,555 ha of lowland dipterocarp forests in various stages of recovery, after commercial selective logging ceased in 2005. Rich in biodiversity representative of the Sundaic lowlands, it is also recognized as an Important Bird and Biodiversity Area (IBA; BirdLife International, 2017). Since its establishment, Harapan has faced mounting conservation challenges: as of 2018, it had lost ~25,000 ha of forest cover to illegal logging and encroachment, and another ~30,000 ha was damaged by El Niño-related drought and fires in 2015 (Fig. 1), particularly in its eastern and the northern regions. Despite these challenges, Harapan's remaining forests stayed contiguous and largely demonstrated signs of recovery through natural regeneration, and at some heavily degraded sites through active tree planting (Fig. 1).

Wildlife trapping and hunting, especially of birds, has been persistent in Harapan (pers. comm. with local bird trappers and Harapan staff, 2018), aided by a network of seasonally navigable roads and rivers that allowed access to most places within the area (Fig. 1), and the lack of anti-poaching patrols except for those targeting a few charismatic mammal species. Anecdotal evidence indicated that bird trapping in Harapan had intensified in the years leading up to our study, likely linked to increasing human accessibility (pers. comm. with Harapan staff, 2018). Trappers used various methods to capture live birds for the pet market, including mist nets, live bird traps, and strong glue. In recent years, the use of shotguns in Harapan to kill hornbills had also been recorded (pers. comm. with bushmeat hunters, 2018), often targeting the Critically Endangered Helmeted Hornbill (*Rhinoplax vigil*) that is prized for its ivory-like casque (Beastall et al., 2016; BirdLife International, 2020).

2.2. *Bird community surveys*

We surveyed bird communities in Harapan in 2009–2011 ('early period' hereafter; Lee and Lindsell, 2011; Hua et al., 2016) and again in 2018 ('current period' hereafter) using point counts. We positioned point count stations ≥200 m apart along line transects that covered a range of forest conditions and human accessibility (as a proxy for trapping pressure; see Section 2.4). In total, we surveyed 636 stations in the early period (Fig. 1). Of these stations, only 287 stations were in the contiguous forest portions of Harapan that were spared from significant fire and deforestation between the early and current periods (Fig. 1), and we confirmed the recovery of their forest habitat via remote sensing analysis (see Section 2.3). We focused on these stations for the current survey, from which we selected 144 stations that covered a range of forest conditions and human accessibility using a stratified random sampling design (Fig. 1).

For both early and current periods, we conducted unlimited radius point counts for the entire bird community that allowed for the correction of imperfect detection in estimating species abundance, excluding nocturnal, wetland, aerial, or raptorial species. We employed 10-min counts in the early period and 12-min counts in the current period. Given our correction for imperfect detection in data analysis (see Section 2.6), the different lengths of point count between the early and current periods should not bias our estimation of species abundance. During each point count, we recorded all birds seen or heard (excluding flyovers), along with their time of initial detection in minutes since the onset of the point count period. The latter information allowed us to use removal models to estimate and correct for species' detection probability (Farnsworth et al., 2002). We conducted all surveys between 05:30–11:30 on days without rain or strong wind, and we recorded the time of the onset of each point count in minutes since dawn ('survey time' hereafter). The early-period surveys were conducted by Harapan's research team led by DCL (551 point count stations; Lee and Lindsell, 2011) and by FH in a separate research project (85 point count stations; Hua et al., 2016), while surveys for the current period were conducted by HSSCS (144 point count stations).

We took two measures to minimize the potential bias in bird community characterization due to different observers conducting surveys. First, we used observer identity as a random effect for detection probability in our removal models, thereby correcting for potential detection differences among observers in estimating species abundance (see Section 2.6). Second, considering that the varying survey skills of the different members of Harapan's research team may bias the ability to detect some small (e.g., White-chested Babbler, *Pellorneum rostratum*) or inconspicuous (e.g., Grey-chested Jungle-Flycatcher, *Cyornis umbratilis*) species, for these prone-to-miss species, we used only the subset of data collected by FH for the early period. We identified these species by assessing the number of times a species was detected out of the pool of point count stations ('detection rate' for short) between the subset of data collected by Harapan's research team versus by FH: we considered a species as prone-to-miss if its detection rate in the former sub-dataset was ≤20 % of that in the latter sub-dataset (Table S1).

2.3. *Quantifying forest condition*

We measured changes in forest condition across the study periods using the metric of top-of-canopy height ('canopy height' hereafter, in meters). We estimated canopy height from a time series of Landsat imagery, using a model derived from LiDAR training data through a machine learning approach. The LiDAR images were collected by TS on October 24, 2014, for a different research project, and they covered 3626 ha (3.7 %) of our survey area (Fig. S1). We processed the LiDAR data to a 0.5-m-resolution and constructed a canopy height layer as described in Swinfield et al. (2019), and we aggregated and resampled the canopy height values to a 30-m resolution to align with Landsat imagery. Next, we used all Landsat imagery covering Harapan within 1 year of each of the two bird surveys and the LiDAR survey to predict canopy height (Asner et al., 2018; Csillik et al., 2019). For this purpose, we converted the surface reflectance values of Landsat imagery to five vegetation indices considered consistent between remotely sensed scenes and suitable for estimating vegetation height (Appendix A; Jin and Sader, 2005; Xue and Su, 2017). We used the vegetation indices from two discrete sets of Landsat images around the LiDAR survey that were two years apart to train a random forest model for predicting canopy height over 75 % of the LiDAR areal coverage (Appendix A), using package 'randomForest' version 4.6 in program R (Breiman and Cutler, 2018; Hastie et al., 2009; R Development Core Team, 2021). Testing using the remaining 25 % of LiDAR data showed good model performance (Fig. S1). We then predicted canopy height for the entire survey area using the vegetation indices derived from the 2009 and 2018 Landsat images (i.e., within 1 year of the bird surveys) and the random forest model.

To represent the canopy height of a given point count station in each period, we averaged the predicted canopy height values over all the pixels within a 100 m radius of the station from the appropriate period ('mean canopy height' hereafter). We opted for a remote sensing approach to measure forest conditions across both study periods in a standardized way and at a scale appropriate to the habitat of most bird species. We additionally used field vegetation survey data collected during both the original (Hua et al., 2016) and current bird surveys to ground truth our remote sensing metric. Our mean canopy height metric was correlated with measurements of tree basal area obtained for a subset of point count stations (early period: $r_{(474)} = 0.31$, $p < 0.01$; current period: $r_{(132)} = 0.2$, $p < 0.05$), indicating its utility in representing forest conditions.

2.4. *Quantifying human accessibility*

For each point count station, we estimated its accessibility to humans as a proxy for the trapping pressure it likely was under, with greater accessibility representing stronger trapping pressure (Harris et al., 2017). The use of this proxy for trapping pressure was necessary due to the difficulty of directly measuring trapping activities across large landscapes over two study periods. Most roads and rivers in Harapan were navigable by motorbikes and boats, which allowed relatively easy access from nearby human settlements. Given that these settlements were observed to be trade hubs for wild-caught birds in and around Harapan, we assumed that the primary determinant of human accessibility to a given location in Harapan would be the effort needed to access it on foot. For each point count station, we calculated its Euclidean distance from the nearest 'easy-access point' (i.e. roads, rivers or trails) as a measure of the difficulty of human access ('access difficulty' hereafter), using the map of Harapan in the package 'FNN' (version 1.1.3; Beygelzimer et al., 2019) in program R (R Development Core Team, 2021). We assumed that habitat conditions inside the forest and the seasonality of the river water levels did not influence the effort taken to access a particular location.

2.5. *Species market demand, habitat association, and IUCN Red List status*

We classified all bird species recorded in our surveys into two trade guilds that represented the relative market demand for them, based on the most up-to-date market survey data for the region (Chng et al., 2015, 2016, 2018a, 2018b; Leupen et al., 2018; Rentschlar et al., 2018; Shepherd et al., 2004, 2016): (1) targeted species (high demand) – species that are highly prized and in high demand for their singing abilities (e.g. songbirds), ornamental attractiveness (e.g. cage birds) or body parts (e.g. helmeted hornbills); and (2) opportunistically trapped species (generic demand) – this includes all other species that are not specifically targeted but nonetheless trapped as 'bycatch' and sold in the market whenever possible. Our classification scheme considered all species as in demand in the market, albeit to different extents. We based this scheme on insights from informal interviews with trappers and local conservationists, which suggested that all trapped birds, if still alive, were supplied to the market. Compared with opportunistically trapped species, we expected that the abundance of targeted species would be more prone to the negative impacts of trapping.

Additionally, we classified all bird species recorded in our surveys into two habitat association guilds, based on the Birds of the World database (Billerman et al., 2020): (1) forest-dependent species – species that prefer primary or mature secondary forests; and (2) generalist species – species that are able to survive in or prefer heavily degraded natural forests, plantations, open areas, or human-dominated landscapes. Compared with generalist species, we expected that the abundance of forest-dependent species would increase more markedly over time as the forest condition improved under restoration (Latja et al., 2016; Owen et al., 2020). Finally, for all bird species recorded in our surveys, we recorded their current IUCN Red List categories, along with descriptions of the threats they face (IUCN, 2019). We compiled this set of information to assess the extent to which the current Red List status and conservation threat assessments reflected the threat posed by trapping as indicated by our research. For species prone to the negative impacts of trapping, we expected the current assessments of their conservation threats to recognize trade-driven trapping as a major threat, and their Red List status to reflect this recognition.

2.6. *Statistical analysis*

2.6.1. *Estimating species abundance, its change, and its relationship with predictor variables*

We used community-level abundance models (Royle, 2004; Yamaura et al., 2011, 2012) under the removal-model framework (Farnsworth et al., 2002) to estimate the abundance of each species – for the area covered by a single point count station – during each study period and its relationship with forest condition and access difficulty. We limited our model-building to species observed during both periods to assess changes in their true abundance over time, because for species not observed in a given survey, it was not possible to estimate their true abundance. Thus, of the 187 species we recorded during both study periods (177 and 132 species during the early and current periods, respectively), we retained 122 species that were recorded in both periods for abundance modeling (Table S2).

To account for imperfect detection under the removal-model framework (Farnsworth et al., 2002), we divided each point count into four time intervals (t); intervals were 2.5 and 3 min for the early and current periods, respectively. While the difference in interval lengths between the early and current periods meant that detection probability applied to different lengths of time, this should not confound the estimation of species abundance, as the number of intervals were the same between the periods. We then tallied the number of individuals for each species that were newly detected during each interval t, which we expressed as $Y_{i,j,k\text{-}t}$ for species i at point count station j during study period k. Similarly, we used $\lambda_{i,j,k}$ to represent species i's true mean abundance at point count station j during study period k. We modeled $\lambda_{i,j,k}$ as a linear function of mean canopy height and access difficulty on a log link (Eq. (1)), after confirming the lack of strong collinearity between these predictor variables for both survey periods (early period: $r_{(656)} = -0.05$, $p = 0.177$; current period: $r_{(656)} = 0.06$, $p = 0.113$).

$$log\left(\lambda_{i,j,k}\right) = \beta_{0\ i,k} + \beta_{1\ i} \times \text{mean canopy height}_{j,k} + \beta_{2\ i,k} \times \text{access difficulty}_{j,k} \tag{1}$$

To parameterize Eq. (1) in a community-level abundance model (Royle, 2004; Yamaura et al., 2012, 2011), we assumed that coefficients at the species level (the β's in Eq. (1)) followed a normal distribution that characterized the community-level response. We denoted the mean of the normal distributions for these community-level coefficients as $\beta_{0c\ k}$, β_{1c}, and $\beta_{2c\ k}$, respectively, with c denoting the community level. We fixed the coefficient for mean canopy height ($\beta_{1\ i}$ and β_{1c}) across the two study periods, as the response of a species to habitat quality is unlikely to drastically change within around ten years unless there was extreme selection pressure (e.g. Grant et al., 2017). However, we allowed the coefficient for access difficulty ($\beta_{2\ i,k}$ and $\beta_{2c\ k}$) to change across study periods, considering that trapping pressure and its influence on species abundance may have changed over time in Harapan. We modeled the realized abundance of species i at point count station j during study period k, $N_{i,j,k}$, as a Poisson draw from the mean $\lambda_{i,j,k}$ (Eq. (2)).

$$N_{i,j,k} \sim Poisson\left(\lambda_{i,j,k}\right) \tag{2}$$

As individual birds were detected (thus 'removed') during each successive interval within a point count, we calculated the abundance of birds that remained to be detected during each interval, $N_{i,j,k\text{-}t}$ following Eq. (3).

$$\begin{aligned} N_{i,j,k-1} &= N_{i,j,k} \\ N_{i,j,k-2} &= N_{i,j,k-1} - Y_{i,j,k-1} \\ N_{i,j,k-3} &= N_{i,j,k-2} - Y_{i,j,k-2} \\ N_{i,j,k-4} &= N_{i,j,k-3} - Y_{i,j,k-3} \end{aligned} \tag{3}$$

We modeled the observed count for each interval $Y_{i,j,k\text{-}t}$ as a binomial variable with $N_{i,j,k\text{-}t}$ trials and detection probability $p_{i,j,k}$, assuming that for species i at point count station j during study period k, this probability was consistent across all intervals (Eq. (4)).

$$Y_{i,j,k-t} \sim Binomial\left(N_{i,j,k-t},\ p_{i,j,k}\right) \tag{4}$$

We modeled $p_{i,j,k}$ as a linear function of the survey time (i.e. the time at which the point count took place, measured in minutes since dawn; scaled and centered) on a logit link, treating the identity of observer m as a random effect (Eq. (5)). We considered all members of Harapan's research team as one observer. We assumed a linear relationship between the detection of birds and survey time to reduce the risk of overparameterization (Fig. S2).

$$\text{logit}\left(p_{i,j,k}\right) = \alpha_{0\ i,m} + \alpha_{1\ i,k} \times \text{survey time}_{j,k} \tag{5}$$

We fitted all models in a Bayesian framework using JAGS (Plummer, 2003) with the packages 'rjags' (version 4–10; Plummer, 2016) and 'r2jags' (version 0.6–1; Su and Yajima, 2015) in R (R Development Core Team, 2021). We used uninformative priors, and we ran the model with 100,000 iterations on three chains, with a burn-in of 90,000 and a thinning value of 5. We evaluated the convergence of the model using the Rhat value (mean Rhat of our model = 1.002), which should ideally be close to 1 (Plummer, 2012). Having already a covariate-heavy model, we decided against using a spatial term quantifying landscape configuration in our model to reduce overfitting or parameter identifiability. Using the Moran's I test for spatial autocorrelation among the number of species detected across point count stations, we found a weak autocorrelation in the early period (Moran's $I = 0.22$, $p < 0.01$), and a near-random distribution in the current period (Moran's $I = 0.07$, $p < 0.01$).

From the above models, we derived the mean abundance across all point count stations for each species, by taking the median of the posterior distributions. We denote these mean abundances hereafter as $\overline{\lambda}_E$ and $\overline{\lambda}_C$ for the early and current periods, respectively. For the $\overline{\lambda}_E$ and $\overline{\lambda}_C$ of each species, we also derived their 89 % Bayesian equal-tailed credible intervals (89 % ETIs hereafter; Kruschke, 2014; Makowski et al., 2019; McElreath, 2018) to gauge the uncertainty in their estimation. We additionally derived these metrics for the entire community in each survey period. Finally, we derived the median and 89 % ETI for the difference between $\overline{\lambda}_C$ and $\overline{\lambda}_E$ (denoted as $\Delta\overline{\lambda}$ hereafter) at both the species and community levels, and for all model coefficients.

2.6.2. *Assessing the impacts of trapping pressure on avifaunal recovery*

We first assessed the impacts of trapping pressure on avifaunal recovery by considering the changes over time in model-estimated β_2 (i.e. the relationship between species abundance and access difficulty). We did this for each species and the entire community. A positive β_2 indicates higher abundance in less accessible areas, likely linked to the negative impacts of trapping. If β_2 became more positive over time, it would indicate intensified negative impacts of trapping on species abundance. For species that had a more positive β_2 in the current period, we further quantified the degree to which intensified trapping impacts may have reduced its abundance recovery, compared to what would have been predicted purely based on improved forest conditions. To do this, for each species and the entire community, we used Eq. (1) to calculate a counterfactual current mean abundance across all point count stations (denoted as $\overline{\lambda}_{Counter}$ hereafter) under a counterfactual scenario where the negative impacts of trapping did not intensify. For each point count station, we applied its values of mean canopy height and access difficulty to Eq. (1), using the coefficients derived from the models above except for β_2, for which we used the coefficient for the early period. We then calculated the difference between $\overline{\lambda}_C$ and $\overline{\lambda}_{Counter}$ for each species and the entire community. A negative value would represent a deficit in a species' abundance recovery ('recovery deficit' hereafter) attributed to the intensification of trapping over time.

We further calculated and plotted $\overline{\lambda}_C$ - $\overline{\lambda}_{Counter}$ for the entire community across a raster grid of Harapan to visualize the community-level recovery deficit and to identify a 'deficit zone' of avian abundance recovery in Harapan. This deficit zone corresponds to the areas where species' abundance recovery linked to improvements in forest conditions was dampened by the decline caused by trapping. We followed the same approach as above, except that we applied Eq. (1) to the mean canopy height and access difficulty values of each grid cell instead of each point count station. Finally, we also checked post hoc whether the abundance and coefficients derived from our model differed with the trade and habitat association guilds of different species.

3. Results

From the 144 point count stations we sampled during both the early (2009–2011) and current (2018) periods (Fig. 1), we recorded a total of 187 bird species from both periods combined. Of these, 55 species were detected only during the early period and 10 species only during the current period (Table S3). We used 122 species recorded in both periods for abundance modeling (Table S2). Among the species that were only detected in the early period, 76 % were opportunistically trapped species and 56 % were habitat generalists. Among the species recorded only during the current period, 90 % were opportunistically trapped species, with an equal proportion belonging to forest specialists and habitat generalists.

3.1. *Changes in forest condition and trapping pressure*

Over the study period, the mean canopy height metric increased across forest areas in Harapan that did not experience significant fire, degradation, or deforestation (Fig. 1), including at the point count stations resampled (mean difference = 0.38 m, 95 % CI = −0.04, 0.79; paired *t*-test, $t_{20} = 1.8, p = 0.08$; Fig. S3). Forests in Harapan had become more accessible over time: the mean access difficulty decreased from 1.32 km (SD = 1.29 km) in the early period to 0.72 km (SD = 0.57 km) in the current period. The Euclidean distance of the least accessible point count station from the nearest easy-access point also decreased from 6.71 km in the early period to 2.70 km in the current period. We found no relationship between changes in mean canopy height and access difficulty, indicating that improvements in forest condition occurred across the study area, even in areas of high accessibility (Fig. S4).

3.2. *Changes in bird species abundance and their relationship with forest condition change*

For the 122 bird species analyzed, 45.1 % of species showed significantly greater mean abundance in the current period compared with the early period (i.e., 89 % ETI of $\Delta\overline{\lambda} > 0$). No species showed significantly lower mean abundance over time (i.e., 89 % ETI of $\Delta\overline{\lambda} < 0$; Fig. 2a). At the community level, the average increase in abundance was 0.69 (89 % ETI: −0.07 to 1.46), and we did not detect a significant relationship between species abundance and forest condition (median β_1: −0.02 with 89 % ETI: −0.34 to 0.31).

3.3. *Relationship between species abundance and trapping pressure*

Coinciding with increased human accessibility, we found that the negative impacts of trapping on bird species abundance had most likely intensified over time. First, the proportion of species whose abundance significantly increased with increasing access difficulty (i.e., 89 % ETI for $\beta_2 > 0$) had tripled over the study period, increasing from 5.4 % in the early period to 16.2 % in the current period (Fig. 3). In comparison, the proportion of species whose abundance significantly decreased with increasing access difficulty (i.e., 89 % ETI for $\beta_2 < 0$) declined from 6.9 % to 1.5 % between the two periods (Fig. 3). Second, 48.4 % of species increased in the degree to which their abundance was associated with increasing access difficulty: their β_2 in the current period either became significantly positive (from being non-significant in the early period), or became more positive, or acquired a narrower 89 % ETI (Fig. 3). At the community level, β_2 increased slightly over time between the early (median: −0.04 with 89 % ETI: −0.47 to 0.37) and current periods (median: 0.25 with 89 % ETI: −0.68 to 1.17).

3.4. *Recovery deficit of species abundance*

We found that 15 % of the species analyzed exhibited a significant recovery deficit (i.e., negative difference between $\overline{\lambda}_C$ and $\overline{\lambda}_{Counter}$, with

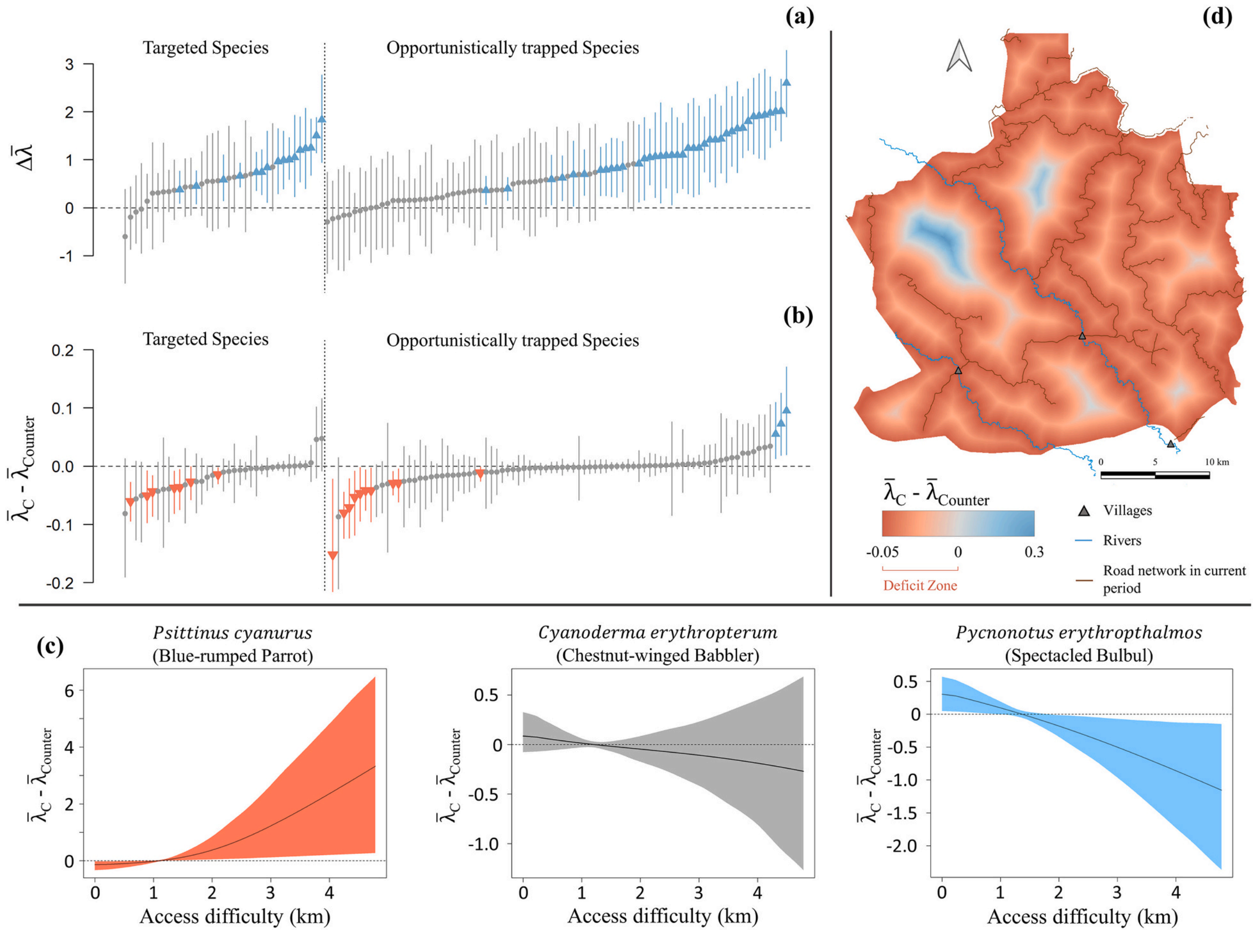

Fig. 2. The recovery of bird species abundance in Harapan and the impacts of trapping pressure. (a) Changes in mean species abundance between the early and current periods ($\Delta\bar{\lambda}$). (b) The difference between mean species abundance in the current period and the counterfactual scenario where trapping pressure did not intensify ($\bar{\lambda}_C$ - $\bar{\lambda}_{Counter}$). Negative values indicate a deficit in abundance recovery attributed to the intensification of trapping pressure. (c) The difference between mean species abundance in the current period and the counterfactual scenario ($\bar{\lambda}_C$ - $\bar{\lambda}_{Counter}$) for three example species, across a gradient of access difficulty within Harapan. Colours correspond to the those in panel b. (d) Spatial patterns of the community-level recovery deficit ($\bar{\lambda}_C$ - $\bar{\lambda}_{Counter}$) predicted in relation to the current access difficulty at Harapan. Deficit zone (red) is areas within Harapan where species' abundance recovery linked to improvements in forest conditions was dampened by trapping. For panels (a) and (b), each bar represents the Bayesian equal-tailed credible intervals (89 % ETI) for one species. Species with significantly positive values (89 % ETI > 0) are in blue (median values shown with upward triangles), species with significantly negative values (89 % ETI < 0) are in red (median values shown with downward triangles), and species with non-significant values are in grey (median values shown in grey circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

89 % ETI < 0; Fig. 2b). In contrast, $\bar{\lambda}_C$ was greater than $\bar{\lambda}_{Counter}$ for only 2.3 % of the species analyzed. The deficit was primarily driven by reductions in bird abundances in areas of greater human accessibility across Harapan, as demonstrated by the concentration of the 'deficit zone' of avian abundance recovery (i.e., region where $\bar{\lambda}_C$ - $\bar{\lambda}_{Counter} < 0$) within ~1 km from easy-access points at the community level (mean width of the deficit zone from access points: 475 m, range width: 0–1117 m; Fig. 2c).

3.5. Difference in abundance recovery between trade and habitat association guilds

A similar proportion of targeted and opportunistically trapped species exhibited positive changes in mean abundance between study periods ($\Delta\bar{\lambda}$; Table 1). Relative to opportunistically trapped species, a higher proportion of targeted species exhibited significantly positive β_2 (i.e. the relationship between abundance and accessibility) in the current period. More targeted species also had a significant recovery deficit (i.e. negative difference between $\bar{\lambda}_C$ and $\bar{\lambda}_{Counter}$; Table 1). We found no difference in the width of the deficit zones for targeted (mean 473 m, range 0–1093 m) versus opportunistically trapped species (mean 477 m, range 0–1136 m). We found that a similar proportion of forest-dependent and generalist species exhibited positive changes in mean abundance ($\Delta\bar{\lambda}$) between study periods (Table 1). Relative to generalist species, we found that a higher proportion of forest-dependent species exhibited significantly positive β_2 in the current period and greater recovery deficits (Table 1).

3.6. The extent to which the threat of trapping was reflected by IUCN threat assessments

Comparing negative impacts of trapping on species abundance against current IUCN threat assessments, we found that exploitation or wildlife trade has yet to be formally recognized as a conservation threat by the IUCN Red List for 15 species. For 21 species that were negatively affected by trapping in Harapan: they either exhibited a significant recovery deficit, or their abundance significantly increased with increasing access difficulty in the current period, current IUCN assessments identified exploitation or wildlife trade to be a threat for only six of them, and most of the species are currently classified as Least Concern (52 % of species) or Near Threatened (33 % of species; Table S4).

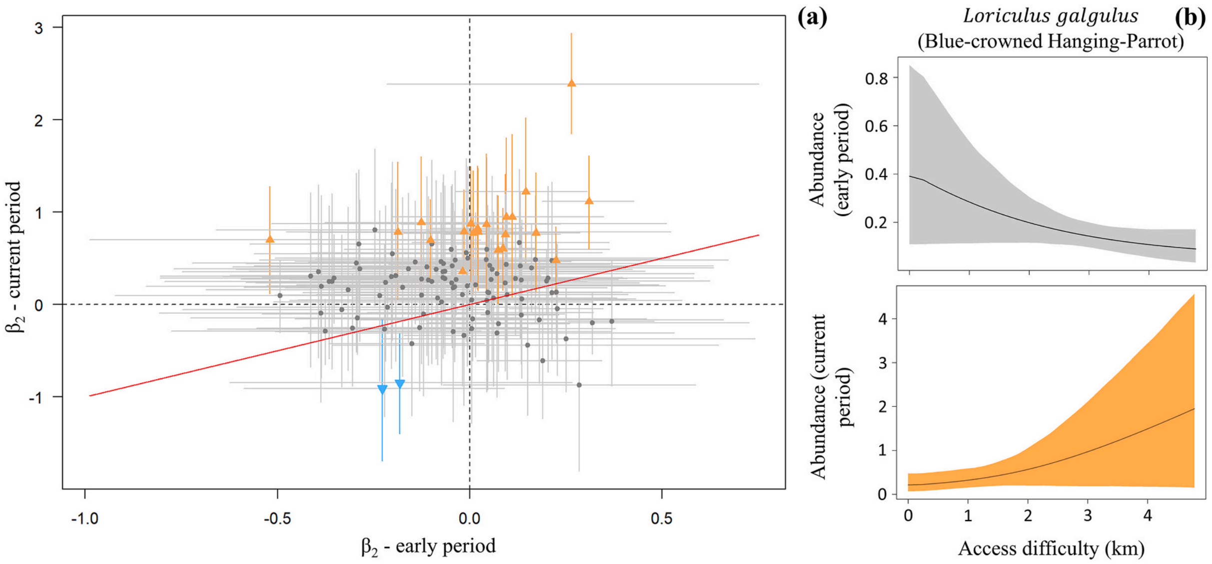

Fig. 3. Estimated relationship between species abundance and access difficulty (β_2). (a) β_2 for each species in the early period and current period, with bars representing 89 % Bayesian equal-tailed credible intervals (89 % ETI). Species with significantly positive β_2 in the current period (89 % ETI for $\beta_2 > 0$) are in orange, with their median β_2 values shown with upward triangles; species with significantly negative β_2 in the current period (89 % ETI for $\beta_2 < 0$) are in blue, with their median β_2 values shown with downward triangles; species with non-significant β_2 are shown with grey circles. Red line represents the 1:1 line. β_2 becoming more positive over time (median values above the red line) indicates intensified negative impacts of trapping on species abundance. (b) Relationship between species abundance and access difficulty for an example species in the early and current periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion and conclusion

Our study shows that bird abundance significantly increased during a decade of forest regeneration and protection at a flagship site of tropical forest restoration in the lowlands of Sumatra. However, we also found indications of increasingly strong impacts of bird trapping on species abundance, which could hamper the conservation success of forest restoration. While most species showed signs of recovery over almost ten years of forest restoration at Harapan (Fig. 2a), for at least 16.2 % of species, the intensifying trapping pressure (Fig. 3) dampened this recovery (Fig. 2b & c). Species prized in the pet trade and those dependent on late-successional forest habitat were particularly concentrated in remote, inaccessible areas (Table 1). We also found that although trapping is likely to significantly impact bird species in Indonesia, the current IUCN Red List (IUCN, 2019) considers trapping a threat to only a few of them (Table S4). Our findings demonstrate the potential of forest protection and regeneration in recovering Southeast Asia's avian diversity but highlight the urgency of tackling the intensifying threat of pet trade.

4.1. *Forest restoration and recovery of avian species*

Given appropriate conditions and recovery time, tropical forest restoration can allow biodiversity to recover, potentially to levels close to those found in primary forests (Crouzeilles et al., 2016; Gilroy et al., 2014; Rozendaal et al., 2019). Our results suggest that avian abundance recovery could happen rapidly within regenerating forests in lowland Sumatra, with notable abundance increases observed within a 10-year period. However, significant conservation gains are only possible if the recovering biodiversity is not jeopardized by factors beyond the scope of restoration. In the case of Harapan, financial and personnel resources supporting conservation have totaled approximately 20 million USD, with an annual operating cost of 1.48–2.5 million USD (Buergin, 2016; Diana and Jong, 2018; Silalahi et al., 2017). It is encouraging that this investment is associated with broad recovery in forest conditions and overall avian populations (Fig. 2a), but the level of recovery is likely to be lower than what could have been achieved in the absence of growing levels of trapping (Benítez-López et al., 2017; Morton et al., 2021). As many bird species play key roles in the regeneration and functioning of forest ecosystems, such as seed dispersal (Morrison and Lindell, 2012; de la Peña-Domene et al., 2014), declines driven by trapping could lead to cascading ecological impacts that further limit the effectiveness of forest restoration (Gardner et al., 2019).

4.2. *Threat of trade-driven trapping on tropical forest conservation*

Our study adds to the growing evidence that increasing levels of trade-driven trapping constitutes a significant threat to Indonesia's forest avifauna (Symes et al., 2018). Evidence from market surveys and communications with local experts (Harapan field staff and the trappers themselves) suggest that bird trapping is generally indiscriminate in its methods, in part because markets accept most species and because there is high mortality of birds along the supply chain (Chng et al., 2015, 2018b; Shepherd, 2006; Shepherd et al., 2004). These factors together incentivize trappers to maximize capture rates (Jepson and Ladle, 2005; Shepherd et al., 2004). As trapping depletes local bird populations, the economic incentive for indiscriminately trapping any species will likely intensify, with or without increases in market demand (Beastall et al., 2016; Courchamp et al., 2006; Shepherd, 2012; TRAFFIC, 2018). This could explain the fact that even opportunistically trapped species showed negative effects of trapping pressure in our dataset (Table 1). The impacts of trapping on wildlife populations are further exacerbated by the rapid loss of forest habitat across Southeast Asia, which not only directly threatens biodiversity persistence, but also facilitates human access by expanding the road and trail network (Harris et al., 2017; Hughes, 2018; Margono et al., 2012).

4.3. *Impacts of trapping pressure and IUCN threat assessments*

Multiple threatened species detected in our surveys showed significant negative impacts of trapping pressure, and we found that for 15 species, trapping has yet to be formally recognized by IUCN as a conservation threat (Table S4). As an example, aside from species such as the Endangered Greater Green Leafbird, *Chloropsis sonnerati,* for which

Table 1

Proportion of species in different trade and habitat association guilds that exhibit significant effects of forest recovery and trapping. The effect is positive if the 89 % Bayesian equal-tailed credible intervals are above 0 (89 % ETI > 0) and negative if 89 % ETI < 0. $\Delta\bar{\lambda}$ refers to changes in mean species abundance between the early and current periods, where a positive change shows recovery in bird species abundance. β_1 is model-estimated relationship between species abundance and canopy height, where a positive β_1 indicates higher abundance in areas with tall canopy, likely linked to forest recovery. β_2 is model-estimated relationship between species abundance and access difficulty, where a positive β_2 indicates higher abundance in less accessible areas, likely linked to the negative impacts of trapping. $\bar{\lambda}_C$ - $\bar{\lambda}_{Counter}$ refers to changes in mean species abundance between the current period and the counterfactual scenario. Negative values of $\bar{\lambda}_C$ - $\bar{\lambda}_{Counter}$ indicate a deficit in a species' abundance recovery attributed to the intensification of trapping pressure over time.

	Targeted (%)	Opportunistically trapped (%)	Forest specialist (%)	Generalist (%)
$\Delta\bar{\lambda}$ (change in abundance over time)				
Positive	43.2	46	47.4	40.9
Negative	0	0	0	0
β_1 (relationship between abundance and canopy height)				
Positive	5.4	9.4	12.8	0
Negative	10.8	12.9	9.0	18.2
β_2 (relationship between abundance and access difficulty, early period)				
Positive	5.4	5.9	6.4	4.5
Negative	8.1	7.1	7.7	6.8
β_2 (relationship between abundance and access difficulty, current period)				
Positive	27.0	13.0	20.5	11.4
Negative	0	2.4	1.3	2.3
$\bar{\lambda}_C$- $\bar{\lambda}_{Counter}$ (difference between the current period and the counterfactual scenario with no increase in trapping pressure)				
Negative (Recovery deficit)	18.9	13.0	16.7	11.4
Positive	0	3.5	2.6	2.3

the threat of trapping has been well recognized (Eaton et al., 2017), our models suggested that the Dark-necked Tailorbird, *Orthotomus atrogularis*, Blue-crowned Hanging-Parrot, *Loriculus galgulus*, and Asian Fairy-bluebird, *Irena puella* (all Least Concern), may also be negatively affected by trapping. In addition, many Least Concern and Near Threatened species exhibited significant negative signals of trapping pressure (Table S4), possibly indicating looming population declines if the current trend continues.

4.4. Caveats to our findings

Three caveats to our results warrant discussion. First, because our early and current bird surveys were conducted by different surveyors and at different survey time lengths, the observed difference in species abundance between study periods may have been influenced by these effects. We have taken measures to statistically alleviate this potential issue to the extent possible. Second, while we were able to assess the increases in canopy height for low forest canopies (typically <15 m) accurately, the potential canopy height increases of tall forests were more challenging to assess due to the known issue of saturation in predicting tree height using LiDAR data (Hansen et al., 2016; Swinfield et al., 2019). Yet our resampled point count locations were most likely in tall forests, because we intentionally sampled them from the region in Harapan that did not experience fire or deforestation. This may at least in part be responsible for the observed weak relationship between species abundance and mean canopy height. Third, we did not consider landscape features in our models, and even though we found spatial autocorrelation to be weak and near random, these factors may have influenced the estimation of bird population recovery (Bhakti et al., 2018; Carrara et al., 2015; Diniz-Filho et al., 2003; Morante-Filho et al., 2021).

4.5. Recommendations for conservation actions

The threats that trapping poses to forest birds call for urgent conservation intervention. Here we provide several recommendations for Indonesia. First, the incentive to trap should be decreased by effective anti-trapping/poaching patrols, law enforcement of illegal selling of birds in markets, and penalties for lawbreakers, aided by alternative livelihood schemes (Leupen et al., 2018; López-Bao et al., 2015; Miller et al., 2019). Employing local communities and where possible, bird trappers in patrolling and as birdwatching guides could provide them with economic incentives to forego trapping or engage in conservation (Widmann and Widmann, 2008). Second, region-wide threat assessments of the severity and extent of trade and trapping should be conducted on all bird species in Southeast Asia and check if localized threats we detected reflect broader patterns. Such assessments should use a combination of market- and field-based surveys to inform site-specific, targeted conservation interventions, such as in situ management of species, habitat (including nest site provisioning) and conservation breeding (Collar et al., 2012; M. Eaton et al., 2015b; Harris et al., 2015; Kurniandaru, 2008; Pain et al., 2006). These assessments should also pre-emptively cover species not yet found in large quantities in markets and should consider potential taxonomic changes (Eaton et al., 2016). Third, behavioral change interventions that target consumers and other actors in the trade supply chain should be conducted, for example by encouraging singing competition categories exclusively for birds from commercial captive breeding or 'ranching', particularly for high-profile species such as the White-rumped Shama *Copsychus malabaricus* (Burivalova et al., 2017; Veríssimo, 2013). Efforts should be made to better understand and address the underlying drivers of wild bird trapping through a collaborative, multi-stakeholder approach, such as that showcased by the Asian Songbird Trade Specialist Group (Burivalova et al., 2017; Marshall et al., 2019; Shepherd and Cassey, 2017). Counter-intuitively, investing in active habitat restoration could increase accessibility, which may in turn increase hunting pressure. We recommend that restoration projects phase out unrequired access roads, while regularly monitoring them even after their abandonment (Kleinschroth et al., 2016).

Forest restoration is urgently needed in many tropical regions that have experienced extensive deforestation and forest degradation, including Southeast Asia (Edwards et al., 2019; FAO and UNEP, 2020; Wilcove et al., 2013). However, its effectiveness in terms of biodiversity recovery could be compromised by wildlife trapping and exploitation. The increased accessibility of degraded forests compounds this challenge (Hughes, 2018). The realization of the conservation promise of forest restoration therefore hinges critically not only on effective restoration actions but also on addressing wildlife trapping.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.109901.

CRediT authorship contribution statement

H.S. Sathya Chandra Sagar: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration. **James J. Gilroy:** Conceptualization, Methodology, Resources, Validation, Writing – review & editing, Visualization, Supervision. **Tom Swinfield:** Formal analysis, Writing – review & editing. **Zuzana Burivalova:** Visualization, Writing – review & editing. **Ding Li Yong:** Resources, Writing – review & editing. **Elva Gemita:** Resources, Project administration, Writing – review & editing. **Novriyanti Novriyanti:** Project administration, Writing – review & editing. **David C. Lee:** Investigation, Writing – review & editing. **Muhammad Nazri Janra:** Investigation, Writing – review & editing. **Andrew Balmford:** Supervision, Funding acquisition, Writing – review & editing. **Fangyuan Hua:** Conceptualization, Methodology, Funding acquisition, Validation, Supervision, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We gratefully acknowledge the funding support from the joint AEC-OBC Conservation Grant (No. P1250) provided by the Oriental Bird Club and the Ecology Arboriculture Landscape, Sir Philip Reckitt Educational Trust travel grant, and European Commission's Joint Master's Degree Fellowship (FPA 2023 – 0224/ 532524-1-FR-2012-1-ERA MUNDUS-EMMC). We sincerely thank S. Kumaran, F. Syamsuri, F. Hasudungan, and PT Restorasi Ekosistem Indonesia for helping us to acquire research permits (126/SIP/FRP/E5/Dit.KVIV/2018) and for providing logistical support throughout the fieldwork. We thank Iwan and Andi for their assistance while collecting bird community data in the field. We also thank the anonymous reviewers for their constructive comments. H.S.S. C. thanks M. Persche and B.R. Shrestha for their detailed and helpful comments on the manuscript. H.S.S.C. thanks M. Persche for support while completing the manuscript.

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