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Trade-driven trapping dampens the biodiversity benefits of forest restoration in Southeast Asia.

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ABSTRACT

Tropical forest restoration stands to deliver important conservation gains in lowland Southeast Asia, which has suffered some of the world's highest rates of forest degradation and loss. This promise, however, may be undermined by defaunation driven by ubiquitous wildlife trapping in the region, particularly for forest birds that are part of the multi-million-dollar pet trade. To date, quantification of the impacts of trade-driven trapping on rates of biodiversity recovery from forest restoration has been limited. Here, we use a unique long-term survey dataset to ask how trade-driven trapping may interfere with the expected recovery of avian community under forest restoration, at a flagship ecosystem restoration site in the lowland rainforests of Sumatra, Indonesia. We show that tropical forest restoration is associated with the increases in the abundance of 88% of bird species over time. However, impacts of trapping within more accessible areas of the forest meant that this recovery was dampened for 74% of bird species, relative to levels expected as a result of the magnitude of forest recovery observed. Most species (80%) showed increasingly positive relationships between abundance and site remoteness over the period, a pattern that was found for both species targeted for the pet trade (85% of species) and those trapped opportunistically or as 'bycatch' (78% of species). We emphasize the urgency of tackling the emerging threat of pet trade to Southeast Asia's avian diversity, not least to ensure the effectiveness of efforts towards forest restoration.

Keywords:

Birds, conservation, nature-based climate solutions, reforestation, tropical rainforest, wildlife trade

1. INTRODUCTION

Tropical forests worldwide have undergone widespread loss and degradation (Barlow et al., 2018; Edwards et al., 2019), with severe consequences for biodiversity, people, and critical ecosystem services (Gibson et al., 2011; Watson et al., 2018). While the protection of existing 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). This is particularly true for Southeast Asia (Sodhi et al., 2010; Wilcove et al., 2013), where only 8.4% of the historical old-growth forest remains intact (Potapov et al., 2017). The future of biodiversity in this region, among the richest in the world, depends on the effective and timely restoration of its forest habitats (Cosset and Edwards, 2017; Edwards et al., 2014, 2009; Senior et al., 2019). Increasing calls for, and uptake of forest restoration in Southeast Asia (Chazdon et al., 2017; Edwards et al., 2019; FAO and UNEP, 2020) offers some hope for the region's biodiversity. The realization of which, however, hinges on ensuring the recovery of biodiversity in forests undergoing restoration.

Across Southeast Asia, wildlife trapping driven by the pet trade is a threat to biodiversity, particularly for forest birds (J. A. Eaton et al., 2015; Harris et al., 2017; Symes et al., 2018). The pet bird trade in Southeast Asia is estimated to be worth hundreds of millions of dollars annually (Gokkon, 2018; Marshall et al., 2019; Parry, 2019) and affects thousands of species (Scheffers et al., 2019), particularly species targeted for singing competitions and pet-keeping (Jepson, 2010; 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 (Shepherd et al., 2004). There is evidence that the scale of trade has increased over the past decade (Marshall et al., 2019), driven in part by increased accessibility of forest areas due to forest loss and degradation (Harris et al., 2017). Limited field evidence has linked trade-driven trapping to widespread decreases in wild bird populations (Harris et al., 2017). Consequently, in forests undergoing restoration, trade-driven trapping may dampen the recovery of avian diversity in areas being managed for ecosystem restoration (Harris et al., 2015; Harrison et al., 2016). To date, however, empirical understanding of the extent to which this may be happening is lacking.

In this study, we evaluated the recovery pattern of avian diversity under forest restoration over time in a region that has been increasingly impacted from exposure to trade-driven trapping. We conducted bird surveys at a flagship ecosystem restoration site in the now heavily modified lowlands of Sumatra, Indonesia, sampling across gradients of forest condition and trapping pressure. Our surveys were in two time windows that spanned almost ten years of forest restoration activities and that coincided with intensifying trade-driven trapping in Southeast Asia (Marshall et al., 2019). We examined how community-wide species abundance changed over time, and how the expected abundance recovery of forest species under restoration was affected by concomitant intensifying impacts of trapping pressure. We additionally assessed how changes in species abundance over time varied with species' market demand and ecological traits, and whether species' current IUCN Red List status evaluations captured the threats posed by trapping.

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 and as of 2018, it covered 98 555 ha of lowland dipterocarp forest in various stages of recovery after commercial selective logging ceased in 2005. It has been jointly managed by a consortium of conservation organizations with heavy financial investment and on-the-ground presence since 2008, with the main goal of recovering biodiversity in the post-logging forests (Harrison and Swinfield, 2015; Hua et al., 2016). 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: it has 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. SII). Despite these challenges, Harapan's remaining forests have largely demonstrated signs of recovery through natural regeneration and active tree planting efforts (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 allows access to most places within Harapan (Fig. 1). There is anecdotal evidence that bird trapping has intensified in recent years, most likely linked to easier access to forest because of continued deforestation and forest fragmentation (pers. comm. with Harapan staff, 2018). Trappers use various methods to capture live birds for the pet market, including mist nets, live bird traps, and birdlime. In recent years, the use of shotguns in Harapan to kill hornbills has also been recorded (pers. comm. with bushmeat hunters, 2018), often targeting the Critically Endangered helmeted hornbill (*Rhinoplax vigil*; BirdLife International 2020) that is prized for its ivory-like casque (Beastall et al., 2016).

2.2 Bird community surveys

We surveyed bird communities in Harapan in 2009–2011 ('early period' hereafter; Lee & 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 remoteness from human settlements ('remoteness' hereafter). We used remoteness from human settlements as a proxy for the trapping pressure on birds because more remote areas are less accessible to trapping, and less cost-effective for trappers given the difficulty of keeping trapped birds alive on longer journeys to markets (Harris et al., 2017). In total, we surveyed 636 stations in the early period (Fig. 1). Of these, a subset of 287 stations were spared from significant forest degradation or loss within a 300-m buffer between the early and current periods and were, in turn, experiencing forest recovery (Fig. SII), as assessed through remote sensing analysis (see 'Quantifying forest condition' below). Consequently, we considered these stations appropriate for assessing the effects of forest recovery and bird trapping without the confounding

effects of habitat disturbance. We resurveyed 144 of these eligible stations in the current period, using a stratified random sampling design to ensure that they covered a range of forest conditions and remoteness (Fig. 1).

For both early and current periods, we conducted unlimited-radius point counts that allowed for the correction of imperfect detection in estimating species abundance. We employed 10-minute counts in the early period and 12-minute counts in the current period. 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 05:50 - 10:30 on days without rain or strong wind, and we recorded the time of the onset of each point count in minutes since sunrise ('survey time' hereafter). The early-period surveys were conducted by Harapan's biodiversity 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 caused by different observers conducting the early and current surveys. First, we used observer identity as a random effect covariate for detection probability in our removal models (see below). Second, because the subset of early data collected by Harapan's biodiversity team may have been associated with lower detection probabilities for at least some species (particularly small or otherwise inconspicuous species) compared with that collected by FH, we compiled a list of these potential 'prone-to-miss species', for which we retained early-period data collected by FH only. We labeled a species as prone-to-miss if its detection rate (i.e., number of times it was detected out of the pool of point count stations) in the survey data collected by Harapan's biodiversity team was $\leq 20\%$ of that in the survey data collected by FH (Table SI1). Additionally, among the species observed, we excluded nocturnal and wetland species, along with mobile and low-density species such as raptors, for which our survey method may not be appropriate.

2.3 Quantifying forest condition

We measured changes in forest condition across the study periods using the metric of top-of-canopy heights ('TCH' hereafter), which we estimated from a time series of Landsat imagery using a model derived from LiDAR training data through a machine learning approach. The LiDAR dataset was collected on October 24, 2014 and covered 3,626 ha (3.7%) of our survey area (Fig. SI2). We processed the LiDAR data to a 0.5-m-resolution TCH model as described in Swinfield et al. (2019), and aggregated and resampled the TCH values to a 30-m resolution to align with Landsat imagery. We used all Landsat imagery covering Harapan within 1 year of the bird and LiDAR surveys to predict TCH (Asner et al., 2018; Csillik et al., 2019). For this purpose, we converted the surface reflectance values of Landsat imagery to five vegetation indices (VIs) considered consistent between remotely sensed scenes and suitable for estimating vegetation height (Appendix A; Jin & Sader 2005; Xue & Su 2017). We used the VIs from two discrete sets of Landsat images two years apart (in 2013 and 2015, i.e. within 1 year of the LiDAR surveys; Hastie et al. 2009) to train a random forest model for predicting TCH over 75% of the LiDAR areal coverage (Appendix A), using package 'randomForest' (version 4.6; Breiman and Cutler, 2018) under program R (R Development Core Team, 2018). Validation using the remaining 25% of LiDAR data showed good model performance (Fig. SI2). We then predicted TCH over the entire survey area using the VIs derived from the 2009 and 2018 Landsat images (i.e., within 1 year of the bird surveys) and the above random forest model. For a given point count station in a given period, we averaged the predicted TCH values over all the pixels within a 100 m radius of the station, to represent the TCH of the forest area around the station ('mean TCH' hereafter).

2.4 Quantifying forest accessibility and remoteness

For each point count station, we used its Euclidian distance from the nearest roads, rivers, or forest edges to represent its remoteness from human settlements, which we in turn used as a proxy for the trapping pressure on forest birds (Harris et al., 2017). The use of a proxy was necessary due to the difficulty of directly measuring trapping pressure across large landscapes. Given that most roads and rivers in Harapan were navigable by motorbikes or boats, which allowed relatively easy access from nearby human settlements, we assumed that the primary determinant of a location's trapping pressure would be the effort taken to access it on foot. For each point count station, we therefore estimated this effort by calculating its Euclidean distance from the nearest 'easy-access point' (i.e. roads, rivers, or forest edges), using the map of Harapan in the package 'FNN' (version 1.1.3; Beygelzimer et al. 2019) under program R (R Development Core Team, 2018). We assumed that habitat conditions inside the forest and the seasonality of river water levels did not influence the effort taken to access a particular location.

2.5 Species market demand, ecological traits, and IUCN Red List status

We classified all bird species recorded in our surveys into two trade guilds representing their relative market demand, based on the best available market survey data for the region (Shepherd et al., 2004): (1) targeted species (high demand) – species that are highly prized and in high demand for their singing abilities (songbirds), ornamental attractiveness (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 for the above reasons, but that are nonetheless trapped as 'bycatch' and sold in the market whenever possible. This classification scheme thus considered all species as in demand at the market, albeit to different extents. This scheme was based on insights from our informal interviews with trappers and local conservationists, which suggested that all trapped birds, if still alive, would be 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 ecological guilds representing their dependence on undisturbed forest conditions, 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).

2.6 Statistical analysis

2.6.1 Bayesian community abundance models.

We used community-level abundance models (Royle, 2004; Yamaura et al., 2012, 2011) under the removal-model framework (Farnsworth et al., 2002) to estimate the abundance of each species during each study period and its relationship with forest condition and remoteness. Because of our focus on measuring changes in species abundance over time, we limited our analysis to species that were observed during both surveys. Thus, of the 190 species we detected during either study periods (177 and 143 species during the early and current periods, respectively), we retained 130 species that were detected in both periods for our final analysis (Table SI2).

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). We tallied the number of individuals for each species that were newly detected during each interval t , which we expressed as $Y_{i,j,k-t}$ 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 , i.e. that expected under the forest condition and remoteness represented by the

point count station. We modeled $\lambda_{i,j,k}$ as a linear function of mean TCH and remoteness on a log link (Formula 1).

$$\log(\lambda_{i,j,k}) = \beta_{0\ i,k} + \beta_{1\ i} \times \text{mean TCH}_{j,k} + \beta_{2\ i,k} \times \text{remoteness}_{j,k} \quad \dots\dots\dots (1)$$

To parameterize Formula 1 in a community-level abundance model (Royle, 2004; Yamaura et al., 2012, 2011), we assumed species-level coefficients follow 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. We fixed the coefficient for mean TCH ($\beta_{1\ i}$) across the two study periods, as the response of a species to habitat quality is unlikely to drastically change within ten years unless there was extreme selection pressure (e.g. Grant et al., 2017). However, we allowed the coefficient for remoteness ($\beta_{2\ i,k}$) to change across study periods, as we hypothesized that relationships between species abundance and forest remoteness may have changed over time with increased trapping. We modeled the actual (i.e. 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 $\lambda_{i,j,k}$ (Formula 2).

$$N_{i,j,k} \sim \text{Poisson}(\lambda_{i,j,k}) \quad \dots\dots\dots (2)$$

As individual birds were detected (thus ‘removed’) during each successive interval within a point count, the abundance of birds that remained to be detected during each interval, $N_{i,j,k-t}$, is calculated as in Formula 3:

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

where the observed count for each interval $Y_{i,j,k-t}$ is modelled as a binomial variable with $N_{i,j,k-t}$ 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 (Formula 4).

$$Y_{i,j,k-t} \sim \text{Binomial}(N_{i,j,k-t}, p_{i,j,k}) \quad \dots\dots\dots (4)$$

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 after sunrise; scaled and centered) on a logit link, treating the identity of observer m as a random effect (we considered all Harapan staff as one observer; Formula 5).

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

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) under program R (R Development Core Team, 2018). 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). From the posterior distributions of the model, we derived, for each species in each survey period, the median values and 95% Bayesian credible intervals (BCIs hereafter) for mean abundance $\bar{\lambda}$ averaged across all point count stations (denoted hereafter as $\bar{\lambda}_E$ and $\bar{\lambda}_C$ for the early and current periods, respectively), as well as for all model coefficients. Comparing the current versus early periods, we additionally derived the median values and BCIs for the relative change between $\bar{\lambda}_C$ and $\bar{\lambda}_E$

(denoted as $\Delta\bar{\lambda}$ hereafter) and in the coefficient for remoteness (denoted as $\Delta\beta_2$ hereafter), for each species as well the community average.

2.6.2 Assessing the impacts of trapping pressure on avifaunal recovery. We first assessed the impacts of trapping pressure on avifaunal recovery using $\Delta\beta_2$ obtained above. A more positive $\Delta\beta_2$ would indicate that over time, species abundance became increasingly associated with less accessible areas (i.e., areas of lower trapping pressure). We additionally assessed how these changes may have influenced species abundance recovery over time due to improved forest conditions associated with restoration. To do this, we calculated, for each species, a counterfactual current $\bar{\lambda}$ (denoted as $\bar{\lambda}_{\text{Counter}}$ hereafter) representing the expected change in species abundance in the absence of any changes in β_2 (effect of remoteness) between the early and current survey periods. We additionally derived the median values and BCIs for the relative change between $\bar{\lambda}_E$ and $\bar{\lambda}_{\text{Counter}}$ (denoted as $\Delta\bar{\lambda}_{\text{Counter}}$ hereafter), for each species as well the community average. We derived $\bar{\lambda}_{\text{Counter}}$ by predicting species' λ for each point count station under the current TCH and remoteness conditions, but with β_2 (i.e., the effect of remoteness) fixed at the level estimated for that species in the early period (Formula 6).

$$\log(\lambda_{\text{counter } i,j,2}) = \beta_{0\ i,2} + \beta_{1\ i} \times \text{mean TCH}_{j,2} + \beta_{2\ i,1} \times \text{remoteness}_{j,2} \quad \dots\dots\dots (6)$$

We then calculated the difference between $\Delta\bar{\lambda}$ and $\Delta\bar{\lambda}_{\text{Counter}}$, where a negative difference represented the deficit in abundance recovery ('recovery deficit' hereafter) attributed to the potential increase in trapping pressure over time. Finally, we visualized this difference (i.e., $\Delta\bar{\lambda} - \Delta\bar{\lambda}_{\text{Counter}}$) across Harapan for each species as well as the entire community to identify a 'risk zone' of recovery deficit, where species abundance recovery linked to forest recovery could not compensate for the decline in species abundance caused by trapping. Here we used the above fitted models (Eq. 1 & Eq. 6) to derive posterior mean estimates of $\bar{\lambda}_E$, $\bar{\lambda}_C$ and $\bar{\lambda}_{\text{Counter}}$ across a raster grid of Harapan, using the current values for TCH and Euclidian distances from each grid cell to the nearest easy-access points.

2.6.3 Relating the impacts of trapping pressure to species traits and IUCN Red List categories. We assessed how estimated impacts of trapping pressure differed between guilds defined by species' market demand and ecological traits, using four metrics that represented species-level impacts of trapping pressure: the effect of remoteness (β_2) in the current period, the change in remoteness effect over time ($\Delta\beta_2$), the change in species overall abundance over time ($\Delta\bar{\lambda}$), and the difference between $\Delta\bar{\lambda}$ and $\Delta\bar{\lambda}_{\text{Counter}}$. We assessed the proportion of species in each guild that exhibited different responses in each of these metrics and used analysis of variance (ANOVA) to compare the means of each metric between guilds. Finally, we compared $\Delta\beta_2$ with species' current IUCN Red List categories to understand if and to what extent the threat of trapping had been commensurably represented by these assessments.

3. RESULTS

3.1 Species' abundance changes over time

We observed broadly improving forest condition at Harapan over the study period, as represented by overall positive changes in TCH (Fig. 1) in areas that did not experience anthropogenic disturbances (Fig. SII). Of the 130 bird species analyzed, we found broad increases in their abundance over time. Specifically, 36% of species showed significantly positive $\Delta\bar{\lambda}$ (95% BCI for $\Delta\bar{\lambda} > 0$), meaning that their average abundance increased significantly over time, while an additional 53% showed tendencies of positive $\Delta\bar{\lambda}$ (median for $\Delta\bar{\lambda} > 0$, although its 95% BCI overlapped with zero; Fig. 2a). While no species showed significantly negative $\Delta\bar{\lambda}$ (95% BCI for $\Delta\bar{\lambda} < 0$), 12% showed tendencies of negative $\Delta\bar{\lambda}$ (median for $\Delta\bar{\lambda} < 0$, although its 95% BCI overlapped with zero; Fig. 2a). On the community level, the mean $\Delta\bar{\lambda}$ across all species was 0.67 (95% BCI: -0.28 to 1.62; Fig. 2a; this represents the mean increase in bird

individual numbers for the area covered by a single point count station). Despite the consistent changes in overall forest condition and species abundance, we did not find a clear relationship between them: the community-level coefficient for mean TCH, β_{1c} was -0.02, with a 95% BCI of -0.42 to 0.39.

3.2 Impacts of trapping pressure on species abundance and recovery

We found negative impacts of our proxy measure for trapping pressure on species abundance for the majority of species studied. In the early study period, only 5% of species analyzed showed significantly positive β_2 , the effect of forest remoteness on species abundance (95% BCI for $\beta_2 > 0$), with 39% showing tendencies of positive β_2 (median for $\beta_2 > 0$, although it's 95% BCI overlapped with zero), but these proportions increased to 9% and 68%, respectively, in the current period (Fig. SI3). On the community level, this effect increased from -0.04 (95% BCI: -0.47 to 0.37) with β_0 -2.90 (95% BCI: -3.58 to -2.24) in the early period to 0.25 (95% BCI: -0.68 to 1.17) with β_0 -2.13 (95% BCI: -3.10 to -1.11) in the current period. Most species also showed increases in their degree of association with forest remoteness over time, with 6% of species showing significantly positive $\Delta\beta_2$, and an additional 74% showing tendencies of positive $\Delta\beta_2$ (Fig. 2b). Overall, on the community level, $\Delta\beta_2$ exhibited a tendency to increase over time ($\Delta\beta_{2c} = 0.30$, 95% BCI: -0.73 to 1.31; Fig. 2b). Concomitant to these signatures of trapping pressure, we found that forests in Harapan had also become more accessible over time: the Euclidean distance of the least accessible point count station from the nearest easy-access point decreased from 6.7 km in the early period to 2.7 km in the current period.

The impacts of trapping pressure had a dampening effect on the recovery of avian species abundance compared to what would have been expected because of improved forest condition. Specifically, this recovery deficit (i.e., negative difference between $\Delta\bar{\lambda}$ and $\Delta\bar{\lambda}_{\text{Counter}}$) was significant (95% BCI < 0) for 7% of the species analyzed, with an additional 67% of species showing tendencies of being significant (median < 0 , although it's 95% BCI overlapped with zero; Fig. 2c), whilst at the community level it was -0.05 (95% BCI: -0.26 to 0.24; Fig. 2c). This recovery deficit was primarily driven by reductions in bird abundances in areas of higher accessibility across Harapan, thus defining a community-level 'risk zone' within 1 km from easy-access points (Fig. 2d). On the species level, the remoteness at which the risk zones ended differed across species (Fig. SI4).

3.3 Relevance of species' market demand, ecological traits, and IUCN threat status

Targeted species on average showed stronger signals of the negative impacts of trapping pressure on population abundance, relative to opportunistically trapped species. A higher proportion of targeted species exhibited positive β_2 in the current period (Fig. 3a), positive $\Delta\beta_2$ (Fig. 3b), and greater recovery deficit as represented by negative difference between $\Delta\bar{\lambda}$ and $\Delta\bar{\lambda}_{\text{Counter}}$ (Fig. 3c). Correspondingly, a lower proportion of targeted species exhibited positive changes in mean abundance between study periods ($\Delta\bar{\lambda}$; Fig. 3d). It should be noted, however, that these differences were not statistically significant (Fig. 3). Contrary to our expectations, we did not find a difference in the remoteness at which the risk zones ended for targeted versus opportunistically trapped species: for both guilds, this remoteness was around 1 km from easy-access points (Fig. SI5). We did not find notable differences in the above metrics between forest-dependent and generalist species (Fig. SI6).

Comparing the effect of forest remoteness between study periods (the estimated mean of $\Delta\beta_2$) for each species with their current IUCN Red List category revealed that the threat of trapping on species populations has generally not been captured well by IUCN threat assessments (IUCN 2019; Fig. 4). For the 104 species that exhibited significantly positive or tendencies of positive $\Delta\beta_2$ (indicative of increasingly negative impacts of trapping on abundance), most of them are currently classed as Least Concern (51% of species) or Near Threatened (25% of species; Table SI2), and trapping is formally recognized by IUCN as a threat for only 10 of them; along with one additional species that exhibits negative $\Delta\beta_2$.

4. DISCUSSION AND CONCLUSION

Using a unique community-level dataset spanning almost ten years from a flagship site of tropical forest restoration in the lowlands of Sumatra, we provide evidence that escalating bird trapping driven by the pet trade has the potential to hamper the conservation success of forest restoration. We show that while most species exhibited signs of abundance recovery under forest restoration at Harapan (Fig. 2a), the intensifying negative signatures of trapping pressure on species abundance (Fig. 2b & Fig. SI3) have dampened this recovery (Fig. 2c) and limited it to less accessible areas (Fig. 2d). We also show that species particularly prized in the pet trade were generally more negatively affected (Fig. 3). Finally, we show that although trapping is likely to impact a large number of species in Southeast Asia as shown in our study site, the current IUCN Red List (IUCN, 2019) considers few of them as being affected by trapping (Fig. 4). Our findings highlight the urgency of tackling the emerging threat of pet trade to Southeast Asia's avian diversity, not least to ensure the effectiveness of the often expensive efforts of forest restoration.

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). However, this is possible only if the recovering biodiversity is not jeopardized by factors outside the scope of restoration. Particularly for restoration initiatives aimed at achieving conservation goals, tackling other threats to safeguard the hard-won biodiversity gain of restoration is paramount. 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 (Buerger, 2016; Diana and Jong, 2018; Silalahi et al., 2017). It is encouraging that this investment is associated with broad recovery in avian populations (Fig. 2a), but the level of recovery is likely to be far lower than would have been achieved had the avifauna not been subjected to sustained trapping (Fig. 2c). As many bird species play key roles in the regeneration and functioning of forest ecosystems (e.g. through seed dispersal, Morrison & 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).

Our study adds to the growing evidence that trade-driven trapping of forest birds constitutes a grave threat to Southeast Asia's forest avifauna (Symes et al., 2018), especially in Indonesia. Evidence from market surveys (Chng et al., 2018, 2015; Shepherd, 2006) 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 (Shepherd et al., 2004) and there is high mortality of birds along the supply chain. 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); possibly explaining similar risk zone's remoteness we observed for both targeted and opportunistically trapped species (Fig. SI5). 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 (Margono et al., 2012), but also facilitates trapper access by expanding the road and trail network (Harris et al., 2017; Hughes, 2018). Multiple threatened species detected in our surveys showed significant negative impacts of trapping pressure, along with several species, for which trapping has yet to be formally recognized as a conservation threat (Fig. 4 & Table SI2). As an example, aside from the Endangered Greater Green Leafbird *Chloropsis sonnerati* for which the threat of trapping has been well recognized (Eaton et al., 2017), our models suggested that the Yellow-bellied Bulbul *Alophoixus phaeocephalus* (Least Concern), Sooty Barbet *Caloramphus hayii*, and Blue-rumped Parrot *Psittinus cyanurus* (both Near Threatened) were also negatively affected, significantly, by trapping (Table SI2). In addition, a large number of species of lower conservation concern exhibited significant, or near significant, negative signals of

trapping pressure (Fig. 4 & Table SI2), possibly indicating looming population declines if the current trend continues.

Two caveats to our findings warrant discussion. First, because our early and current bird surveys were conducted by different surveyors, the observed difference in species abundance between study periods may have in part been an artifact of observer effects. While we have taken measures to alleviate this potential problem, these measures cannot fully rule out the possibility that differences in observer detection abilities may have contributed to the increased species abundance found in the current period. This issue, however, is often inevitable for studies or monitoring efforts that cover a large temporal span. Second, while we were able to assess the increases in TCH for low forest canopies (typically < 15 m) accurately, the potential TCH increases of tall forests were more challenging to assess due to the well-known saturation of tree height predictions using LiDAR data (Hansen et al., 2016; Swinfield et al., 2019). This bias should be at least in part responsible for the observed weak relationship between species abundance and mean TCH. Nonetheless, as our inferences focused on the relationship between species abundance and remoteness as a proxy for trapping pressure (i.e., β_2), we note that neither of the above caveats undermines our central finding that trapping pressure hampered the conservation gains of forest restoration for avian diversity at Harapan.

The threats that trapping poses to forest birds call for urgent conservation intervention. Here we provide several practical recommendations for Southeast Asia. First, effective anti-trapping/poaching patrols and law enforcement (Miller et al., 2019), including penalties to lawbreakers as deterrents (Leupen et al., 2018; López-Bao et al., 2015), coupled with alternative livelihood schemes should be adopted to decrease trapping incentives. Employing local communities and where possible, bird trappers in patrolling and as birdwatching guides could provide them with economic incentives to forego trapping and/or engage in conservation, and to cultivate a genuine long-term interest in supporting conservation (Widmann and Widmann, 2008). Second, to provide the basis for devising conservation actions, region-wide threat assessments on 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 the broader situation. Such assessments should use a combination of market- (Harris et al., 2015) and field-based surveys to inform site-specific, targeted conservation interventions (as an example, see Eaton et al. 2015b). These interventions could include *in situ* management of species (Pain et al., 2006) and habitat (including nest site provisioning; e.g. Kurniandaru 2008), conservation breeding (Collar et al., 2012), and possibly, commercial captive breeding or ‘ranching’ (J. A. Eaton et al., 2015) of key, high-profile species such as the White-rumped Shama, *Copsychus malabaricus* (Palko et al., 2011). 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). More broadly, efforts should be made to better understand and address the underlying drivers of wild bird trapping (Burivalova et al., 2017; Marshall et al., 2019) through a collaborative, multi-stakeholder approach, such as that showcased by the Asian Songbird Trade Specialist Group (Shepherd and Cassey, 2017), and to explore behavioral change interventions that target consumers and other components of the trade supply chain (Veríssimo, 2013).

Forest restoration is urgently needed in many tropical regions that have experienced extensive deforestation and forest degradation (Edwards et al., 2019), including Southeast Asia (FAO and UNEP, 2020; Wilcove et al., 2013). However, its effectiveness to recover biodiversity could be compromised by wildlife trapping and more broadly, exploitation, as our study demonstrated. The increased accessibility of degraded forests compounds this challenge (Hughes, 2018). The realization of the conservation promise of forest restoration (Strassburg et al., 2020), therefore, hinges critically on not only effective restoration actions but also on how effectively we can manage local stakeholder partnerships and protect these forest areas from other anthropogenic threats.

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FIGURES

Fig. 1. Distribution of point count stations and changes in forest condition over time at Harapan Rainforest. Point count stations surveyed during the early period (2009-2011) are displayed in purple; those surveyed during both the early and current (2018) periods are displayed in yellow. The map also displays changes in forest condition as represented by TCH (top-of-canopy height) in meters, estimated from Landsat imagery using a LiDAR training dataset. The road and river network and village locations in and around Harapan in the current period are also displayed.

Fig. 2. The recovery pattern of bird species abundance in Harapan and the impacts it sustained from the trapping pressure. (a) Changes in mean species abundance between the early and current periods ($\Delta\bar{\lambda}$). (b) Changes in the effect of remoteness on species abundance between the early and current periods ($\Delta\beta_2$); y-axis is standardized, and a unit change in remoteness is equal to a Z score of 1021 m. (c) The difference between $\Delta\bar{\lambda}$ and $\Delta\bar{\lambda}_{Counter}$ (i.e., changes in mean species abundance between early and counterfactual current period); negative values of $\Delta\bar{\lambda} - \Delta\bar{\lambda}_{Counter}$ indicates recovery deficit - dampened abundance recovery because of intensifying trapping pressure. (d) Model-predicted spatial patterns of the community-level recovery deficit ($\Delta\bar{\lambda} - \Delta\bar{\lambda}_{Counter}$), mapped in relation to the current easy-access point network (road, river, and forest edges) at Harapan. For panels (a)-(c), values were provided for the entire community and separately for the targeted and opportunistically trapped guilds (left-most section), as well as separately for individual species belonging to the targeted and opportunistically trapped guilds (middle and right-most sections, respectively; each bar represents one species); across all three panels, species are ordered in the same order of decreasing $\Delta\bar{\lambda}$ within each guild.

Fig. 3. Comparison between the targeted and opportunistically trapped species with regard to the negative effects of trapping pressure on their abundance, as represented by (a) positive β_2 in the current period, (b) positive $\Delta\beta_2$ between the early and current periods, (c) positive $\Delta\bar{\lambda}$ between the early and current periods, and (d) negative $\Delta\bar{\lambda} - \Delta\bar{\lambda}_{\text{Counter}}$. For each of the above four metrics, comparisons concerned (1) the proportion of species in each guild that exhibited responses indicative of more severe negative effects of trapping pressure (pie chart in the upper portion of each panel), as well as (2) ANOVA test of the metric values between the two guilds as represented by jittered box plots (lower portion of each panel; each point represents an individual species).

Fig. 4. The extent to which the threat of trapping pressure on our study species was captured by the IUCN Red List assessments. We represented the threat of trapping pressure by $\Delta\beta_2$ between the early and current periods, with species binned into 0.1-wide $\Delta\beta_2$ intervals. Those species whose $\Delta\beta_2$ were significantly different from zero (95% BCI not overlapping with zero) are highlighted, as are species currently recognized by IUCN to be threatened by hunting/trapping.