1 **Title of the paper:**
2 Trade-driven trapping dampens the biodiversity benefits of forest restoration in Southeast Asia.
3
4

5 **Author Information:**
6 H S Sathya Chandra Sagar [1,2], James J. Gilroy [1], Tom Swinfield [3,4], Ding Li Yong [5], Elva Gemita [6],
7 Novriyanti Novriyanti [7], David C. Lee [8], Muhammad Nazri Janra [9], Andrew Balmford [2], Fangyuan Hua
8 [2,10]
9

10 *Author affiliations:*
11
12   1. School of Environmental Science, University of East Anglia, Norwich Research Park, Norwich,
13   Norfolk, NR4 7TJ, United Kingdom
14   2. Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, CB2
15   3QZ, United Kingdom
16   3. Department of Plant Sciences, University of Cambridge Conservation Research Institute,
17   Cambridge, CB2 3QZ, United Kingdom.
18   4. Centre for Conservation Science, Royal Society for the Protection of Birds, Cambridge, CB2
19   3QY, United Kingdom
20   5. BirdLife International (Asia), 354 Tanglin Road, #01-16/17, Tanglin International Centre,
21   Singapore, 247672, Singapore
22   6. PT Restorasi Ekosistem Indonesia, Jl. Dadali No. 32, Bogor 16161, Indonesia
23   7. Department of Forestry, Faculty of Agriculture, Universitas Lampung, Jl. Prof. Dr. Ir. Sumantri
24   Brojonegoro, RW.No: 1, Gedong Meneng, Kec. Rajabasa, Kota Bandar Lampung, Lampung
25   35141, Indonesia.
26   8. School of Applied Sciences, University of South Wales, Pontypridd CF37 4BD, United Kingdom
27   9. Department of Biology, Andalas University, Limau Manis, Pauh, Padang City, West Sumatra
28   25175, Indonesia
29   10. Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Haidian
30   District, Beijing, China
31

32 **Corresponding authors:**
33
34 **H S Sathya Chandra Sagar**
35 School of Environmental Science, University of East Anglia, Norwich Research Park, Norwich,
36 Norfolk, NR4 7TJ, United Kingdom.
37 Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, CB2 3QZ,
38 United Kingdom.
39 Email: sathyachandrasagar@gmail.com
40
41 **James Gilroy**
42 School of Environmental Science, University of East Anglia, Norwich Research Park, Norwich,
43 Norfolk, NR4 7TJ, United Kingdom.
44 Email: j.gilroy@uea.ac.uk
45
46 **Fangyuan Hua**
47 Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, CB2 3QZ,
48 United Kingdom.
49 Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Haidian District,
50 Beijing, China.
51 Email: fhua@pku.edu.cn

1

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.

103 In this study, we evaluated the recovery pattern of avian diversity under forest restoration over time in a
104 region that has been increasingly impacted from exposure to trade-driven trapping. We conducted bird
105 surveys at a flagship ecosystem restoration site in the now heavily modified lowlands of Sumatra,
106 Indonesia, sampling across gradients of forest condition and trapping pressure. Our surveys were in two
107 time windows that spanned almost ten years of forest restoration activities and that coincided with
108 intensifying trade-driven trapping in Southeast Asia (Marshall et al., 2019). We examined how
109 community-wide species abundance changed over time, and how the expected abundance recovery of
110 forest species under restoration was affected by concomitant intensifying impacts of trapping pressure.
111 We additionally assessed how changes in species abundance over time varied with species' market
112 demand and ecological traits, and whether species' current IUCN Red List status evaluations captured the
113 threats posed by trapping.
114
115 **2. METHODS**
116
117 **2.1 Study site**
118 We conducted our study in the Harapan Rainforest ('Harapan' hereafter), which straddles the provinces of
119 Jambi and South Sumatra in Sumatra, Indonesia (2°08′ S, 103°22′ E, 50–80 m a.s.l.; Fig. 1). Harapan was
120 established as Indonesia's first ecosystem restoration concession in 2007 and as of 2018, it covered 98
121 555 ha of lowland dipterocarp forest in various stages of recovery after commercial selective logging
122 ceased in 2005. It has been jointly managed by a consortium of conservation organizations with heavy
123 financial investment and on-the-ground presence since 2008, with the main goal of recovering
124 biodiversity in the post-logging forests (Harrison and Swinfield, 2015; Hua et al., 2016). Rich in
125 biodiversity representative of the Sundaic lowlands, it is also recognized as an Important Bird and
126 Biodiversity Area (IBA; BirdLife International, 2017). Since its establishment, Harapan has faced
127 mounting conservation challenges: it has lost ~25 000 ha of forest cover to illegal logging and
128 encroachment, and another ~30 000 ha was damaged by El Niño-related drought and fires in 2015 (Fig.
129 SI1). Despite these challenges, Harapan's remaining forests have largely demonstrated signs of recovery
130 through natural regeneration and active tree planting efforts (Fig. 1).
131
132 Wildlife trapping and hunting, especially of birds, has been persistent in Harapan (pers. comm. with local
133 bird trappers and Harapan staff, 2018), aided by a network of seasonally navigable roads and rivers that
134 allows access to most places within Harapan (Fig. 1). There is anecdotal evidence that bird trapping has
135 intensified in recent years, most likely linked to easier access to forest because of continued deforestation
136 and forest fragmentation (pers. comm. with Harapan staff, 2018). Trappers use various methods to capture
137 live birds for the pet market, including mist nets, live bird traps, and birdlime. In recent years, the use of
138 shotguns in Harapan to kill hornbills has also been recorded (pers. comm. with bushmeat hunters, 2018),
139 often targeting the Critically Endangered helmeted hornbill (*Rhinoplax vigil*; BirdLife International 2020)
140 that is prized for its ivory-like casque (Beastall et al., 2016).
141
142 **2.2 Bird community surveys**
143 We surveyed bird communities in Harapan in 2009-2011 ('early period' hereafter; Lee & Lindsell 2011;
144 Hua et al. 2016) and again in 2018 ('current period' hereafter) using point counts. We positioned point
145 count stations ≥200 m apart along line transects that covered a range of forest conditions and remoteness
146 from human settlements ('remoteness' hereafter). We used remoteness from human settlements as a proxy
147 for the trapping pressure on birds because more remote areas are less accessible to trapping, and less cost-
148 effective for trappers given the difficulty of keeping trapped birds alive on longer journeys to markets
149 (Harris et al., 2017). In total, we surveyed 636 stations in the early period (Fig. 1). Of these, a subset of
150 287 stations were spared from significant forest degradation or loss within a 300-m buffer between the
151 early and current periods and were, in turn, experiencing forest recovery (Fig. SI1), as assessed through
152 remote sensing analysis (see 'Quantifying forest condition' below). Consequently, we considered these
153 stations appropriate for assessing the effects of forest recovery and bird trapping without the confounding

3

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

157

158   For both early and current periods, we conducted unlimited-radius point counts that allowed for the
159   correction of imperfect detection in estimating species abundance. We employed 10-minute counts in the
160   early period and 12-minute counts in the current period. During each point count, we recorded all birds
161   seen or heard (excluding flyovers), along with their time of initial detection in minutes since the onset of
162   the point count period. The latter information allowed us to use removal models to estimate and correct
163   for species' detection probability (Farnsworth et al., 2002). We conducted all surveys between 05:50 -
164   10:30 on days without rain or strong wind, and we recorded the time of the onset of each point count in
165   minutes since sunrise ('survey time' hereafter). The early-period surveys were conducted by Harapan's
166   biodiversity team led by DCL (551 point count stations; Lee and Lindsell, 2011) and by FH in a separate
167   research project (85 point count stations; Hua et al., 2016), while surveys for the current period were
168   conducted by HSSCS (144 point count stations).

169

170   We took two measures to minimize the potential bias in bird community characterization caused by
171   different observers conducting the early and current surveys. First, we used observer identity as a random
172   effect covariate for detection probability in our removal models (see below). Second, because the subset
173   of early data collected by Harapan's biodiversity team may have been associated with lower detection
174   probabilities for at least some species (particularly small or otherwise inconspicuous species) compared
175   with that collected by FH, we compiled a list of these potential 'prone-to-miss species', for which we
176   retained early-period data collected by FH only. We labeled a species as prone-to-miss if its detection rate
177   (i.e., number of times it was detected out of the pool of point count stations) in the survey data collected
178   by Harapan's biodiversity team was ≤20% of that in the survey data collected by FH (Table SI1).
179   Additionally, among the species observed, we excluded nocturnal and wetland species, along with mobile
180   and low-density species such as raptors, for which our survey method may not be appropriate.

181

182   **2.3 Quantifying forest condition**
183   We measured changes in forest condition across the study periods using the metric of top-of-canopy
184   heights ('TCH' hereafter), which we estimated from a time series of Landsat imagery using a model
185   derived from LiDAR training data through a machine learning approach. The LiDAR dataset was
186   collected on October 24, 2014 and covered 3,626 ha (3.7%) of our survey area (Fig. SI2). We processed
187   the LiDAR data to a 0.5-m-resolution TCH model as described in Swinfield et al. (2019), and aggregated
188   and resampled the TCH values to a 30-m resolution to align with Landsat imagery. We used all Landsat
189   imagery covering Harapan within 1 year of the bird and LiDAR surveys to predict TCH (Asner et al.,
190   2018; Csillik et al., 2019). For this purpose, we converted the surface reflectance values of Landsat
191   imagery to five vegetation indices (VIs) considered consistent between remotely sensed scenes and
192   suitable for estimating vegetation height (Appendix A; Jin & Sader 2005; Xue & Su 2017). We used the
193   VIs from two discrete sets of Landsat images two years apart (in 2013 and 2015, i.e. within 1 year of the
194   LiDAR surveys; Hastie et al. 2009) to train a random forest model for predicting TCH over 75% of the
195   LiDAR areal coverage (Appendix A), using package 'randomForest' (version 4.6; Breiman and Cutler,
196   2018) under program R (R Development Core Team, 2018). Validation using the remaining 25% of
197   LiDAR data showed good model performance (Fig. SI2). We then predicted TCH over the entire survey
198   area using the VIs derived from the 2009 and 2018 Landsat images (i.e., within 1 year of the bird surveys)
199   and the above random forest model. For a given point count station in a given period, we averaged the
200   predicted TCH values over all the pixels within a 100 m radius of the station, to represent the TCH of the
201   forest area around the station ('mean TCH' hereafter).

202

203   **2.4 Quantifying forest accessibility and remoteness**

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

216 **2.5 Species market demand, ecological traits, and IUCN Red List status**
217 We classified all bird species recorded in our surveys into two trade guilds representing their relative
218 market demand, based on the best available market survey data for the region (Shepherd et al., 2004): (1)
219 targeted species (high demand) – species that are highly prized and in high demand for their singing
220 abilities (songbirds), ornamental attractiveness (cage birds) or body parts (e.g. helmeted hornbills); and
221 (2) opportunistically trapped species (generic demand) – this includes all other species that are not
222 specifically targeted for the above reasons, but that are nonetheless trapped as 'bycatch' and sold in the
223 market whenever possible. This classification scheme thus considered all species as in demand at the
224 market, albeit to different extents. This scheme was based on insights from our informal interviews with
225 trappers and local conservationists, which suggested that all trapped birds, if still alive, would be supplied
226 to the market. Compared with opportunistically trapped species, we expected that the abundance of
227 targeted species would be more prone to the negative impacts of trapping.

229 Additionally, we classified all bird species recorded in our surveys into two ecological guilds representing
230 their dependence on undisturbed forest conditions, based on the Birds of the World database (Billerman et
231 al., 2020): (1) forest-dependent species – species that prefer primary or mature secondary forests; and (2)
232 generalist species – species that are able to survive in or prefer heavily degraded natural forests,
233 plantations, open areas, or human-dominated landscapes. Compared with generalist species, we expected
234 that the abundance of forest-dependent species would increase more markedly over time as the forest
235 condition improved under restoration (Latja et al., 2016; Owen et al., 2020). Finally, for all bird species
236 recorded in our surveys, we recorded their current IUCN Red List categories, along with descriptions of
237 the threats they face (IUCN, 2019).

239 **2.6 Statistical analysis**

241 **2.6.1 Bayesian community abundance models**. We used community-level abundance models (Royle,
242 2004; Yamaura et al., 2012, 2011) under the removal-model framework (Farnsworth et al., 2002) to
243 estimate the abundance of each species during each study period and its relationship with forest condition
244 and remoteness. Because of our focus on measuring changes in species abundance over time, we limited
245 our analysis to species that were observed during both surveys. Thus, of the 190 species we detected
246 during either study periods (177 and 143 species during the early and current periods, respectively), we
247 retained 130 species that were detected in both periods for our final analysis (Table SI2).

249 To account for imperfect detection under the removal-model framework (Farnsworth et al., 2002), we
250 divided each point count into four time intervals (t; intervals were 2.5 and 3 min for the early and current
251 periods, respectively). We tallied the number of individuals for each species that were newly detected
252 during each interval t, which we expressed as $Y_{i,j,k-t}$ for species i at point count station j during study
253 period k. Similarly, we used $\lambda_{i,j,k}$ to represent species i's true mean abundance at point count station j
254 during study period k, i.e. that expected under the forest condition and remoteness represented by the

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

258 $$\log (\lambda_{i,j,k}) = \beta_{0\ i,k} + \beta_{1\ i} \times \text{mean TCH}_{j,k} + \beta_{2\ i,k} \times \text{remoteness}_{j,k} \qquad \text{..…………… (1)}$$

260 To parameterize Formula 1 in a community-level abundance model (Royle, 2004; Yamaura et al., 2012,
261 2011), we assumed species-level coefficients follow a normal distribution that characterized the
262 community-level response; we denoted the mean of the normal-distributions for these community-level
263 coefficients as $\beta_{0c\ k}$, β_{1c}, and $\beta_{2c\ k}$, respectively. We fixed the coefficient for mean TCH ($\beta_{1\ i}$) across the
264 two study periods, as the response of a species to habitat quality is unlikely to drastically change within
265 ten years unless there was extreme selection pressure (e.g. Grant et al., 2017). However, we allowed the
266 coefficient for remoteness ($\beta_{2\ i,k}$) to change across study periods, as we hypothesized that relationships
267 between species abundance and forest remoteness may have changed over time with increased trapping.
268 We modeled the actual (i.e. realized) abundance of species i at point count station j during study period k,
269 $N_{i,j,k}$, as a Poisson draw from the mean $\lambda_{i,j,k}$ (Formula 2).

271 $$N_{i,j,k} \sim Poisson\ (\lambda_{i,j,k}) \qquad \text{……………. (2)}$$

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

276 $$N_{i,j,k\text{-}1} = N_{i,j,k}$$

277 $$N_{i,j,k\text{-}2} = N_{i,j,k\text{-}1} - Y_{i,j,k\text{-}1}$$

278 $$N_{i,j,k\text{-}3} = N_{i,j,k\text{-}2} - Y_{i,j,k\text{-}2}$$

279 $$N_{i,j,k\text{-}4} = N_{i,j,k\text{-}3} - Y_{i,j,k\text{-}3} \qquad \text{……………. (3)}$$

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

283 $$Y_{i,j,k\text{-}t} \sim Binomial\ (N_{i,j,k\text{-}t}, p_{i,j,k}) \qquad \text{..…..……… (4)}$$

284 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,
285 measured in minutes after sunrise; scaled and centered) on a logit link, treating the identity of observer m
286 as a random effect (we considered all Harapan staff as one observer; Formula 5).

287 $$\text{logit}\ (p_{i,j,k}) = \alpha_{0\ i,m} + \alpha_{1\ i,k} \times \text{survey time}_{j,k} \qquad \text{……………. (5)}$$

289 We fitted all models in a Bayesian framework using JAGS (Plummer, 2003) with the packages 'rjags'
290 (version 4-10; Plummer 2016) and 'r2jags' (version 0.6-1; Su and Yajima 2015) under program R (R
291 Development Core Team, 2018). We used uninformative priors, and we ran the model with 100,000
292 iterations on three chains, with a burn-in of 90,000 and a thinning value of 5. We evaluated the
293 convergence of the model using the Rhat value (mean Rhat of our model = 1.002), which should ideally
294 be close to 1 (Plummer, 2012). From the posterior distributions of the model, we derived, for each species
295 in each survey period, the median values and 95% Bayesian credible intervals (BCIs hereafter) for mean
296 abundance $\bar{\lambda}$ averaged across all point count stations (denoted hereafter as $\bar{\lambda}_E$ and $\bar{\lambda}_C$ for the early and
297 current periods, respectively), as well as for all model coefficients. Comparing the current versus early
298 periods, we additionally derived the median values and BCIs for the relative change between $\bar{\lambda}_C$ and $\bar{\lambda}_E$

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

301

302   **2.6.2 Assessing the impacts of trapping pressure on avifaunal recovery**. We first assessed the impacts
303   of trapping pressure on avifaunal recovery using $\Delta\beta_2$ obtained above. A more positive $\Delta\beta_2$ would indicate
304   that over time, species abundance became increasingly associated with less accessible areas (i.e., areas of
305   lower trapping pressure). We additionally assessed how these changes may have influenced species
306   abundance recovery over time due to improved forest conditions associated with restoration. To do this,
307   we calculated, for each species, a counterfactual current $\bar{\lambda}$ (denoted as $\bar{\lambda}_{Counter}$ hereafter) representing the
308   expected change in species abundance in the absence of any changes in β_2 (effect of remoteness) between
309   the early and current survey periods. We additionally derived the median values and BCIs for the relative
310   change between $\bar{\lambda}_E$ and $\bar{\lambda}_{Counter}$ (denoted as $\Delta\bar{\lambda}_{Counter}$ hereafter), for each species as well the community
311   average. We derived $\bar{\lambda}_{Counter}$ by predicting species' λ for each point count station under the current TCH
312   and remoteness conditions, but with β_2 (i.e., the effect of remoteness) fixed at the level estimated for that
313   species in the early period (Formula 6).

314

315    $\log(\lambda_{counter\ i,j,2}) = \beta_{0\ i,2} + \beta_{1\ i} \times$ mean $TCH_{j,2} + \beta_{2\ i,1} \times$ remoteness$_{j,2}$ …………. (6)

316

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

325

326   **2.6.3 Relating the impacts of trapping pressure to species traits and IUCN Red List categories.** We
327   assessed how estimated impacts of trapping pressure differed between guilds defined by species' market
328   demand and ecological traits, using four metrics that represented species-level impacts of trapping
329   pressure: the effect of remoteness (β_2) in the current period, the change in remoteness effect over time
330   ($\Delta\beta_2$), the change in species overall abundance over time ($\Delta\bar{\lambda}$), and the difference between $\Delta\bar{\lambda}$
331   and $\Delta\bar{\lambda}_{Counter}$. We assessed the proportion of species in each guild that exhibited different responses in
332   each of these metrics and used analysis of variance (ANOVA) to compare the means of each metric
333   between guilds. Finally, we compared $\Delta\beta_2$ with species' current IUCN Red List categories to understand
334   if and to what extent the threat of trapping had been commensurably represented by these assessments.

335

336   **3. RESULTS**

337   **3.1 Species' abundance changes over time**

338   We observed broadly improving forest condition at Harapan over the study period, as represented by
339   overall positive changes in TCH (Fig. 1) in areas that did not experience anthropogenic disturbances (Fig.
340   SI1). Of the 130 bird species analyzed, we found broad increases in their abundance over time.
341   Specifically, 36% of species showed significantly positive $\Delta\bar{\lambda}$ (95% BCI for $\Delta\bar{\lambda} > 0$), meaning that their
342   average abundance increased significantly over time, while an additional 53% showed tendencies of
343   positive $\Delta\bar{\lambda}$ (median for $\Delta\bar{\lambda} > 0$, although its 95% BCI overlapped with zero; Fig. 2a). While no species
344   showed significantly negative $\Delta\bar{\lambda}$ (95% BCI for $\Delta\bar{\lambda} < 0$), 12% showed tendencies of negative $\Delta\bar{\lambda}$ (median
345   for $\Delta\bar{\lambda} < 0$, although its 95% BCI overlapped with zero; Fig. 2a). On the community level, the mean $\Delta\bar{\lambda}$
346   across all species was 0.67 (95% BCI: -0.28 to 1.62; Fig. 2a; this represents the mean increase in bird

347 individual numbers for the area covered by a single point count station). Despite the consistent changes in
348 overall forest condition and species abundance, we did not find a clear relationship between them: the
349 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

351 We found negative impacts of our proxy measure for trapping pressure on species abundance for the
352 majority of species studied. In the early study period, only 5% of species analyzed showed significantly
353 positive β_2, the effect of forest remoteness on species abundance (95% BCI for $\beta_2 > 0$), with 39% showing
354 tendencies of positive β_2 (median for $\beta_2 > 0$, although it's 95% BCI overlapped with zero), but these
355 proportions increased to 9% and 68%, respectively, in the current period (Fig. SI3). On the community
356 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
357 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
358 period. Most species also showed increases in their degree of association with forest remoteness over
359 time, with 6% of species showing significantly positive $\Delta\beta_2$, and an additional 74% showing tendencies of
360 positive $\Delta\beta_2$ (Fig. 2b). Overall, on the community level, $\Delta\beta_2$ exhibited a tendency to increase over time
361 ($\Delta\beta_{2c}$ = 0.30, 95% BCI: -0.73 to 1.31; Fig. 2b). Concomitant to these signatures of trapping pressure, we
362 found that forests in Harapan had also become more accessible over time: the Euclidean distance of the
363 least accessible point count station from the nearest easy-access point decreased from 6.7 km in the early
364 period to 2.7 km in the current period.

365 The impacts of trapping pressure had a dampening effect on the recovery of avian species abundance
366 compared to what would have been expected because of improved forest condition. Specifically, this
367 recovery deficit (i.e., negative difference between $\Delta\bar{\lambda}$ and $\Delta\bar{\lambda}_{Counter}$) was significant (95% BCI < 0) for 7%
368 of the species analyzed, with an additional 67% of species showing tendencies of being significant
369 (median < 0, although it's 95% BCI overlapped with zero; Fig. 2c), whilst at the community level it was
370 -0.05 (95% BCI: -0.26 to 0.24; Fig. 2c). This recovery deficit was primarily driven by reductions in bird
371 abundances in areas of higher accessibility across Harapan, thus defining a community-level 'risk zone'
372 within 1 km from easy-access points (Fig. 2d). On the species level, the remoteness at which the risk
373 zones ended differed across species (Fig. SI4).

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

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

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

393 **4. DISCUSSION AND CONCLUSION**

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

406 Given appropriate conditions and recovery time, tropical forest restoration can allow biodiversity to
407 recover, potentially to levels close to those found in primary forests (Crouzeilles et al., 2016; Gilroy et al.,
408 2014; Rozendaal et al., 2019). However, this is possible only if the recovering biodiversity is not
409 jeopardized by factors outside the scope of restoration. Particularly for restoration initiatives aimed at
410 achieving conservation goals, tackling other threats to safeguard the hard-won biodiversity gain of
411 restoration is paramount. In the case of Harapan, financial and personnel resources supporting
412 conservation have totaled approximately 20 million USD with an annual operating cost of 1.48-2.5
413 million USD (Buergin, 2016; Diana and Jong, 2018; Silalahi et al., 2017). It is encouraging that this
414 investment is associated with broad recovery in avian populations (Fig. 2a), but the level of recovery is
415 likely to be far lower than would have been achieved had the avifauna not been subjected to sustained
416 trapping (Fig. 2c). As many bird species play key roles in the regeneration and functioning of forest
417 ecosystems (e.g. through seed dispersal, Morrison & Lindell 2012; de la Peña-Domene et al. 2014),
418 declines driven by trapping could lead to cascading ecological impacts that further limit the effectiveness
419 of forest restoration (Gardner et al., 2019).

420 Our study adds to the growing evidence that trade-driven trapping of forest birds constitutes a grave threat
421 to Southeast Asia's forest avifauna (Symes et al., 2018), especially in Indonesia. Evidence from market
422 surveys (Chng et al., 2018, 2015; Shepherd, 2006) and communications with local experts, Harapan field
423 staff and the trappers themselves suggest that bird trapping is generally indiscriminate in its methods, in
424 part because markets accept most species (Shepherd et al., 2004) and there is high mortality of birds along
425 the supply chain. These factors together incentivize trappers to maximize capture rates (Jepson and Ladle,
426 2005; Shepherd et al., 2004). As trapping depletes local bird populations, the economic incentive for
427 indiscriminately trapping any species will likely intensify, with or without increases in market demand
428 (Beastall et al., 2016; Courchamp et al., 2006; Shepherd, 2012; TRAFFIC, 2018); possibly explaining
429 similar risk zone's remoteness we observed for both targeted and opportunistically trapped species (Fig.
430 SI5). The impacts of trapping on wildlife populations are further exacerbated by the rapid loss of forest
431 habitat across Southeast Asia, which not only directly threatens biodiversity persistence (Margono et al.,
432 2012), but also facilitates trapper access by expanding the road and trail network (Harris et al., 2017;
433 Hughes, 2018). Multiple threatened species detected in our surveys showed significant negative impacts
434 of trapping pressure, along with several species, for which trapping has yet to be formally recognized as a
435 conservation threat (Fig. 4 & Table SI2). As an example, aside from the Endangered Greater Green
436 Leafbird *Chloropsis sonnerati* for which the threat of trapping has been well recognized (Eaton et al.,
437 2017), our models suggested that the Yellow-bellied Bulbul *Alophoixus phaeocephalus* (Least Concern),
438 Sooty Barbet *Caloramphus hayii,* and Blue-rumped Parrot *Psittinus cyanurus* (both Near Threatened)
439 were also negatively affected, significantly, by trapping (Table SI2). In addition, a large number of
440 species of lower conservation concern exhibited significant, or near significant, negative signals of

9

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

443 Two caveats to our findings warrant discussion. First, because our early and current bird surveys were
444 conducted by different surveyors, the observed difference in species abundance between study periods
445 may have in part been an artifact of observer effects. While we have taken measures to alleviate this
446 potential problem, these measures cannot fully rule out the possibility that differences in observer
447 detection abilities may have contributed to the increased species abundance found in the current period.
448 This issue, however, is often inevitable for studies or monitoring efforts that cover a large temporal span.
449 Second, while we were able to assess the increases in TCH for low forest canopies (typically < 15 m)
450 accurately, the potential TCH increases of tall forests were more challenging to assess due to the well-
451 known saturation of tree height predictions using LiDAR data (Hansen et al., 2016; Swinfield et al.,
452 2019). This bias should be at least in part responsible for the observed weak relationship between species
453 abundance and mean TCH. Nonetheless, as our inferences focused on the relationship between species
454 abundance and remoteness as a proxy for trapping pressure (i.e., β_2), we note that neither of the above
455 caveats undermines our central finding that trapping pressure hampered the conservation gains of forest
456 restoration for avian diversity at Harapan.

457 The threats that trapping poses to forest birds call for urgent conservation intervention. Here we provide
458 several practical recommendations for Southeast Asia. First, effective anti-trapping/poaching patrols and
459 law enforcement (Miller et al., 2019), including penalties to lawbreakers as deterrents (Leupen et al.,
460 2018; López-Bao et al., 2015), coupled with alternative livelihood schemes should be adopted to decrease
461 trapping incentives. Employing local communities and where possible, bird trappers in patrolling and as
462 birdwatching guides could provide them with economic incentives to forego trapping and/or engage in
463 conservation, and to cultivate a genuine long-term interest in supporting conservation (Widmann and
464 Widmann, 2008). Second, to provide the basis for devising conservation actions, region-wide threat
465 assessments on the severity and extent of trade and trapping should be conducted on all bird species in
466 Southeast Asia, and check if localized threats we detected reflect the broader situation. Such assessments
467 should use a combination of market- (Harris et al., 2015) and field-based surveys to inform site-specific,
468 targeted conservation interventions (as an example, see Eaton et al. 2015b) These interventions could
469 include *in situ* management of species (Pain et al., 2006) and habitat (including nest site provisioning; e.g.
470 Kurniandaru 2008), conservation breeding (Collar et al., 2012), and possibly, commercial captive
471 breeding or 'ranching' (J. A. Eaton et al., 2015) of key, high-profile species such as the White-rumped
472 Shama, *Copsychus malabaricus* (Palko et al., 2011). These assessments should also pre-emptively cover
473 species not yet found in large quantities in markets and should consider potential taxonomic changes
474 (Eaton et al., 2016). More broadly, efforts should be made to better understand and address the underlying
475 drivers of wild bird trapping (Burivalova et al., 2017; Marshall et al., 2019) through a collaborative,
476 multi-stakeholder approach, such as that showcased by the Asian Songbird Trade Specialist Group
477 (Shepherd and Cassey, 2017), and to explore behavioral change interventions that target consumers and
478 other components of the trade supply chain (Veríssimo, 2013).

479 Forest restoration is urgently needed in many tropical regions that have experienced extensive
480 deforestation and forest degradation (Edwards et al., 2019), including Southeast Asia (FAO and UNEP,
481 2020; Wilcove et al., 2013). However, its effectiveness to recover biodiversity could be compromised by
482 wildlife trapping and more broadly, exploitation, as our study demonstrated. The increased accessibility
483 of degraded forests compounds this challenge (Hughes, 2018). The realization of the conservation
484 promise of forest restoration (Strassburg et al., 2020), therefore, hinges critically on not only effective
485 restoration actions but also on how effectively we can manage local stakeholder partnerships and protect
486 these forest areas from other anthropogenic threats.

487 **ACKNOWLEDGEMENTS**

REFERENCES

498 Asner GP, Brodrick PG, Philipson C, Vaughn NR, Martin RE, Knapp DE, Heckler J, Evans LJ, Jucker T,
499 Goossens B. 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in
500 Malaysian Borneo. Biological Conservation 217:289–310. DOI: 10.1016/j.biocon.2017.10.020.

501 Barlow J et al. 2018. The future of hyperdiverse tropical ecosystems. Nature 559:517–526.

502 Beastall C, Shepherd CR, Hadiprakarsa Y, Martyr D. 2016. Trade in the Helmeted Hornbill Rhinoplax
503 vigil: the 'ivory hornbill.' Bird Conservation International 26:137–146. DOI:
504 10.1017/S0959270916000010.

505 Beygelzimer A, Kakadet S, Langford J, Arya S, Mount D, Li S. 2019. Package 'FNN': FNN: Fast Nearest
506 Neighbor Search Algorithms and Applications. Version 1.1.3. Available from https://cran.r-project.org/
507 (accessed October 2020).

508 Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS, editors. 2020. Birds of the World. Cornell
509 Laboratory of Ornithology, Ithaca, NY. Available from https://birdsoftheworld.org/ (accessed November
510 2020).

511 BirdLife International. 2017. Forests of Hope site - Harapan Rainforest, Indonesia. Available from
512 http://www.birdlife.org/ (accessed November 2020).

513 BirdLife International. 2020. Species factsheet: *Rhinoplax vigil*. Available from http://www.birdlife.org/
514 (accessed November 2020).

515 Breiman L, Cutler A. 2018. Package 'randomForest': Breiman and Cutler's Random Forests for
516 Classification and Regression. Version 4.6. Available from https://cran.r-project.org/ (accessed October
517 2019).

518 Buergin R. 2016. Ecosystem restoration concessions in Indonesia: conflicts and discourses. Critical Asian
519 Studies 48:278–301. DOI: 10.1080/14672715.2016.1164017.

520 Burivalova Z, Lee TM, Hua F, Lee JSH, Prawiradilaga DM, Wilcove DS. 2017. Understanding consumer
521 preferences and demography in order to reduce the domestic trade in wild-caught birds. Biological
522 Conservation 209:423–431. DOI: 10.1016/j.biocon.2017.03.005.

523 Chazdon R, Brancalion P. 2019. Restoring forests as a means to many ends. Science 365:24–25.

524 Chazdon RL, Brancalion PHS, Lamb D, Laestadius L, Calmon M, Kumar C. 2017. A Policy-Driven
525 Knowledge Agenda for Global Forest and Landscape Restoration. Conservation Letters 10:125–132.
526 DOI: 10.1111/conl.12220.

527 Chng SCL, Eaton JA, Krishnasamy K, Shepherd CR. 2015. In the Market for Extinction: An inventory of
528 Jakarta's bird markets. TRAFFIC Report. Petaling Jaya, Selangor, Malaysia.

529 Chng SCL, Shepherd CR, Eaton JA. 2018. In the market for extinction: birds for sale at selected outlets in
530 Sumatra. TRAFFIC Bulletin 30(1):15-22.

531 Collar NJ, Gardner L, Jeggo DF, Marcordes B, Owen A, Pagel T, Pes T, Vaidl A, Wilkinson R, Wirth R.
532 2012. Conservation breeding and the most threatened birds in Asia. BirdingAsia 18:50–57.

533 Cosset CCP, Edwards DP. 2017. The effects of restoring logged tropical forests on avian phylogenetic
534 and functional diversity. Ecological Applications 27:1932–1945. DOI: 10.1002/eap.1578.

535 Courchamp F, Angulo E, Rivalan P, Hall RJ, Signoret L, Bull L, Meinard Y. 2006. Rarity value and
536 species extinction: the anthropogenic Allee effect. PLOS Biology 4. DOI: 10.1371/journal.pbio.0040415.

537 Crouzeilles R, Curran M, Ferreira MS, Lindenmayer DB, Grelle CEV, Rey Benayas JM. 2016. A global
538 meta-Analysis on the ecological drivers of forest restoration success. Nature Communications 7. DOI:
539 10.1038/ncomms11666

540 Csillik O, Kumar P, Mascaro J, O'Shea T, Asner GP. 2019. Monitoring tropical forest carbon stocks and
541 emissions using Planet satellite data. Scientific Reports 9:17831. DOI: 10.1038/s41598-019-54386-6

542 de la Peña-Domene M, Martínez-Garza C, Palmas-Pérez S, Rivas-Alonso E, Howe HF. 2014. Roles of
543 birds and bats in early tropical-forest restoration. PloS one 9: e104656. DOI:
544 10.1371/journal.pone.0104656.

545 Diana E, Jong HN. 2018. End of funding dims hopes for a Sumatran forest targeted by palm oil growers.
546 Mongabay. Available from https://news.mongabay.com/ (accessed March 2020).

547 Eaton JA, Chng SCL, Miller AE. 2017. Second South-east Asian Songbird Crisis Summit. TRAFFIC
548 Bulletin 29(1):3-4.

549 Eaton JA, Shepherd CR, Rheindt FE, Harris JBC, van Balen S, Wilcove DS, Collar NJ. 2015a. Trade-
550 driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. Forktail:1–12.

551 Eaton JA, van Balen S, Brickle NW, Rheindt FE. 2016. Birds of the Indonesian Archipelago: Greater
552 Sundas and Wallacea. Lynx. Spain.

553 Eaton M, Aebischer N, Brown A, Hearn R, Lock L, Musgrove A, Noble D, Stroud D, Gregory R. 2015b.
554 Birds of Conservation Concern 4: the population status of birds in the UK, Channel Islands and Isle of
555 Man. British Birds 108:708–746.

556 Edwards DP et al. 2014. Selective-logging and oil palm: Multitaxon impacts, biodiversity indicators, and
557 trade-offs for conservation planning. Ecological Applications 24:2029–2049. DOI: 10.1890/14-0010.1

558 Edwards DP, Ansell FA, Ahmad AH, Nilus R, Hamer KC. 2009. The value of rehabilitating logged
559 rainforest for birds. Conservation Biology 23:1628–1633. DOI: 10.1111/j.1523-1739.2009.01330.x

560 Edwards DP, Socolar JB, Mills SC, Burivalova Z, Koh LP, Wilcove DS. 2019. Conservation of Tropical
561 Forests in the Anthropocene. Current Biology 29: R1008–R1020.

562 FAO, UNEP. 2020. The State of the World's Forests 2020. Forests, biodiversity and people. Accessed
563 from http://www.fao.org/ (accessed August 2020).

564 Farnsworth GL, Pollock KH, Nichols JD, Simons TR, Hines JE, Sauer JR. 2002. A removal model for
565 estimating detection probabilities from point-count surveys. The Auk 119:414–425.

566 Gardner CJ, Bicknell JE, Baldwin-Cantello W, Struebig MJ, Davies ZG. 2019. Quantifying the impacts
567 of defaunation on natural forest regeneration in a global meta-analysis. Nature Communications 10:4590.
568 DOI: 10.1038/s41467-019-12539-1.

569   Gibson L et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature
570   478:378–381.

571   Gilroy JJ, Woodcock P, Edwards FA, Wheeler C, Baptiste BLG, Uribe CAM, Haugaasen T, Edwards DP.
572   2014. Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism.
573   Nature Climate Change 4:503–507. DOI: 10.1038/nclimate2200.

574   Gokkon B. 2018. Indonesia gives in to bird traders, rescinds protection for 3 species. Mongabay.
575   Available from https://news.mongabay.com/ (accessed March 2020).

576   Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J. 2017. Evolution caused by extreme
577   events. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160146.

578   Hansen MC, Potapov P V, Goetz SJ, Turubanova S, Tyukavina A, Krylov A, Kommareddy A, Egorov A.
579   2016. Mapping tree height distributions in Sub-Saharan Africa using Landsat 7 and 8 data. Remote
580   Sensing of Environment 185:221–232. DOI: 10.1016/j.rse.2016.02.023.

581   Harris JBC et al. 2017. Measuring the impact of the pet trade on Indonesian birds. Conservation Biology
582   31:394–405. DOI: 10.1111/cobi.12729.

583   Harris JBC, Green JMH, Prawiradilaga DM, Giam X, Hikmatullah D, Putra CA, Wilcove DS. 2015.
584   Using market data and expert opinion to identify overexploited species in the wild bird trade. Biological
585   Conservation 187:51–60. DOI: 10.1016/j.biocon.2015.04.009.

586   Harrison RD, Sreekar R, Brodie JF, Brook S, Luskin M, O'Kelly H, Rao M, Scheffers B, Velho N. 2016.
587   Impacts of hunting on tropical forests in Southeast Asia. Conservation Biology 30:972–981. DOI:
588   10.1111/cobi.12785.

589   Harrison RD, Swinfield T. 2015. Restoration of Logged Humid Tropical Forests: An Experimental
590   Programme at Harapan Rainforest, Indonesia. Tropical Conservation Science 8:4–16. DOI:
591   10.1177/194008291500800103.

592   Hastie T, Tibshirani R, Friedman J. 2009. The elements of statistical learning: data mining, inference, and
593   prediction. Springer Science & Business Media. Springer-Verlag, New York.

594   Hua F, Yong DL, Janra MN, Fitri LM, Prawiradilaga D, Sieving KE. 2016. Functional traits determine
595   heterospecific use of risk-related social information in forest birds of tropical South-East Asia. Ecology
596   and Evolution 6:8485–8494. DOI: 10.1002/ece3.2545.

597   Hughes AC. 2018. Have Indo-Malaysian forests reached the end of the road? Biological Conservation
598   223:129–137. DOI: 10.1016/j.biocon.2018.04.029.

599   IUCN. 2019. The IUCN Red List of Threatened Species. Available from http://www.iucnredlist.org
600   (accessed October 2020).

601   Jepson P. 2010. Towards an Indonesian bird conservation ethos: reflections from a study of bird-keeping
602   in the cities of Java and Bali. Pages 313–330 in Tidemann SC, Gosler A, editors. Ethno-ornithology:
603   Birds, indigenous peoples, culture and society: Routledge, UK.

604   Jepson P, Ladle RJ. 2005. Bird-keeping in Indonesia: Conservation impacts and the potential for
605   substitution-based conservation responses. Oryx 39:442–448.

606   Jin S, Sader SA. 2005. Comparison of time series tasseled cap wetness and the normalized difference
607   moisture index in detecting forest disturbances. Remote sensing of Environment 94:364–372. DOI:
608   10.1016/j.rse.2004.10.012.

609   Kurniandaru S. 2008. Providing nest boxes for Java sparrows Padda oryzivora in response to nest site loss
610   due to building restoration and an earthquake, Prambanan Temple, Java, Indonesia. Conservation
611   Evidence 5:62–68.

612   Latja P, Valtonen A, Malinga GM, Roininen H. 2016. Active restoration facilitates bird community
613   recovery in an Afrotropical rainforest. Biological Conservation 200:70–79. DOI:
614   10.1016/j.biocon.2016.05.035.

615   Lee DC, Lindsell JA. 2011. Biodiversity of Harapan Rainforest: Summary report on baseline surveys of
616   mammals, birds, fish, herptiles, butterflies and habitat. Royal Society for Protection of Birds. Sandy, UK.

617   Leupen BTC, Krishnasamy K, Shepherd CR, Chng SCL, Bergin D, Eaton JA, Yukin DA, Hue SKP,
618   Miller A, NEKARIS KA-I. 2018. Trade in White-rumped Shamas Kittacincla malabarica demands strong
619   national and international responses. Forktail Journal of Asian Ornithology 34:1–8.

620   Lewis SL, Wheeler CE, Mitchard ETA, Koch A. 2019. Restoring natural forests is the best way to remove
621   atmospheric carbon. Nature 568:25–28.

622   López-Bao J V et al. 2015. Toothless wildlife protection laws. Biodiversity and Conservation 24:2105–
623   2108. DOI: 10.1007/s10531-015-0914-8

624   Margono BA, Turubanova S, Zhuravleva I, Potapov P, Tyukavina A, Baccini A, Goetz S, Hansen MC.
625   2012. Mapping and monitoring deforestation and forest degradation in Sumatra (Indonesia) using Landsat
626   time series data sets from 1990 to 2010. Environmental Research Letters 7. DOI: 10.1088/1748-
627   9326/7/3/034010.

628   Marshall H, Collar NJ, Lees AC, Moss A, Yuda P, Marsden SJ. 2019. Spatio-temporal dynamics of
629   consumer demand driving the Asian Songbird Crisis. Biological Conservation:108237. DOI:
630   10.1016/j.biocon.2019.108237.

631   Miller AE, Gary D, ansyah J, Sagita N, Muflihati, Kartikawati, Adirahmanta SN. 2019. Socioeconomic
632   Characteristics of Songbird Shop Owners in West Kalimantan, Indonesia. Tropical Conservation Science.
633   DOI: 10.1177/1940082919889510.

634   Morrison EB, Lindell CA. 2012. Birds and bats reduce insect biomass and leaf damage in tropical forest
635   restoration sites. Ecological Applications 22:1526–1534. DOI: 10.1890/11-1118.1.

636   Owen KC, Melin AD, Campos FA, Fedigan LM, Gillespie TW, Mennill DJ. 2020. Bioacoustic analyses
637   reveal that bird communities recover with forest succession in tropical dry forests. Avian Conservation
638   and Ecology 15 (1): 25. DOI: 10.5751/ACE-01615-150125.

639   Pain DJ, Martins TLF, Boussekey M, Diaz SH, Downs CT, Ekstrom JMM, Garnett S, Gilardi JD,
640   McNiven D, Primot P. 2006. Impact of protection on nest take and nesting success of parrots in Africa,
641   Asia and Australasia. Animal Conservation 9:322–330. DOI: 10.1111/j.1469-1795.2006.00040.x.

642   Palko I V, Kalyakin M V, Thinh N V. 2011. Nesting of the White-rumped Shama (Copsychus
643   malabaricus) in southern Vietnam. Bonner Zoologische Monographien 57:185-191.

644   Parry RL. 2019. Indonesian craze for songbird contests is gambling with their lives. The Times. Available
645   from https://www.thetimes.co.uk/ (accessed March 2020).

646   Plummer M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.
647   Proceedings of the 3rd international workshop on distributed statistical computing. Vienna, Austria.

648   Plummer M. 2012. JAGS Version 3.3.0 user manual. International Agency for Research on Cancer, Lyon,
649   France.

14

Plummer M. 2016. Package 'rjags': Bayesian graphical models using MCMC. Version 3. Available from https://cran.r-project.org/ (accessed November 2018).

Potapov P et al. 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances 3. DOI: 10.1126/sciadv.1600821.

R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Royle JA. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. Biometrics 60:108–115. DOI: 10.1111/j.0006-341X.2004.00142.x.

Rozendaal DMA, Bongers F, Aide TM, Alvarez-Dávila E, Ascarrunz N, Balvanera P, Becknell JM, Bentos T V, Brancalion PHS, Cabral GAL. 2019. Biodiversity recovery of Neotropical secondary forests. Science Advances 5. DOI: 10.1126/sciadv.aau3114.

Scheffers BR, Oliveira BF, Lamb I, Edwards DP. 2019. Global wildlife trade across the tree of life. Science 366:71–76.

Senior RA, Hill JK, Edwards DP. 2019. Global loss of climate connectivity in tropical forests. Nature Climate Change 9:623–626. DOI: 10.1038/s41558-019-0529-2.

Shepherd CR. 2006. The bird trade in Medan, north Sumatra: An overview. BirdingASIA 5:16–24.

Shepherd CR. 2012. The owl trade in Jakarta, Indonesia: a spot check on the largest bird markets. BirdingASIA 18:58–59.

Shepherd CR, Cassey P. 2017. Songbird trade crisis in Southeast Asia leads to the formation of IUCN SSC Asian Songbird Trade Specialist Group. Journal of Indonesian Natural History 5:3–5.

Shepherd CR, Sukumaran J, Wich SA. 2004. Open season: An analysis of the pet trade in Medan, Sumatra, 1997-2001. TRAFFIC Southeast Asia Report. Petaling Jaya, Selangor, Malaysia.

Silalahi M, Utomo AB, Walsh TA, Ayat A, Bashir S. 2017. Indonesia's ecosystem restoration concessions. Unasylva 68: 63-70.

Sodhi NS et al. 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. Biological Conservation. DOI: 10.1016/j.biocon.2009.12.029.

Strassburg BBN et al. 2020. Global priority areas for ecosystem restoration. Nature. 586, 724–729.

Su Y-S, Yajima M. 2015. Package 'R2jags': Using R to run 'JAGS.' Version 0.5-7. Available from https://cran.r-project.org/ (accessed November 2018).

Swinfield T, Lindsell JA, Williams J V, Harrison RD, Gemita E, Schönlieb CB, Coomes DA. 2019. Accurate Measurement of Tropical Forest Canopy Heights and Aboveground Carbon Using Structure from Motion. Remote Sensing 11:928.

Symes WS, Edwards DP, Miettinen J, Rheindt FE, Carrasco LR. 2018. Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. Nature Communications 9:4052. DOI: 10.1038/s41467-018-06579-2.

TRAFFIC. 2018. Massive wild bird seizures reflect soaring pressure on Sumatran birds. Available from https://www.traffic.org/ (September 2019).

Veríssimo D. 2013. Influencing human behaviour: an underutilised tool for biodiversity management. Conservation Evidence 10:29–31.

689 Watson JEM et al. 2018. The exceptional value of intact forest ecosystems. Nature Ecology and Evolution
690 2:599–610. DOI: 10.1038/s41559-018-0490-x.

691 Widmann P, Widmann IL. 2008. The cockatoo and the community: ten years of Philippine Cockatoo
692 Conservation Programme. Birding Asia 10:23–29.

693 Wilcove DS, Giam X, Edwards DP, Fisher B, Koh LP. 2013. Navjot's nightmare revisited: logging,
694 agriculture, and biodiversity in Southeast Asia. Trends in ecology & evolution 28:531–540.

695 Xue J, Su B. 2017. Significant remote sensing vegetation indices: A review of developments and
696 applications. Journal of Sensors. Hindawi. DOI: 10.1155/2017/1353691.

697 Yamaura Y, Andrew Royle J, Kuboi K, Tada T, Ikeno S, Makino S. 2011. Modelling community
698 dynamics based on species-level abundance models from detection/non detection data. Journal of applied
699 ecology 48:67–75.

700 Yamaura Y, Royle JA, Shimada N, Asanuma S, Sato T, Taki H, Makino S. 2012. Biodiversity of man-
701 made open habitats in an underused country: a class of multispecies abundance models for count data.
702 Biodiversity and Conservation 21:1365–1380. DOI: 10.1007/s10531-012-0244-z.

703 Zvoleff A. 2020. Package 'glcm': Calculate Textures from Grey-Level Co-Occurrence Matrices
704 (GLCMs). Version version 1.6.5. Available from https://cran.r-project.org/ (accessed March 2020).

705

706 **FIGURES**

707
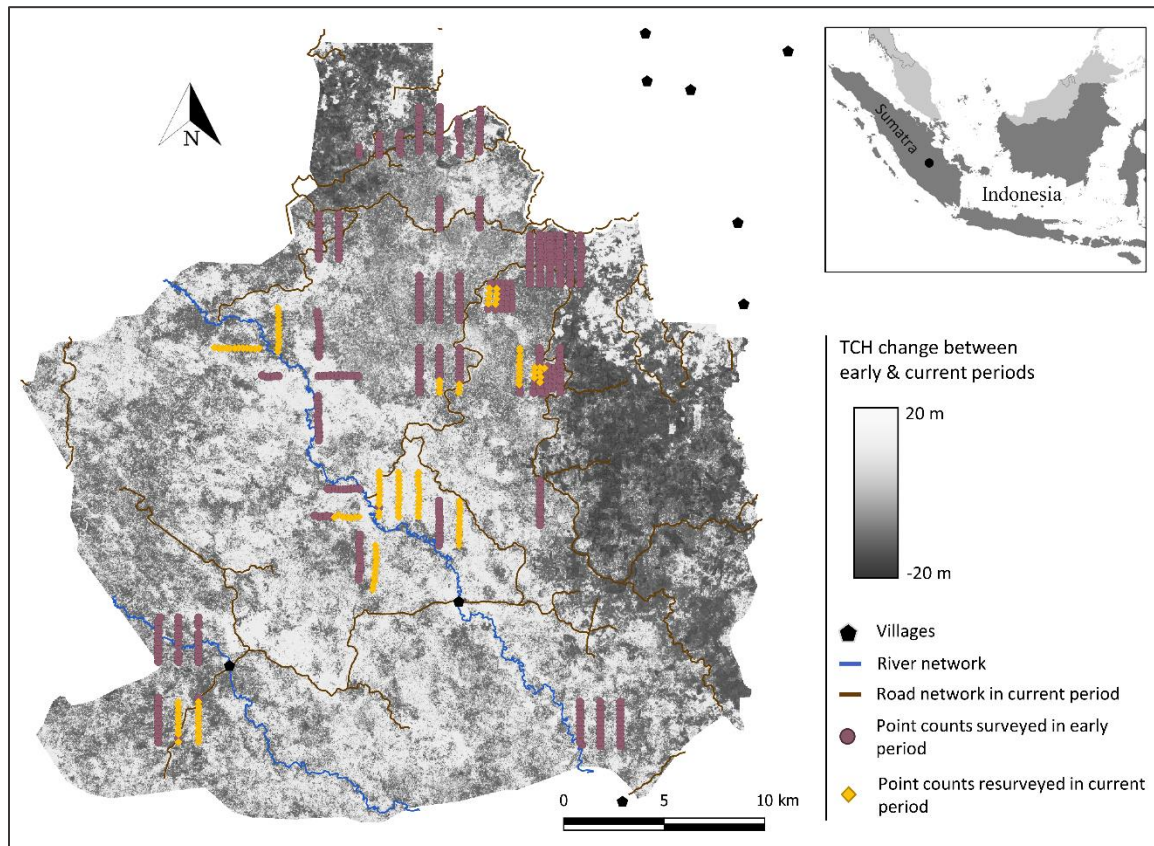
Fig. 1. Distribution of point count stations and changes in forest condition over time at Harapan Rainforest. Point count stations surveyed during the early period (2009-2011) are displayed in purple; those surveyed during both the early and current (2018) periods are displayed in yellow. The map also 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.
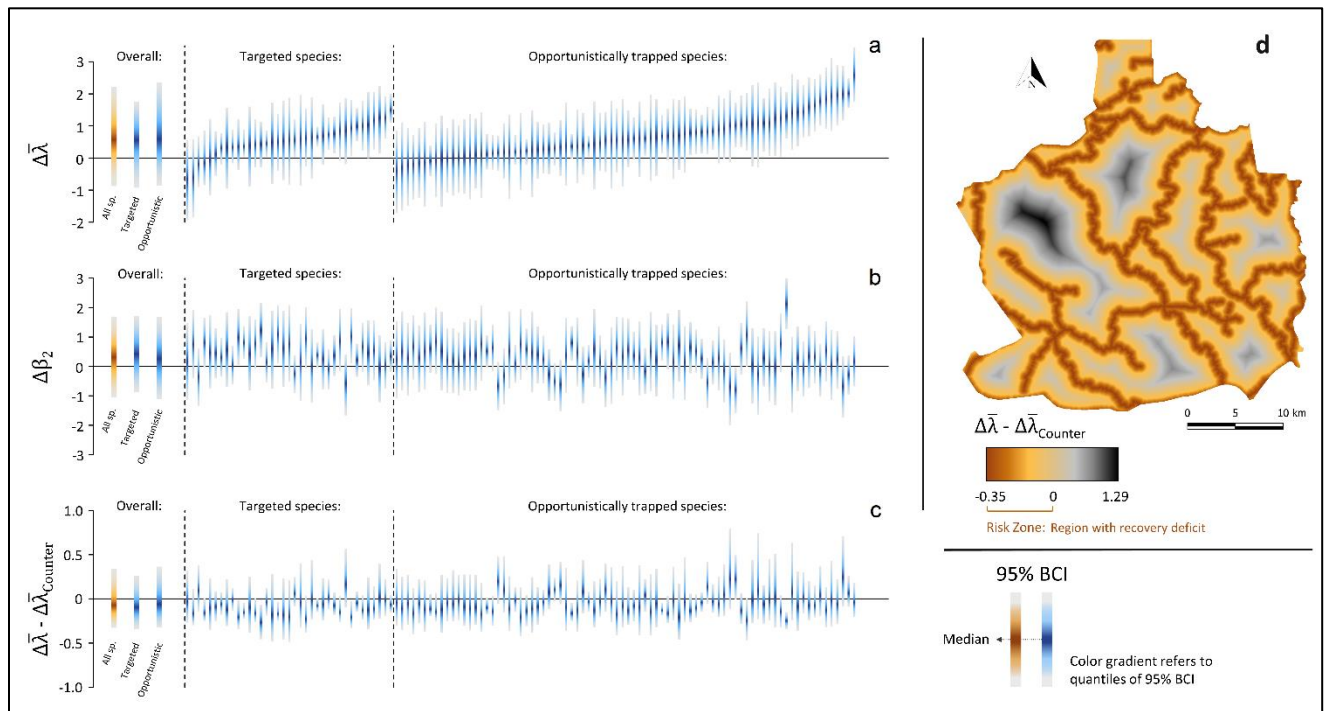

Fig. 2. The recovery pattern of bird species abundance in Harapan and the impacts it sustained from the trapping pressure. (a) Changes in mean species abundance between the early and current periods ($\Delta\bar{\lambda}$). (b) Changes in the effect of remoteness on species abundance between the early 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.

17

736
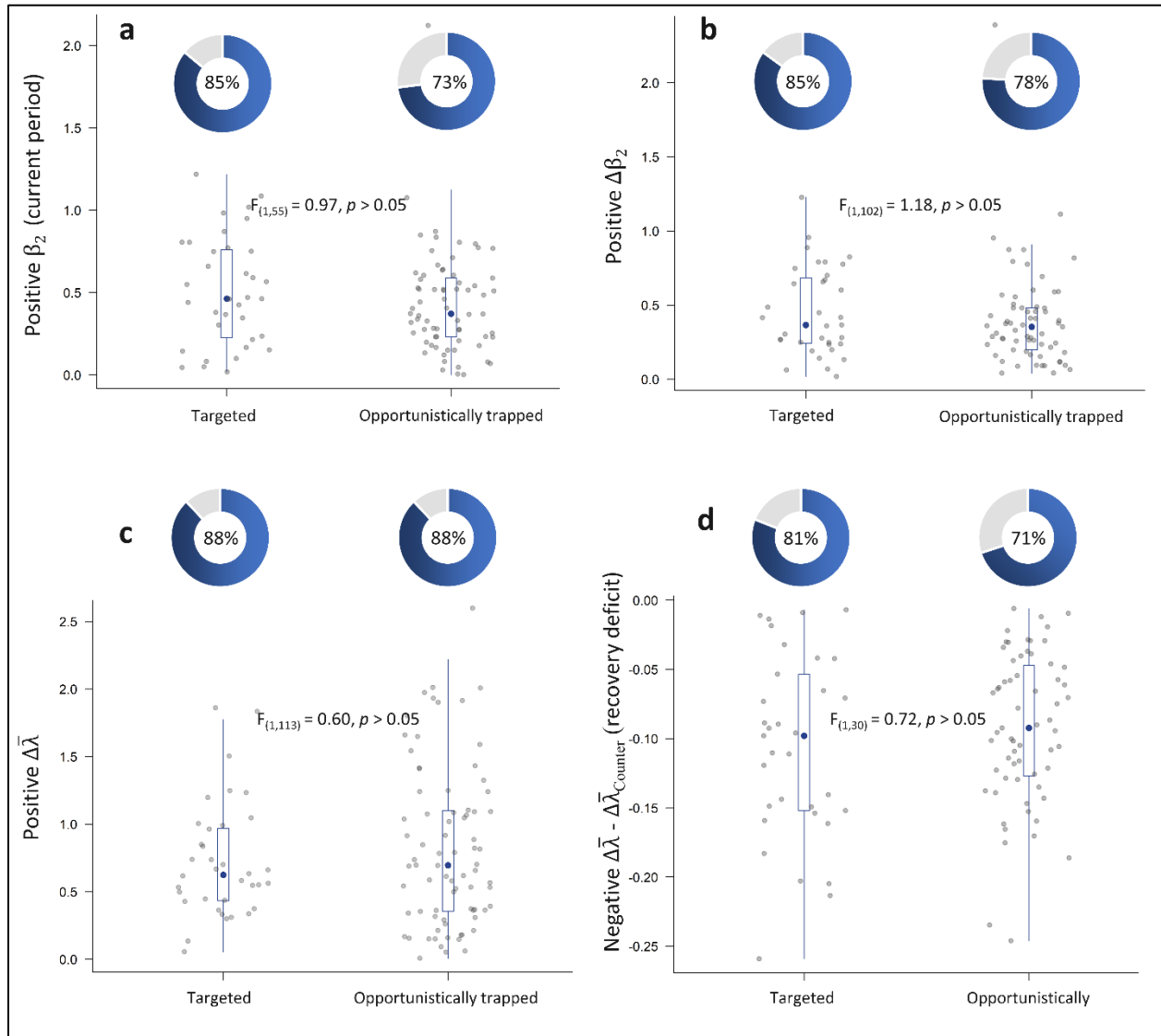
737
738
739 Fig. 3. Comparison between the targeted and opportunistically trapped species with regard to the negative
740 effects of trapping pressure on their abundance, as represented by (a) positive β_2 in the current period, (b)
741 positive $\Delta\beta_2$ between the early and current periods, (c) positive $\Delta\bar{\lambda}$ between the early and current periods,
742 and (d) negative $\Delta\bar{\lambda}$ - $\Delta\bar{\lambda}_{Counter}$. For each of the above four metrics, comparisons concerned (1) the
743 proportion of species in each guild that exhibited responses indicative of more severe negative effects of
744 trapping pressure (pie chart in the upper portion of each panel), as well as (2) ANOVA test of the metric
745 values between the two guilds as represented by jittered box plots (lower portion of each panel; each point
746 represents an individual species).
747

18
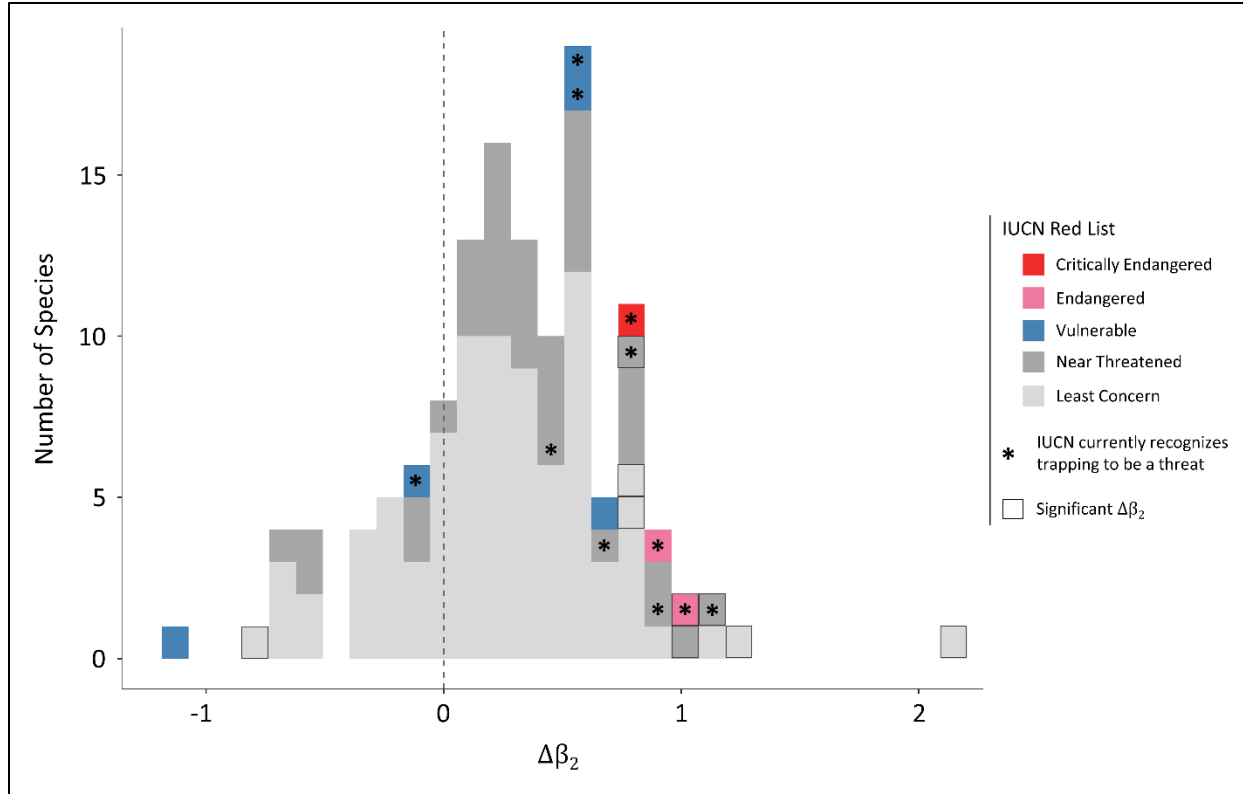
Fig. 4. The extent to which the threat of trapping pressure on our study species was captured by the IUCN
Red List assessments. We represented the threat of trapping pressure by $\Delta\beta_2$ between the early and current
periods, with species binned into 0.1-wide $\Delta\beta_2$ intervals. Those species 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.