1    **Title:** Below the canopy: global trends in forest vertebrate populations and their drivers

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13   **Abstract**

14   Global forest assessments use forest area as a proxy indicator of biodiversity status, which may

15   mask below-canopy pressures driving forest biodiversity loss and 'empty forest' syndrome. The

16   status of forest biodiversity is important not only for species conservation but also because species

17   loss can have consequences for forest health and carbon storage. We aimed to develop a global

18   indicator of forest specialist vertebrate populations to improve assessments of forest biodiversity

19   status. For this purpose we used the Living Planet Index methodology, developing a weighted

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20  composite Forest Specialist Index for the period 1970-2014. We then investigated potential drivers

21  of forest vertebrate population change, including tree cover change, to determine whether forest

22  area is a good proxy for forest biodiversity. The effects of satellite-derived tree cover trends and

23  other pressures on the average rate of change of forest vertebrate populations were analysed. We

24  reviewed the literature to gain more context-specific information relating to drivers of forest

25  specialist population change. On average, forest vertebrate populations declined by 53% between

26  1970 and 2014. We found little evidence of a consistent global effect of tree cover change on forest

27  vertebrate populations but a significant negative effect of exploitation threat on forest specialists.

28  However, time-series cross-correlation analyses showed some forest specialist populations are

29  closely aligned to tree cover change. The literature review identified several drivers of population

30  change that cannot be detected remotely and may cause populations to change independently of

31  tree cover. Forest vertebrate populations have more than halved since the 1970s. In conclusion, we

32  found that forest area is a poor proxy of forest biodiversity status. For forest biodiversity to recover,

33  we must monitor and manage all threats to vertebrates, including those below the canopy.

34

37

**Introduction**

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40  As we approach the 2020 deadline for the Aichi Biodiversity Targets under the Convention on

41  Biological Diversity (CBD), the continuing loss of biodiversity remains a seemingly intractable

42  environmental challenge (Ceballos et al., 2015) with grave implications for human wellbeing and

43     the supply of valuable ecosystem services (Dirzo et al., 2014). Some 322 vertebrates have become

44     extinct since 1500, and more than 27% of all assessed extant species are threatened with extinction

45     (Dirzo et al., 2014; IUCN, 2019).  At a global scale, the average abundance of monitored vertebrate

46     populations declined by 60% between 1970 and 2014 (WWF, 2018). With the average rate of

47     vertebrate species loss over the last century being up to 100 times the background rate, there is

48     little doubt that we have entered an era representing the sixth mass extinction (Ceballos et al.,

49     2015).

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51     Deforestation has been a significant driver of this worldwide biodiversity crisis. Over a century

52     ago most clearance was of temperate forests (Brooks, Pimm, & Oyugi, 1999) leading to observed

53     species extinctions (Pimm & Askins, 1995), whilst in the last decades the main deforestation

54     frontiers and risks to biodiversity have been in the tropics (Gibbs et al., 2010; Myers, 1993; Song

55     et al., 2018). Tropical forests are some of the most biodiverse ecosystems on Earth, harbouring

56     over half the world's terrestrial species (Groombridge & Jenkins, 2003). Yet deforestation and

57     degradation of tropical forests have reduced their land coverage from 12% to less than 5%

58     (Brandon, 2014), primarily as a result of large-scale industrial and local subsistence agriculture

59     (Hosonuma et al., 2012) as well as logging, fires and fragmentation (Lewis, Edwards, & Galbraith,

60     2016). This represents a loss of important resources and habitat for humanity (between 1.2 and 1.5

61     billion people are directly dependent on ecosystem services provided by tropical forests; (Vira et

62     al., 2015) as well as biodiversity, with far-reaching implications for the climate system (Lewis et

63     al., 2016) and global carbon cycle (McNicol, Ryan, & Mitchard, 2018; Sullivan et al., 2017).

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3

65  Land use change is predicted to continue as a major driver of terrestrial biodiversity loss for the

66  rest of this century (Sala et al., 2000). In order to assess the impacts of land conversion pressures,

67  it is crucial to develop national-to-global scale biodiversity measurements (Scholes et al., 2008).

68  Yet, in the absence of a global measure of the status of forest biodiversity, forest area has been

69  employed as a proxy indicator during global target setting and monitoring processes. Under the

70  Strategic Plan for Biodiversity 2011-2020, for example, Aichi Target 5 focuses on halving the rate

71  of loss of forests and other natural habitats by 2020 (CBD, 2010). The suite of indicators for

72  Sustainable Development Goal 15 ('Life on land') of the 2030 Agenda on Sustainable

73  Development includes forest area as a proportion of total land area, and the proportion of forest

74  and other ecosystems covered by protected areas (UN DESA, 2017). Similarly, indicators used to

75  monitor biodiversity conservation in the Forest Resources Assessment of the Food and

76  Agricultural Organisation (FAO) comprise area of primary forest, forest area designated for the

77  conservation of biodiversity, and forest area in legally established protected areas (FAO, 2016).

78  However, the pertinence of forest area as a proxy indicator of forest biodiversity has never been

79  tested. While habitat loss is the major driver of forest biodiversity loss, a focus on forest area alone

80  risks masking other pressures on forest vertebrates that can operate below the canopy in

81  conjunction with or independently of forest cover change. Consequently, areas with stable or

82  increasing forest cover might be experiencing undetected declines in forest vertebrates, leading to

83  so-called 'empty forests' that appear intact but have lost many of their large animals (Redford,

84  1992).

85

86  Understanding the status of forest biodiversity is important not only for species conservation but

87  also because biodiversity loss can have consequences for forest health and carbon stocks). The

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88    status of the world's forests is a critical factor in the avoidance of dangerous climate change, with

89    almost all scenarios consistent with meeting the 1.5 degree target requiring the maintenance and

90    expansion of forest area. Forests are well recognised in the Paris Agreement on climate change for

91    their potential to reduce emissions, act as carbon sinks, and deliver "non-carbon benefits",

92    including biodiversity conservation. Concurrently, the conservation of biodiversity in forests can

93    have direct carbon benefits. Recent research has shed light on the important role that some forest

94    vertebrates, particularly large birds and primates, play in forest regeneration and long-term carbon

95    storage (Gardner, Bicknell, Struebig, & Davies, 2017). A loss or reduction in forest vertebrates

96    from regions with a high proportion of large-seeded animal-dispersed tree species, such as Africa,

97    Asia and the Neotropics, can lead to carbon losses in forests (Bello et al., 2015; Osuri et al., 2016;

98    Poulsen, Clark, & Palmer, 2013). Defaunation therefore threatens the role that forests play as

99    essential carbon stores and sinks, risking the investments made by governments and non-state

100   actors in forests as carbon 'banks'.

101

102   Using the Living Planet Index (LPI) methodology (Collen et al., 2009; McRae, Deinet, & Freeman,

103   2017) we aimed to develop the first global indicator of forest vertebrate specialist populations to

104   improve assessments of forest biodiversity status. We then assessed whether trends in forest

105   vertebrate populations were related to changes in tree cover, using satellite-derived tree cover

106   datasets that matched the forest vertebrate data in space and time. If forest cover were a good

107   indicator of forest biodiversity, we would expect to find a positive relationship between forest

108   vertebrate population change and tree cover change. We therefore tested two hypotheses:

109       1. Forest vertebrates are in decline worldwide

110       2. Forest vertebrate population change is positively correlated to tree cover change.

111

**Materials and Methods**

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114     **Development of a Forest Specialists Index**

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116     The Living Planet Database (LPD) contains time-series abundance data for over 22,000 vertebrate

117     populations including more than 4,200 species across the globe with the earliest records dating

118     back to the 1950s (www.livingplanetindex.org). In order to be eligible for the LPD, data must

119     cover at least 2 years, be collected at the same location using consistent monitoring methods and

120     be traceable. The data is collated from a range of sources, including peer-review literature, grey

121     literature, online databases and data holders. In addition to abundance data, metadata associated

122     with each population is entered into the database. This additional information allows the

123     disaggregation of populations based on, for example, taxa, region, biome, or habitat association.

124

125     The decision to develop an indicator for forest specialists as opposed to all forest species follows

126     the approach, but not the same method of selection, as the indicators developed for European birds

127     (Gregory et al., 2005). Given that specialists depend entirely on forests, and non-specialists may

128     be generalists or specialists of other habitats, their use in this indicator would provide a better

129     representation of ecosystem health. We defined forest specialists using the habitat coding from the

130     IUCN Red List (IUCN, 2019). Those with "Forest" listed as one of the major habitats for that

131     species were considered forest generalists, whilst those with only "Forest" listed as the major

132     habitat were considered forest specialists. This definition of specialist is narrow as the "Forest"

133     category from the IUCN Red List refers to natural habitat and does not include artificial habitats

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134   such as plantations. The forest specialists dataset comprised 268 forest specialist species (455

135   populations): 135 birds, 89 mammals, 19 reptiles and 25 amphibians. See Appendix S1 in

136   Supporting Information for a breakdown by realm and taxonomic class.

137

138   We followed the approach of the diversity-weighted Living Planet Index (McRae et al., 2017) to

139   create a weighted index proportional to the species richness of each biogeographic realm and taxa

140   in the data set; also to enable results to be compared to the global Living Planet Index. In order to

141   calculate weightings for each taxa and realm, the total number of vertebrate species from each

142   taxonomic class and biogeographic realm that has "Forest" listed as a habitat was taken from the

143   IUCN Red List. Unlike for birds, mammals and amphibians, the coverage of reptile assessments

144   in the IUCN Red List is not comprehensive so we did not have a full list of forest reptile species

145   globally. However, the number of forest reptiles by realm was considered usable given that the

146   proportion of reptile species in each realm was similar to amphibians and also because spatial

147   patterns of species richness tends to be similar among other vertebrate groups (Grenyer et al.,

148   2006).

149

150   To create the subsets for the indicator, we disaggregated the data according to three taxonomic

151   groups (mammals, birds, herptiles) by five realms (Nearctic, Palearctic, Neotropical, Afrotropical,

152   Indo-Pacific). Combining amphibians and reptiles into a herptile group and Indo-Malaya,

153   Australasia and Oceania into a single Indo-Pacific realm was a response to low data availability

154   for these subsets. The final combinations yielded a total of 14 subsets as there were no time-series

155   data available for Palearctic herptiles.

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7

157 The Forest Specialist Index was calculated using the R package rlpi

158 (https://github.com/Zoological-Society-of-London/rlpi) following the approach in McRae et al.

159 (2017). The weightings calculated above for forest species were applied to each of the 14 subsets.

160

161 **Drivers of forest vertebrate population change**

162

163 *Forest populations and tree cover change*

164

165 We selected all forest specialists and generalists that were surveyed at a specific location (defined

166 as a discrete area such as a national park or sample area of a forest; a non-specific location

167 comprises a larger survey area such as a province or country). For each population, the period

168 encompassing the first and last year of survey data is subsequently referred to as the study period.

169 Many population records do not have data available for every year of the study period. We

170 determined annual predicted abundance values per population by fitting Generalised Additive

171 Models (GAMs) to the time-series population data where survey data was available for at least 6

172 years and linear regressions where data was available for between 2 and 5 years, following

173 Spooner, Pearson, & Freeman (2018).

174

175 In order to assess the relationship between tree cover change and forest vertebrate populations, we

176 required a continuous measure of tree cover spanning multiple years and at a biologically useful

177 resolution. Various global datasets exist that provide continuous tree cover values for multiple

178 years and vary in tree cover definition, spatial resolution, temporal coverage and frequency

179 (Appendix S2). Currently, the highest resolution global datasets (e.g. ~30-m) are available for a

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180  shorter temporal coverage than some datasets with a coarser resolution. Higher resolution datasets

181  allow more fine-scale detection of changes in vegetation cover, while longer-term datasets increase

182  the likelihood of detecting a relationship between tree cover change and population change by

183  increasing the number of populations and years that can be analysed. We opted to run our analyses

184  twice, once using the shorter-term 30-m Landsat Global Forest Change dataset (hereafter referred

185  to as the Hansen dataset; Hansen et al., 2013) and once using the longer-term 5.6-km MEASURES

186  VCF5KYR 1982-2016 dataset which includes annual fractional tree cover and bare ground cover

187  values (hereafter referred to as the Song dataset; Song et al., 2018). In addition to fractional tree

188  cover in 2000 and 2010 (2010 layer accessed from USGS Land Cover Institute, 2017), the Hansen

189  dataset provides annual tree cover loss as a binary presence/absence value for 2000 to 2017,

190  defined as complete stand replacement or a change from a forest to a non-forest state within a

191  pixel. This information allows the estimation of deforestation rates, but may mask fine-scale

192  changes within pixels such as a reduction (but not complete loss) in tree cover and assigns gradual

193  losses that occur over multiple years to a single year.

194

195  It is important to note that, while these datasets may refer to 'forest cover', none differentiate

196  between natural, semi-natural or non-natural forests (such as plantations). Thus, while losses (or

197  gains) in tree cover might reflect deforestation (or regeneration) in natural forests, in plantations

198  this might reflect harvest (or growth) of products grown specifically for human extraction that may

199  provide lower quality habitat for forest vertebrate populations. Systematically collected global data

200  on tree plantations are lacking. The Global Forest Watch (GFW) Tree Plantations layer records

201  tree plantations in a single year (2013/2014) for only seven countries (Brazil, Cambodia,

202  Colombia, Indonesia, Liberia, Malaysia, Peru; Petersen et al., 2016) and is therefore unsuitable for

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203  our analyses. A recently released near-global dataset on plantations by GFW (Harris, Goldman, &

204  Gibbes, 2019) is also unsuitable, as the reference year is 2015 and the image interpretation method

205  varied between countries. In the absence of suitable global information distinguishing natural and

206  planted forests, we therefore refer to tree cover rather than forest cover whenever discussing values

207  derived from the spatial tree cover datasets used in this analysis.

208

209  We fitted buffers with a 5-km radius around the central coordinates of each forest population and

210  extracted annual tree cover area and bare ground area for 1982-2016 using the Song dataset and

211  tree cover area in 2000 and 2010 using the Hansen dataset. We additionally extracted annual loss

212  values for 2001-2017 from the Hansen dataset, using per-pixel tree cover in 2000 to estimate how

213  much tree cover was lost per buffer per year. All data extraction was carried out in Google Earth

214  Engine (Gorelick et al., 2017). We visually assessed the change in tree cover over time per location

215  based on the Song dataset and identified substantial inter-annual fluctuations in tree cover at some

216  locations that were unlikely to reflect true changes. To smooth these fluctuations in the Song

217  dataset, GAMs were fitted to the annual tree cover values within each buffer to obtain annual fitted

218  tree cover values.

219

220  We reduced the annual fitted population data to only include years that fell within 1982-2016 when

221  analysing the effects of tree cover change with the Song dataset and 2000-2015 when analysing

222  with the Hansen tree cover dataset. In both cases we removed populations that no longer had ≥2

223  years of data covering a ≥5 year period (Appendix S3 & S4). Average logged rate of change of

224  each remaining population was calculated following Spooner et al. (2018). Using the Song dataset,

225  we reduced the annual fitted tree cover values to match the study period of each population, with

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226    a 1-year lag (i.e. tree cover in year $t$ matched to population data in year $t+1$). We then calculated

227    three predictor variables from the fitted tree cover values: mean tree cover during the study period;

228    mean bare ground cover during the study period; and the tree cover trend over the study period,

229    taken as the year coefficient from an ordinary least squares regression of annual fitted tree cover

230    on year. We also calculated three predictor variables from the Hansen dataset: tree cover in 2000;

231    the area of tree cover lost over the study period (based on loss data only); and the proportional

232    change in tree cover between 2000 and 2010 (as these are the two years with percent tree cover

233    per pixel available). We removed populations with zero tree cover in all years from the analyses,

234    leaving 1668 generalist and 175 specialist populations in the analyses using the Song dataset

235    compared with 685 generalist and 74 specialist populations in the analyses with the Hansen dataset

236    (see Appendices S3 and S4 for a breakdown by realm and taxonomic class, respectively).

237

238    *Additional drivers of forest population change*

239

240    Forest vertebrates are affected by many drivers that may occur independently of, or in conjunction

241    with, tree cover change, and some of this information is stored in the LPD. Each time-series in the

242    LPD has metadata associated with it that provide ancillary information about the population,

243    including threat information. If the source of the population data specified the existence of any

244    threats to the population, this was categorised as climate change, disease, exploitation, habitat

245    degradation/change, habitat loss, invasive species/genes or pollution, and was recorded in the LPD.

246    Exploitation, including the hunting, persecution, indirect killing or collection of wild individuals

247    for trade, is likely to be a key driver of some forest vertebrates and can occur independently of tree

248    cover change. We therefore included in our analyses a binary variable specifying whether the

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249   primary threat to the population was or was not exploitation. It is possible that body size may

250   impact species' sensitivity to forest change (Henle et al., 2004). To investigate this effect, we took

251   adult body mass values per species from the Amniote (Myhrvold et al., 2015), AmphiBIO

252   (Oliveira, São-Pedro, Santos-Barrera, Penone, & Costa, 2017) and EltonTraits 1.0 (Wilman et al.,

253   2014) databases. Where species-level body mass information was not available, we assigned the

254   species the mean body mass of its genus, family or order (higher taxonomic ranks used where data

255   was unavailable for lower ranks). The body mass values were logged (base 10) to normalise them.

256   We calculated additional predictor variables using independently derived global spatial datasets.

257   We calculated the density of roads within the study area, defined as the total length of roads within

258   each population's 5-km buffer, using the gROADS v1 dataset (CIESIN & ITOS, 2013). We used

259   the UN-Adjusted Gridded Population of the World Version 4 dataset (CIESIN, 2016) to calculate

260   the mean Human Population Density (HPD) within each buffer in the year 2000. Finally, we

261   calculated the mean travel time to the nearest city or densely populated area for each buffer from

262   the Accessibility to Cities 2015 dataset (Weiss et al., 2018).

263

264   *Model structure*

265

266   At some locations multiple populations were monitored over the same period, so we chose to fit a

267   model to the data that would take into account their non-independence. For each predictor variable

268   we fitted mixed effects models using the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2015)

269   with the average rate of change of each population as the dependent variable, location as a random

270   effect and the predictor as a fixed effect. We fitted separate models for each predictor variable to

271   identify any relationships between these variables and population change. To determine whether a

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272  predictor variable was a significant driver of population change, we calculated Akaike's

273  Information Criterion (AIC) for all models and compared them with the AIC of the null model

274  including only a random effect of location. We considered a predictor variable to have significantly

275  improved the model fit if inclusion of the variable lowered the AIC by at least 2 compared to the

276  null model  (Burnham & Anderson 2004).

277

278  We fitted these models to all forest populations (generalists and specialists) and additionally to

279  forest specialist populations only. All analyses were carried out in the statistical software R

280  version 3.5.1 (R Core Team, 2018).

281

282  *Influential genera*

283

284  We wished to determine whether any groups of species were having a significant influence on the

285  models. In the absence of any groups of influential species, models iteratively excluding one group

286  at a time would not produce substantially different model estimates. We used the 'influence.ME'

287  package (Nieuwenhuis, Grotenhuis, & Pelzer, 2012) to produce estimates from models that

288  iteratively excluded the influence of each genus, where each predictor variable was fitted in a

289  univariate mixed effects model with genus as a random effect. We used the "sigtest" function to

290  test whether excluding any genus changed the statistical significance of any of the predictor

291  variables in our models. We then examined the influential genus to determine the cause and

292  repeated our analyses with the genus omitted.

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295    *Forest specialist literature review*

296

297    We additionally carried out population-level time series cross-correlation analyses to assess the

298    relationship between annual forest specialist abundance and tree cover. For each population we

299    assessed the correlation between annual fitted population abundance and annual fitted tree cover

300    values using the Song tree cover dataset. As population change may lag behind tree cover change,

301    for instance when a loss of habitat causes a reduction in fecundity or juvenile survival but not adult

302    mortality, we assessed the correlation between population abundance and tree cover allowing for

303    the existence of a time lag, selecting the lag that gave the strongest correlation. Because these

304    populations are forest specialists we assumed that they were more likely to have a positively

305    correlated relationship with tree cover change. Therefore we initially checked for a significant

306    positive correlation between the annual abundance estimates and tree cover, and only checked for

307    a significant negative relationship in the absence of a positive relationship. Populations were

308    therefore categorised as positively, inversely or uncorrelated with tree cover. A cross-correlation

309    was considered significant if its absolute value exceeded the double square root of the number of

310    years of data that were used in that specific cross-correlation analysis. This follows the

311    approximate (large-sample) standard deviation for the usual Pearson-correlation-coefficient-based

312    n independent observations on pairs of independent measurements. We note that we are applying

313    this threshold for filtering not for formal statistical testing.

314

315    To identify any common themes in the forest specialist populations that appear to be responding

316    to tree cover change, we reviewed the source literature of the populations that we categorised as

317    positively or inversely correlated with tree cover. We extracted qualitative information relating to

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318    forest type (natural or plantation), forest utilisation (e.g. logging, hunting, recreational use), drivers

319    of forest cover change (e.g. regeneration, fire, storm damage, disease, invasive species) and drivers

320    of population change (e.g. change in habitat, change in food availability, predator control,

321    increased predation, poaching or protection from poaching, invasive species, climate change,

322    disease).

323

324    **Results**

325    **Forest Specialist Index**

326

327    The Forest Specialist Index declined by 53% between 1970 and 2014 (Fig 1A; Index value: 0.47;

328    range 0.30-0.73). This indicates an average decline in 455 monitored populations of forest

329    specialists at an annual rate of 1.7% per year. The decline in the index was steepest between 1970

330    and 1976. The percentage of all species that had an annual declining trend was consistently

331    between 50 and 65% during the time period except for the late 1980s, early 2000s and 2013-4

332    when the proportion dropped below half (Appendix S5). These time periods are illustrated by

333    corresponding changes in the index to a slower decline. There is an increase in the percentage of

334    increasing annual trends in 2013 and 2014 and the percentage in 2014 is the highest out of all 44

335    years; this pattern is noticeable across all taxa (Fig 1B-D).  There were more declining years than
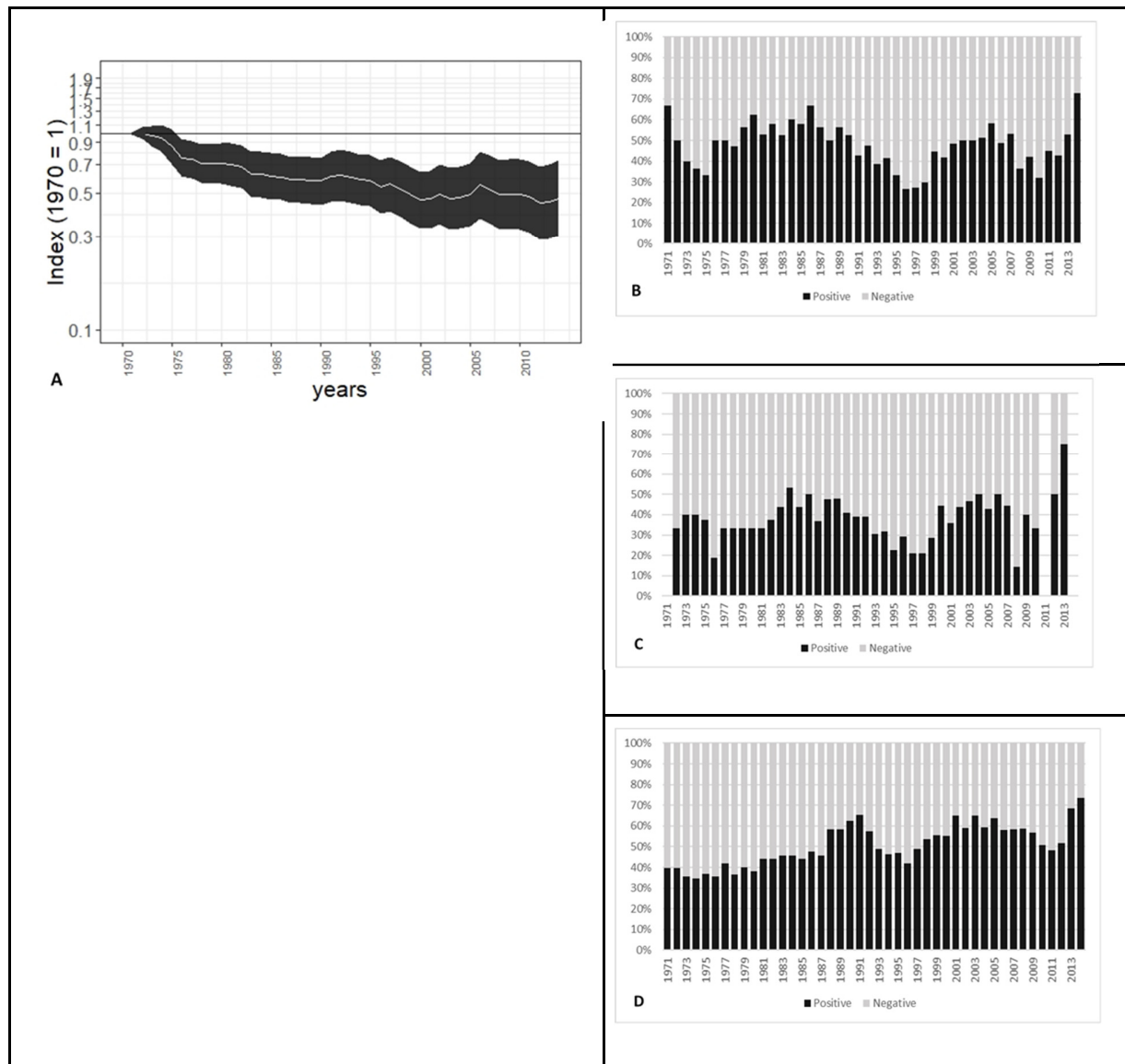
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337

**Fig 1: Weighted index of population change for 268 forest specialist species (A). Solid line shows the weighted index values and shaded region shows the 95% confidence for the index. Percentage of annual species trends which are increasing (positive) or declining (negative) for mammals (B), herptiles (C) and birds (D)**

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16

343 increasing among species trends for mammals (53% of all annual data points) and herptiles (63%

344 of all annual data points); the reverse was true for birds where there were more increasing years

345 (52% of all annual data points). For all taxa, the percentage of increasing and declining annual

346 trends varied across the time series (Fig 1B-D). The number of declining species trends from

347 tropical realms and tropical forest biomes was greater than increasing, while the reverse was true

348 of temperate realms and temperate forest biomes (Appendix S6).

349

350 **Drivers of forest vertebrate population change**

351

352 We identified one genus (*Gyps*) that had a large influence on the model estimates. Gyps vultures

353 are a group of generalist species that have declined severely since the 1990s because of accidental

354 poisoning from the veterinary drug diclofenac (Oaks et al., 2004), and are therefore a very specific

355 case that does not reflect responses of forest populations to any of the widespread pressures we

356 have investigated. We therefore excluded Gyps vultures from our analyses.

357

358 Mixed effects models including specialist and generalist forest populations and using the long-

359 term Song tree cover dataset showed no evidence of a relationship between forest population

360 change and mean tree cover, mean bare ground, exploitation, HPD, mean travel time or road

361 density (Table 1). Positive effects of tree cover trend over the study period and body size (both

362 $p<0.05$) suggested some relationship between these predictor variables and population change (Fig

363 2), but effect sizes were zero or close to zero with confidence intervals overlapping the zero line,

364 and a comparison of AIC values with the null model showed the fit of the models were not

365 significantly improved by including either variable (Table 1).

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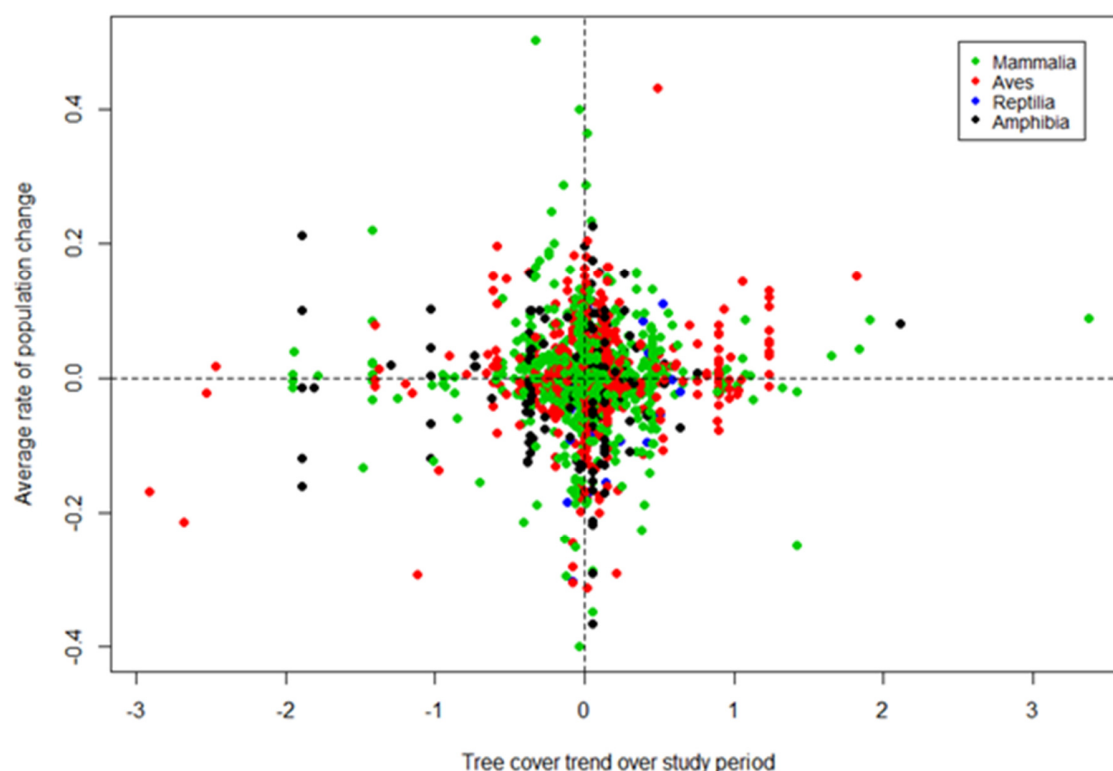
**Fig 2. Average rate of change of forest vertebrate populations (specialists and generalists) with abundance data covering at least a 5 year range between 1982 and 2016 from the Living Planet Database, and tree cover trend within a 5-km radius of each population's study location calculated over the same period as the population data from remotely-sensed tree cover data (Song et al., 2018). Green = mammals, Red = birds, Blue = reptiles, Black = amphibians. N = 1668.**

374

We found a significant negative effect of exploitation on forest specialist population change, although this was based on exploitation being the primary threat of just 12 out of 175 forest specialist populations. We found no evidence of a relationship between forest specialist population change and any other predictor variable (Table 2).

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379

380 Mixed effects models including forest specialists and generalists and using the Hansen tree cover

381 dataset suggested a positive effect of HPD and body mass (both p<0.05) on forest population

382 change, but a comparison of AIC with the null model showed this was not significant. There was

383 no evidence of any relationships between population change and any other variables (Appendix

384 S7). We found no significant relationships between any predictors and population change when

385 repeating the analyses using only forest specialist data (Appendix S8).

386

387 **Table 1. Average rate of forest population change regressed on fixed predictor effects with a**

388 **random effect of location: mixed effect model results for forest vertebrate populations**

389 **(generalists and specialists). Populations had at least 2 years of data covering at least a 5 year**

390 **period from 1982-2016. Tree cover variables calculated using the Song et al (2018) dataset.**

391 **N = 1668.**

| Fixed effect | Estimate | CI | p-value | AIC | ΔAIC |
|---|---|---|---|---|---|
| NULL | *NA* | *NA* | *NA* | -4113.666 | 0 |
| Tree cover trend | 0.01 | 0.00 – 0.02 | 0.033 | -4107.464 | 6.202 |
| Body mass | 0.00 | 0.00 – 0.01 | 0.002 | -4109.732 | 3.934 |
| Mean tree cover | -0.00 | -0.01 – 0.00 | 0.501 | -4102.222 | 11.444 |

19

| | | | | | |
|---|---|---|---|---|---|
| Mean bare ground | 0.00 | -0.01 – 0.01 | 0.857 | -4102.885 | 10.781 |
| Exploitation (Y) | 0.00 | -0.01 – 0.02 | 0.800 | -4103.753 | 9.913 |
| HPD | 0.00 | -0.00 – 0.01 | 0.144 | -4103.674 | 9.992 |
| Road density | -0.00 | -0.00 – 0.00 | 0.901 | -4096.325 | 17.341 |
| Mean travel time | -0.00 | -0.01 – 0.01 | 0.707 | -4102.185 | 11.481 |

392

393

394 **Table 2. Average rate of forest population change regressed on fixed predictor effects with a**

395 **random effect of location: mixed effect model results for forest vertebrate populations**

396 **(specialists only). Populations had at least 2 years of data covering at least a 5 year period**

397 **from 1982-2016. Tree cover variables calculated using the Song et al. (2018) dataset. N = 175.**

398

| Fixed effect | Estimate | CI | p | AIC | ΔAIC |
|---|---|---|---|---|---|
| NULL | *NA* | *NA* | *NA* | -461.632 | 3.409 |
| Tree cover trend | 0.02 | -0.01 – 0.04 | 0.126 | -454.989 | 10.052 |

20

| Body mass | -0.00 | -0.01 - 0.00 | 0.305 | -451.438 | 13.603 |
|---|---|---|---|---|---|
| Mean tree cover | -0.02 | -0.06 – 0.03 | 0.437 | -454.560 | 10.481 |
| Mean bare ground | 0.02 | -0.02 – 0.07 | 0.287 | -454.991 | 10.05 |
| Exploitation (Y) | -0.09 | -0.14 – -0.04 | 0.001 | -465.041 | 0 |
| HPD | -0.01 | -0.02 – 0.01 | 0.472 | -452.625 | 12.416 |
| Road density | -0.00 | -0.00 – 0.00 | 0.310 | -448.816 | 16.225 |
| Mean travel time | 0.01 | -0.01 – 0.04 | 0.242 | -453.894 | 11.147 |

399

400 Cross-correlation analyses between annual forest specialist abundance and annual tree cover

401 identified 40 populations with positively correlated relationships and 31 populations with inversely

402 correlated relationships. 104 populations had no correlation with tree cover. A review of the

403 literature of the 71 populations that were positively or negatively correlated with tree cover found

404 some common themes. All populations that were monitored in areas where forest regeneration (10

405 populations) or extreme events (3 populations) were specified as a driver of forest cover change

406 displayed a positively correlated relationship with tree cover, and populations in areas where

407 logging was present also tended to have a positively correlated relationship (6/9 populations). In

21

408   all cases where invasive species control was specified as a driver of population change (4

409   populations), populations had a positively correlated relationship with tree cover. Populations

410   monitored in forests where hunting was present (not necessarily targeting that species) tended to

411   be negatively inversely correlated with tree cover (11/14 populations), and all hunted populations

412   (5 populations) had an inversely correlated relationship with tree cover. Populations that were

413   noted as being affected by climate change also tended to be inversely correlated with tree cover

414   (10/11 populations). Other specified drivers of population change, such as habitat change, food

415   availability, disease and increased predation were infrequent and less consistently associated with

416   populations that were positively or inversely correlated with tree cover.

417

418   **Discussion**

419

420   Our results indicate that, on average, the global abundance of forest specialists more than halved

421   from 1970 to 2014. The finding was consistent among mammal and herptiles but less so among

422   birds, especially from temperate forests. Trends are worse in the tropics, as might be expected

423   given the more rapid rates of forest loss in tropical regions (FAO, 2016) over that period. The final

424   years of the index, 2013 and 2014, showed an increasing trend as a result of a greater proportion

425   of increasing annual trends among species than in previous years, across all taxa. As there have

426   been other increasing trend years in the index throughout the time-series followed by a decline

427   (1991-2, 2001-2, 2004-6), it is not possible to say at this stage whether the latest upturn in the

428   Forest Specialist Index is a sign of a significant improvement in the abundance of forest specialists.

429

22

430  In understanding the overall reduction in the rate of decline of the index after 2000, we need to

431  consider three factors which are pertinent to interpreting trends in composite indices: species with

432  increasing trends entering the data set, species with declining trends leaving the data set and

433  improvement in species trends from declining to increasing during this time period. The first two

434  factors result from turnover in the species data that contributes to the index as data are not available

435  for all 44 years for all species. This turnover in data is observed in our data set, suggesting that the

436  reduced rate of decline may not entirely reflect overall improving status for species in the data set,

437  rather a change in the underlying data coupled with some species recoveries. This highlights a

438  limitation of composite indices such as this where the temporal representation of species data is

439  not comprehensive across the time-series (Buckland & Johnston, 2017) and illustrates the need for

440  diagnostics to accompany interpretation as well as additional data to strengthen the index. In

441  addressing the third factor, and in order to eliminate any effect of data turnover, we looked at

442  species with data present in all decades. These are predominantly bird species from the Nearctic

443  which are well monitored over the long-term. After an initial decline, the average trend for this set

444  of species does show an improvement to stability from the mid-2000s, but this trend is not yet

445  increasing (Appendix S9). The stabilisation of trends in forest bird species in the Nearctic is

446  consistent with other findings (BirdLife International, 2018). It is worth noting that species

447  biodiversity data is currently skewed away from where species richness is greatest (Collen, Ram,

448  Zamin, & McRae, 2008), limiting our ability to identify and address threats in some of the most

449  biodiverse areas on the planet. The lack of population time-series in the Living Planet Database

450  from forest hotspots in Africa, Asia and the Amazon highlights this issue. To develop a more

451  representative picture of the status of forest biodiversity and drivers of population change, these

23

452    data gaps need to be filled. This will require greater investment in systematic, long-term, on-the-

453    ground monitoring of forest vertebrates and improved data sharing within the research community.

454

455    It has been claimed that, whilst remote sensing allows rigorous and quantitative monitoring of

456    forest cover change, processes of defaunation are more cryptic and difficult to track (Dirzo et al.,

457    2014), even occurring in large protected habitats (Peres & Palacios, 2007). Our results lend support

458    to this assessment that forest cover alone is inadequate as an indicator of forest biodiversity. We

459    did not find significant evidence of a consistent relationship between forest vertebrate populations

460    and tree cover change in the surrounding area. Analyses such as these would benefit from a global,

461    systematically-developed dataset categorising forest areas into natural or planted forests, with

462    temporal information detailing when each plantation was established. This would allow tree cover

463    loss or gains within plantations to be identified, allowing for more rigorous checks of the

464    relationship between populations of forest-dwelling species and natural forest cover change. A

465    recently released database by GFW offers a promising development in this respect, but its start

466    date of 2015 precludes its use in the current study (Harris et al., 2019).

467

468    Positively correlated relationships between tree cover change and population trends were evident

469    for some forest vertebrates included in our analyses, but this was not detected across all populations

470    and other factors appear to have masked this relationship at a global level. By reviewing the source

471    literature of forest specialist populations we investigated common factors associated with

472    populations that displayed a positive or inverse correlation with tree cover change. We found

473    examples of multiple pressures driving population declines (such as poaching, climatic conditions

474    and disease) and conservation interventions supporting population recovery (such as the control of

24

475    invasive species and forest regeneration). All populations in areas undergoing natural or managed

476    native forest regeneration had a positively correlated relationship with tree cover change, while

477    populations specified as being threatened by climatic conditions, such as an increasing intensity of

478    La Niña events, tended to be inversely correlated with tree cover change. Similarly, the exploited

479    populations identified in our literature review, exclusively mammalian species, had a inversely

480    correlated relationship with tree cover change. Given that we also found a significant negative

481    effect of exploitation on forest specialist population change, this suggests that the impact of

482    exploitation on mammalian forest specialists is strong enough to decouple the expected positively

483    correlated relationship between these populations and tree cover change.

484

485    Our finding of exploitation as a key driver of forest specialist population decline supports evidence

486    presented elsewhere. An analysis of threat information for 8688 species on the IUCN Red List of

487    Threatened Species identified over-exploitation alongside agriculture (principally crop and

488    livestock farming) as the main drivers of biodiversity loss (Maxwell, Fuller, Brooks, & Watson,

489    2016). Climate change is considered to be an increasingly important driver in the future (Foden et

490    al., 2013; Maxwell et al., 2016). Indeed, its impact is already evident: an analysis of bird and

491    mammal data in the Living Planet Database found the rate of climate warming, but not land

492    conversion, a strong driver of population change (Spooner et al., 2018). The intensification of

493    climate and other global environmental changes are predicted to interact with overexploitation and

494    other pressures to lead to severe future degradation of tropical forests unless alternative, non-

495    destructive development pathways are followed (Lewis et al., 2016). With most drivers of change

496    interacting in space, time and organisational level (Liu et al., 2015), ultimately an explicitly linked

25

497   set of forest biodiversity indicators may be more useful than reliance on any individual indicator

498   to understand and communicate forest biodiversity trends and guide policy (Butchart et al., 2010).

499

500   The Forest Specialist Index should be among such a set of indicators. This indicator, as developed

501   here, has now been put forward through the Biodiversity Indicators Partnership to measure

502   progress towards Aichi Targets 5, 7 and 12 (https://www.bipindicators.net/indicators/living-

503   planet-index/living-planet-index-forest-specialists) and would complement existing indicators in

504   monitoring progress towards SDG 15, the post-2020 framework under the CBD and in the delivery

505   of the Paris Agreement. As such, it would also be a valuable inclusion in the Global Core Set of

506   forest-related indicators as being coordinated by the FAO.

507

508   The findings presented here also demonstrate the importance of complementing satellite remote

509   sensing-derived datasets with repeated on the ground species surveys and site-specific threat

510   information when assessing the status of forest biodiversity and drivers of species population

511   change. While remote sensing data has undoubtedly improved our ability to independently monitor

512   and assess changes in forest cover, there are many additional drivers of forest population change

513   that can only be identified by looking below the canopy. A focus on forest cover alone risks

514   masking below-canopy processes, such as defaunation, with grave consequences not only for

515   forest biodiversity but also long-term forest health and carbon storage (Bello et al., 2015; Gardner

516   et al., 2017; Poulsen et al., 2013). Therefore, we must not lose sight of the crucial role that site-

517   level species monitoring plays in understanding trends and drivers of forest biodiversity change.

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26

520 **Acknowledgements**

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693 **Supporting Information**

694 Appendix S1. Number of species and populations in the forest specialist index by realm and
695 taxonomic class
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|  | Afrotropical | | Indopacific | | Nearctic | | Neotropical | | Palearctic | |
|---|---|---|---|---|---|---|---|---|---|---|
|  | Species | Populations | Species | Populations | Species | Populations | Species | Populations | Species | Populations |
| Birds | 1 | 1 | 27 | 44 | 45 | 47 | 60 | 75 | 8 | 42 |
| Mammals | 27 | 49 | 19 | 32 | 6 | 32 | 31 | 54 | 6 | 14 |
| Reptiles and amphibians | 5 | 5 | 7 | 11 | 4 | 11 | 27 | 37 | 0 | 0 |

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720  Appendix S2. Specifications of some global tree cover datasets with continuous vegetation fields
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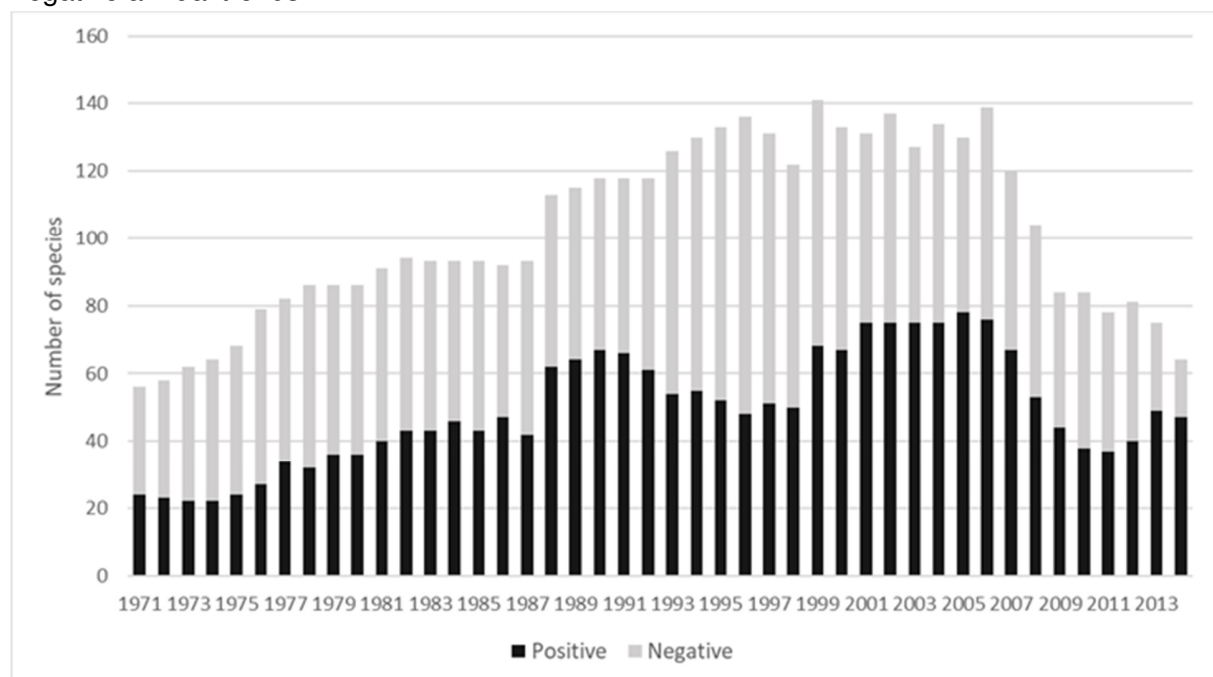| Dataset name | Definition of tree cover | Spatial resolution | Temporal coverage/ cadence | Reference |
|---|---|---|---|---|
| Landsat Global Forest Change | Canopy closure for all vegetation taller than 5 meters in height. | 30 m | Fractional tree cover available for 2000 and 2010 only; tree cover loss available for 2001-2017 | Hansen et al (2013) |
| Landsat VCF (GLCF) | The percentage of horizontal ground in each 30-m pixel covered by woody vegetation greater than 5 meters in height | 30 m | 2000, 2005, 2010 | (Sexton et al., 2013) |
| MEASURES VCF5KYR | The proportion of the ground covered by the vertical projection of tree crowns. Trees are defined as all vegetation taller than 5 meters in height. | 0.05 degree (5600 m) | 1982-2016, annual | Song et al (2018) |
| MODIS VCF | Percent of the pixel covered by tree canopy equal to or greater than 5 m in height. | 250 m | 2000-2015, annual | (DiMiceli et al., 2015) |

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729  Appendix S3. Number of forest populations (generalists and specialists) and forest specialist
730  populations per realm included in analyses using long-term and short-term tree cover datasets.
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| Analysis | Realm | All forest populations | Forest specialist populations |
|---|---|---|---|
| Long-term (Song) | Afrotropical | 365 | 36 |
| | Australasia | 64 | 3 |
| | Indo-Malayan | 98 | 20 |
| | Nearctic | 321 | 14 |
| | Neotropical | 315 | 76 |
| | Oceania | 30 | 12 |
| | Palearctic | 475 | 14 |
| Short-term (Hansen) | Afrotropical | 172 | 12 |
| | Australasia | 42 | 3 |
| | Indo-Malayan | 52 | 10 |
| | Nearctic | 96 | 2 |
| | Neotropical | 127 | 43 |
| | Oceania | 0 | 0 |
| | Palearctic | 196 | 4 |

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746  Appendix S4. Number of forest populations (generalists and specialists) and forest specialist
747  populations per taxonomic class included in analyses using long-term and short-term tree cover
748  datasets.

| Analysis | Taxa | All forest populations | Forest specialist populations |
|---|---|---|---|
| Long-term (Song) | Amphibians | 154 | 19 |
| | Birds | 701 | 73 |
| | Mammals | 767 | 78 |
| | Reptiles | 46 | 5 |
| Short-term (Hansen) | Amphibians | 52 | 2 |
| | Birds | 251 | 33 |
| | Mammals | 348 | 34 |
| | Reptiles | 34 | 5 |

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774 Appendix S5. Number of species trends in the FSI annually, with proportions of positive and
775 negative annual trends



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800 Appendix S6. Number of average declining, increasing and stable (less than 5% change in
801 abundance) species trends in tropical and temperate realms (A) and biomes (B). Nine species
802 were not located in a forest biome (where forest is the dominant habitat type), so were not
803 included in B.
804

| A Realm | Decline | Increase | Stable |
|---|---|---|---|
| Temperate realms (Nearctic, Palearctc) | 25 | 35 | 7 |
| Tropical realms (Afrotropical, Neotropical, Indo-Pacific) | 99 | 83 | 19 |
| B Biome | Decline | Increase | Stable |
| Temperate forest biomes (including Mediterranean and boreal) | 29 | 39 | 7 |
| Tropical forest biomes (including mangrove) | 89 | 76 | 19 |

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828 Appendix S7. Model results from mixed effects models of average rate of population change of
829 forest generalists and specialists regressed on fixed predictor effects with a random effect of
830 location. Populations had at least 2 years of data covering at least a 5 year period from 2000-
831 2015. Tree cover variables calculated using the Hansen dataset. N = 685.
832

| Fixed effect | Estimate | CI | p-value | AIC |
|---|---|---|---|---|
| NULL | *NA* | *NA* | *NA* | -1479.421 |
| Tree cover 2000 | -0.00 | -0.01 – 0.01 | 0.769 | -1468.794 |
| Total tree loss | 0.00 | -0.00 – 0.01 | 0.736 | -1467.425 |
| Tree cover change 2000-2010 | -0.00 | -0.03 – 0.02 | 0.822 | -1470.524 |
| Body mass | 0.00 | 0.00 – 0.01 | 0.021 | -1472.199 |
| Exploitation (Y) | 0.02 | -0.01 – 0.04 | 0.244 | -1472.025 |
| HPD | 0.01 | 0.00 – 0.02 | 0.023 | -1473.445 |
| Road density | 0.00 | -0.00 – 0.00 | 0.607 | -1463.679 |
| Mean travel time | -0.01 | -0.02 – 0.00 | 0.234 | -1470.392 |

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834  Appendix S8. Model results from mixed effects models of average rate of population change of
835  forest specialists regressed on fixed predictor effects with a random effect of location. Populations
836  had at least 2 years of data covering at least a 5 year period from 2000-2015. Tree cover variables
837  calculated using the Hansen dataset. N = 74.
838

| Fixed effect | Estimate | CI | p-value | AIC |
|---|---|---|---|---|
| NULL | *NA* | *NA* | *NA* | -158.048 |
| Tree cover 2000 | -0.02 | -0.07 – 0.03 | 0.445 | -151.075 |
| Total tree loss | 0.00 | -0.01 – 0.02 | 0.735 | -148.242 |
| Tree cover change 2000-2010 | 0.06 | -0.27 – 0.40 | 0.719 | -154.474 |
| Body mass | -0.00 | -0.01 – 0.01 | 0.832 | -147.690 |
| Exploitation (Y) | -0.05 | -0.12 – 0.01 | 0.091 | -153.850 |
| HPD | -0.00 | -0.02 – 0.02 | 0.981 | -148.417 |
| Road density | -0.00 | -0.00 – 0.00 | 0.374 | -145.234 |
| Mean travel time | 0.00 | -0.03 – 0.03 | 0.925 | -149.413 |

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842    Appendix S9. Abundance index for 74 species from the FSI with data present throughout all
843    decades from 1970 to 2014 (these are primarily birds from the Nearctic)
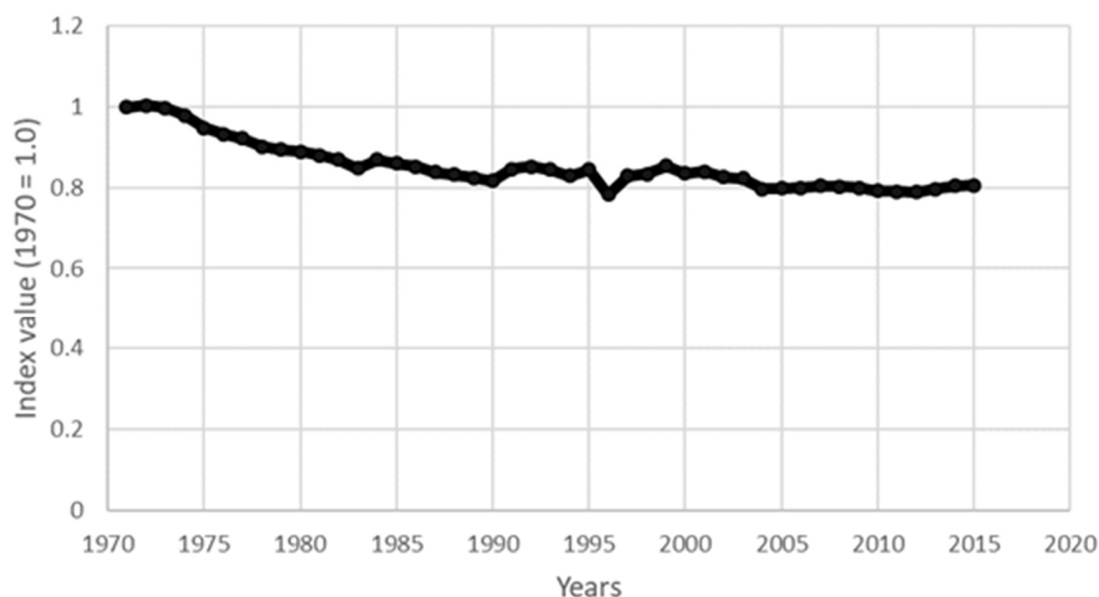


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