Climate-driven variation in dispersal ability predicts responses to forest fragmentation in birds

Thomas L. Weeks[1,2]*, Matthew G. Betts[3], Marion Pfeifer[4], Christopher Wolf[3], Cristina Banks-Leite[1], Luc Barbaro[5,6], Jos Barlow[7], Alexis Cerezo[8], Christina M. Kennedy[9], Urs G. Kormann[10], Charles J. Marsh[11,12], Pieter I. Olivier[13,14], Benjamin T. Phalan[15], Hugh P. Possingham[16], Eric M. Wood[17], Joseph A. Tobias[1]

[1]*Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot, SL5 7PY, UK.*

[2]*Department of Life Sciences, Natural History Museum London, Cromwell Rd, South Kensington, London SW7 5BD, UK.*

[3]*Forest Biodiversity Research Network, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA.*

[4]*School of Natural and Environmental Sciences, Newcastle University, Newcastle Upon Tyne NE1 7RU, UK*

[5]*Dynafor, University of Toulouse, INRAE, Castanet-Tolosan, France.*

[6]*CESCO, Museum National d'Histoire Naturelle, CNRS, Sorbonne-University, Paris, France*

[7]*Lancaster Environmental Centre, Lancaster University, Lancaster LA1 4YQ, UK*

[8]*Foundation for Ecodevelopment and Conservation (FUNDAECO), 25 calle, 2-39, zona 1. Ciudad de Guatemala, Guatemala. C. P. 0101*

[9]*Global Protect Oceans, Lands and Waters Program, The Nature Conservancy, Fort Collins, CO, 80524, USA*

[10]Swiss Ornithological Institute, Sempach CH-6204, Switzerland

[11]Department of Ecology and Evolution & Yale Center for Biodiversity and Global Change,

Yale University, New Haven, Connecticut, USA

[12]Center for Biodiversity and Global Change, Yale University, New Haven, CT, USA

[13]M.A.P Scientific Services, Pretoria 0081, South Africa

[14]Department of Zoology and Entomology, University of Pretoria, 0083, South Africa

[15]Centre for Conservation of Atlantic Forest Birds, Parque das Aves, Foz do Iguaçu, PR

85859-899, Brazil

[16]School of Biological Sciences, The University of Queensland, St Lucia 4072 Australia

[17]Department of Biological Sciences, California State University Los Angeles, 5151 State

University Drive, Los Angeles, California 90032, USA

*Corresponding author: t.weeks19@imperial.ac.uk (T.L. Weeks)

ORCID iDs: 0000-0002-2525-3900 (T.L. Weeks), 0000-0002-7100-2551 (M.G. Betts),

0000-0002-6775-3141 (M. Pfeifer), 0000-0002-5519-3845 (C. Wolf), 0000-0002-0091-

2857 (C. Banks-Leite), 0000-0001-7454-5765 (L. Barbaro), 0000-0003-4992-2594 (J.

Barlow), 0000-0001-8497-9276 (A. Cerezo), 0000-0001-8902-8728 (C. M. Kennedy),

0000-0001-9875-4836 (U.G. Kormann), 0000-0002-0281-3115 (C.J. Marsh), 0000-

0001-7876-7226 (B. T. Phalan), 0000-0001-7755-996X (H.P. Possingham), 0000-0003-

2787-6451 (E.M. Wood), 0000-0003-2429-6179 (J.A. Tobias).

Type of paper: Article

Running head: Dispersal predicts responses to forest fragmentation

Abstract

Species sensitivity to forest fragmentation varies latitudinally, peaking in the tropics. A prominent explanation for this pattern is that historical landscape disturbance at higher latitudes has removed fragmentation-sensitive species or promoted the evolution of more resilient survivors. However, it is unclear whether this so-called extinction filter is the dominant driver of geographic variation in fragmentation sensitivity, particularly because climatic factors may also cause latitudinal gradients in dispersal ability, a key trait mediating sensitivity to habitat fragmentation. Here we combine field survey data with a morphological proxy for avian dispersal ability (hand-wing index) to assess responses to forest fragmentation in 1034 bird species worldwide. We find that fragmentation sensitivity is strongly predicted by dispersal limitation, and that other factors – latitude, body mass, and historical disturbance events – have relatively limited explanatory power after accounting for species differences in dispersal. We also show that variation in dispersal ability is only weakly predicted by historical disturbance and more strongly associated with intra-annual temperature fluctuations (seasonality). Our results suggest that climatic factors play a dominant role in driving global variation in the impacts of forest fragmentation, emphasising the need for more nuanced environmental policies which take into account local context and associated species traits.

Keywords: birds, dispersal, habitat fragmentation, functional traits, land-use change, forest conservation

Main text

Introduction

Habitat fragmentation is a major driver of biodiversity decline [1-3]. At a global scale, the impacts are often most apparent in forest species, many of which are poorly adapted to land-use change caused by anthropogenic disturbance, including urbanisation, logging and agricultural expansion [4]. Forest fragmentation threatens many species by creating barriers to connectivity among fragmented populations [5-7], in conjunction with 'edge effects' and habitat loss, resulting in reduced availability of habitat and other resources [8]. The strength of these impacts varies widely, both across species and geographically, with a prominent latitudinal gradient in sensitivity to forest fragmentation reported in some taxonomic groups [9, 10]. Despite numerous studies focusing on the effects of forest fragmentation at local and landscape scales, the mechanisms driving these global patterns in fragmentation sensitivity remain unclear [11].

One proposed mechanism – based on the concept of 'extinction filters' – is that geographical variation in fragmentation sensitivity is driven by differential patterns of extinction whereby fragmentation-sensitive species have already been lost from landscapes which have historically incurred higher levels of environmental disturbance [12]. This concept is sometimes expanded beyond the effects of extinction to include the impacts of historical disturbance on surviving species, which are more likely to have evolved adaptations to persist in fragmented landscapes [9]. Thus, through both extinction and evolution, species surviving periods of intense disturbance are predicted to have one or more traits – including stronger dispersal ability, wider ecological niches, smaller area requirements, and 'faster' life history strategies – making them more

5

100 resilient to current levels of habitat fragmentation (Fig. 1a). Accordingly, if landscapes

101 exposed to the strongest or most frequent historical disturbances are clustered towards

102 higher latitudes (Fig. 2a), extinction filters may explain the latitudinal gradient in

103 fragmentation sensitivity (Fig. 2c).

104   Although previous analyses have shown that extinction filters contribute to

105 global patterns in fragmentation sensitivity [9], additional mechanisms are almost

106 certainly involved, perhaps playing a dominant role. Even in the absence of historical

107 disturbance or extinction, natural selection is expected to generate latitudinal gradients

108 in niche-related or life-history traits, many of which are adaptations to intra-annual

109 climatic fluctuation (seasonality) [13] (Fig. 1c). In particular, fragmentation sensitivity

110 may be accentuated by dispersal limitation [2], which appears to be most prevalent in

111 tropical biota [14] (Fig. 2b).

112   Recent global analyses focusing on birds – the study taxa with the most

113 comprehensive data available – reveal that climatic seasonality predicts variation in

114 dispersal ability, even when accounting for latitude [15]. At higher latitudes, and in

115 highly seasonal tropical environments such as savannahs and dry forests, many species

116 have mobile lifestyles, characterised by seasonal territoriality, flocking in the non-

117 breeding season, spatial resource tracking and migratory behaviour [16, 17].

118 Conversely, in many tropical forest birds, stable climatic conditions and the consequent

119 year-round availability of food resources give rise to sedentary lifestyles, characterised

120 by ecological specialisation, year-round territoriality and reduced natal dispersal

121 distance [18-21]. The concept is not limited to birds as reduced dispersal distance is

122 also evident in many other tropical forest animals [22] and plants [23] for similar

123 reasons.

124   Variation in dispersal limitation is linked to fragmentation sensitivity in birds

125   because less dispersive species have reduced gap-crossing ability [24-26] increasing

126   rates of extinction in habitat patches and reducing the likelihood of recolonization after

127   extinction events [18, 27]. Equally, if lineages evolving at high latitudes are inherently

128   more dispersive as a result of ecological adaptation to widely fluctuating intra-annual

129   climatic regimes, their sensitivity to forest fragmentation may be reduced (Fig. 1). The

130   reported latitudinal gradient in dispersal limitation [14, 15] may therefore cause the

131   parallel gradient in species sensitivity to forest fragmentation [9, 10, 26] (Fig. 2d),

132   potentially even explaining the apparent relationship between fragmentation sensitivity

133   and historical disturbance (Fig. 2).

134   To provide a more nuanced analysis of the relative roles of different

135   mechanisms, we estimate fragmentation sensitivity of bird species reported by field

136   surveys in 22 countries (Fig. 2). We quantify the effect of fragmentation on these

137   populations, based on their aversion to forest edges, accounting for continuous

138   gradients in tree-cover [28]. We then use Bayesian phylogenetic mixed effect models to

139   assess whether fragmentation sensitivity is best predicted by historical disturbance or

140   hand-wing index (HWI) – a metric of wing shape that predicts dispersal distance [21]

141   and gap-crossing ability in forest birds [29, 30]. We use negative (inverse) hand-wing

142   index score (nHWI), i.e. dispersal limitation, because this helps to clarify the

143   mechanistic link with fragmentation sensitivity (see Methods).

144   Historical disturbance and dispersal limitation are not mutually exclusive

145   hypotheses. Rather, dispersal limitation is one of several potential underlying

146   mechanisms for the effects of historical disturbance (Fig. 1). A history of disturbance

147   may lead to the decline and extinction of dispersal-limited species and could also drive

148   selection for increased dispersal ability in surviving lineages [31, 32]. Nonetheless, if

149 fragmentation sensitivity is more strongly associated with dispersal than disturbance,

150 this would imply a primary role for other factors. We examine this possibility further by

151 testing whether historical disturbance or climatic seasonality influence fragmentation

152 sensitivity directly or via downstream effects on dispersal (HWI). Taken together, these

153 analyses offer new insights into the relative roles of extinction filters and ecological

154 adaptation, with implications for the design of effective conservation strategies in

155 fragmented ecosystems.

156

157 **Results**

158 We compiled data from 31 study landscapes spanning from 0.8–62.6 degrees latitude

159 (Fig. 2) and sampling sites with high historical disturbance (n = 16) and low historical

160 disturbance (n = 15; see Methods and Supplementary Dataset 1). Intensive field surveys

161 recorded 1564 populations of 1034 bird species, of which BirdLife International [33]

162 treated 276 as "Forest-specialists" and 874 as "Forest-associated" (i.e. the same 276

163 species combined with a further 598 species with medium forest dependency). The

164 remaining 160 species are not associated with forest (Supplementary Dataset 1). To

165 focus our analyses on relevant populations, we only assigned fragmentation sensitivity

166 to Forest-specialists (Restricted analyses) and Forest-associated species (Expanded

167 analyses; see Methods). Analyses were conducted at three different levels – landscapes,

168 populations and species – depending on the hypothesis being tested (see Methods).

169

170 **Historical disturbance and dispersal limitation**

171 We estimated latitude and historical disturbance for each study landscape (n = 31)

172 using the approach described by Betts et al. [9] and then inferred dispersal limitation

173 (nHWI) for all study species (n = 1034) using global data on wing morphology [15, 34]

174 (see Methods). In line with predictions (Fig. 2a), we found a correlation between the

175 latitude of study landscapes and the level of historical disturbance increasing towards

176 the poles (*W*-statistic: 183, *P* = 0.013) (Extended Data Fig. 1). Similarly, we found the

177 expected opposite gradient in dispersal limitation (Fig. 2b) with mean assemblage

178 nHWI (*n* = 31) decreasing with latitude ($\hat{\beta}$: -0.007, *P* < 0.001) (Extended Data Fig. 2),

179 consistent with global patterns of avian dispersal ability [15].

180

181 **Patterns of fragmentation sensitivity**

182 Based on patterns of abundance with respect to distance from forest edge, most

183 (225/382; 58.9%) "Forest-specialist" populations and many (583/1302; 44.8%)

184 "Forest-associated" populations were classified as "Forest-core" (i.e. BIOFRAG software

185 assigned them a "Forest" habitat preference and a "Core" affinity, suggesting edge-

186 intolerance; see Methods). We restricted classification as fragmentation sensitive to

187 these two groups in our Restricted and Expanded analyses, respectively. In our

188 Restricted analysis, we found that 14.4% (*n* = 225) of all study populations (*n* = 1564)

189 were fragmentation sensitive, increasing to 37.3% (*n* = 583) in our Expanded analysis

190 (see Methods). Despite being more prevalent in some clades (e.g. suboscine passerines)

191 than others (Fig. 3a), fragmentation sensitivity was widespread across our sample and

192 its phylogenetic signal ranged from low (Expanded sample, *d* = 0.83) to moderate

193 (Restricted sample, *d* = 0.57).

194   The proportion of fragmentation sensitive bird populations in each assemblage

195 (*n* = 31) decreased with absolute latitude (Extended Data Fig. 3a & b), supporting

196 predictions (Fig. 2) based on the results of previous studies [9, 10]. In our Restricted

197 analyses, the mean proportion of fragmentation sensitive species in low disturbance

198 landscapes (12%) was approximately double that found in high disturbance landscapes

199   (5%), with similar results in Expanded analyses (37% versus 18%, respectively) (Fig.

200   3b), as well as previous analyses based on a subset of the same data [9]. At the

201   landscape level, we found a strong positive correlation between mean dispersal

202   limitation (nHWI) and the proportion of fragmentation sensitive species in each

203   assemblage. This result was similar in both the Restricted ($\hat{\beta}$ = 2.926, P = 0.009; Fig. 3a)

204   and Expanded analyses ($\hat{\beta}$ = 2.790, P = 0.004: Extended Data Fig. 4).

205

206   **Drivers of fragmentation sensitivity**

207   The Bayesian posterior distributions from our analysis of 1564 study populations

208   indicate that species sensitivity to forest fragmentation was best explained by dispersal

209   limitation (nHWI), both in our Restricted and Expanded analyses (Fig. 4). Indeed, once

210   our models included nHWI, all other covariates explained little additional variation in

211   the likelihood of a species being classified as fragmentation sensitive. In each case, the

212   posterior distributions of these co-variates became centered close to 0, suggesting that

213   their relationship with fragmentation sensitivity is accounted for by dispersal limitation

214   (Fig. 4; Extended Data Table 1).

215   We included body size in our models because larger-bodied species have greater

216   space requirements and may be forced to cross gaps between habitat patches more

217   often, either to access different parts of their territory or to obtain sufficient food [24,

218   35]. In our Restricted analysis, we found a weak (non-significant) positive effect of body

219   mass on fragmentation sensitivity (Fig. 4a) with a stronger effect size for the interaction

220   term between body mass and dispersal limitation (nHWI). However, credible intervals

221   include 0 and the effect is reduced in our Expanded analyses (Fig 4b).

222   Our classification of disturbed landscapes spans different time-scales, including

223   both ongoing or deep-time natural disturbances (fires, storms & glaciation) as well as

224 more recent anthropogenic disturbance (forest loss). To assess whether these temporal

225 scales have different implications for fragmentation sensitivity, we re-classified

226 disturbance as either anthropogenic (forest loss) or natural (fires, storms & glaciation),

227 then re-ran our models (see Supplementary materials). In both cases, the main results

228 were unchanged, with similar posterior distributions to those produced from our main

229 model (Extended Data Fig. 5 & 6; Table S1 & S2).

230

231 **Historical versus climatic mechanisms**

232 Our analyses suggest that dispersal limitation (nHWI) plays a dominant role in shaping

233 patterns of fragmentation sensitivity, but what drives variation in dispersal ability?

234 Given that a combination of both historical and climatic factors is potentially involved

235 (Fig. 1), we explored the relative roles of disturbance history, latitude, and seasonality

236 in generating patterns of dispersal limitation (Table S3). Using local-scale metrics for

237 each of these covariates (i.e. calculated at the landscape-level), we found a negative

238 association between disturbance history and nHWI (Fig. 5a). However, when we added

239 landscape latitude to the model, the strongest correlation with nHWI switched from

240 disturbance history to latitude (Fig. 5b), suggesting that other latitudinal factors may

241 predominate. Indeed, when we include seasonality as a third covariate, we found that

242 seasonality is the only significant driver of dispersal limitation, whereas disturbance

243 history and latitude explained little additional variation (Fig. 5c). When we re-ran these

244 analyses using data from the full species distribution (i.e. disturbance, latitude and

245 climate data averaged across species breeding ranges), results were similar (Extended

246 Data Fig. 7; Table S4). Despite the correlation between historical disturbance, latitude

247 and climate variables, collinearity between these predictors was checked via variance

248 inflation factors (VIFs) and found to be acceptable (< 6) in all models.

11

249   The proportion of variance in dispersal limitation (nHWI) explained by each

250   model was modest, although the full trivariate model explained substantially more

251   variance ($R^2 = 0.056$) than either the univariate ($R^2 = 0.009$) or bivariate models ($R^2 =$

252   0.041). Furthermore, of the total variance explained by the full model, we found that

253   seasonality explained the majority (59.35%), whereas historical disturbance (5.93%)

254   and latitude (34.71%) have comparatively limited explanatory power (Fig. 5d-f).

255   Results were similar regardless of whether we averaged species-level data at the local

256   landscape level or across the breeding range of each species (see Methods; Extended

257   Data Fig. 7). The switch in both statistical significance and explanatory power towards

258   seasonality in the full model suggests that the effects of disturbance and latitude in

259   simpler models are mostly explained by co-occurring effects of seasonality. This

260   conclusion was further supported by a phylogenetic structural equation model, which

261   identified the fundamental driver of variation in dispersal limitation as seasonality, not

262   historical disturbance (see Supplementary materials; Fig. S1).

263

264   **DISCUSSION**

265   We have shown that dispersal limitation estimated from wing morphology (nHWI), and,

266   to a lesser extent, the interaction between nHWI and body mass, are key predictors of

267   fragmentation sensitivity in birds. Although these global gradients in dispersal

268   limitation may be shaped by historical factors, particularly latitudinal variation in

269   natural or anthropogenic disturbance [9, 36, 37], our results reveal that the main driver

270   of this pattern is a strong environmental mechanism associated with intra-annual

271   climatic variation, i.e. seasonality [15].

272   It could be argued that seasonality is simply another form of disturbance, and

273   that our findings highlight an additional example of extinction filters shaping the

274   distribution of fragmentation sensitive species. However, this conceptualisation seems

275   inappropriate because seasonality is not explicitly historical, it is an ongoing process by

276   which species adaptations arise gradually through natural selection, and rarely by

277   extinction [13, 38]. In this context, dispersal limitation offers a more general mechanism

278   that helps to explain the link previously identified between historical disturbance and

279   fragmentation sensitivity [9], and also provides a framework for understanding how

280   climate shapes the responses of biodiversity to land-use change [39]. Ultimately, the

281   role of dispersal limitation highlights a mechanism by which population decline or

282   extinction can be driven by fragmentation *per se*, as opposed to area effects [40].

283

284   **Dispersal as a unifying mechanism**

285   In their global analysis, Betts et al. [9] reported a strong latitudinal gradient in

286   sensitivity to forest fragmentation, in line with previous studies suggesting that tropical

287   forest species are on average less equipped to cope with forest fragmentation for a

288   range of physiological reasons, including low dispersal, aversion to light, and adaptation

289   to the cooler and more stable temperatures of tropical forest interiors [10, 41, 42]. The

290   reduced proportion of fragmentation sensitive species in high disturbance sites was

291   thought to reflect an extinction filter, whereby fragmentation sensitive species were

292   already lost from assemblages. Our analyses reveal the same patterns, with a

293   progressive decrease in the proportion of fragmentation-sensitive species from low to

294   high latitudes (Extended Data Fig. 4) and a similar decrease in the proportion of

295   fragmentation sensitive species from low disturbance to high disturbance sites (Fig. 3a).

296   However, once variation in morphological dispersal constraints is accounted for, both

297   patterns become non-significant, suggesting that the effects of dispersal override those

298   of landscape history.

13

299   Similarly, the widespread finding that dietary groups differ in their sensitivity to

300   fragmentation (e.g. [43-45]) might not be related to diet and food abundance *per se* but

301   rather the fact that dispersal limitation (nHWI) varies significantly within and between

302   trophic niches (Extended Data Fig. 8). Specialist invertivores, for example, tend to be

303   more dispersal-limited than other dietary groups, including nectarivores, granivores

304   and omnivores, which typically have more mobile lifestyles [15]. Moreover, sensitivity

305   to fragmentation appears to vary widely within specialised trophic niches, including

306   invertivores [45, 46] and frugivores [47, 48]. This within-guild variation can be

307   explained by differences in dispersal ability among members of the same trophic group.

308   For example, terrestrial and understorey insectivores are generally less dispersive and

309   more sensitive to habitat fragmentation than canopy or aerial insectivores [14, 42],

310   suggesting that flight efficiency and gap crossing ability outweigh diet as the key factor

311   determining responses to fragmentation in tropical forests [29, 30].

312   The effect of dispersal limitation on fragmentation sensitivity makes sense in

313   light of evidence from observational (e.g. [24, 49]) and experimental studies (e.g. [29,

314   30]) indicating that forest bird species with reduced dispersal capacity are much less

315   inclined to cross gaps of inhospitable habitat. For a substantial proportion of tropical

316   forest species, constrained gap-crossing ability reduces population connectivity in

317   forested landscapes [24] and constrains recolonisation of isolated habitat fragments

318   after local extinction events [18]. This impact is compounded by an increased hostility

319   of matrix (non-forest) habitats to forest specialists which are often constrained by

320   specialised ecological traits unsuited to typical matrix conditions [27, 50-52]. In effect,

321   hostile matrix gaps present a greater barrier to movements of forest specialists,

322   theoretically increasing the cost of dispersal limitation [53-55]. We see evidence of this

323 higher cost in the larger effect sizes of dispersal limitation (nHWI) in our Restricted

324 versus Expanded analyses.

325   Previous studies have suggested that dispersal limitation accentuates the

326 negative impacts of tropical forest loss [56] and fragmentation [2], or highlighted

327 associations between fragmentation sensitivity and other traits related to dispersal,

328 including sedentary or non-migratory lifestyles [10, 57, 58]. Our results go further in

329 showing that dispersal limitation is a pervasive underlying mechanism potentially

330 mediating or driving the effects of historical disturbance [9], habitat preference [56]

331 and diet [45] on fragmentation sensitivity. Thus, while it is often assumed that the

332 impacts of fragmentation *per se* on biodiversity are mediated primarily by edge effects

333 (e.g. [3, 40]), our findings highlight the importance of gap effects, with variation in the

334 ability to cross habitat gaps being a key determinant of which species win or lose in

335 fragmented environments [24-26].

336

337 **Caveats and clarifications**

338 Our results appear to conflict with long-term studies at one locality in Amazonian Brazil

339 which found no significant relationship between forest fragmentation sensitivity and

340 dispersal limitation in birds [59, 60]. However, this previous finding may be explained by

341 methodological issues because dispersal ability was only scored indirectly through

342 expert opinion and the study landscape was not consistently fragmented. At times,

343 substantial regrowth was allowed to develop between fragments [61], no doubt

344 increasing the movement of species with poor dispersal ability through the disturbed

345 landscape [62]. Our analyses based on a more objective metric, estimated over a larger

346 sample of species and landscapes, show that dispersal limitation is a powerful predictor

347 of latitudinal gradients in fragmentation sensitivity. Thus, we find no support for the

348   hypothesis that highly sedentary tropical species are under reduced pressure to cross

349   habitat gaps, hence alleviating the impacts of fragmentation [59, 60]. While inverse

350   relationships between dispersal limitation and fragmentation sensitivity may occur

351   temporarily, or in partially fragmented landscapes with large patch-size, the opposite

352   pattern predominates at global scales.

353   We only find weak and inconclusive support for the effect of body size in our full

354   models, in line with several previous studies of vertebrates [63-65]. However, the

355   interaction term between body size and dispersal limitation receives stronger support

356   in both models, presumably because larger-bodied species typically require larger areas

357   of habitat to meet their resource requirements and sustain a viable population of

358   individuals [66, 67]. These larger home ranges are more easily fragmented, increasing

359   the need to move between habitat patches [35]. In both these cases, the spatial context

360   means that larger-bodied species only thrive in fragmented landscapes if they can easily

361   move across matrix gaps. Thus, species with both large body size and poor dispersal

362   suffer a "double jeopardy" and are particularly sensitive to habitat fragmentation [24].

363   A final point to consider is the BIOFRAG sampling design, which focuses on edge

364   tolerance rather than occurrence in isolated fragments [28]. It is not immediately

365   obvious why dispersal limitation should influence edge tolerance any more than other

366   traits associated with edge aversion, including year-round territoriality, restriction to

367   ground or understorey habitats, light sensitivity, thermal intolerance and a slow-paced

368   life history strategy [41, 42, 68, 69]. One possibility is that dispersal limitation may

369   indicate edge sensitivity through correlation with these other traits, although they are

370   all strongly related to latitude and seasonality [14, 27], which have much weaker effect

371   than dispersal limitation in our models. In addition, we excluded BIOFRAG sites where

372   continuous forest was over-sampled, and restricted our additional sampling to highly

373   fragmented landscapes containing many isolated forest patches with correspondingly

374   high ratio of edge to core (see Supplementary materials). Therefore, our measure of

375   fragmentation sensitivity strongly reflects the extent to which species persist in isolated

376   habitat patches compared to continuous areas of forest. The difficulty of crossing hostile

377   matrix gaps is almost certainly the dominant impact of dispersal limitation in such

378   landscapes [18].

379

380   **Dispersal limitation: cause or consequence?**

381   If major historical disturbance events led to fragmented forest landscapes that

382   disfavoured species with poor dispersal, then extinction filters – as conceptualised by

383   Betts *et al.* [9] – may directly shape the patterns we detect in wing morphology.

384   However, we only found inconclusive evidence for this relationship in univariate

385   models (Fig. 5; Extended Data Fig. 7). The weakness of these simplified models is that

386   disturbance appears to be correlated with seasonality (Extended Data Fig. 9), so a

387   univariate analysis may pick up a signal from seasonality rather than disturbance *per se.*

388   We addressed this problem using two different types of complex models (i.e.

389   multivariate and structural equation models), both of which reveal that dispersal traits

390   are best explained, not by historical disturbance, but by temperature variability.

391   Our findings align with the view that high-dispersal traits of high-latitude species

392   are adaptations to seasonality – i.e. part of a behavioural strategy or program, typically

393   involving either migration or movement between sites, to allow survival during periods

394   of the year when there is little or no production of food in the breeding area (see [17]).

395   For example, many avian insectivores breeding in boreal forests are migratory or highly

396   dispersive, and therefore capable of surviving in fragmented landscapes, or recolonising

397   habitat patches after local extinction events [27, 70]. Seasonality is by far the strongest

398   predictor of latitudinal variation in avian wing morphology, with dispersal adaptations

399   peaking in the most seasonal landscapes [15]. This fits a more general pattern of

400   increased dispersal ability and decreased fragmentation sensitivity at higher latitudes

401   where climatic variability results in strong selection for niche flexibility [14, 23].

402   Our analyses suggest that climatic effects predominate in shaping global patterns

403   of dispersal limitation and hence fragmentation sensitivity in birds. However, this does

404   not exclude a role for other drivers. All models presented here detect large variation in

405   the effect of species-level covariates on the likelihood of a species being classified as

406   fragmentation sensitive. We found some, albeit weak, support for an effect of landscape-

407   level predictors, including historical disturbance. Several other candidate traits were

408   not included in our models. Thus, although the latitudinal gradient of fragmentation

409   sensitivity in birds appears to be primarily driven by natural selection for increased

410   dispersal ability at higher, more seasonal latitudes, a variety of other behavioural,

411   ecological and historical factors may contribute to variance across species in sensitivity

412   to forest fragmentation.

413   Further studies are needed to understand the combined roles of climate,

414   disturbance regimes, and dispersal limitation in shaping the response of biodiversity to

415   environmental change. Current attempts to disentangle the influence of seasonality

416   from historical disturbance are limited by data quality. In particular, treatment of

417   disturbance as a coarse binary variable increases uncertainty in our analyses. Further

418   resolution of the issue requires higher-quality disturbance data, which may be available

419   in the near future for some regions (e.g., maps of fire history are under construction for

420   North America). Ultimately, the combination of habitat fragmentation and climate

421   change may be the most severe threat hanging over species with poor dispersal ability,

422 since these tend to decline in fragmented landscapes, and then disappear altogether

423 when they cannot track climates [71, 72].

424

425 **Conclusions**

426 Ecological traits can provide highly resolved information about a species' fundamental

427 niche [73-75], so it makes sense that variation in traits such as dispersal limitation may

428 drive responses to habitat fragmentation. Given that dispersal limitation also peaks at

429 the equator [14, 15], we conclude that dispersal traits offer a compelling explanation for

430 widely reported spatial gradients in fragmentation sensitivity [9, 10, 76]. Our results

431 also highlight how avian wing morphology provides a simple metric to identify

432 communities and species most sensitive to fragmentation, with potential uses in land-

433 use management and the design of protected area networks.

434   These findings have important implications, both for understanding the

435 mechanisms causing fragmentation effects, and formulating appropriate management

436 interventions. Our results are consistent with previous studies suggesting that forest

437 fragmentation will have more severe effects on tropical species [9, 10], and provide

438 strong evidence that this pattern reflects inherent differences among species in their

439 ability to cope with edge effects and to disperse across deforested terrain. A major

440 management implication is that maintaining structural connectivity between forest

441 fragments (i.e. corridors and 'stepping stones' of natural habitat) is a priority

442 worldwide, and particularly urgent in the tropics. Taken together, our results highlight

443 the need for flexible and dynamic conservation strategies tailored to local contexts,

444 including climatic conditions and associated species adaptations.

445

446 **Methods**

447 To estimate fragmentation sensitivity of species populations, we used BIOFRAG

448 software [28] to analyse a refined and updated version of the BIOFRAG dataset [77].

449 BIOFRAG provides a direct estimate of the effects of landscape-level fragmentation on

450 each population of each species [9, 28] (see Supplementary material). Populations of the

451 same species may be identified as fragmentation sensitive in some landscapes and

452 insensitive in others. We define fragmentation-sensitive populations as those avoiding

453 forest edges in fragmented landscapes and occurring mainly in the forest core. We

454 follow methods explained in greater depth elsewhere [9, 28, 77], summarising the key

455 points in the following sections, with details of updates and modifications.

456

457 **Study landscapes and surveys**

458 We compiled bird assemblage data from published surveys of fragmented forest

459 landscapes, coupled with fragmentation data extracted from GIS vegetation layers. The

460 core sample was downloaded from the BIOFRAG database, containing species

461 abundance from 32 abundance surveys and tree-cover maps of associated study

462 landscapes from the year 2000 [9, 77]. We excluded 11 studies from our analysis

463 because of potential pseudoreplication (see Supplementary materials). To expand our

464 sample, we gathered further post-1998 bird survey data from (or cited within) forest

465 fragmentation studies via a literature search of Web of Science core collection, using the

466 default "Topic" search for literature published after 2010, with terms: Birds OR Bird OR

467 Avian AND Forest OR Wood* OR Rainforest AND Sample OR Survey OR Census AND

468 Fragment* AND Plot* OR Site* AND Abundance.

469   After adding 10 new studies to the original BIOFRAG dataset, the final sample

470 contained 31 survey datasets sampled between 1998 and 2013 across six continents

471 (Africa, 3; South America, 5; North America, 10; Europe, 7; Asia, 3; Oceania, 3) (Fig. 1,

472 Supplementary dataset 1). We calculated the absolute latitude of each study landscape

473 as the centroid latitude of all the sampling points within each survey, using the

474 geosphere package in R [78]. In all cases, surveys targeted both forest and non-forest

475 matrix with varying levels of tree-cover heterogeneity and multiple (average = 153)

476 sampling locations. We omitted surveys reporting only presence-absence, and limited

477 our sampling to surveys reporting abundance or relative abundance of bird species at

478 each sampling location. We converted raw abundance estimates to relative abundance

479 to allow comparison across the full sample of landscapes. Although we limited sampling

480 to landscapes in which the original forest cover had become fragmented by a non-forest

481 matrix, this included a range of forest types embedded in various matrix types

482 (Supplementary dataset 1).

483   We included mist-netting, point-count and line-transect surveys in our sample

484 and account for differences in survey method among studies using a mixed-effects

485 modelling approach. We excluded studies using multiple survey methods inconsistenly

486 across the study landscape. Accurate geolocation of avian populations is key to

487 identifying the affinity of species to forest edges. However, geolocation is challenging in

488 field surveys, particularly in dense forest where detectability of birds is often low and

489 95% of birds are identified through auditory signals [79-81]. To maximise accuracy of

490 geolocation, we excluded point-count radii greater than 100 m and transects larger than

491 100 x 100m. Our sample contains four mist-nets surveys, all located in Brazilian tropical

492 forests. Although sampling bird communities using mist-nets leads to inaccuracies in

493 abundance estimates based on capture rate [82], they have the advantage that

494 identification and geolocation of mist-netted bird species is generally accurate.

495

496 **Forest fragmentation and edge effects**

497   To estimate responses of bird species to fragmentation, we began by combining bird

498   survey data with information on habitat. We downloaded tree-cover maps and non-

499   habitat masks for the year 2000 at 30m resolution [82, 83], using the following methods

500   replicated from previous studies [9, 28]. We set the value of each pixel in the tree-cover

501   maps to the percentage tree cover within each 30 m × 30 m pixel (hereafter termed

502   "point cover"). The non-habitat masks estimate forest cover as a binary value (forest

503   and non-forest) which we use to identify forest edge boundaries with improved

504   precision. To create map layers for each study landscape, we then extracted and

505   cropped the tree-cover and non-habitat mask layers to a minimum convex polygon with

506   a 5 km buffer around the sampling points, using Google Earth Engine [84]. To minimize

507   distortion of the distance and direction between sample points, we projected maps and

508   sample points into azimuthal equidistant projection (AEQD), giving coordinates in

509   meters with origin equal to the sample points centroid [9].

510   Following methods proposed by Pfeifer et al. [28], we quantified the level of edge

511   influence (EI) within a specified radius from sample points. We used BIOFRAG software

512   to calculate 30m resolution EI maps using the tree-cover maps downloaded from Google

513   Earth Engine. We then specified the "Depth of Edge influence" (DEI) – i.e. the size of

514   radius – for each pixel, and calculated the level of tree cover heterogeneity as a function

515   of the mean and standard deviation of point-cover values within the DEI radius. DEI was

516   set to 1 km as default, with adjustments where necessary according to the scale of

517   particular datasets (see Supplementary materials).

518   Forest edges within the DEI radius strongly influence the EI value, meaning that

519   EI is representative of both the amount of forest edge surrounding each pixel, and the

520   local tree cover variation, accounting for edge shape and patch size. We also

521   implemented a Gaussian filter to smooth the point-cover values within the DEI radius,

522   with a stronger smoothing effect on values farther away from the focal pixel.

523   Implementing this filter ensures that variation in tree cover closer to the focal pixel has

524   a larger impact on the EI value, in line with the assumption that the strength of edge

525   effects is related to their proximity to the sampling location [28].

526   EI for each grid cell I can be expressed as

527

528    $$EI_i = \max(\sigma C, |C - C_i|) \times sign(C - C_i)$$

529

530   where C is the landscape average of tree cover per pixel, C_i is the percent tree cover at

531   each pixel and σC is the standard deviation of habitat cover at the landscape scale.

532

533   **Habitat preference and edge affinity**

534   We used EI and point-cover maps for each study landscape to classify each species into

535   three categories of habitat preference (Forest/Matrix/Generalist) and three categories

536   of edge affinity (Core/Edge/noPref), resulting in nine different combinations (Table S5).

537   Classification was based on relative abundances of species across a range of point-cover

538   and EI values through a Naïve Bayes Classifier based approach (see Supplementary

539   materials). We restricted our sample to populations with a "Forest" habitat preference

540   and then assigned populations to a binary response variable (fragmentation sensitive or

541   fragmentation insensitive) based predominantly on their edge affinity classification.

542   A potential source of inaccuracy in classifications of habitat preference and edge

543   affinity arises because tree cover may change between the time of survey and the year

544   2000 when our tree cover maps were created. Tree-cover change may mean that values

545   extracted from the EI and tree-cover maps do not represent the point-cover and

546   surrounding tree-cover heterogeneity at the time of the survey. However, when we ran

23

547   a sensitivity analysis to assess the influence of post-survey tree-cover change, we found

548   that these changes have only minor effects on our results and do not alter the

549   conclusions from our main analyses (see Supplementary materials; Fig. S2).

550

551   **Assigning fragmentation sensitivity to bird populations**

552   Previous studies assumed that populations classified as "Forest-core" by the BIOFRAG

553   algorithm are fragmentation sensitive, based on the premise that avoidance of forest

554   edge habitats indicates sensitivity to edge effects [9, 28]. However, this approach can be

555   sensitive to inaccurate geolocation of species observation points, reducing confidence in

556   estimates of edge affinity, potentially resulting in open-country bird species being

557   classified as Forest-core species.

558   To reduce the number of misclassified populations, we limited assignment of

559   fragmentation sensitivity to 225 populations of 165 species classified by BirdLife

560   International [33] as having a high forest dependency ("Forest specialist"), in addition

561   to qualifying as Forest-core. We also relaxed the threshold by including less-specialised

562   species, leading to classification of 583 populations of 418 species with either high or

563   medium forest dependency ("Forest associated"), in addition to Forest-core status.

564   Further details of how species were assigned to high and medium forest dependency

565   are provided by Buchanan et al. [85]. Analyses based on these two definitions of

566   fragmentation sensitivity are referred to as "Restricted" and "Expanded" analyses,

567   respectively. Restricting the assignment of fragmentation sensitivity to either Forest-

568   specialist or Forest-associated species meant that 60 populations of 53 species were

569   identified as insensitive to forest-fragmentation despite being classified as "Forest-core"

570   species (Table S6). These species are highly unlikely to be sensitive to forest

571   fragmentation because most are abundant in non-forest habitats, favouring open areas,

572   gardens or forest edges (e.g., *Elaenia chiriquensis*, *Molothrus ater, Serinus serinus*,

573   *Thraupis sayaca*).

574   We examined latitudinal patterns of fragmentation sensitivity by extracting the

575   centroid latitude of species geographical ranges from published data [34]. To assess

576   whether fragmentation sensitivity was non-randomly distributed across the global bird

577   phylogeny [86], we created a majority rule consensus tree from 100 random

578   phylogenies downloaded from BirdTree (www.birdtree.org), using the Hackett

579   backbone. We then quantified phylogenetic signal in fragmentation sensitivity as the

580   sum of changes in estimated nodal values for binary traits (d) [87]. Values of d close to 0

581   indicate that fragmentation sensitivity is phylogenetically conserved; values close to 1

582   suggest a random distribution across the phylogenetic tree. In our dataset, families with

583   a high proportion of fragmentation-sensitive species tend to be sedentary and largely

584   restricted to the tropics, such as Trogonidae (Restricted: 70% sensitive; Expanded: 93%

585   sensitive), Furnariidae (Restricted: 53% sensitive; Expanded: 61% sensitive,) and

586   Pycnonotidae (Restricted: 47% sensitive; Expanded: 47% sensitive).

587

588   **Historical disturbance**

589   We estimated historical disturbance for each study landscape using the methods

590   described by Betts et al. [9]. The likely impact of different types of historical disturbance

591   was quantified using four sets of maps: glaciated areas at the last glacial maximum [88];

592   high intensity forest crown fires [89]; tropical storms [90]; and long-term

593   anthropogenic forest loss (see Supplementary Materials). Using the AEQD projection,

594   we overlaid these map layers onto a minimum convex polygon with a 5km buffer

595   around each sample point. To align with Betts et al. [9], we converted historical

596 disturbance to a binary variable (High/Low), with landscapes scored as High

597 disturbance if any disturbance layer was detected across the majority (>50%) of the

598 landscape (see Supplementary materials).

599   Treating disturbance as a binary variable is simplistic but makes sense inasmuch

600 as all forms of disturbance may have severe impacts on biodiversity regardless of

601 whether they act independently or in combination with other factors. A potential

602 weakness is that this approach groups together forms of disturbance operating over

603 very different timescales. Natural disturbances act over deep time whereas

604 anthropogenic disturbances operate on a shallower timescale and often at smaller

605 spatial scale. To account for this temporal distinction, we created three binary

606 disturbance variables – "natural" (fires, glaciation, storms), "anthropogenic" (recent

607 forest loss), and "any" (all the above) – then modelled their effect on fragmentation

608 sensitivity separately.

609

610 **Dispersal limitation**

611 To estimate variation in dispersal ability across species, we compiled Hand-wing Index

612 (HWI) for all 1034 study species using global datasets [15, 34]. HWI is a measure of

613 wing-shape – and specifically wing-elongation – correlated with wing aspect ratio [91,

614 92]. HWI is therefore linked to flight efficiency, with high values of HWI strongly

615 indicative of dispersive, migratory or aerial lifestyles [15, 21]. HWI predicts dispersal

616 distance in birds [21, 93], thus providing a morphological metric widely used as a proxy

617 for dispersal ability in macroecological studies [15, 94-97]. Variation of HWI across our

618 study sample (n = 1034 species) is large (range = 1.9–71.8; mean = 22.7; SD = 12.2) and

619 broadly representative of all birds (n = 9993; mean = 25.7; SD = 15.06; see Fig. S3a).

620   The relationship between HWI and dispersal ability is positive [21, 93] whereas

621   its relationship with dispersal limitation is negative (high HWI reflects low dispersal

622   limitation). To reflect this inversion and to ease the interpretation of analyses, we take

623   the negative of the species mean trait value (nHWI) as a proxy of dispersal limitation

624   (i.e. high nHWI reflects high dispersal limitation). We found dispersal traits are

625   distributed fairly evenly throughout the phylogenetic tree of our sample (Fig. 2b),

626   suggesting that variation in nHWI is not especially biased by particular taxonomic

627   groups. To conduct analyses at the assemblage level, we summarised the average level

628   of dispersal limitation (nHWI) in each study landscape (n = 31) by taking the mean

629   dispersal limitation score for all species present at that site.

630

631   **Body size**

632   Small species with high HWI (e.g. swallows) are often far more dispersive than large

633   species with low HWI (e.g. kiwis), highlighting why HWI provides a more accurate

634   prediction of avian dispersal ability than more traditional metrics, such as body mass.

635   Although initial analyses reported an association between body size and dispersal

636   distance in birds [98, 99], body size does not predict avian dispersal ability at global

637   scales [15]. Nonetheless, body size is an important correlate of fragmentation sensitivity

638   [50] and dispersal [100] in animals, as well an important morphological predictor of

639   threat status and fragmentation sensitivity [50, 101]. We therefore account for variation

640   in body size by including species mean body mass as a covariate in our models and

641   assess interactions between body mass and dispersal. Such interactions are predicted if

642   the effects of dispersal limitation are accentuated in species with larger body size,

643   owing to their inherent characteristics, including low population density, slow

644   reproductive output and susceptibility to hunting [68, 101-103]. Body mass estimates

645   are extracted from recently updated global datasets [34].

646

647   **Defining scales**

648   We performed analyses using data calculated across three different scales. Landscape-

649   level analyses (e.g. Fig. 3b) used geographical or climatic data extracted from the

650   landscape or species-specific data averaged across all species within the landscape

651   assemblage (e.g. community mean dispersal limitation). Population-level analyses (e.g.

652   Fig. 4) used data specific for each population and therefore capture intra-specific

653   variation (e.g. fragmentation sensitivity varying across different localities). Species-level

654   analyses (e.g. Fig. S1) use data averaged across all populations of the same species (e.g.

655   fragmentation sensitivity), generated at species level (e.g. mean body mass) [34], or

656   extracted from GIS layers and averaged across all cells of the species distributional

657   range (e.g. range-wide seasonality).

658

659   **Seasonality**

660   To tease apart the effects of dispersal limitation (nHWI) from other correlated traits

661   associated with seasonal climates, we included seasonality in our models. For

662   landscape-level analyses, we quantified seasonality at the centroid of survey points for

663   each study landscape (n = 31). Using these centroids, we extracted local intra-annual

664   temperature variation from WorldClim.org [104], at 2.5 minute resolution ($\sim$5km^2)

665   with raster cell values equal to the standard deviation in local mean monthly

666   temperatures across the year. For species-level analyses, we also extracted this metric

667   of seasonality across the distribution of each species by calculating an average from all

668   raster cells overlapping the species' breeding range (see Supplementary materials)

669

Statistical analyses

671 We performed a generalised linear model to assess whether community mean dispersal

672 limitation (nHWI) is related to the overall fragmentation sensitivity of bird assemblages

673 at the landscape level. To avoid overdispersion in our residuals, we calculated the

674 proportion of fragmentation sensitive species in each of our 31 study landscapes and

675 modelled whether this proportion was dependent on community mean dispersal

676 limitation (nHWI) using a quasi-binomial error structure.

677 To assess the effect of predictor variables on species sensitivity to habitat

678 fragmentation at the species level, we performed multivariate Bayesian phylogenetic

679 mixed effects models on each of our fragmentation sensitivity methods (for model

680 design and rationale, see Table S7). In both Expanded and Restricted analyses, we

681 modelled the effects of historical disturbance, absolute latitude, seasonality, dispersal

682 limitation, and body mass (as well as an interaction term between body mass and

683 dispersal limitation) on the likelihood of being classified as fragmentation sensitive.

684 Seasonality and body mass were logarithmically scaled prior to analysis. We included

685 study and species as random effects to account for repeated sampling of particular

686 species across multiple studies, as well as the non-independence of species sampled

687 within the same study landscape (Extended Data Table 1). To allow accurate effect-size

688 comparisons between continuous variables and our binary disturbance variable, we

689 standardized all continuous variables by 2 standard deviations [105]. Collinearity

690 between predictor variables was checked via variance inflation factors (VIFs) and found

691 to be acceptable (< 10).

692 To perform sensitivity analyses, we re-ran the same set of models with minor

693 adaptations (see Supplementary materials). First, we replaced the binary historical

694 disturbance variable with subsets restricted to anthropogenic and natural disturbances.

695 To account for possible conflation between dispersive traits and migratory behaviour,

696 we removed long-distance migrants from our sample and re-ran our Restricted analysis

697 (Fig. S4). Finally, to ensure results were not driven by exteme values of nHWI, we

698 repeated our analyses with Apodiformes removed from the dataset (see Supplementary

699 materials).

700 Models were constructed using the brms package in R [106] with markov chain

701 iterations and priors kept consistent across all models. We selected 10000 total

702 iterations with a 2000-iteration warmup-phase. We used the no u-turn sampler (NUTS)

703 to reduce autocorrelation between successive iterations and as such no thinning was

704 required. We assigned weakly informative priors, normal (0,10), to the slope

705 parameters and the intercept as recommended by Gelman [107]. Each of our models ran

706 four markov chains in parallel which were assessed for convergence. We used 100

707 random trees from the global bird phylogeny [86], as described above, and ran all of our

708 models separately across this sample of trees. This resulted in 400 chains per model

709 which were then combined to produce our final posterior distribution accounting for

710 phylogenetic uncertainty [108]. We report estimated effect sizes ($\hat{\beta}$) as the means of the

711 posterior distributions, along with 95% credible intervals (Extended Data Table 1). The

712 effects of each of our variables on fragmentation sensitivity were inferred through

713 assessment of posterior distributions.

714

715 **Inferring causal mechanisms**

716 To identify drivers of fragmentation sensitivity, we constructed structural equation

717 models (SEMs) using the phylopath package in R [109]. The results of SEMs provide

718 insight into the relative importance of different drivers, but should be treated with

719   caution given the hierarchical complexity of our data structure (see Supplementary

720   materials; Fig. S1). Therefore, in addition, we modelled the effects of historical

721   disturbance, latitude and seasonality on nHWI (Table S3 & S4) to test the role of these

722   factors in explaining variation in dispersal limitation across study species (n = 1034).

723   Given that extinction filters may act at a local scale through removing and then

724   preventing recolonisation by maladapted species in the landscape [12], we calculated

725   historical disturbance, latitude and seasonality using landscape-level data. For each

726   species, we used GIS layers to extract the historical disturbance score (binary variable:

727   High = 1, Low =0), local temperature variation [104] and absolute latitude of the

728   landscape centroid, for all landscapes where the species was present. We then averaged

729   these scores to obtain species-level values based on variables extracted from the

730   relevant study landscapes.

731   We then ran three phylogenetic generalised least-squared models using 100

732   random phylogenies (see above) for (1) all study species, (2) residents, short distance

733   migrants and partial migrants (i.e. excluding long-distance migrants), and (3) residents

734   only. Data and definitions for these migratory classes are provided by Tobias & Pigot

735   [110]. In each case (1–3), we first assessed the relationship between historical

736   disturbance and nHWI as a univariate model. Second, we added latitude as an additional

737   covariate, and third, we added seasonality as a third covariate. Multicolinearity between

738   the three covariates was addressed by assessment of VIFs and found to be acceptable

739   (VIF < 6). For each model, we established the relative proportion of independent

740   variance explained by each driver using hierarchical partitioning implemented with the

741   R package *hier.part* [111]. Evolutionary drivers such as habitat disturbance and climate

742   may act on species traits at regional rather than local scales, so we re-ran these analyses

743   with disturbance, seasonality and latitude estimated across the distribution of each

744   study species (see Supplementary materials).

745

Data availability statement

All data are available at:

https://github.com/tomlweeks1994/Dispersal_mediates_fragmentation_sensitivity

Code availability statement

The code to conduct analyses and replicate figures is available at:

https://github.com/tomlweeks1994/Dispersal_mediates_fragmentation_sensitivity

Acknowledgements

Author contributions

TLW and JAT conceived and developed the study, with input from MGB, MP and CW. Data from particular sites were contributed by MB, CB-L, LB, JB, AC, CMK, UGK, CJM, PIO, BTP, HPP and EMW. TLW integrated datasets and ran all analyses with support from CW and MGB. TLW wrote the first version of the manuscript and designed all figures

770   with input from JAT. All authors contributed to subsequent drafts and gave final

771   permission for publication.

772

773 Competing interests

774   The authors declare no conflict of interest.

775

776

777 ORCID

778	Thomas L. Weeks	0000-0002-2525-3900
779	Matthew G. Betts	0000-0002-7100-2551
780	Christopher Wolf	0000-0002-5519-3845
781	Marion Pfeifer	0000-0002-6775-3141
782	Cristina Banks-Leite	0000-0002-0091-2857
783	Luc Barbaro	0000-0001-7454-5765
784	Jos Barlow	0000-0003-4992-2594
785	Alexis Cerezo	0000-0001-8497-9276
786	Christina M. Kennedy	0000-0001-8902-8728
787	Urs G. Kormann	0000-0001-9875-4836
788	Charled J. Marsh	0000-0002-0281-3115
789	Benjamin T. Phalan	0000-0001-7876-7226
790	Hugh P. Possingham	0000-0001-7755-996X
791	Eric M. Wood	0000-0003-2787-6451
792	Joseph A. Tobias	0000-0003-2429-6179

793

794

Figures
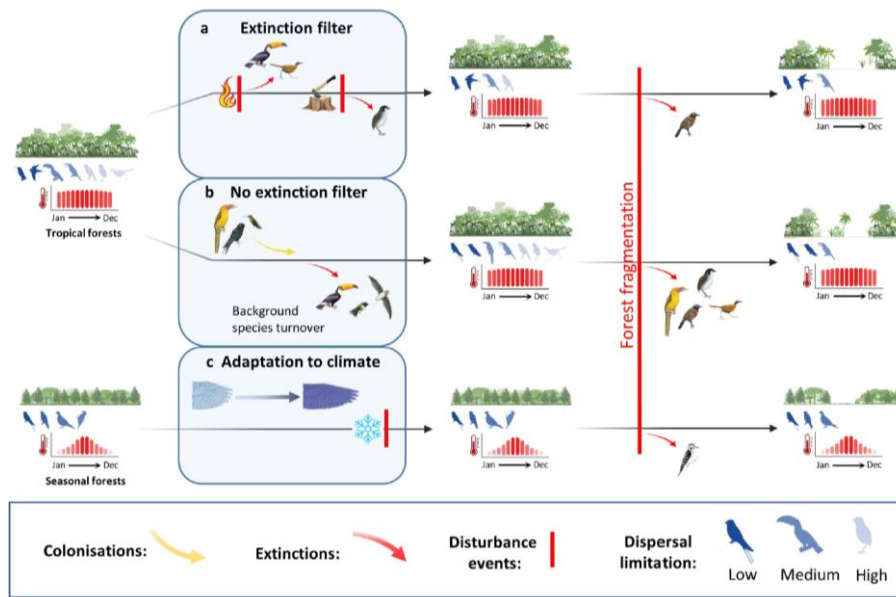
Fig. 1 | Hypotheses predicting the distribution of fragmentation-sensitive species.
The top pathway (**a**) illustrates how 'extinction filters' linked to historical disturbances
(e.g. fire & anthropogenic forest loss) can be non-random, removing species traits
associated with sensitivity to disturbance, and retaining more resilient survivors.
Tropical bird communities that have largely avoided severe historical disturbance
theoretically contain more species with disturbance-sensitive traits (e.g. poor dispersal,
ecological specialisation), accentuating the impacts of forest fragmentation (**b**).
Background turnover of species – shown in (**b**) but present in all pathways – is random
with respect to disturbance-sensitive traits. A different mechanism involves the
evolution of flight adaptations to cope with seasonal fluctuations in temperature and
resources (e.g. vegetation, insects, flowers, fruit). In birds, the predominant adaptation
to seasonality involves increased mobility (e.g. local dispersal; long-distance migration),
so highly seasonal communities lack dispersal-limited species, potentially increasing
their resilience to forest fragmentation (**c**) in comparison with climatically stable
regions (**b**). Relative species richness is shown by the number of bird silhouettes in the
community.
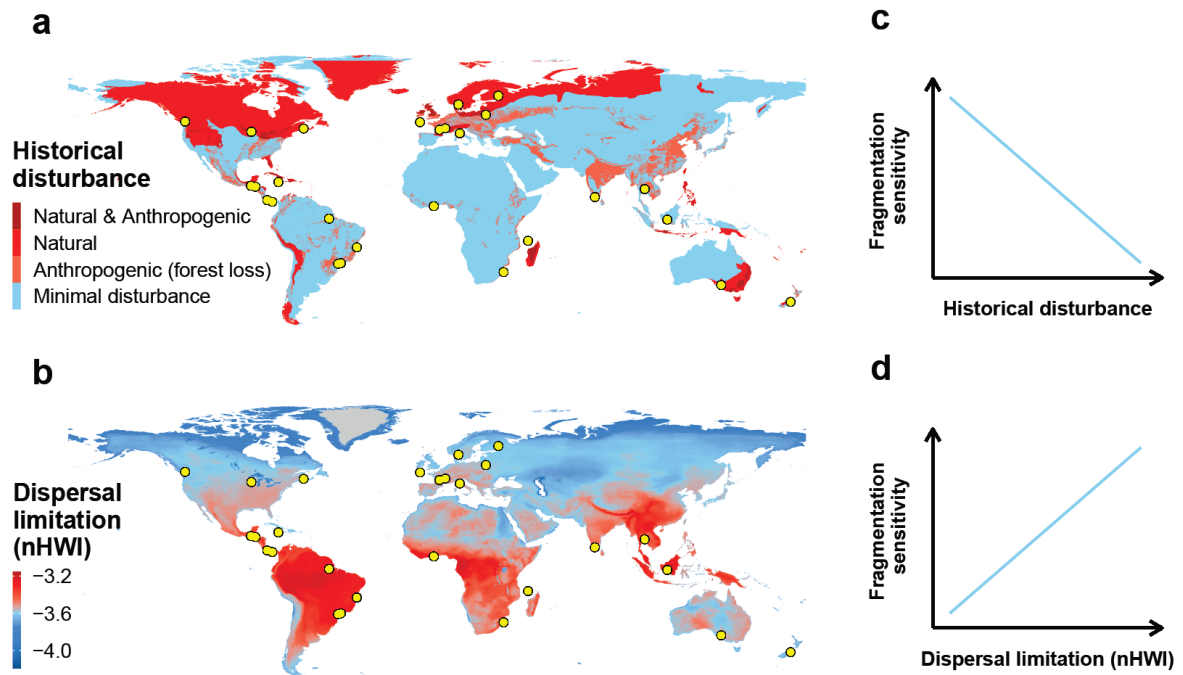
Fig. 2 | Global patterns of landscape disturbance and dispersal limitation. **a**) The

presence of natural (e.g. major fires, storms, glaciation) or anthropogenic historical

disturbances recorded in each grid cell. Natural disturbance pressures (bright red) have

typically persisted for longer periods of time and may cause complete removal of forest

biota (e.g. Glaciation). Anthropogenic forest loss (pale red) represents more recent

disturbance that often alters composition of local assemblages without complete

eradication. **b**) Variation in negative (i.e. inverse) hand-wing index (nHWI), averaged

across species occurring in each grid cell, ranging from low (blue) to high (red)

dispersal limitation. Dispersal limitation data are calculated from measurements of

10562 bird species, logarithmically scaled for visualization [log(1/nHWI)]. Yellow dots

show study landscapes (21 from BIOFRAG; 10 from additional sampling). Grid cells in **a**)

and **b**) are 2.5 arc minutes. Right-hand panels show hypothetical relationships:

extinction filters predict that fragmentation sensitivity is negatively associated with

historical disturbance (**c**); dispersal-related mechanisms predicts that fragmentation

sensitivity is positively associated with dispersal limitation (**d**).
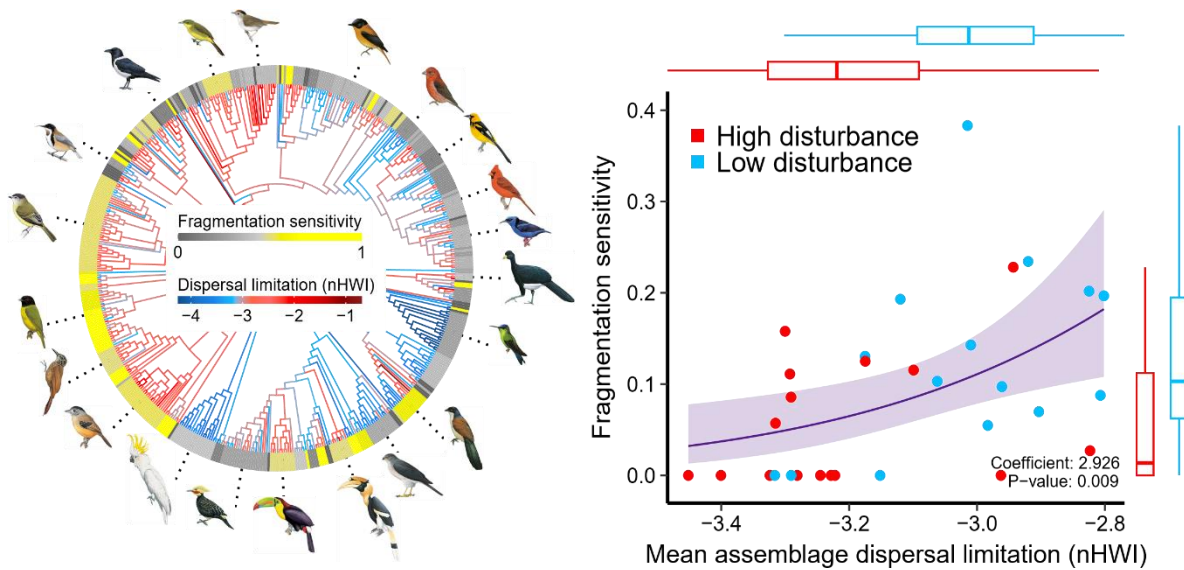
Fig. 3 | Fragmentation sensitivity increases with dispersal limitation in bird

assemblages. **a)** Variation in fragmentation sensitivity and dispersal ability plotted on a

consensus phylogenetic tree. Each branch represents a genus (*n* = 441), with data at tips

averaged across families (*n* = 115) for visualization. Branch colours indicate dispersal

limitation (least dispersive species in red); tip colours show the proportion of

fragmentation-sensitive species in each family (Expanded analysis; most sensitive in

yellow). **b)** Data points (coloured by level of historical disturbance) are means for 31

study landscapes. For each assemblage, fragmentation sensitivity is assigned to Forest-

core species with high forest dependency (Restricted analysis), and mean dispersal

limitation is the negative (i.e. inverse) hand-wing index (nHWI) averaged across all

species; nHWI is logarithmically scaled [log(1/HWI)] for visualization. Statistics are

from a generalized linear model with quasi-binomial errors;purple line shows model fit

(R^2 = 0.180); shaded region shows 95% confidence intervals. Boxplots in (**b**) show the

same distributions with median value, interquartile range, and whiskers to extreme

values (outliers are data points >1.5x quartiles). Results for the Expanded sample are

shown in Extended Data Fig. 4.

847
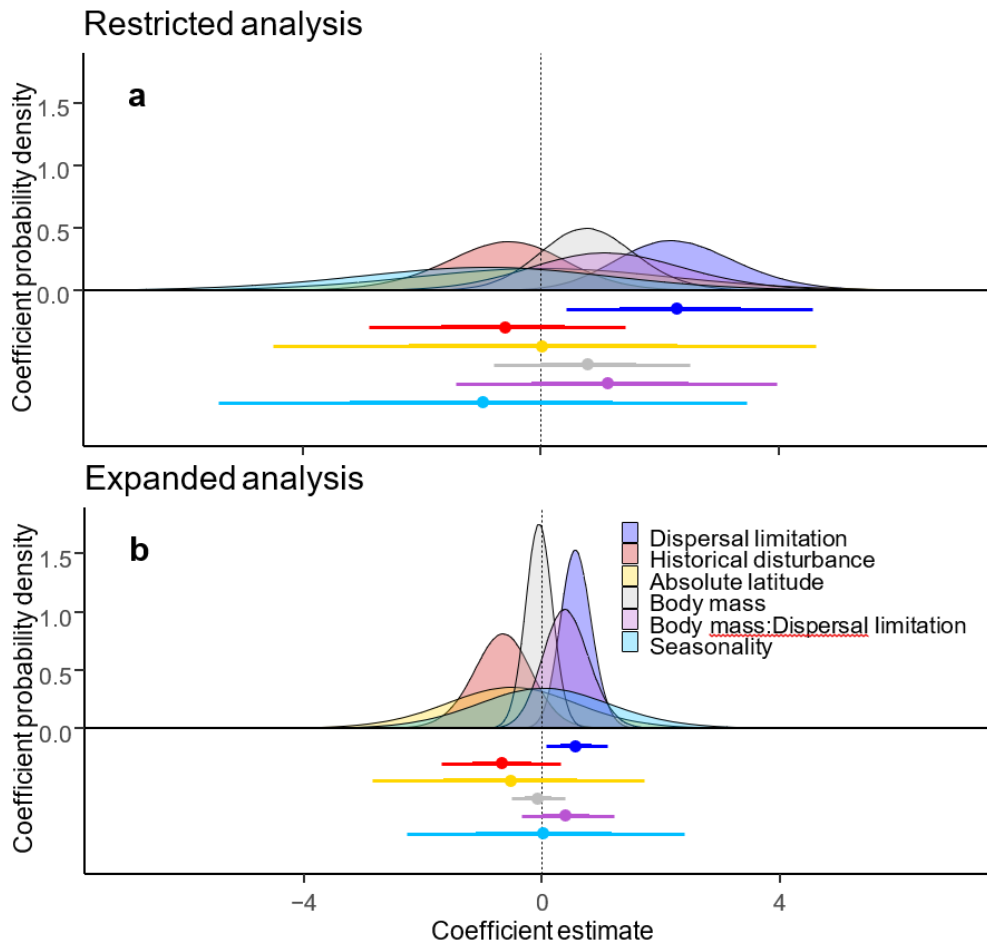
Fig. 4 | Dispersal limitation (nHWI) explains variation in fragmentation sensitivity. Results of Bayesian phylogenetic mixed effect models predicting fragmentation sensitivity for all 1564 bird populations (n = 1034 species). Populations were classified as fragmentation sensitive if they were identified as 'Forest-core' by BIOFRAG. Restricted analysis assigned fragmentation sensitivity only to 'Forest specialists' (**a**); Expanded analysis assigned fragmentation sensitivity to both 'Forest specialist' and 'Forest associated' species (**b**; see Methods). Bayesian posterior distribution is shown above the line; effect size estimates with credible intervals (CI) below the line (68%: thick errorbars; 95%: thin errorbars). High effect sizes indicate a positive association with fragmentation sensitivity; low effect sizes indicate a negative association. Historical disturbance is a binary variable (1/0) calculated using all disturbance layers (e.g. forest loss, glaciation, storms & fires)

860
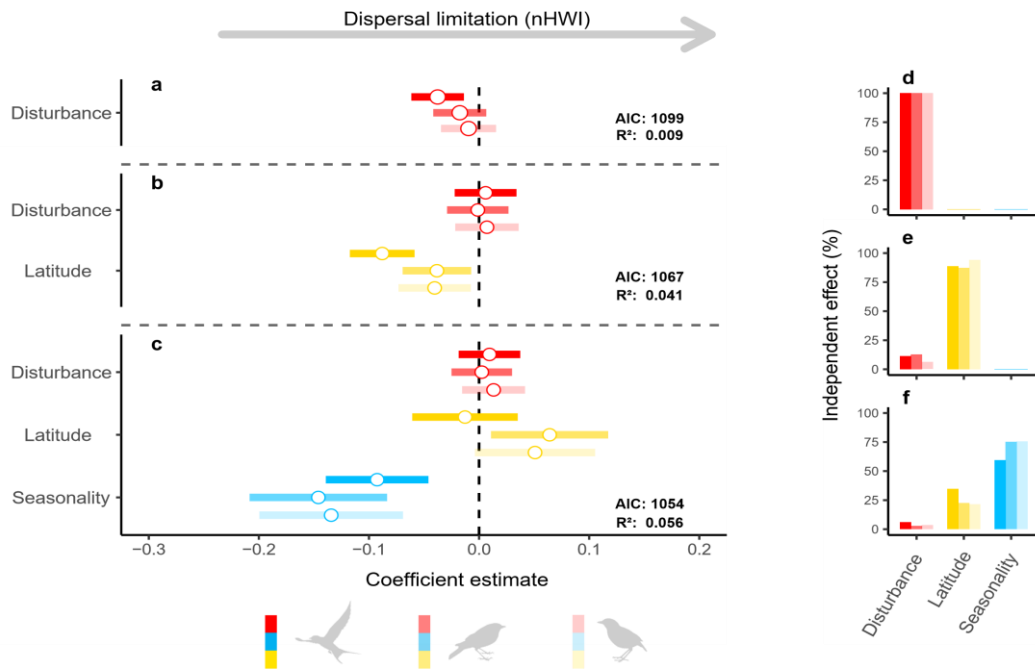
Fig. 5 | Predictors of dispersal limitation in birds. Results shown are outputs of phylogenetic generalized least squares models predicting dispersal limitation (nHWI) across all bird species sampled, including long-distance migrants (swallow image, dark bars; n = 1034); only resident species and short distance/partial migrants (thrush image, medium bars; n = 921); or resident species only (pitta image, pale bars; n = 858). Panels present three sets of models with increasing complexity: a univariate model with single predictor (**a, d**), and multivariate models with two (**b, e**) and three (**c, f**) predictors. Each predictor is calculated at the species-level by averaging across landscapes where each species is present. Disturbance (red) is the local binary disturbance scores, latitude (yellow) is the absolute latitude of the landscape centroids and seasonality (blue) is the standard deviation of mean monthly temperature values. Panels **a-c** show effect size estimates with 95% confidence intervals; a negative effect indicates reduced dispersal limitation (i.e. increased dispersal ability). R^2 and AIC values are calculated for full sample models only. Panels **d-f** show the proportion of independent variation explained by each model covariate, calculated using hierarchical partitioning.

References

878   1.   Brook, B., Sodhi, N., & Bradshaw, C. (2008). Synergies among extinction drivers

879   under global change. *Trends in Ecology & Evolution*, **23**, 453–460.

880   https://doi.org/10.1016/j.tree.2008.03.011

881   2.   Ewers, R. M., & Didham, R. K. (2006). Confounding factors in the detection of

882   species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

883   https://doi.org/10.1017/S1464793105006949

884   3.   Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-

885   Pinto, H., ... & Prevedello, J. A. (2020). Indirect effects of habitat loss via habitat

886   fragmentation: A cross-taxa analysis of forest-dependent species. *Biological*

887   *Conservation*, **241**, 108368. https://doi.org/10.1016/j.biocon.2019.108368

888   4.   Wade, T. G., Riitters, K. H., Wickham, J. D., & Jones, K. B. (2003). Distribution and

889   causes of global forest fragmentation. *Conservation Ecology*, **7**, 7.

890   https://doi.org/10.5751/es-00530-070207

891   5.   Grantham, H. S., Duncan, A., Evans, T. D., Jones, K. R., Beyer, H. L., Schuster, R.,

892   Walston, J., Ray, J. C., Robinson, J. G., Callow, M., Clements, T., Costa, H. M.,

893   DeGemmis, A., Elsen, P. R., Ervin, J., Franco, P., Goldman, E., Goetz, S., Hansen, A., ...

894   Watson, J. E. M. (2020). Anthropogenic modification of forests means only 40% of

895   remaining forests have high ecosystem integrity. *Nature Communications*, **11**, 5978.

896   https://doi.org/10.1038/s41467-020-19493-3

897   6.   Hanski, I. (1998). Metapopulation dynamics. *Nature*, **396**, 41–49.

898   https://doi.org/10.1038/23876

899   7.   Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts,

900   S. C. et al. (2018). Moving in the Anthropocene: Global reductions in terrestrial

901 mammalian movements. *Science,* **359**: 466–469.

902 https://doi.org/10.1126/science.aam9712

903 8. Murcia, C. (1995). Edge effects in fragmented forests: Implications for conservation.

904 *Trends in Ecology & Evolution*, **10**, 58–62. https://doi.org/10.1016/S0169-

905 5347(00)88977-6

906 9. Betts, M. G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D. B.,

907 Barlow, J., Eigenbrod, F., Faria, D., Fletcher, R. J., Hadley, A. S., Hawes, J. E., Holt, R. D.,

908 Klingbeil, B., Kormann, U., Lens, L., Levi, T., Medina-Rangel, G. F., Melles, S. L., …

909 Ewers, R. M. (2019). Extinction filters mediate the global effects of habitat

910 fragmentation on animals. *Science*, **366**, 1236–1239.

911 https://doi.org/10.1126/science.aax9387

912 10. Bregman, T. P., Sekercioglu, C. H., & Tobias, J. A. (2014). Global patterns and

913 predictors of bird species responses to forest fragmentation: Implications for

914 ecosystem function and conservation. *Biological Conservation*, **169**, 372–383.

915 https://doi.org/10.1016/j.biocon.2013.11.024

916 11. Banks-Leite, C., Betts, M. G., Ewers, R. M., Orme, C. D. L., Pigot, A. L. (2022) The

917 macroecology of landscape ecology. *Trends in Ecology and Evolution*. 2961,

918 https://doi.org/10.1016/j.tree.2022.01.005

919 12. Balmford, A. (1996). Extinction filters and current resilience: the significance of

920 past selection pressures for conservation biology. *Trends Ecology & Evolution*, **11**,

921 193–196.

922 13. Varpe, Ø. (2017). Life history adaptations to seasonality. *Integrative and*

923 *Comparative Biology*, **57**, 943–960. https://doi.org/10.1093/icb/icx123

924 14. Salisbury, C. L., Seddon, N., Cooney, C. R., & Tobias, J. A. (2012). The latitudinal

925 gradient in dispersal constraints: Ecological specialisation drives diversification in

926   tropical birds. *Ecology Letters*, **15**, 847–855. https://doi.org/10.1111/j.1461-

927   0248.2012.01806.x

928 15. Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C.,

929   MacGregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J. A. (2020). Ecological

930   drivers of global gradients in avian dispersal inferred from wing morphology.

931   *Nature Communications*, **11**, 2463. https://doi.org/10.1038/s41467-020-16313-6

932 16. Dynesius, M., & Jansson, R. (2000). Evolutionary consequences of changes in

933   species' geographical distributions driven by Milankovitch climate oscillations.

934   *Proceedings of the National Academy of Sciences*, **97**, 9115–9120.

935   https://doi.org/10.1073/pnas.97.16.9115

936 17. Winger, B. M., Auteri, G. G., Pegan, T. M., & Weeks, B. C. (2019). A long winter for the

937   Red Queen: Rethinking the evolution of seasonal migration. *Biological*

938   *Reviews*, **94**, 737–752. https://doi.org/10.1111/brv.12476

939 18. Moore, R. P., Robinson, W. D., Lovette, I. J., & Robinson, T. R. (2008). Experimental

940   evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters*,

941   **11**, 960–968. https://doi.org/10.1111/j.1461-0248.2008.01196.x

942 19. Stutchbury, B.J.M. & Morton, E.S. (2001). *Behavioral ecology of tropical birds.*

943   Academic Press, London, UK.

944 20. Tobias, J. A., Sheard, C., Seddon, N., Meade, A., Cotton, A. J., & Nakagawa, S. (2016)

945   Territoriality, social bonds, and the evolution of communal signaling in birds.

946   *Frontiers in Ecology & Evolution*, **4**, 74. https://doi.org/10.3389/fevo.2016.00074

947 21. Weeks, B.C., O'Brien, B.K., Sheard, C., Claramunt, S., Chu, J.J., & Tobias, J.A. (2022).

948   Morphological adaptations linked to flight efficiency and aerial lifestyle determine

949   natal dispersal distance in birds. *Functional Ecology*. Early View

950   https://doi.org/10.1111/1365-2435.14056

951

952   22. Terborgh, J. (1992). *Diversity and the tropical rainforest*. New York: Scientific

953   American Library.

954   23. Jocque, M., Field, R., Brendonck, L., & De Meester, L. (2010). Climatic control of

955   dispersal-ecological specialization trade-offs: A metacommunity process at the

956   heart of the latitudinal diversity gradient? *Global Ecology and Biogeography*, **19**,

957   244–252. https://doi.org/10.1111/j.1466-8238.2009.00510.x

958   24. Lees, A. C., & Peres, C. A. (2009). Gap-crossing movements predict species

959   occupancy in Amazonian forest fragments. *Oikos*, **118**, 280–290.

960   https://doi.org/10.1111/j.1600-0706.2008.16842.x

961   25. Robertson, O. J., & Radford, J. Q. (2009). Gap-crossing decisions of forest birds in a

962   fragmented landscape. *Austral Ecology*, **34**, 435–446.

963   https://doi.org/10.1111/j.1442-9993.2009.01945.x

964   26. Tobias, J. A., Şekercioğlu, Ç. H., & Vargas, H. F. (2013). Bird conservation in tropical

965   ecosystems: challenges and opportunities. *Key Topics in Conservation Biology*, **2**,

966   258–276. https://doi.org/10.1002/9781118520178.ch15

967   27. Stratford, J. A., & Robinson, W. D. (2005). Gulliver travels to the fragmented tropics:

968   Geographic variation in mechanisms of avian extinction. *Frontiers in Ecology and*

969   *the Environment*, **3**, 85–92. https://doi.org/10.2307/3868515

970   28. Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J.,

971   Butchart, S. H. M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze,

972   N., Faria, D., Hadley, A., Harris, S. M., Klingbeil, B. T., Kormann, U., Lens, L., Medina-

973   Rangel, G. F., … Ewers, R. M. (2017). Creation of forest edges has a global impact on

974   forest vertebrates. *Nature*, **551**, 187–191. https://doi.org/10.1038/nature24457

975   29. Claramunt, S., Hong, M., & Bravo, A. (2022) The effect of flight efficiency on gap-

976   crossing ability in Amazonian forest birds. *Biotropica*, **54**, 860-868.

977   https://doi.org/10.1111/btp.13109

978   30. Naka, L.N., Costa, B. M. S., Lima, G. R., & Claramunt, S. (2022). Riverine Barriers as

979   Obstacles to Dispersal in Amazonian Birds. *Front. Ecol. Evol.* 10:846975.

980   31. Cheptou, P. O., Hargreaves, A. L., Bonte, D., & Jacquemyn, H. (2017). Adaptation to

981   fragmentation: Evolutionary dynamics driven by human influences. *Philosophical*

982   *Transactions of the Royal Society B: Biological Sciences*, **372**, 20160037.

983   https://doi.org/10.1098/rstb.2016.0037

984   32. Scheffers, B. R., Shoo, L., Phillips, B., Macdonald, S. L., Anderson, A., VanDerWal, J.,

985   Storlie, C., Gourret, A., Williams, S. E. (2017). Vertical (arboreality) and horizontal

986   (dispersal) movement increase the resilience of vertebrates to climatic instability.

987   *Global Ecology and Biogeography*, **26**, 787–798.

988   https://doi.org/10.1111/geb.12585

989   33. BirdLife International. (2021). *BirdLife Data Zone*. Available online at: http://www.

990   birdlife.org/datazone [Accessed January 24, 2021].

991   34. Tobias, J. A., Sheard, C., Pigot, A., Devenish, A., Yang, J., Sayol, F. et al. (2022).

992   AVONET: morphological, ecological and geographical data for all birds. *Ecology*

993   *Letters*. **25**, 581–597. https://doi.org/10.1111/ele.13898.

994   35. Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that

995   affect populations in complex landscapes. *Oikos*, **65**, 169-175.

996   36. Baltzer, J. L., Veness, T., Chasmer, L. E., Sniderhan, A. E., & Quinton, W. L. (2014).

997   Forests on thawing permafrost: Fragmentation, edge effects, and net forest loss.

998   *Global Change Biology*, **20**, 824–834. https://doi.org/10.1111/gcb.12349

999   37. Stephens, S. L., Burrows, N., Buyantuyev, A., Gray, R. W., Keane, R. E., Kubian, R., Liu,

1000   S., Seijo, F., Shu, L., Tolhurst, K. G., & Van Wagtendonk, J. W. (2014). Temperate and

1001   boreal forest mega-fires: Characteristics and challenges. *Frontiers in Ecology and*

1002   *the Environment*, **12**, 115–122. https://doi.org/10.1890/120332

1003 38. Williams, C. M., Ragland, G. J., Betini, G., Buckley, L. B., Cheviron, Z. A., Donohue, K. et

1004   al. (2017). Understanding evolutionary impacts of seasonality: an introduction to

1005   the symposium. *Integrative and Comparative Biology*, **57**, 921–933.

1006   https://doi.org/10.1093/icb/icx122

1007 39. Schulte to Bühne, H., Tobias, J. A., Durant, S. M., & Pettorelli, N. (2020). Improving

1008   predictions of climate change–land use change interactions. *Trends in Ecology &*

1009   *Evolution*, **36**, 29–38.

1010 40. Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annual*

1011   *Review of Ecology, Evolution, and Systematics*, **48**, 1-23.

1012   https://doi.org/10.1146/annurev-ecolsys-110316-022612

1013 41. Jirinec, V., Rodrigues, P.F., Amaral, B.R. and Stouffer, P.C. (2022). Light and

1014   temperature niches of ground-foraging Amazonian insectivorous birds. *Ecology*,

1015   **103,** e3645. https://doi.org/10.1002/ecy.3645

1016 42. Stratford, J. A., & Stouffer, P. C. (2015). Forest fragmentation alters microhabitat

1017   availability for Neotropical terrestrial insectivorous birds. *Biological Conservation*,

1018   **188**, 109–115. https://doi.org/10.1016/j.biocon.2015.01.017

1019 43. Kennedy, C. M., Grant, E. H. C., Neel, M. C., Fagan, W. F., & Marra, P. P. (2011).

1020   Landscape matrix mediates occupancy dynamics of Neotropical avian

1021   insectivores. *Ecological Applications*, **21**, 1837-1850. https://doi.org/10.1890/10-

1022   1044.1

1023 44. Kennedy, C. M., Marra, P. P., Fagan, W. F., & Neel, M. C. (2010). Landscape matrix

1024   and species traits mediate responses of Neotropical resident birds to forest

1025   fragmentation in Jamaica. *Ecological Monographs*, **80**, 651–669.

1026   https://doi.org/10.1890/09-0904.1

1027   45.   Sekercioglu, Ç. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D., & Sandí, R. F.

1028   (2002). Disappearance of insectivorous birds from tropical forest fragments.

1029   *Proceedings of the National Academy of Sciences*, **99**, 263–267.

1030   https://doi.org/10.1073/pnas.012616199

1031   46.   González-Gómez, P. L., Estades, C. F., & Simonetti, J. A. (2006). Strengthened

1032   insectivory in a temperate fragmented forest. *Oecologia*, **148**, 137–143.

1033   https://doi.org/10.1007/s00442-005-0338-3

1034   47.   Donoso, D. S., Grez, A. A., & Simonetti, J. A. (2003). Effects of forest fragmentation on

1035   the granivory of differently sized seeds. *Biological Conservation*, **115**, 63–70.

1036   https://doi.org/10.1016/S0006-3207(03)00094-6

1037   48.   Watson, J., Watson, A., Paull, D., & Freudenberger, D. (2003). Woodland

1038   fragmentation is causing the decline of species and functional groups of birds in

1039   southeastern Australia. *Pacific Conservation Biology*, **8**, 261–270.

1040   https://doi.org/10.1071/pc030261

1041   49.   Lens, L., Van Dongen, S., Norris, K., Githiru, M., & Matthysen, E. (2002). Avian

1042   persistence in fragmented rainforest. *Science*, **298**, 1236–1238.

1043   https://doi.org/10.1126/science.1075664

1044   50.   Keinath, D. A., Doak, D. F., Hodges, K. E., Prugh, L. R., Fagan, W., Sekercioglu, C. H.,

1045   Butchart, S. H. M., & Kauffman, M. (2017). A global analysis of traits predicting

1046   species sensitivity to habitat fragmentation. *Global Ecology and Biogeography*, **26**,

1047   115–127. https://doi.org/10.1111/geb.12509

1048   51.   Paton, G. D., Shoffner, A. V., Wilson, A. M., & Gagné, S. A. (2019). The traits that

1049   predict the magnitude and spatial scale of forest bird responses to urbanization

1050   intensity. *pLoS ONE*, **14**, 1–20. https://doi.org/10.1371/journal.pone.0220120

1051

1052   52.   Robinson, W. D., Rourke, B., Stratford, J. A. (2021). Put some muscle behind it:

1053   Understanding movement capacity of tropical birds. *Ornithology* **138**, ukaa068.

1054   https://doi.org/10.1093/ornithology/ukaa068

1055   53.   Ehlers Smith, D. A., Si, X., Ehlers Smith, Y. C., & Downs, C. T. (2018). Seasonal

1056   variation in avian diversity and tolerance by migratory forest specialists of the

1057   patch-isolation gradient across a fragmented forest system. *Biodiversity and*

1058   *Conservation*, **27**, 3707–3727. https://doi.org/10.1007/s10531-018-1622-y

1059   54.   Harris, R. J., & Reed, J. M. (2002). Behavioral barriers to non-migratory movements

1060   of birds. *Annales Zoologici Fennici*, **39**, 275–290.

1061   55.   Kormann, U., Scherber, C., Tscharntke, T., Klein, N., Larbig, M., Valente, J. J., et al.

1062   (2016). Corridors restore animal-mediated pollination in fragmented tropical

1063   forest landscapes. *Proceedings of the Royal Society B: Biological Sciences*, **283**,

1064   20152347. https://doi.org/10.1098/rspb.2015.2347

1065   56.   Socolar, J. B., & Wilcove, D. S. (2019). Forest-type specialization strongly predicts

1066   avian responses to tropical agriculture. *Proceedings of the Royal Society B:*

1067   *Biological Sciences*, **286**, 20191724. https://doi.org/10.1098/rspb.2019.1724

1068   57.   Barbaro, L., & Van Halder, I. (2009). Linking bird, carabid beetle and butterfly life-

1069   history traits to habitat fragmentation in mosaic landscapes. *Ecography*, **32**, 321–

1070   333. https://doi.org/10.1111/j.1600-0587.2008.05546.x

1071   58.   Cuervo, J. J., & Møller, A. P. (2020). Demographic, ecological, and life-history traits

1072   associated with bird population response to landscape fragmentation in Europe.

1073   *Landscape Ecology*, **35**, 469–481. https://doi.org/10.1007/s10980-019-00959-9

1074   59.   Ferraz, G., Nichols, J. D., Hines, J. E., Stouffer, P. C., Bierregaard, R. O., & Lovejoy, T. E.

1075   (2007). A large-scale deforestation experiment: Effects of patch area and isolation

1076   on Amazon birds. *Science*, **315**, 238–241.

1077   https://doi.org/10.1126/science.1133097

1078   60.   Van Houtan, K. S., Pimm, S. L., Halley, J. M., Bierregaard, R. O., & Lovejoy, T. E.

1079   (2007). Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology*

1080   *Letters*, **10**, 219–229. https://doi.org/10.1111/j.1461-0248.2007.01004.x

1081   61.   Rutt, C. L., Jirinec, V., Cohn-Haft, M., Laurance, W. F., Stouffer, P. C. (2019) Avian

1082   ecological succession in the Amazon: A long-term case study following

1083   experimental deforestation. *Ecol. Evol.*, **9**, 13850–13861.

1084   https://doi.org/10.1002/ece3.5822

1085   62.   Jirinec, V., Burner, R. C., Amaral, B. R., Bierregaard, R. O., Fernandez-Arellano, G,

1086   Hernández-Palma, A., Johnson, E. I., Lovejoy, T. E., Powell, L. L., Rutt, C. L., Wolfe, J.

1087   D., Stouffer, P.C. (2021). Morphological consequences of climate change for resident

1088   birds in intact Amazonian rainforest. *Science Advances*, **7**, eabk1743.

1089   https::://doi.org/10.1126/sciadv.abk1743

1090   63.   Sigel, B. J., Douglas Robinson, W., & Sherry, T. W. (2010). Comparing bird

1091   community responses to forest fragmentation in two lowland Central American

1092   reserves. *Biological Conservation*, **143**, 340–350.

1093   https://doi.org/10.1016/j.biocon.2009.10.020

1094   64.   Vetter, D., Hansbauer, M. M., Végvári, Z., & Storch, I. (2011). Predictors of forest

1095   fragmentation sensitivity in neotropical vertebrates: A quantitative review.

1096   *Ecography*, **34**, 1–8. https://doi.org/10.1111/j.1600-0587.2010.06453.x

1097   65.   Watling, J. I., & Donnelly, M. A. (2006). Fragments as islands: A synthesis of faunal

1098   responses to habitat patchiness. *Conservation Biology*, **20**, 1016–1025.

1099   https://doi.org/10.1111/j.1523-1739.2006.00482.x

1100   66.   Laforge, A., Archaux, F., Coulon, A., Sirami, C., Froidevaux, J., Gouix, N., et al.

1101   (2021). Landscape composition and life-history traits influence bat movement and

1102   space use: Analysis of 30 years of published telemetry data. *Global Ecology and*

1103   *Biogeography*, **30**, 2442–2454

1104 67. Schoener, T.W. (1968). Sizes of feeding territories among birds. *Ecology*, **49**, 123–

1105   141.

1106 68. Albaladejo-Robles, G., Böhm, M., & Newbold, T. (2022). Species life-history

1107   strategies affect population responses to temperature and land-cover

1108   changes. *Global Change Biology.* https://doi.org/10.1111/gcb.16454

1109 69. Latimer, C. E., & Zuckerberg, B. (2021). Habitat loss and thermal tolerances

1110   influence the sensitivity of resident bird populations to winter weather at regional

1111   scales. *Journal of Animal Ecology*, **90**, 317–329. https://doi.org/10.1111/1365-

1112   2656.13332

1113 70. Schmiegelow, F.K.A., Machtans, C.S., & Hannon, S.J. (1997). Are boreal birds resilient

1114   to forest fragmentation? An experimental study of short-term community

1115   responses. *Ecology*, **78**, 1914–1932. https://doi.org/10.1890/0012-

1116   9658(1997)078[1914:ABBRTF]2.0.CO;2

1117 71. Early, R., & Sax, D.F. (2011), Analysis of climate paths reveals potential limitations

1118   on species range shifts. *Ecology Letters*, **14**, 1125–1133.

1119   https://doi.org/10.1111/j.1461-0248.2011.01681.x

1120 72. Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat,

1121   I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., &

1122   Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*,

1123   **122**, 1532–1540. https://doi.org/10.1111/j.1600-0706.2013.00399.x

1124 73. Cadotte, M. W., Arnillas, C. A., Livingstone, S. W., & Yasui, S. L. E. (2015). Predicting

1125   communities from functional traits. *Trends in Ecology and Evolution*, **30**, 510–511.

1126   https://doi.org/10.1016/j.tree.2015.07.001

1127   74.   McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community

1128   ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.

1129   https://doi.org/10.1016/j.tree.2006.02.002

1130   75.   Pigot, A. L., Jetz, W., Sheard, C., & Tobias, J. A. (2018). The macroecological dynamics

1131   of species coexistence in birds. *Nature Ecology and Evolution*, **2**, 1112–1119.

1132   https://doi.org/10.1038/s41559-018-0572-9

1133   76.   Lindell, C. A., Riffell, S. K., Kaiser, S. A., Battin, A. L., Smith, M. L., & Sisk, T. D. (2007).

1134   Edge responses of tropical and temperate birds. *Wilson Journal of Ornithology*, **119**,

1135   205–220. https://doi.org/10.1676/05-133.1

1136   77.   Pfeifer, M., Lefebvre, V., Gardner, T. A., Arroyo-Rodriguez, V., Baeten, L., Banks-Leite,

1137   C., Barlow, J., Betts, M. G., Brunet, J., Cerezo, A., Cisneros, L. M., Collard, S., D'Cruze,

1138   N., da Silva Motta, C., Duguay, S., Eggermont, H., Eigenbrod, F., Hadley, A. S., Hanson,

1139   T. R., … Ewers, R. M. (2014). BIOFRAG – a new database for analyzing BIOdiversity

1140   responses to forest FRAGmentation. *Ecology and Evolution*, **4**, 1524–1537.

1141   https://doi.org/10.1002/ece3.1036

1142   78.   Hijmans, R. J., Williams, E., & Chris, V. (2017). *Package "Geosphere"* https://cran.*r-*

1143   *project.org/web/packages/geosphere/geosphere.pdf*.

1144   79.   Alldredge, M. W., Simons, T. R., & Pollock, K. H. (2007). A field evaluation of distance

1145   measurement error in auditory avian point count surveys. *Journal of Wildlife*

1146   *Management*, **71**, 2759–2766. https://doi.org/10.2193/2006-161

1147   80.   Mayhew, R. J., Tobias, J. A., Bunnefeld, L., & Dent, D. H. (2019). Connectivity with

1148   primary forest determines the value of secondary tropical forests for bird

1149   conservation. *Biotropica*, **51**, 219–233. https://doi.org/10.1111/btp.12629

1150   81.   Miller, D. A. W., Weir, L. A., McClintock, B. T., Grant, E. H. C., Bailey, L. L., & Simons, T.

1151   R. (2012). Experimental investigation of false positive errors in auditory species

1152   occurrence surveys. *Ecological Applications*, **22**, 1665–1674.

1153   https://doi.org/10.1890/11-2129.1

1154   82. Robinson, W. D., Lees, A. C., & Blake, J. G. (2018). Surveying tropical birds is much

1155   harder than you think: a primer of best practices. *Biotropica*, **50**, 846–849.

1156   https://doi.org/10.1111/btp.12608

1157   83. Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina,

1158   A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A.,

1159   Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of

1160   21st-century forest cover change. *Science*, **342**, 850–853.

1161   https://doi.org/10.1126/science.1244693

1162   84. Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017).

1163   Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote*

1164   *Sensing of Environment*, **202,** 18–27. https://doi.org/10.1016/j.rse.2017.06.031

1165   85. Buchanan, G.M., Donald, P.F., & Butchart, S.H.M. (2011). Identifying priority areas

1166   for conservation: a global assessment for forest-dependent birds. *PLoS ONE*, **6**,

1167   e29080.

1168   86. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global

1169   diversity of birds in space and time. *Nature*, **491**, 444–448.

1170   https://doi.org/10.1038/nature11631

1171   87. Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat

1172   types: a new measure of phylogenetic signal strength in binary traits. *Conservation*

1173   *Biology*, **24**, 1042-1051. https://doi.org/10.1111/j.1523-1739.2010.01455.x

1174   88. Ray, N., & Adams, J. M. (2001). A GIS-based vegetation map of the world at the last

1175   glacial maximum (25,000-15,000 BP). *Internet Archaeology*, **11**, 1–44.

1176   https://doi.org/10.11141/ia.11.2

1177 89. Lavorel, S., Flannigan, M. D., Lambin, E. F., & Scholes, M. C. (2007). Vulnerability of

1178   land systems to fire: Interactions among humans, climate, the atmosphere, and

1179   ecosystems. *Mitigation and Adaptation Strategies for Global Change*, **12**, 33–53.

1180   https://doi.org/10.1007/s11027-006-9046-5

1181 90. Met Office. (2018). *Met Office location of tropical cyclones*. Available online at:

1182   https://www.metoffice.gov.uk/weather/learn-about/weather/types-of-

1183   weather/hurricanes/location [Accessed January 24, 2021].

1184 91. Kipp, F. A. (1959). Der Handflügel-Index als flugbiologisches MaB. *Die Vogelwarte*,

1185   **20**, 77086.

1186 92. Lockwood, R., Swaddle, J. P., & Rayner, J. M. V. (1998). Avian wingtip shape

1187   reconsidered: Wingtip shape indices and morphological adaptations to migration.

1188   *Oikos*, **29**, 273–292.

1189 93. Claramunt, S. (2021). Flight efficiency explains differences in natal dispersal

1190   distances in birds. *Ecology*, **102**, 1–12. https://doi.org/10.1002/ecy.3442

1191 94. Kennedy, J. D., Borregaard, M. K., Jønsson, K. A., Marki, P. Z., Fjeldså, J., & Rahbek, C.

1192   (2016). The influence of wing morphology upon the dispersal, geographical

1193   distributions and diversification of the corvides (Aves; passeriformes). *Proceedings*

1194   *of the Royal Society B: Biological Sciences*, **283**, 20161922

1195   https://doi.org/10.1098/rspb.2016.1922

1196 95. Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., ... &

1197   Tobias, J. A. (2020). Macroevolutionary convergence connects morphological form

1198   to ecological function in birds. *Nature Ecology & Evolution*, **4**, 230-239.

1199   https://doi.org/10.1038/s41559-019-1070-4

1200 96. Stoddard, M. C., Yong, E. H., Akkaynak, D., Sheard, C., Tobias, J. A., & Mahadevan, L.

1201   (2017). Avian egg shape: Form, function and evolution. *Science*, **356**, 1249–1254.

1202   https://doi.org/10.1126/science.aaj1945

1203   97. White, A. E. (2016). Geographical barriers and dispersal propensity interact to limit

1204   range expansions of himalayan birds. *American Naturalist*, **188**, 99–112.

1205   https://doi.org/10.1086/686890

1206   98. Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1998). Patterns of natal

1207   and breeding dispersal in birds. *Journal of Animal Ecology*, **67**(4), 518–536.

1208   https://doi.org/10.1046/j.1365-2656.1998.00215.x

1209   99. Sutherland, G. D., Harestad, A. S., Price, K., & Lertzman, K. P. (2000). Scaling of natal

1210   dispersal distances in terrestrial birds and mammals. *Ecology and Society*, **4**, 16.

1211   https://doi.org/10.5751/es-00184-040116

1212   100. Santini, L., Di Marcc, M., Visconti, P., Baiserc, D., Boitanl, L., & Rondinini, C. (2013).

1213   Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix*, **24**, 181–

1214   186. https://doi.org/10.4404/hystrix-24.2-8746

1215   101. Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest,

1216   W., Orme, C. D. L., & Purvis, A. (2005). Multiple causes of high extinction risk in

1217   large mammal species. *Science*, **309**, 1239–1241.

1218   https://doi.org/10.1126/science.1116030

1219   102. Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. (2004). The scaling of animal space

1220   use. *Science*, **306**, 266–268. https://doi.org/10.1126/science.1102138

1221   103. Peres, C.A. (2001) Synergistic effects of subsistence hunting and habitat

1222   fragmentation on Amazonian forest vertebrates. *Conservation Biology*, **15**, 1490–

1223   1505. https://doi.org/10.1046/j.1523-1739.2001.01089.x

1224   104. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high

1225   resolution interpolated climate surfaces for global land areas. *International Journal*

1226   *of Climatology*, **25**, 1965-1978. https://doi.org/10.1002/joc.1276

1227 105. Gelman, A. (2008). Scaling regression inputs by dividing by two standard

1228   deviations. *Statistics in Medicine*, **27**, 2865–2873.

1229   https://doi.org/10.1002/sim.3107

1230 106. Bürkner, P. C. (2017). Brms: An R package for Bayesian multilevel models using

1231   Stan. *Journal of Statistical Software*, **80**, 1–28.

1232   https://doi.org/10.18637/jss.v080.i01

1233 107. Gelman, A. (2006). Prior distributions for variance parameters in hierarchical

1234   models. *International Society for Bayesian Analysis*, **1**, 515–533.

1235   https://doi.org/10.1002/cjs.5550340302

1236 108. Nakagawa, S., & De Villemereuil, P. (2019). A general method for simultaneously

1237   accounting for phylogenetic and species sampling uncertainty via rubin's rules in

1238   comparative analysis. *Systematic Biology*, **68**, 632–641.

1239   https://doi.org/10.1093/sysbio/syy089

1240 109. Van der Bijl, W. (2018). Phylopath:Easy phylogenetic path analysis in R. PeerJ, 6,

1241   e4718. https://doi.org/10.7717/peerj.4718

1242 110. Tobias, J. A., & Pigot, A. L. (2019). Integrating behaviour and ecology into global

1243   biodiversity conservation strategies. *Philosophical Transactions of the Royal*

1244   *Society B: Biological Sciences*, **374**, 20190012.

1245   https://doi.org/10.1098/rstb.2019.0012

1246 111. Nally, M. R. & Walsh, C. J. (2004). Hierarchical partitioning public-domain software.

1247   *Biodiversity and Conservation*, **13**, 659–660.

1248

1249

1250