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11   **High critical forest habitat thresholds of native bird communities in Afrotropical**

12   **agroforestry landscapes**

13

14   **Abstract**

15   Our knowledge on the nature of forest species responses to deforestation remains ambiguous.

16   Moreover, most previous research took place in fragmented landscapes or did not take into

17   account the diversity of ecological features among the studied species. Understanding the

18   relationship between forest cover and functional guilds inside a bird community may serve as

19   a valuable tool to assess how much forest is necessary to conserve significant portions of

20   forest species. We sampled birds (198 species, 6 883 encounters) along a full gradient of

21   deforestation across 4 000 km² of forest-dominated landscapes in Southwest Cameroon. We

22   applied multivariate adaptive regression splines to model α-, β- and γ-richness of various bird

23   guilds in relation to forest cover. Overall, β- and γ-richness remained constant above 42%

24   forest cover. However, total α-richness as well as all richness partitions of Guinea-Congo

25   biome-restricted, large-bodied arboreal foliage gleaning, tree nesting, and frugivorous species

26   declined when forest cover was below 74%. Moreover, ant-followers and terrestrial

27   insectivores showed their highest diversity at zero deforestation. In contrast, open-land,

28   granivorous, opportunistic insectivorous and widespread species strongly increased below

29   42% forest cover. High β-diversity at intermediate deforestation conditions indicate that the

30   sharp decline of original forest bird diversity may only be compensated by habitat and

foraging generalists, which benefit from high habitat heterogeneity. Our study implies that Afrotropical forest bird diversity decreases non-linearly with forest loss. Critical habitat thresholds above 70% are much higher than previously reported and highlight the need for conservation measures of large intact forest remnants.

Keywords: African bird diversity; bird guilds; deforestation; diversity partitioning; forest cover; multivariate adaptive regression splines

1. Introduction

For more than two decades, there has been a debate on how much forest is needed to maintain diversity in a landscape context. In his pioneering review on the effects of woodland cover on bird and mammal species, Andrén (1994) argued for a minimum of 10% to 30% forest cover needed to preserve a substantial portion of original species diversity. In the following years, numerous field studies on various taxa have found support for a critical threshold hypothesis. Whereas several bird (e.g. Cushman and McGarigal, 2003; Radford et al., 2005), invertebrate (e.g. Bergman et al., 2004), and multi-taxa studies (Banks-Leite et al., 2014; Ochoa-Quintero et al., 2015) are in line with Andrén's proposed threshold range, others suggest a minimum forest cover level of 40% to 50% for amphibians (e.g. Gibbs, 1998), invertebrates (Schmidt and Roland, 2006), birds (e.g. Martensen et al., 2012; Morante-Filho et al., 2015), and mammals (Reunanen et al., 2004). Moreover, some authors have failed to find evidence of non-linear relations between forest cover and species richness or occurrence in birds (e.g. Villard et al., 1999) as well as lizards and birds (Lindenmayer et al., 2005). Besides an undeniable effect of landscape configuration (Fahrig, 2003; Villard et al., 1999), these contradicting results suggest that species' responses to deforestation are determined by their

55 ecological characteristics (Andrén, 1994; Luck and Daily, 2003; Maas et al., 2009). Although

56 many of the before-mentioned studies focused on birds, our knowledge on the response

57 patterns of functional guilds of complete bird communities remains limited. Respective

58 studies are needed to predict ecological consequences related to land-use change and

59 deforestation (Lewis, 2009), which can influence conservation management efforts in forested

60 landscapes (Metzger and Décamps, 1997).

61 Conversion of forests to simplified land-use systems usually leads to changes in bird species

62 composition with altered proportions of functional groups and less specialized bird

63 communities (Harvey and Villalobos, 2007; Maas et al., 2009; Şekercioğlu, 2012). Some

64 groups have been found to persist at high levels of species richness or even increase at

65 intermediate disturbance or forest cover levels, i.e. as nectarivores or frugivores. This is

66 presumably due to high primary productivity and food availability in systems such as

67 agroforests (Gomes et al., 2008; Waltert et al., 2005). Large-bodied and insectivorous species

68 tend to decrease with increasing deforestation rates and get replaced by small-sized and

69 granivorous or omnivorous species that become highly abundant in open agricultural areas

70 (Newbold et al., 2012; Senior et al., 2013).

71 Until today, very little is known about the effects of deforestation and land-use intensification

72 on functional bird diversity in the Guineo-Congolian forest belt. Our study area lies within the

73 heart of the Gulf of Guinea forest, which represents the largest continuous forest block in the

74 biodiversity hotspot West African forests (Oates et al., 2004). In this region, land-use change

75 from a growing human population and from industrial oil palm expansion is imminent (Linder

76 and Palkovitz, 2016). In this study, we aimed to identify potential critical habitat thresholds

77 for various guilds. We applied multivariate adaptive regression splines on bird data collected

78 along a deforestation gradient from 0% to 100% at a local scale. The diversity measures used

79 are based on diversity partitioning (alpha, beta, and gamma richness) as well as a series of

80 diversity indices with increasing community weights. We hypothesized that relationships

81 between diversity in bird guilds and forest cover are non-linear. We further hypothesized that

82 critical habitat thresholds would be guild-specific and appear at intermediate deforestation

83 levels for habitat, feeding and foraging generalists and at lower deforestation levels for more

84 specialized forest bird species.

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86 **2. Material and methods**

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88 *2.1. Study area*

89 The study was conducted inside the Korup region in the Ndian Division of Southwest

90 Cameroon (4°54'N to 5°23'N and 8°44'E to 9°7'E). The altitude varies between 50 and 800 m

91 a.s.l. The average yearly rainfall is 5 272 mm and the average daily temperature ranges from a

92 minimum of 22.7 to a maximum of 30.6 °C (Chuyong et al., 2004). The study area (Fig. 1) is

93 part of the largest continuous rainforest block in Western Africa, the Cross-Sanaga-Bioko

94 coastal forests, located within the Gulf of Guinea Biodiversity Hotspot (Oates et al., 2004).

95 The area is sparsely populated, with small villages and agroforests both inside and around the

96 Korup National Park (KNP). For birds, Rodewald et al. (1994) listed 390 species in Korup

97 National Park and its surroundings, of which twelve were considered as endemic montane

98 forest species for the Cross-Sanaga region.One of the few intensified land-use systems in the

99 region, an oil palm plantation estate of PAMOL Plantations Plc., is located at the southern end

100 of KNP, separated from the park by the Mana River. This plantation (5 804 ha) was set up

101 with oil palms (*Elaeis guineensis*) in 1928.

102 *2.2. Bird sampling*

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103   We systematically sampled bird communities around twelve villages, equitably distributed in

104   three different landscapes, namely 1) inside evergreen rainforest in KNP, 2) in the

105   agroforestry landscapes outside the park and 3) in PAMOL. We used the center of each

106   settlement to define the mid point of a grid consisting of nine 1 km × 1 km blocks (Fig. 1). Of

107   these nine blocks, the four extreme corner blocks were sampled, resulting in 48 sampled

108   blocks in twelve sample sites. Since we know from own bird surveys in the region (e.g.

109   Waltert et al., 2005) that nine repeats are sufficient to saturate species accumulation curves

110   and derive reliable richness estimates (Colwell, 2016), we placed nine sample points within

111   each sample block, spaced 333 m each (Fig. 1). Hence, we also complied with the

112   recommended minimum distance between sample points to avoid multiple counting (250 m;

113   Ralph et al., 1995). Therefore, we surveyed a total of 432 sample points across the whole

114   study area.

115   We began bird point count sampling (Ralph et al., 1995) in June and July 2013, and finalized

116   the survey from May to June 2014. In both years, the survey team consisted of one expert

117   ornithologist (FNM) and one assistant (mainly EV and DK). At each sample point we once

118   recorded all seen or heard bird species for a period of ten minutes in the morning (6-11 h) or

119   afternoon (15-18 h). Bird species identification followed Borrow and Demey (2001). To

120   reduce disturbance caused by noises and movements of the survey team, we opened paths to

121   the sample points at least one day before data collection and waited for at least two minutes

122   after the arrival at each point before starting the sample protocol. Only presence-absence data

123   were taken and flyovers, i.e. birds not interacting with the surveyed area, were discarded

124   before analyses.

125

126   *2.3. Data analysis*

127 Following Fotso et al. (2001), Fry et al. (2004), and Waltert et al. (2005), we classified the

128 recorded bird species by feeding guild (carnivorous, frugivorous, granivorous, insectivorous,

129 nectarivorous, and omnivorous), foraging guild (arboreal foliage gleaner, sallyier foliage

130 gleaner, bark gleaner, sallyier, terrestrial and opportunistic miscellaneous insectivore), habitat

131 preference (forest specialists, generalists, and open-land species), nest site affiliation (ground,

132 bush, shrub, and tree breeders), and range size (Guineo-Congolian biome-restricted and non-

133 biome-restricted species). Additionally, we categorized large canopy frugivores (turacos,

134 parrots, and hornbills), ant-followers, which track the raids of army or driver ants of the genus

135 *Dorylus* to prey on animals flashed by the ants (including occasional ant-followers; Peters and

136 Okalo, 2009; Willis, 1985), and size classes of arboreal foliage gleaners (small, medium, and

137 large)

138 We combined satellite imagery interpretation and ground-truthing to assess forest cover. For

139 this, we searched the NASA archive for the most recent LANDSAT images prior to the field

140 survey in 2013. Since from 2003 on, all images contain stripes, several cloud-free scenes per

141 year were needed to cover the entire study area. Barely cloud contaminated LANDSAT

142 ETM+ images (30 m pixel size) were found for January 2013/December 2012 and November

143 2012/December 2012 for the southern/central and most northern part of our study area,

144 respectively. We created forest cover maps for each sample grid and print them for ground

145 truthing, which we performed with locals from the closest settlements. At every sample site

146 we spent at least four days walking a minimum of 5 km pathways through each 1 km²

147 sampling block to increase the accuracy of forest cover estimates and detect most recent

148 changes due to farm opening. We used GPS devices for field work and processed all maps in

149 ESRI ArcGIS 10.3.

150 We did not estimate detection probably, since neither a distance sampling nor an occupancy

151 modelling approach was followed. Previous work in the region showed that>90% of bird

observations were of acoustic nature so that results are highly likely unbiased by habitat

except from the smaller canopy dwelling nectarivores who seemingly are underrecorded in

high forest compared to secondary habitats (Waltert et al., 2005). However, we standardized

observer and sampling efforts (see also Methods 2.2) to limit sources of heterogeneity.

Therefore, our count statistics were referred to as indices (Yoccoz et al., 2001) and focused

our analysis and discussion solely on relative diversity changes. We used two different

approaches to dissect the structure of bird communities. First, since previous research pointed

out that beta diversity is more consistent between taxa and, therefore, provides a higher

indicator value than alpha (or gamma) diversity (Kessler et al., 2009; Schulze et al., 2004), we

analyzed the response of within-microhabitat (at sampling points; referring to alpha richness,

α), between-microhabitat (beta, β) and within-sampling block (1 km²; gamma, γ) species

richness. We followed the additive partitioning method (equation 1; Veech, 2002), which

allows straightforward comparison of species assemblage partitions.

Eq. (1) $\gamma = \alpha + \beta$

Since alpha is calculated as mean species richness per sample point (Veech, 2002), it also

serves as an equivalent to the relative abundance of the sample block and can, therefore, be

interpreted as the niche breadth of a focus guild or group. In adddition, richness estimates for

γ-richness were done using the classical formula of the first-order Jackknife estimator in

EstimateS 9.1 (Colwell, 2016).

Second, to assess the effect of community weights and their implication on diversity values

within analysed bird groups, we used Shannon (equation 2) and Rényi's entropy (equation 3)

to calculate a series of diversity indices from order one to four (Tóthmérész, 1995):

Eq. (2) $x_{sh} = -\sum_{i=1}^{S} p_i ln p_i$

Eq. (3) $x_{re} = \left(-ln \sum_{i=1}^{S} p_i^q\right)/(1-q)$

176   where p is the frequency of species i, derived from its relative abundance, and q is the order of

177   the diversity index value x.

178   Since we compared responses of different diversity measures, we converted the indice values

179   into effective numbers (D) of species following Jost (2006; equation 4).

180   Eq. (4) $D = \exp(x)$

181   We examined the change of bird diversity along the gradient of forest cover using

182   multivariate adaptive regression splines (MARS) based on linear models (Friedman, 1991)

183   through the *earth* package in R version 3.4.1 (Milborrow, 2016; R Core Team, 2017). We

184   allowed a maximum number of six terms before pruning. We used cross-validation (with 30

185   cross-validations and five cross-validation folds) as well as classical backward pruning and

186   selected the better fitting model by comparison of the generalized R^2 value.

187   Finally, we analyzed the response of all recorded bird species to forest cover using

188   redundancy analysis (RDA) through the *vegan* package in R (Oksanen et al., 2016). The

189   species matrix was constrained using forest cover and Hellinger transformed prior to the

190   analyses, which allows a RDA with species data tables that contain many zeros (Legendre and

191   Gallagher, 2001). F-values and p-values were obtained by permutation tests based on 999

192   permutations.

193   We tested for spatial autocorrelation in model residuals using a spatial correlogram and global

194   Morans'I test for spatial autocorrelation in the *ade4* (Dray et al., 2007) and *ncf* packages

195   (Bjørnstad and Cai, 2018) for R. These packages assesses p-values using randomization.

196   Neither Moran's I test ($I_{\text{Total community}} = -0.101$, $p = 0.999$) nor the correlogram (Fig. S1) of the

197   total community model on observed γ-diversity indicated spatial autocorrelation. At the level

198   of bird guilds and groups, we focused our discussion on the non-autocorrelated models (two

199   out of thirty models showed spatial autocorrelation; Table S1).

200

3. Results

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We recorded a total of 6,883 bird encounters and 198 bird species along 432 sampling points

(Table S2). They belonged to 43 families, with Pycnonotidae (22 species) being the most

species-rich family in the study area followed by Sylviidae (13) and Ploceidae (11). All

encountered birds could be identified to species level. At sampleblock level (1 km²), we

recorded slightly more species in agroforestry matrices outside the national park than inside,

whereas species richness in the oil palm plantation was the lowest (Table 1).

209

3.1. Bird guild responses to forest cover

With the exception of some groups (ground and bush nest builders, carnivorous and

omnivorous feeders, sallier foragers, and bark gleaners), our MARS models obtained high R^2

values above 0.30 (Fig. 2, 3). Observed and estimated total gamma richness of the total

community reached their maxima at 42% of forest cover, remaining stable above. Whereas

beta richness, which accounted for almost 70% of the observed species richness across the

gradient of forest cover, showed the same pattern, alpha richness only peaked at 74% of forest

cover (Fig. 2).

Only few bird guilds showed similar responses to that of the entire community (insectivorous

feeders, sallier-foliage gleaners, and medium-sized arboreal foliage gleaners). Frugivorous,

forest specialists, biome-restricted, and large canopy bird richness indicators, however,

reached their maximum at 74% of forest cover. Alpha and gamma richness of large-sized

arboreal foliage gleaners increased until 81% of forest cover, whereas its beta component and

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223   the estimated gamma richness peaked at 92%. The highly specialized group of ant-following

224   birds did not show any threshold response to forest cover. This guild showed the highest

225   values for all diversity components at 100% forest cover. For terrestrial insectivorous, tree-

226   nesting, and arboreal foliage gleaning birds the alpha richness peaked at high forest cover

227   rates, whereas their beta components already formed brinks at 42%. However, the observed

228   gamma richness of these groups also peaked at 74% of forest cover (Fig. 2).

229   At intermediate forest cover, habitat generalists, nectarivores and shrub-nesters showed

230   highest beta and gamma richness at intermediate forest cover rates of 15% to 42%. However,

231   the alpha richness in nectarivorous and shrub-nesting birds peaked at higher forest cover rates,

232   whereas it remained nearly unchanged across the entire gradient in granivores (Fig. 2).

233   Among the different feeding guilds, only granivores were found in high species numbers at

234   low forest cover. Their beta and gamma richness was highest between 0% and 42% forest

235   cover and lower above, whereas their alpha diversity remained low across the entire gradient

236   with a small peak at 0% forest cover (Fig. 2). The response of open-habitat specialists was

237   even more pronounced: all species richness components dropped down to zero at 81% and

238   were highest at 0% forest cover. Only beta richness remained stable at a high level below 42%

239   forest cover. The group of non-biome-restricted species showed a threshold at 15% forest

240   cover, above which all diversity components decreased. The response of miscellaneous

241   insectivorous foragers was more complex. Whereas within- and beta richness decreased

242   across the gradient with thresholds at 42% and 74% of forest cover, observed and estimated

243   gamma richness were lowest at 74% and highest between 0% and 42% of forest cover (Fig.

244   S2).

245

246   *3.2. Effects of community weights*

247   The general pattern of most guild responses to forest did not differ when adding weight to

248   frequent species (Fig. 3 and Fig. S3). Generally, effective numbers decreased with increasing

249   order of the diversity index and, therefore, increases and declines appeared to be less steep.

250   For some groups, such as insectivorous, biome-restricted and non-biome-restricted species,

251   we observed dissimilarities of more than 50% in effective numbers across the gradient

252   between order zero (species richness) and Rényi's fourth-order entropy. In contrast, some

253   groups did not differ greatly, such as nectarivorous, terrestrial insectivorous, and medium-

254   sized arboreal foliage gleaners. Effective numbers of forest specialist, frugivorous, large

255   canopy, and ant-following species only decreased strongly in highly forested blocks when

256   adding community weights, but remained on a generally low level in open areas (Fig. 3).

257   However, in some groups the thresholds at which species numbers remain stable changed

258   with higher orders of diversity indices. This was the case for the total bird community, the

259   arboreal foliage gleaners and the non-biome-restricted species, where the threshold shifted

260   from lower (15% and 42%) to higher forest cover rates (42% and 74%). When adding

261   community weights, habitat generalists reached a single peak at 42% forest cover and

262   decreased below, while open-land species remained stable below the same threshold instead

263   of showing an increase of species numbers. The more weight we added to frequent species,

264   the more pronounced became the decline and increase of miscellaneous and terrestrial

265   insectivorous bird guilds, respectively, along the gradient of forest cover. Shrub-breeding

266   species numbers peaked at intermediate forest cover in first order but not second to fourth

267   order diversity indices.

268

269   *3.3. Species-specific responses to forest cover*

270   Forest cover explained a significant part of the variance in bird species composition

271   (proportion of constrained inertia = 31.54%; *Pseudo-F$_{1,46}$* = 21.19, *p* = 0.001) within the

272   redundancy analyses. Bird communities related to high forest cover were dominated by

273   biome-restricted species, which are mainly either arborial foliage gleaners or terrestrial

274   insectivores (Table 2, Fig. S4-S11). We also observed a significant share of ant-following

275   birds in highly forested areas with only a few common species, such as African thrush

276   (*Turdus pelios*) and common bulbul (*Pycnonotus barbatus*), remaining in open areas.

277   Widespread, open-land, granivorous, and miscellaneous insectivorous species were mainly

278   negatively associated with forest cover. Species that showed a weak response to forest cover

279   were mainly insectivores with various foraging strategies (Table 2).

280

281   **4. Discussion**

282

283   *4.1. Differential responses to changes in forest cover*

284   Our results support previous findings of low species numbers in bird assemblages of highly

285   deforested landscapes (e.g. Andrén, 1994; Martensen et al., 2012; Waltert et al., 2005). Above

286   42% forest cover, overall gamma richness remained stable, but species composition changed

287   strongly along the gradient of forest cover.

288   The response pattern to deforestation of insectivore gamma richness was congruent with that

289   of the entire bird community, though showing a more pronounced decline below 42% forest

290   coverage. Low tree, bush, and liana density and diversity under intensified land-use have

291   presumably reduced bark and foliage gleaners' richness; instead, opportunistic miscellaneous

292   insectivores were more prominent. Though small- and medium-sized foliage gleaners also

293   showed diversity declines below 74% remaining forest cover, large foliage gleaner were

294   affected the most, already decreasing at 81%. This might be attributed to greater energy

295   requirements that might not be met due to bottom-up effects of reduced or changed resource

296   availability (Senior et al., 2013). Among the group of insectivorous birds, terrestrial foragers

297   were most sensitive to deforestation. While beta richness started declining below 74% forest

298   cover, alpha species diversity as well as diversity indices under community weight even

299   indicate a steady decline without any threshold. Warmer microclimate due to lower canopy

300   cover as well as lacking leaf litter might change the ground arthropod fauna and, therefore,

301   negatively affect the foraging opportunities of terrestrial insectivores (Waltert et al., 2005).

302   Ant-following birds also showed a severe and steady decline in alpha, beta as well as gamma

303   richness along the entire gradient of deforestation. Only few of the recorded 26 ant-following

304   bird species are omnivorous (*Andropadus latirostris*, *Baeopogon indicator*, *Pycnonotus*

305   *barbatus*, *Thescelocichla leucopleura*), whereas most are highly specialized and depend on

306   the occurrence of army ant raids. Those specialists are believed to be among the first to

307   disappear in altered tropical rainforest environments (Peters et al., 2008). Various studies

308   documented the higher-order effects of fragmented forests associated with the rapid loss of

309   specialized ant-following birds (e.g. Peters and Okalo, 2009; Turner, 1996). In small forest

310   fragments in Western Kenya, the decline of highly specialized ant-followers was associated

311   with changes in army ant composition. Although overall army ant abundances remained

312   stable, the forest-dependent army ant species, *Dorylus wilverthii*, declined along with forest

313   fragment size, whereas *Dorylus molestus* increased (Peters and Okalo, 2009). The latter is a

314   generalist found in various habitats from forest to dry bushland (Gotwald, 1995). However, its

315   diurnal activity strongly depends on humidity, ceasing when conditions are too dry (Willis,

316   1985), which has in turn a negative effect on the foraging success of ant-following birds.

317   Although the ecological mechanisms behind the decline of ant-followers under deforestation

13

318   regimes in West Africa are not yet studied, Peters and Okalo's (2009) findings underline the

319   importance of high forest cover for the conservation of this highly sensitive bird guild.

320   Thirteen granivorous bird species were recorded throughout the study area with increasing

321   richness from forested to open areas. Whereas the granivorous blue-headed wood dove

322   (*Turtur brehmeri*) seemed to be a characteristic species for natural forests, six other species

323   were recorded exclusively in deforested areas. In line with previous studies (Clough et al.,

324   2009; Şekercioğlu, 2012; Waltert et al., 2005), diversity in granivores was highest at low

325   forest coverage attributed to higher food availability due to the increased abundance and

326   diversity of herbs and grasses under open conditions (Waltert et al., 2005).

327   Also, nectar-feeding birds seem to thrive with some deforestation. In previous studies,

328   nectarivores often showed highest species richness in moderately human-modified landscapes

329   (e.g. Schulze et al., 2004; Şekercioğlu, 2012), but low diversity in highly deforested and

330   homogeneous land-use systems, such as oil palm plantations (Clough et al., 2009; Tscharntke

331   et al., 2008). In addition, higher species richness in nectarivores was found not to be related to

332   their abundance, which seems to decrease more pronouncedly with increasing habitat

333   modification (Newbold et al., 2013; Waltert et al., 2004). This is in line with our results,

334   which show highest gamma richness between 15-42%, whereas relative abundance was

335   highest above 42%. On the one hand, hump-shaped richness patterns of nectarivores might be

336   explained by higher productivity and greater food resources in agroforestry matrices

337   (Şekercioğlu, 2012; Tscharntke et al., 2008). On the other hand, it might also be attributed to

338   sampling limitations: canopy nectarivores are very difficult to detect in natural forests due to

339   small sizes and thin vocalizations. Presence-absence data of nectarivores might therefore be

340   biased towards human-modified landscapes and conclusions on conservation management

341   implications should be drawn with caution (Waltert et al., 2005).

342   In accordance with previous studies (e.g. Gomes et al., 2008; Martensen et al., 2012),

343   diversity values of frugivorous birds showed a pronounced response to deforestation, with a

344   sharp decrease below 74% of forest cover. Compared to forests, structurally diverse

345   agroforestry systems may retain a similiar frugivore species richness and up to 75% of

346   frugivore abundance (Harvey and Villalobos, 2007). However, the composition of frugivorous

347   assemblages also depends on floristic characteristics (Luck and Daily, 2003) as well as on the

348   proximity of natural rainforest (Moran and Catterall, 2014). Presumably due to low resource

349   availability, frugivores may not sustain in highly deforested areas (Senior et al., 2013). This

350   particularly accounts for large canopy frugivores, which are known to depend on large forest

351   remnants (Galetti et al., 2013). Apart from the semi-granivorous grey parrot (*Psittacus*

352   *erithacus*), which used to regularly feed on oil palm nuts in plantation areas, this group was

353   nearly absent in sample blocks with less than 42% of remaining forest cover. Yet, large

354   canopy frugivores are of special conservation concern, since they are important long-distance

355   dispersers of large seeds, while being prone to poaching (Galetti et al., 2013).

356   Ground-nesting birds seem to benefit marginally from the open nature of industrial

357   agricultural systems, which might be due to the limited presence of mammal predators

358   (unpubl. data, DK). Bush-breeders, on the other hand, show an opposite, albeit weak,

359   response, with slightly higher alpha and gamma richness above 42% and 74% of forest cover,

360   respectively. Presumably due to more heterogeneous and abundant nesting sites, some

361   infrequent shrub-breeding species profited from half-open habitats, whereas tree-nesting bird

362   richness naturally depends on high forest cover. Also the proportion of species with unknown

363   breeding ecology was higher in forested areas, which reflects the need for more research on

364   the ecology of forest-dependent birds.

365   The most distinct differences we observed between forested and open areas were in regard to

366   biogeographic distribution of the recorded bird species. Whereas Guineo-Congolian biome-

367 restricted species clearly dominated the bird assemblages in highly forested blocks, their alpha

368 and gamma richness strongly declined below 74% forest cover. On the contrary, widespread

369 species, such as Senegal coucal (*Centropus senegalensis*), barn swallow (*Hirundo rustica*) or

370 black kite (*Milvus migrans*), showed highest richness in deforested landscapes below 15%

371 forest cover. In addition, also within the non-biome-restricted species group, we found

372 differential responses to forest cover related to distribution; whereas beta and gamma richness

373 of species bound to the African tropics dropped below 15% forest cover. The rest of the group

374 (cosmopolitans and species distributed in Africa, sub-Saharan Africa as well as the Old

375 World) showed highest abundance and diversity in fully deforested blocks (Fig. S3). This

376 highlights that landscapes under high land-use intensity and environmental homogenization

377 are not only prone to biotic simplification (Maas et al., 2009), but also to alienation of species

378 assemblages, even if closely borded by natural habitat.

379 For some studied bird groups we could not detect clear response patterns: Whereas omnivores

380 might have indeed the ability to adapt to habitat changes due to feeding plasticity, the graphs

381 of aerial feeders and carnivores are presumably artifacts. Due to their prolonged foraging

382 flights, they are more likely to be recorded in open sampling conditions, independently from

383 their abundance or richness.

384 *4.2. Bird species composition at intermediate deforestation*

385 According to the intermediate disturbance hypothesis, which predicts maximum local species

386 richness at intermediate disturbance levels (Gomes et al., 2008; Horn, 1975), we expected to

387 find highest diversity values in areas with intermediate forest coverage. However, we only

388 observed this pattern in a few bird guilds, such as the small-sized arboreal foliage gleaners

389 and the shrub-nesting species, for which gamma richness peaked around 42% to 74% of forest

390 cover. In addition, in many groups the proportion of beta richness tended to be higher at

391 intermediate levels of forest cover as e.g. in arboreal foliage gleaners, terrestrial insectivores

392 and biome-restricted species, indicating higher species turnover rates due to greater habitat

393 heterogeneity, even if the landscape is human-modified (Andrén, 1994, Tscharndtke et al.,

394 2012). Presumably, for the same reason alpha and gamma richness of most guilds including

395 the total bird community already showed a threshold at 42% of forest cover, albeit not

396 forming any peak at this level. It seems instead that the landscape mosaic at intermediate

397 forest cover provides a wider range of different habitat types, whereas highly forested areas

398 maintain the capacity to harbor a large species pool due to manifold niche diversification

399 (Martensen et al., 2012). Species richness in forest specialists remained high above a level of

400 74% but dropped by one third already at 42% of forest cover. This loss could only be

401 compensated by an increase of generalists and open-land specialists, which benefit from non-

402 forest habitat structures. Another contribution to constantly high total species richness at

403 intermediate forest levels could be caused by an edge effect. As the study took place within

404 the large continuous forest block in and around KNP, most sample blocks of intermediate

405 forest cover were located in the immediate vicinity of (near-)primary forest. Spill-over of

406 birds and/or their prey from the surrounding mature forest might have contributed to the high

407 species richness in the agroforestry matrices (Lucey and Hill, 2012; Pardini et al., 2010).

408

409 *4.3. Critical forest thresholds in tropical bird conservation*

410 Although several studies already documented changes in bird diversity along a gradient of

411 habitat modification (e.g. Maas et al., 2009; Şekercioğlu, 2012) or forest cover (e.g.

412 Martensen et al., 2012; Radford et al., 2005) in various settings, our study is the first to

413 illustrate how the rate of forest cover affects functional bird diversity in an African forest-

414 dominated landscape. In general, the response pattern to deforestation found for gamma

415 richness is in line with previous references of minimum habitat requirements of 40-50% cover

416 to preserve bird diversity (Banks-Leite et al., 2014; Martensen et al., 2012; Morante-Filho et

417   al., 2015; Ochoa-Quintero et al., 2015), though still higher than the 10-30% initially proposed

418   by Andrén (1994). However, it might be misleading to solely base conservation management

419   strategies on diversity values of the overall bird community, since that might mask important

420   changes in species composition, and might therefore not address conservation needs of

421   ecological bird groups of particular conservation concern (Batáry et al., 2011; Maas et al.,

422   2009; Morante-Filho et al., 2015). If a fully forested sampling block would be cleared down

423   to a minimum habitat threshold of about 40% as indicated by the response of the bird

424   community as a whole, the bird assemblage would lose more than 30% of the frugivorous,

425   large canopy, and biome-restricted species as well as 40% of the terrestrial insectivores, large

426   foliage gleaners and ant-followers. In addition, granivorous, opportunistic miscellaneous

427   insectivorous, and wide-spread species would immigrate, leading to richness increases of

428   more than 250%, 150% and 200%, respectively. Such a dramatic deviation from a natural bird

429   species composition might have profound and cascading effects on ecosystem processes and

430   services (Banks-Leite et al., 2014). For instance, highly specialized native insectivores may

431   hardly be replaceable by other more generalist taxa in regard to natural pest-control

432   (Şekercioğlu et al., 2004). Also, the decline of nectarivores and frugivores, including large

433   canopy species, which serve as important pollinators and (long-distance) seed dispersers

434   (Luck and Daily, 2003; Moran and Catterall, 2014; Şekercioğlu, 2012), may have severe

435   impacts on the reproduction of some plants species and, therefore, on the floral species

436   richness and composition (Clough et al., 2009; Galetti et al., 2013). Consequently, in order to

437   maintain a bird community functionally similar to the original one, the preservation of a

438   minimum of 70% of forest cover may be needed. Such a critical habitat threshold reflects

439   those of the most specialized forest bird groups and allows for higher-order diversity indices

440   of the overall bird community. Additionally, this would also preserve a substantial proportion

441   of the highly sensitive groups of terrestrial insectivores and ant-followers.

442 Besides bird species richness alone may already serve as a comparable good indicator for

443 overall species richness (Gardner et al., 2008), we have a good knowledge on the ecology of

444 this species groups, including niches used. Therefore, bird guild analyses may help to explain

445 functional diversity of an ecological system and diversity changes in bird guilds should be

446 seriously taken into account for conservation efforts. We provide the first analysis of bird

447 diversity responses to forest cover loss based on data from continuous mature forest, which is

448 only interrupted by loosely scattered settlements and their associated productive land. Such

449 productive land can already hold forest cover rates above 70% (see also Table 1) because it

450 consists of a heterogeneous matrix of primary and secondary forests as well as

451 compartmentalized farmland with shade trees. On the one hand, the Korup region can,

452 therefore, serve as a model to illustrate responses of an original Afrotropical forest bird

453 assemblage to changes in forest cover. On the other hand, these circumstances form the basis

454 to align forest conservation with sustainable development efforts in the West African forest

455 region. While sustaining the well-established network of protected areas (Harvey and

456 Villalobos, 2007; Marsden et al., 2006), conservation and development schemes are well-

457 advised to strengthen smallholder farming (Uezo et al. 2008) instead of industrial plantation

458 agriculture to meet nutritional and economic needs (Linder and Palkovitz 2016).

459

Conflict of interests

476   The authors declare no financial or other conflict of interests.

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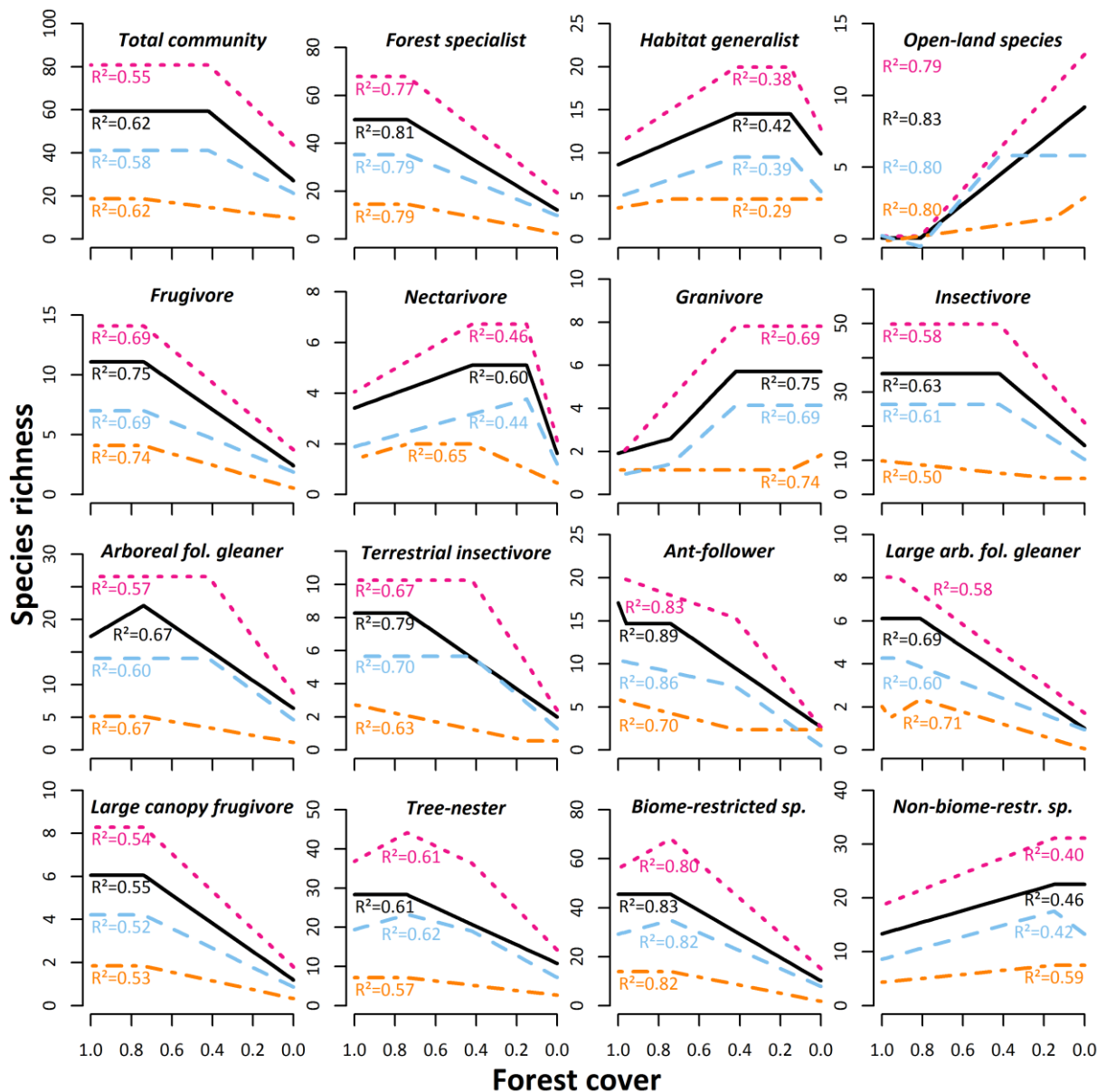
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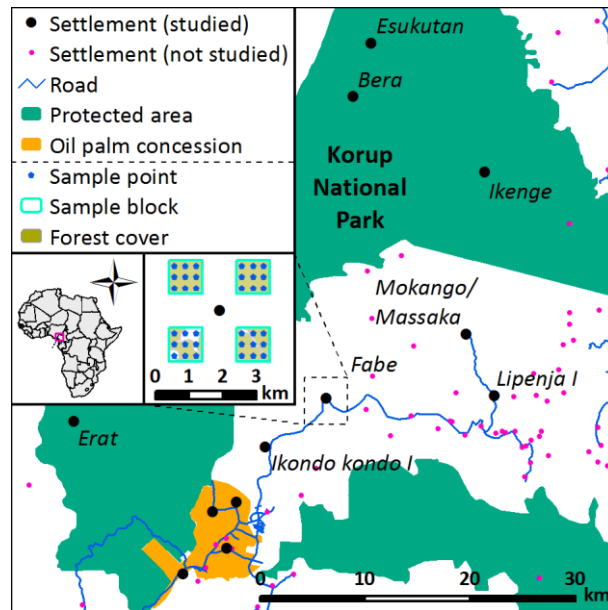
Fig. 1. Map of the study area in Southwest Cameroon and an illustration of the study design at settlement level.(here: Fabe village).

654

Fig. 2. Response patterns of within-microhabitat (alpha; orange dot-dashed line), between-microhabitat (beta; skyblue dashed line), observed (black solid line) and estimated within-block (gamma; pink dotted line) species richness to changes in forest cover in most studied bird groups (see Fig. S1 for the remaining groups) corresponding to the best-fitting MARS models; richness estimates are based on the classical first-order Jackknife estimator.

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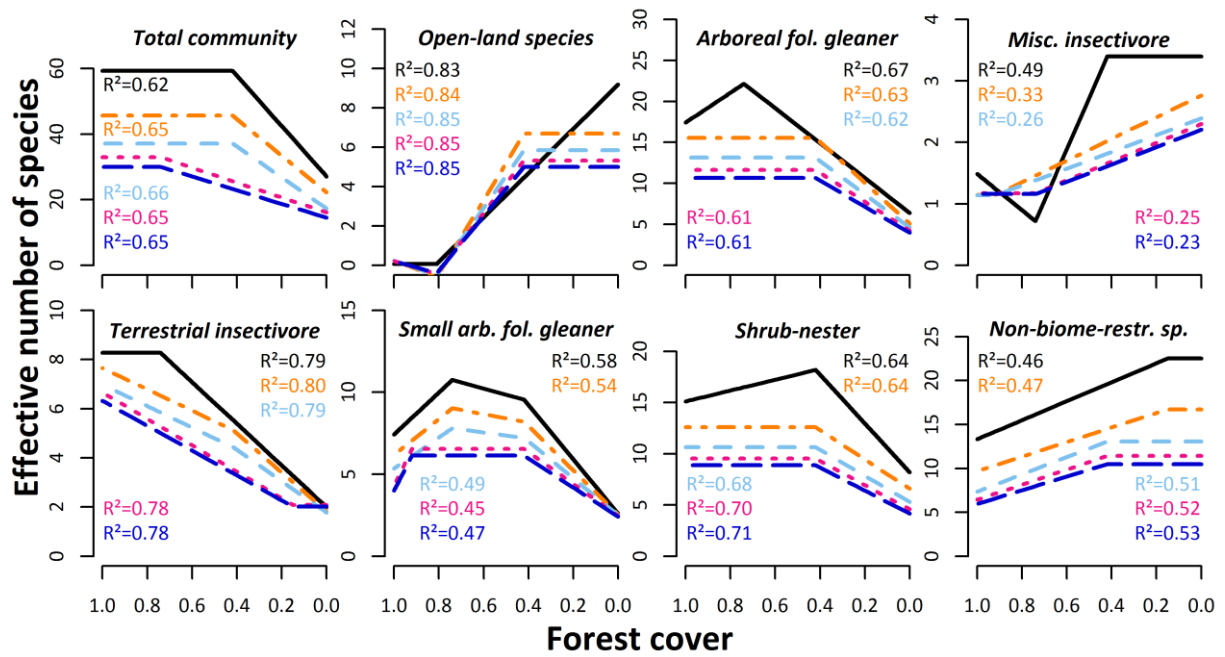
Fig. 3. Response patterns of observed within-block (gamma) species richness (black solid line),
Shannon (orange dot-dashed line) as well as Rényi's second-order (skyblue dashed line), third-order
(pink dotted line) and fourth-order entropy (blue coarse-dashed line) species richness to changes in
forest cover in some studied bird groups (see Fig. S3 for the remaining groups) corresponding to the
best-fitting MARS models; all diversity indices are expressed in effective numbers (see Jost 2006).

667

668

669   Table 1. Summary of forest cover and species richness figures as well as sampling effort at sampling
670   block level (1 km²) in the three survey landscapes; means are presented with SD; richness estimates
671   are based on the classical first-order Jackknife estimator; KNP – Korup National Park, UAF –
672   unprotected agroforestry matrix; OPP – oil palm plantation.

	Forest cover			**Sampling effort (min)**	**γ-diversity at 1 km² (n)**				
	mean	min	max		total	mean observed	mean expected	min	max
KNP	0.88 (±0.14)	0.52	1.00	1440	140	58.31 (±9.26)	78.09 (±13.60)	44	78
UAF	0.87 (±0.11)	0.64	1.00	1440	145	60.38 (±11.14)	82.60 (±15.93)	38	82
OPP	0.10 (±0.13)	0.00	0.42	1440	123	37.50 (±11.54)	53.72 (±17.90)	23	62

673

674

Table 2. Bird species with strongest (positive and negative) and weakest association with forest cover in the RDA; RDA axis 1 is fully associated with forest cover (see Fig S1). Habitat preference: F – forest species, G – generalist, O – open-land species; Feeding guild: F – frugivore, G – granivore, I – insectivore, O – omnivore; Insectivore foraging guild: AFG – arboreal foliage gleaner, MISC – opportunistic miscellaneous insectivore, SA – sallyier, SFG – sallyier foliage gleaner, T – terrestrial insectivore; AFG size group: L – large, M – medium, S – small; Nest site: B – bush, G – ground, S – shrub, T – tree; Geographical range: A – Africa, BR – biome-restricted (Guineo-Congolian endemic), SUB – sub-Saharan Africa, TRA – tropical Africa; Others: Ant – Ant-follower, LCB – large canopy bird.

Scientific Name	RDA1 Score	Habitat	Feeding	Foraging	AFG Size	Nesting	Range	Others
Positive association with forest cover								
Criniger chloronotus	-0.29	F	I	AFG	L	S	BR	Ant
Deleornis fraseri	-0.29	F	I	AFG	S	T	BR	-
Bleda syndactyla	-0.29	F	I	T	-	B	BR	Ant
Illadopsis rufipennis	-0.27	F	I	T	-	B	BR	Ant
Neocossyphus poensis	-0.27	F	I	T	-	-	BR	Ant
Bleda notata	-0.27	F	I	T	-	S	BR	Ant
Turtur afer	-0.27	F	G	-	-	B	TRA	-
Ceuthmochares aereus	-0.26	F	I	AFG	L	S	TRA	-
Sarothrura pulchra	-0.26	F	I	-	-	G	BR	-
Tricholaema hirsuta	-0.26	F	I	AFG	S	B	BR	-
Negative association with forest cover								
Cisticola anonymus	0.35	O	I	MISC	-	G	BR	-
Lonchura bicolor	0.34	O	G	-	-	T	TRA	-
Camaroptera brachyura	0.34	G	I	MISC	-	B	SUB	-
Platysteira cyanea	0.33	O	I	SA	-	T	TRA	-
Streptop. semitorquata	0.33	F	G	-	-	T	SUB	-
Turdus pelios	0.31	G	I	T	-	T	TRA	Ant
Estrilda melpoda	0.30	O	G	-	-	G	TRA	-
Pycnonotus barbatus	0.30	G	O	-	-	S	A	Ant
Cinnyris chloropygius	0.28	G	N	-	-	S	TRA	-

Ploceus ocularis	0.28	G	I	AFG	M	S	TRA	-

Weak association with forest cover

Chrysococcyx cupreus	0.01	G	I	AFG	M	S	TRA	-
Camaroptera chloronota	-0.01	F	I	AFG	S	G	BR	-
Malimbus scutatus	-0.02	F	I	SFG	-	T	BR	-
Ceyx picta	-0.02	G	I	MISC	-	O	TRA	-
Gymnobucco calvus	-0.03	G	F	-	-	T	BR	-
Camaroptera superciliaris	-0.03	F	I	AFG	S	S	BR	-
Halcyon malimbica	-0.03	F	I	MISC	-	S	TRA	-
Tockus fasciatus	-0.04	F	O	-	-	T	BR	LCB
Nigrita fusconota	-0.04	F	I	AFG	S	S	BR	-
Andropadus virens	0.05	G	I	MISC	-	G	TRA	Ant

684