

FOREST FRAGMENTATION IN AN AFRICAN BIODIVERSITY HOTSPOT IMPACTS
MIXED-SPECIES BIRD FLOCKS

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ABSTRACT

The effect of forest fragmentation on mixed-species foraging bird flocks has been poorly evaluated, particularly in African forests. We examined the consequences of forest fragmentation on such flocks in the East Usambara Mountains, Tanzania, by addressing ecological as well as behavioural components. We counted these flocks in five small (<31 ha), isolated fragments and six widely spaced continuous forest sites. Given that flock cohesion and stability might be facilitated via positive interactions of leader or nuclear species, we focused on one putative nuclear species, the square-tailed drongo (*Dicrurus ludwigii*), and using playback of its vocalisations, we evaluated (i) if its vocalisations attracted flocking birds as expected by a nuclear species, and (ii) if loss of this species in fragments contributed to flock declines. We found that flocks in forest fragments had smaller sizes, reduced species richness, a reduced proportion of understorey specialists, a higher proportion of forest generalists and non-forest species, and were more variable in size and composition compared to flocks observed in continuous forest. Furthermore, flocks in fragments were composed of a higher proportion of omnivores than insectivores. Despite lower absolute abundance in fragments, *D. ludwigii* was observed in 86% of natural occurring flocks in both fragments and continuous forest, and flocks with *D. ludwigii* were significantly larger than those without it—especially in the continuous forest. Playback vocalisations of *D. ludwigii* attracted flocks of similar abundance and species richness in fragments and continuous forest, but a vastly different composition, confirming (i) its nuclear role and (ii) that, in fragments, flock assemblages had a distinct composition, with a high proportion of forest generalists and non-forest species. Loss or diminished abundance of nuclear species due to fragmentation may be an important factor that affects the presence and composition of mixed-species flocks. Given that 67% of flocking species forage in the understorey, and that insectivores were more negatively affected in fragments than omnivores, the implications of our findings are relevant for conservation in tropical forests.

Keywords: avian flocks; Eastern Arc; experimental playback; forest fragmentation; nuclear species; mutualism

1. Introduction

Mixed-species foraging flocks (hereafter mixed-species flocks) are common in avian communities globally (Moynihan, 1962; Hutto, 1994), but are especially important components of tropical forests (Munn and Terborgh, 1979; Powell, 1985; Thiollay, 1999; Sridhar et al., 2009). These groups of different bird species move and forage together (Swynnerton, 1915; McClure, 1967), and are considered important in structuring avian communities (Vernon, 1980; Terborgh, 1990). A number of ecological, fitness and social advantages have been attributed to mixed-species flock formation (Greenberg, 2000), including increased foraging efficiency (Clark and Mangel, 1984; Hino 1998, Satischandra et al., 2007), and protection from potential predators while in the flock (Terborgh, 1990; Thiollay, 1999; Sridhar et al., 2009). Ultimately, regularity of participation in such flocks increases survival odds (Jullien and Clobert, 2000; Cruz-Angón et al., 2008), and can thus be a measure of fitness, likely explaining why such flocking behaviour is commonly encountered in various ecosystems.

Flock development, cohesion and stability are likely facilitated by the presence of one or more leader or nuclear species (Winterbottom, 1943; Hutto, 1994; Goodale and Beauchamp, 2010). Nuclear species are defined as those species that lead flocks, behave conspicuously, occur in a high proportion of flocks and are rarely found outside of such flocks (Hutto, 1994). These characteristics may make a nuclear species easy to identify and follow through dense foliage, conferring a variety of advantages to other flock participants, as well as on the nuclear species itself (Goodale and Beauchamp, 2010). Two types of nuclear species have been identified: those that

function as ‘sentinels’ (Greig-Smith, 1981) versus those that are ‘intraspecifically gregarious’ (see Goodale and Kotagama, 2005). Using playback experiments, either or both of these types of nuclear species have been indirectly shown to strongly attract other birds (Goodale and Kotagama, 2005). These lines of evidence suggest that the positive interactions between nuclear species and flock participants help facilitate the cohesion and stability of mixed-species flocks. Loss of such species through human disturbance could therefore affect flock formation and dynamics.

Forest fragmentation, the process by which continuous forest is broken into smaller and often isolated forest patches, is one of the leading agents of species extinctions at local and global scales (Newmark, 1991; Şekercioglu et al., 2002; Bregman et al., 2014). Fragmentation might affect flock formation via the loss of nuclear species (see Stouffer and Bierregaard, 1995; Maldonado-Coelho and Marini, 2000; Lee et al., 2005). Moreover, the structure and cohesion of foraging flocks might be affected by reduced representation of specific foraging guilds. For instance, understory insectivores are among the guilds most vulnerable to fragmentation (Newmark, 1991; Stouffer and Bierregaard, 1995; Şekercioglu et al., 2002; Arcilla et al., 2015; Buechley et al., 2015), and many species in this guild frequently participate in mixed-species flocks (Stouffer and Bierregaard, 1995; van Houtan et al., 2006; Goodale et al., 2013). Until recently, few studies have examined the effects of forest fragmentation and other human-aided disturbances on such flocks, and these have been limited largely to the Neotropics and Australasia (Stouffer and Bierregaard, 1995; Maldonado-Coelho and Marini, 2000; Maldonado-Coelho and Marini, 2004; Lee et al., 2005; van Houtan et al., 2006; Sridhar and Sankar, 2008; Mokross et al., 2014; Goodale et al., 2014). In Afrotropical forests, many of which continue to be fragmented or degraded at alarmingly high rates (Rudel, 2013), the stability and diversity of mixed-species flocks remain practically unstudied.

The Eastern Arc Mountains of Tanzania and south-eastern Kenya (Brooks et al., 2002) is one of the most globally-threatened biodiversity hotspots. Long-term research from the East Usambara Mountains (Newmark, 1991; henceforth EUM), which are one of the northern blocks that comprise the Eastern Arc, has demonstrated that understory insectivores are locally extinct or in very reduced abundances from fragments as small as 31 ha and isolated by extensive tea plantations. Many of these understory species are regular components of flocks in continuous forest (NJC pers.obs.), and yet little is known about why they fail to persist in small fragments. We therefore sought to test the primary hypothesis that forest fragmentation in the EUM negatively impacted mixed-species flocks, and as a corollary, that loss of a putative nuclear species potentially contributes to declines in species that join such flocks.

Forest fragmentation reduces species richness, stability and composition of mixed-species flocks in Neotropical forests, and we expected the same to be true for the EUM. For example, working in the Atlantic forests of south-eastern Brazil, Maldonado-Coelho and Marini (2004) observed 356 flocks in nine forest fragments, and found that species richness and flock size were positively related to fragment area. They also found that flock stability increased with fragment area; results were generally comparable to an earlier study in fewer Atlantic forest fragments (Maldonado-Coelho and Marini, 2000). Based on the capture rates of species pre- and post-fragmentation, van Houtan et al. (2006) showed that species with a higher tendency for flocking behaviour were less likely to persist in small, isolated Amazonian fragments. Given high levels of fragmentation due to tea cultivation in the plateau region of the EUM, we first evaluated if species richness and individual abundance in mixed-species flocks was different in continuous forest versus small, isolated fragments. Furthermore, because insectivores are negatively affected by fragmentation in the EUM (Newmark, 1991), we divided the species that constituted mixed-species flocks into insectivores and omnivores in an effort to determine if guilds were heterogeneously affected by fragmentation. As the fragments chosen were isolated by tea plantations and not connected by secondary growth, we predicted that species richness, composition and abundance would be lower in isolated, small fragments as compared to continuous forest. We also predicted that omnivores would be less

1 affected by fragmentation than insectivores due to their broader dietary needs (Şekercioğlu et al.,
2 2002), and that in these two guilds, understory species with more specialised niche requirements
3 would experience the greatest reduction through fragmentation.

4 During our observational study on mixed-species flocks, and an earlier community level study from
5 2000-2001, we found that one putative sentinel species, the square-tailed drongo (*D. ludwigii*), was
6 rare or absent from some small fragments in the EUM. We therefore used this to our advantage as a
7 natural manipulation and performed playback experiments to test if (i) this was indeed a nuclear
8 species, and (ii) if playback of its vocalisations induced species flocks in fragments as compared to
9 the continuous forest. We selected this drongo species due to previous observations on its
10 behaviour (NJC, pers. obs.), which suggested it was a “sentinel” nuclear species not unlike the
11 greater racket-tailed drongo (*Dicrurus paradiseus*) of South Asian forests (Goodale and Kotagama,
12 2005; Satischandra et al., 2010). We reasoned that insectivores and other guilds use the
13 vocalisations of nuclear species to locate flocks (Goodale and Kotagama, 2005), and that sentinels
14 like the drongo provide a number of positive interactions for flock participants. Using observational
15 data on mixed-species flocks and an experimental playback manipulation of an apparent nuclear
16 species on mixed-species flocks, we provide important evidence on the role of nuclear species in
17 this fragmented biodiversity hotspot. Moreover, our evidence suggests that sentinel nuclear species
18 might be vital toward flock stability and cohesion, including facultative participants. Loss of
19 nuclear species might therefore have important conservation implications, especially in tropical
20 forests, which are rapidly being lost to deforestation worldwide.
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26 **2. Methods**

27 *2.1 Study Area*

28 The study was conducted in Amani Nature Reserve and adjacent forest fragments (Fig. S1). Amani
29 Nature Reserve is 8380 ha in size and includes lowland and submontane forest (4°48'-5°13'S,
30 38°32'-48'E), protecting one of the extensive wet forests of the EUM in northeastern Tanzania,
31 which is part of the Eastern Arc Mountain range. Rising from the coast to 1506 m, the EUM are
32 renowned for exceptionally high biodiversity, and considered a centre for speciation for various
33 taxa (Iversen, 1991; Burgess et al, 2007).
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40 Forest loss and fragmentation on this plateau has been severe over the last two centuries, through
41 clearing for tea estates and, to some extent, intensive subsistence cultivation (e.g. Hamilton and
42 Bensted-Smith, 1989; Newmark, 1991), leading to >50% loss in original forest cover (Newmark,
43 1998). Six remnant forest fragments (0.5, 2, 9, 16, 21 and 31 ha), surrounded by a homogeneous
44 matrix of tea plantation and occurring at 900-1000 m in elevation were used in this study. Tea
45 plantations are monospecific and short, up to 1 m high, with intensive use of fertilisers, herbicides
46 and pesticides: bird diversity is therefore impoverished in this habitat (NJC, pers. obs.). The
47 continuous forest (~3500 ha) is within the nature reserve in the submontane plateau, and six widely
48 separated sites were selected for this study (Fig. S1).
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53 The climate is consistently wet for much of the year. Rain is sustained by constant flow of moist
54 currents from the nearby Indian Ocean, but peak rains occur between mid-March to May and
55 October-November, with a dry period from January to early March. The mean annual rainfall is
56 around 2000 mm, humidity is high, and the mean annual temperature at Amani is 20.6 °C (Hamilton
57 and Bensted-Smith, 1989). Rather constant moisture in the submontane zone has produced a
58 vegetation community dominated by a suite of tree species typical of wet forest. Canopy species
59 that predominate include *Allanblackia stuhlmannii*, *Cephalosphaera usambarensis*, *Parinari*
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1 *excelsa*, *Isobertinia schefflerii*, *Greenwayodendron suaveolens*, *Anisophyllea obtusifolia*,
2 *Myrianthus holstii*, *Macaranga capensis*, *Trilepisium madagascariensis*, *Strombosia scheffleri* and
3 the exotic invasive, *Maesopsis eminii*. Two common emergent species are *Newtonia buchananii*
4 and *Maranthes goetzeniana* and the midstory and understorey are largely dominated by
5 *Leptonychia usambarensis*, *Mesogyne insignis*, *Sorindeia madagascariensis*, and *Alchornea hirtella*.

6 2.2 Observational sampling of flocks

7 Mixed-species flocks can be recognized when two or more species associate and move together in
8 the same direction for about five minutes (Stotz, 1993), and we therefore used this cue to detect
9 such flocks in the study area. We sampled mixed-species foraging flocks in five isolated forest
10 fragments (2, 9, 16, 21 and 31 ha), and six continuous forest sites, each more than 1.5 km from the
11 nearest other site. From May to September 2004, we randomly visited the 11 sites. This five-month
12 period is at the tail end of the heavy rains (May), and the beginning of the cold season (June-
13 August), and transitional warm to short rainy season (September; Hamilton and Bensted-Smith,
14 1989). From late August into September is when the majority of the forest bird community begins
15 breeding, and prior to that is the non-breeding season (Moreau, 1936; Mkongewa et al., 2013).

16 At each site, we walked into the forest until we located a flock. Upon encountering a flock, we
17 walked in the anticipated direction that the flock was moving, then allowed 5 minutes of settling
18 time. Using 8x40 mm binoculars, we observed each flock and recorded the species and the number
19 of individuals of each species for 10 minutes. All observations were conducted between 0630 and
20 1130 AM, and never under rainy or windy conditions. We only counted one flock at each site in a
21 day to satisfy the assumption that flocks were independent from each other. In forest fragments
22 sampled on the same day, we chose fragments in the opposite direction, and far from each other, to
23 minimize double counting flocks as previous observations indicated that some flocking species can
24 fly over the tea plantations between adjacent fragments.

25 2.3 Playback experiment of nuclear species

26 “Sentinel” nuclear species can provide a number of positive interactions to flock attendants
27 (Goodale and Kotagama, 2005). Sentinel nuclear species have an anti-predator function, and differ
28 from interspecifically gregarious nuclear species, which provide anti-predation and foraging
29 benefits (Hino, 1998; Goodale and Kotagama, 2005). Sentinel nuclear species enable other species
30 to move rapidly through the foliage as they follow it, using consistent and conspicuous calling and
31 sallying to attract attention to its location, and similarly, due to their active behaviour and
32 attentiveness, warning participants of impending danger (Goodale and Kotagama, 2005). The
33 square-tailed drongo (*D. ludwigii*) of the EUM exhibits many of these qualities (NJC, pers. obs.),
34 and thereby served as a model putative sentinel nuclear species.

35 In May 2013, we conducted the playback experiment in fragments and continuous forest to evaluate
36 (1) the efficacy of the *D. ludwigii* as a putative nuclear species, and (2) the response of flocking
37 species in fragments where the drongo is mostly absent, as compared to the continuous forest,
38 where it is present. Three continuous sites in Amani Nature Reserve, each >0.75 km apart, and three,
39 isolated forest fragments (0.5, 2 and 9 ha) surrounded by tea plantations were selected for this
40 experiment (Fig. S1).

41 Playbacks consisted of pre-recorded tracks and were classified into three different treatments: (a) a
42 white noise control; (b) a non-flocking species, tambourine dove (*Turtur tympanistria*), common
43 throughout the area, including fragments (Newmark, 1991; Cordeiro et al., 2009), and (c) the
44 putative nuclear species, square-tailed drongo (*D. ludwigii*). Multiple playback recordings of the
45 dove and drongo were acquired from colleagues whose recordings were from eastern Tanzania and
46 south-east Kenya, including the study area. For the drongo, we included the entire repertoire and

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did not exclude true or false alarm calls (see Satischandra et al., 2010), which are characteristics of this species.

At each location, the treatments were played using an iPad equipped with a portable speaker-amplifier (RadioShack Mini Audio Amplifier). To simulate an actual flocking call, the recordings were consistently projected at a volume comparable to their natural amplitude as judged by ear. A series of experimental three trials was conducted at each forest location (n =18). Each trial took place between the hours of 6:00 to 10 AM and 3:30 to 5:00 PM and included the treatment playback: control (white noise), non-flocking species (tambourine dove), and nuclear species (square-tailed drongo). Playback trials were performed when we entered a site and ensured that no mixed species flocks were apparent in the vicinity since we were testing if the playback of a putative nuclear species attracted loosely foraging species and ultimately facilitated the formation of a mixed species flock. Each of the three treatment recordings was 45 s long from start to finish, and was played three times with a 5 s reprieve between each repetition. After a 30 s lull, the cycle of treatment recordings were repeated a second time, and together, comprised a single replicate. For each treatment, we recorded the following within a 5 min period following playback: the species and the number of individuals of each species responding, and the type of response (i.e. direct or vocal). We noted a direct response when a bird was observed moving toward the playback, whereas a vocal response was noted when a bird vocalized in response to the playback within 10 s. Two observers equipped with binoculars collected experimental data. An additional observer acted as the data recorder and controlled the treatment playbacks.

2.4 Statistical Analysis

We ran Generalized Linear Mixed Models (GLMM) in with package lme4 (Bates et al., 2013) in the R 2.15.2 environment (R Core Team, 2012). GLMM fit was examined with plots of fitted data versus standardized model residuals, which in all cases showed a satisfactory fit.

In the results, in keeping with Moran (2003) and Perneger (1998), we present untransformed GLMM probabilities. That is, we do not apply alpha-level corrections (e.g., Bonferroni or False Discovery Rate control (Verhoeven et al., 2005)) because these generate conservative results and inflated rate of Type II (false negative) error. As our study focuses on the effects of forest fragmentation on mixed-species flocks in East Africa, and our results have high relevance to conservation, we suggest that false-negative error should be minimized (Roback and Askins, 2005), because it could lead to underestimation of conservation threats.

All multivariate analyses were done in the vegan 2.0 R package (Oksanen et al., 2013), except for SIMPER, which was performed with PAST 2.17 (Hammer et al., 2001). In the results, data are presented as mean \pm SE.

2.4.1 Observational data of flocks

We used Generalized Linear Mixed Models with Poisson distribution and log-link to test the hypothesis that forest fragmentation affects flock size and species richness. Due to the small numbers of sites in our study, we focused on forest size as the main fragmentation parameter, and did not consider other potentially relevant factors, such as isolation or perimeter/area ratio. In the models, species richness and flock size were the response variables, while log-transformed forest area was entered as fixed effect. Forest area was centred and standardized as advised by Schielzeth (2010) to improve interpretability and comparability of regression coefficients. Sites (six continuous and five fragments) were entered as a random factor. We ran this analysis on three datasets: all the species together, and separately for insectivores and omnivores; feeding guilds were categorised using Birds of Africa (1982-2004).

1 We hypothesized that fragmentation might impact forest-dependent species and understorey
2 specialists more than species with broader ecological requirements (generalists). Therefore, in the
3 forest fragments, the proportion of individuals and species with generalist habitat requirements is
4 expected to increase. To test this hypothesis, we used GLMMs with Gaussian error structure and
5 direct link, where forest area was the fixed factor and site was entered as a random factor. The
6 response variables were (a) the proportion of non-forest species or individuals and (b) the
7 proportion of understorey species or individuals in a flock. Proportions were arcsin-square root
8 transformed to improve model fit. The categorisation of each species as forest versus non-forest
9 dependent was taken from Bennun et al. (1996). Forest dependent species are forest-interior species
10 that occur primarily in undisturbed forest tracts that they depend on for breeding, whereas non-
11 forest dependent include (i) species that inhabit and breed in secondary forest and forest strips, and
12 may occur in the forest interior but are less abundant there (termed forest generalists), and (ii)
13 species from other habitat types abutting forest that may visit but are not dependent on forest for
14 their survival (Bennun et al., 1996). To understand the strata in which flocking species primarily
15 foraged, we used the independent classifications conducted by 21 amateur and professional
16 ornithologists who work in the forest habitats of eastern Africa (unpublished data). Species were
17 then categorised into any of the following strata based on >50% of observer classification to a
18 particular category: understorey, canopy or broad (forages relatively equally in both the understorey
19 and canopy).
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25 We further compared species richness in fragments and continuous forest by plotting sample-based
26 rarefaction curves and their unconditional 95% confidence limits with software EstimatesS 9.1.0
27 (Colwell, 2013). Curves were rescaled to individuals (Gotelli and Colwell, 2001), and compared by
28 observing the overlap of their confidence limits.
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31 In a second step, we performed a multivariate ordination with Detrended Correspondence Analysis
32 (Legendre and Legendre, 1998) to determine whether flocks in continuous forest and fragments
33 differed in terms of their species composition. DCA is an appropriate method to analyse count data,
34 and it uses chi-square distances, which avoid the double-zero problem, i.e. two flocks with different
35 species composition might appear similar due to species that are absent from both flocks. In DCA,
36 units of Axis 1 can be interpreted as the average value of the standard deviation of species turnover,
37 so that a complete species turnover occurs in approximately four units (Legendre and Legendre,
38 1998). We used the entire set of 66 flocks and 48 species, and untransformed count data to perform
39 the DCA ordination, and tested its significance through 999 permutations (Oksanen et al., 2013).
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45 We assessed whether flocks in fragments were more variable in size and composition than those in
46 continuous forest calculating Multivariate Dispersion (MD), a multivariate analogue of Levene's
47 test for homogeneity of variances (Anderson, 2006). Significance of multivariate dispersion was
48 evaluated with 999 permutations. Finally, we calculated Similarity Percentage (SIMPER (Clarke,
49 1993)), which is a method for assessing which taxa are primarily responsible for an observed
50 multivariate difference between groups. In SIMPER and MD, the input matrix contained
51 untransformed counts of the 66 flocks (each flock was kept separate), and we calculated similarity
52 values with Bray-Curtis index, which is not affected by the double-zero problem.
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57 Finally, we assessed the potential nuclear role of the square-tailed drongo (*D. ludwigii*). We used
58 GLMM with Poisson distribution and log-link to compare size and species richness in flocks with
59 and without drongo in both habitats. Factors in these models were drongo (present/absent) and
60 habitat (fragment versus continuous) as well as their interaction, plus site as random factor. We did
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not consider more complex models including date and time, as the number of flocks without drongos was low (5 in continuous forest, 4 in fragments). We used data recorded in a point count study (for points in each site, count duration 15 minutes, unlimited distance) done in 2000-2001 (Cordeiro et al., unpublished data) to independently evaluate the relative abundance of *D. ludwigii* from the same suite of sites. Point count data were analysed with a Poisson GLMM (habitat = fixed; site = random factor).

2.4.2 Playback experiment

Analyses of the experiment followed a similar flow as those of the observational study, however, since the nature of the response of *D. ludwigii* to the playback of its calls is expected to differ from that of heterospecifics, we excluded *D. ludwigii* from all calculations of species richness and abundance. First, we used GLMMs to test the effects of the three experimental treatments on the number and species richness of birds attracted to the playback. Then, we used GLMMs to compare abundance and species richness of bird assemblages attracted by the playback of square-tailed drongo in continuous forest and fragments. We used DCA, MD and SIMPER to compare the species composition of flocks attracted by playback in the two types of habitats.

3. Results

3.1 Observational data on flocks

The 66 flocks (36 in continuous and 30 in fragmented forest) altogether contained 4597 individuals of 49 species; that is 3361 individuals and 41 species in continuous forest, and 1236 individuals and 39 species in fragments. Average flock size was 93.4 ± 4.3 individuals in continuous forest, versus 41.2 ± 2.5 in forest fragments, whereas species richness was respectively 21.2 ± 0.8 and 13.6 ± 0.6 . Of the 49 flocking species, 35% were primarily understorey dwellers, 32% foraged in the understorey and in higher-level strata, and the remaining 33% were canopy dwellers (refer to Table 2). Forest area had a major effect on both total number of individuals and total species richness, which were consistently higher in continuous forest than in forest fragments (GLMM, $p < 0.001$; Table 1). Significantly higher abundance and species richness in continuous forest was also observed when birds were split into omnivores and insectivores (GLMM, all $p \leq 0.001$, Table 1). The loss of species richness and abundance was more marked in insectivores than in omnivores (Fig. 1a-d; two-tailed t-test comparing slopes of regression lines of insectivores and omnivores: $df = 16$ and $p = 0.02$ for both abundance and species richness). Accordingly, insectivores represented $51.7 \pm 1.1\%$ of the individuals and $55.8 \pm 1.0\%$ of species of flocks in continuous forest, but only $39.6 \pm 1.8\%$ and $42.9 \pm 1.4\%$ respectively in forest fragments.

In forest fragments, flocks had an increased component of canopy and forest-generalist and non-forest species, while understorey specialists and forest dependent species were less represented (Fig. 1e-h, Table 1). Accordingly, understorey specialists made $12.9 \pm 0.7\%$ of individuals and $19.9 \pm 1.0\%$ of species in flocks observed in continuous forest, but only $8.8 \pm 1.0\%$ of individuals and $10.7 \pm 1.2\%$ of species in forest fragments. Forest generalists and non-forest species went from $26.6 \pm 1.0\%$ of individuals and $32.2 \pm 1.3\%$ of species in continuous forest, to $39.4 \pm 1.6\%$ of individuals and $47.0 \pm 1.6\%$ of species in fragments.

Confidence intervals of rarefaction curves overlapped broadly (Fig. 2a), suggesting that the lower species richness of flocks in forest fragments was due to the smaller number of individuals that compose these flocks, and not to a smaller pool of species from which the flocks were drawn.

1 DCA ordination showed that convex hulls enclosing flocks observed in continuous forest and forest
2 fragments overlapped in part (Fig. 3a), but nevertheless group centroids were significantly
3 separated in the multivariate space (permutation test, $p < 0.001$), confirming that overall species
4 composition of flocks was different in the two habitats. Flock scores along DCA axis 1 ranged
5 across 2.30 units, suggesting a species turnover of approximately 75% between the axis extremes.
6 Turnover of species was 25% in continuous forest (range of scores on DCA axis 1 = 0.99 units),
7 and 59% in forest fragments (range of scores on axis 1 = 1.75). MD analysis confirmed that flocks
8 in forest fragments were significantly more variable than those in continuous forest (Permutation
9 test, $p = 0.003$, Fig. S4).

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11 SIMPER analysis showed that seven species (four omnivores and three insectivores; Table 2)
12 contributed more than 50% of observed multivariate dissimilarity between flocks in forest
13 fragments and continuous forest. In general, these species were observed only slightly less
14 frequently in fragment flocks, but showed more substantial decrements in individual abundance
15 ($>40\%$) in forest fragments. Among the 21 species with intermediate (1-4%) contribution to
16 multivariate dissimilarity, abundances and frequencies were generally lower in forest fragments, but
17 seven species (*Anthreptes pallidigaster*, *Pogoniulus leucomystax*, *D. ludwigii*, *Nectarinia olivacea*,
18 *Stactolaema leucotis*, *Andropadus virens* and *Terpsiphone viridis*) had rather similar abundance and
19 frequency in the two habitats. Ten of 20 species with multivariate contribution equal or less than 1%
20 were equally or more frequent in flocks observed in forest fragments. These results suggest that in
21 forest fragments, mixed-species foraging flocks tend to lose individuals of regularly flocking
22 (usually forest-dependent) species, but gain a number of irregularly flocking, mostly forest
23 generalists and non-forest species.

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25 The frequency at which *D. ludwigii* was observed in foraging flocks was very similar in continuous
26 forest and in fragments (86.1% versus 86.7% respectively; Table 2). However, in the point count
27 study, relative density of *D. ludwigii* was three times as high in continuous forest than in the
28 fragments (2.2 ± 0.3 versus 0.7 ± 0.3 inds/point; GLMM, $p < 0.0001$). Flocks with *D. ludwigii* were
29 larger than those without this species (excluding *D. ludwigii*: Continuous forest: 72.6 ± 12.5 versus
30 94.0 ± 9.2 individuals; Fragments 36.8 ± 20.6 versus 39.9 ± 4.2 ; GLMM: *D. ludwigii* presence $p <$
31 0.0001 , habitat $p < 0.0001$, *D. ludwigii* X habitat interaction $p = 0.43$). There was no difference in
32 species richness in flocks with and without *D. ludwigii* (Continuous forest: 20.2 ± 3.5 versus
33 20.3 ± 1.7 species/flock; Fragments 12.0 ± 5.1 versus 12.8 ± 1.0 ; GLMM: *D. ludwigii* presence $p =$
34 0.80 , habitat $p < 0.01$, *D. ludwigii* X habitat interaction $p = 0.83$).

3.2 Playback experiment

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36 Playback vocalisations of *D. ludwigii* attracted significantly more individuals (17.8 ± 1.7) and
37 species (3.5 ± 0.8) of birds per replicate than the two other playback treatments (GLMM, $p < 0.0001$).
38 White noise and tambourine dove vocalisations did not differ between them (GLMM, $p = 0.14$;
39 average number of individuals and species attracted, white noise: 0.06 ± 0.06 , tambourine dove:
40 0.39 ± 0.18). Assemblages of birds attracted by the drongo vocalisations did not differ between
41 continuous forest and forest fragments in terms of number of individuals and species richness
42 (GLMM, effect of habitat type on number of individuals, $p = 0.08$; on species richness, $p = 0.25$).

43
44 Confidence intervals of rarefaction curves of birds attracted by drongo vocalisation in continuous
45 forest and forest fragments overlapped broadly (Fig. 2b), suggesting that the two species
46 assemblages were drawn from similarly-sized species pools in the two habitats. Flocks attracted by
47 *D. ludwigii* vocalisations in fragments were equally variable in terms of species composition as
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those attracted in continuous forest (MD analysis permutation test, $p = 0.88$).

Multivariate ordination with DCA showed that species composition of flocks attracted by playback was significantly different between continuous forest and forest fragments (Fig. 3b; permutation test, $p < 0.001$). SIMPER analysis showed that differences between flocks of birds were due mainly to higher abundance of olive sunbird (*Nectarinia olivacea*), collared sunbird (*Anthreptes collaris*) and black-headed apalis (*Apalis melanocephala*) in forest fragments, while yellow-streaked greenbul (*Phyllastrephus flaviostratus*) and Shelley's greenbul (*Andropadus masukuensis*) were attracted more frequently in continuous forest (Table 3).

4. Discussion

Highlighted in this special issue are understory insectivorous birds from tropical forests, which, as compared to other guilds, are among the most negatively impacted by deforestation, fragmentation and habitat degradation in the tropics (Şekercioğlu et al., 2002; Bregman et al., 2014; Powell et al., 2015). Just over two-thirds of the species that participated in mixed-species flocks in the EUM forage primarily in the understory (35%), or in both the understory and canopy (32%). Of the latter grouping, we wish to emphasise that plasticity of foraging height among some of these species may be driven by seasonality, or by frequent occurrence in mixed-species flocks (Dinesen, 1995; Zou et al., 2011; Farine and Milburn, 2013). For example, an African *Andropadus* greenbul species increased its foraging height from a median of 5-6 m when not participating in flocks to 13 m when it joined flocks (Dinesen, 1995). Given the complexity of defining species as solely belong to a single forest stratum we therefore consider the entire 67% of species that forage partially or primarily in the understory as relevant to the focus of this special issue.

To our knowledge, this study is the first to report on forest fragmentation and its impact on heterogeneous mixed-species flocks in an Afrotropical forest. In an earlier study, Peters et al. (2008) focused on understory ant-following flocks in western Kenya, which is altogether a different type of flock that specifically follows army ants as they move along the floor of African forests. Furthermore, our study also appears to be one of the first to experimentally test the role of a nuclear species as an explanation for depauperate forest bird communities in small, isolated fragments, offering us an initial understanding of the importance of such mutualistic relationships.

Forest fragmentation in the EUM produced mixed-species flocks that were smaller than those in the continuous forest, and as a consequence of fewer individuals, they also comprised fewer species. Our results are comparable to several other tropical studies that examined flocks along disturbance gradients. Maldonado-Coelho and Marini (2000, 2004) also found that heterogeneous flocks that were smaller in size and were lower in species richness in small than large fragments of the Atlantic Forest of eastern Brazil. Working along an urban to rural gradient in Malaysia, Lee et al. (2010) also found that the species richness in mixed-species flocks decreased by almost 55% in urban as opposed to forest interior habitats. Conversely, in India (Sridhar and Sankar, 2008), Amazonian Brazil (Mokross et al., 2014), and the Andes (Colorado and Rodewald, 2015), species richness did not change or increased in forest fragments versus continuous forest. The context of habitat heterogeneity, including regenerating vegetation around fragments, can buffer negative impacts on mixed-species flocks (Maldonado-Coelho and Marini, 2000; Brandt et al., 2009; Mokross et al., 2014). In the EUM, tea plantations may present a barrier to dispersal, at least for understory dwellers (Newmark, 1991). This factor, together with empirical evidence showing that smaller fragments maintain low diversity avian communities due to area effects (Newmark, 1991; Stratford and Stouffer, 1999), may in part explain more impoverished naturally occurring flocks in the EUM. While both insectivorous and omnivorous flocking species occurred in lower abundance and species richness in small fragments as compared to continuous forest, understory insectivores

1 showed the highest decrement. Similar results showing loss of insectivorous flocking species,
2 especially from the understorey of African (Peters et al., 2008) and South American forests
3 (Stouffer and Bierregaard, 1995) suggest this to be a pervasive phenomenon worldwide. Deducing
4 the actual causes will require further investigation because insectivores dominate mixed-species
5 flocks.

6 Variability in flock composition in the EUM provides another tier towards understanding mixed-
7 species flocks in fragmented forests. Mixed-species flocks in the EUM fragments were significantly
8 more variable than those in continuous forest, consistent with evidence from ant-following mixed-
9 species flocks in Kenyan fragments (Peters et al., 2008) and mixed-species heterogeneous and
10 understorey flocks of the Atlantic forests of Brazil (Maldonado-Coehlo and Marini, 2004). While
11 we did not mark flocking individuals to evaluate home range sizes, we reason that a core of the
12 individuals and species that strongly associate with flocking maintain stable territories that
13 contribute to the regularity of flock formation (Greig-Smith, 1978; Goodale and Beauchamp, 2010).
14 Thus, lower stability and higher variability of flocks in small fragments is likely explained by (i)
15 territory sizes being too large to be encompassed in such areas compared to continuous forest
16 (Maldonado-Coehlo and Marini, 2004; van Houtan et al., 2006), and (ii) most of the flocking
17 species in fragments are not regular flock members, since many regular member species in
18 continuous forest are not present or very rare in fragments.

19 In forest fragments, the reduced abundance of individuals of regular flocking species, and not the
20 lower species richness of the species pool from which the flocks were drawn, largely explains why
21 flocks were markedly species-poor. Moreover, highly variable flock structure in fragments (Table 2,
22 Fig. 3a) appears to be because a number of facultative species (including forest generalists and non-
23 forest visitors) irregularly joined the flocks in fragments. This pattern was upheld for mixed-
24 species flocks attracted by playback of the drongo vocalisations. Even in this case, flocks were
25 drawn from equally-sized (i.e. similar species richness) pools of species from inside as well as
26 outside the forest, comparable to findings elsewhere (Maldonado-Coehlo and Marini, 2004; Sridhar
27 and Sankar, 2008); however, the compositional differences in flocks between continuous forests
28 and fragments were very marked (Table 3, Fig. 3b). Flock stability is likely driven by flock leaders
29 or nuclear species, and a number of studies have suggested that loss of these species in forest
30 fragments may lead to the disintegration of mixed-species flocks (Stouffer and Bierregaard, 1995;
31 Dolby and Grubb, 1999; Maldonado-Coehlo and Marini, 2004). We used this reasoning to test if
32 this indeed was the case in EUM fragments.

33 Is the square-tailed drongo (*D. ludwigii*) a nuclear species and will playback of its entire repertoire
34 facilitate mixed-species flocks in fragments from which it is absent? We found that this putative
35 sentinel nuclear species attracted a similar number of individuals and species in fragments versus
36 continuous forest, and the distinctive compositional differences between habitats might be more due
37 to substantially different species pools to draw from, rather than the absence of flocking species.
38 We also found that conspecifics attracted to drongo playback were more than seven times lower in
39 fragments; this result was further confirmed from independent census data where the abundance of
40 *D. ludwigii* was three times lower in fragments. Given the similar size and species richness of
41 assemblages attracted by playback in both habitats, this suggests that *D. ludwigii* provides a nuclear
42 role to start flocks, even in fragments. Moreover, from our sampling of naturally occurring mixed-
43 species flocks, three important results corroborated the nuclear role of *D. ludwigii*. First, *D. ludwigii*
44 occurred in almost all flocks in both habitats. Second, flocks with *D. ludwigii* were significantly
45 larger than those without the species, and especially so in continuous forest. Third, species richness
46 did not differ between these comparisons, suggesting that the species pools from which the flocks
47 were drawn were equally sized. Taken together, *D. ludwigii* behaves similarly to the racket-tailed
48 drongo (*D. paradiseus*; Goodale and Kotagama, 2005), a nuclear species in south-west Asian
49 forests. As it sallies for prey, *D. ludwigii* is able to also sense danger, serving a dual function to
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1 attract heterospecifics to help flush prey, and providing protection by visually scanning the forest
2 (Goodale and Kotagama, 2005; Satischandra et al., 2010). A number of ant-following species in
3 the Neotropics function as sentinels, and their nuclear role (Munn and Terborgh, 1979; Thiollay and
4 Jullien, 1998) helps initiate and maintain these groups.

5 Central to this study is the finding that *D. ludwigii* appears imperative to flock formation in the
6 EUM fragments. Working on two types of nuclear species in Sri Lankan forests, sentinel and
7 intraspecifically gregarious species, Goodale and Kotagama (2005) found that playback
8 vocalisations of the two species attracted eight times more insectivores than omnivores and
9 frugivores, when played in combination and only three times more when played independently,
10 (Kotagama and Goodale 2004). Given that nuclear species provide a number of positive
11 interactions with heterospecific flocking species, increasing beneficial associations (Hino, 1998;
12 Srinivasan et al., 2010), and especially among other insectivores, the higher the likelihood that a
13 loss in these species from fragments could cascade into diminished avian communities in tropical
14 forest fragments (Stouffer and Bierregaard, 1995; van Houtan et al., 2006, Lee et al., 2010).
15 *Dicrurus ludwigii* is often found with other putative but gregarious nuclear species such as yellow-
16 streaked greenbul (*P. flaviostratus*) and dark-backed weaver (*Ploceus bicolor*), which are both
17 largely absent from smaller fragments in the EUM. The possibility of a positive-positive
18 interaction among these three species in facilitating mixed-species flocks remains to be tested. As
19 documented in Goodale and Kotagama's (2005) experiment, insectivores use the vocalisations of
20 nuclear species to locate flocks, and either sentinel or gregarious equally attract these species, but
21 having both types of nuclear species would appear to enhance flock formation. Since most of the
22 EUM species that join mixed-species flocks are understorey foragers, and insectivores are among
23 the guilds most negatively impacted in isolated fragments, advancing our understanding of the
24 nuclear role of single to multiple nuclear species should be a conservation priority in this
25 biodiversity hotspot and throughout the tropics.

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48 References

- 49 Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*
50 62, 245–253.
51 Arcilla, N., Holbech, L.H., Kolani, Z., 2015. Recent declines of Upper Guinea forest understory
52 birds as indicators of unsustainable logging and illegal forest exploitation in Ghana, West
53 Africa. *Biol. Conserv.* This SI issue.
54 Bates, D., Maechler, M., Bolker, B.M., 2013. lme4: Linear mixed-effects models using Eigen and
55 R package version 0.999999-2.
56 Bennun, L., Pomeroy, D., Dranzoa, C., 1996. The forest birds of Kenya and Uganda. *J. E. Afr. Nat.*
57 Hist. 85, 23–48.
58 Birds of Africa (1986-2004). Academic Press (vols. 1-6), Christopher Helm (vol. 7).

- 1 Bregman, T.P., Sekercioglu, C.H., Tobias, J.A., 2014. Global patterns and predictors of bird species
2 responses to forest fragmentation: Implications for ecosystem function and conservation.
3 Biol. Conserv. 169, 372–383.
- 4 Buechley, E.R., Şekerciöğlü, C.H., Duguma, G., Ndungu, J.K., Abdu, B., Beyene, T., Muleta, D.,
5 Lens, L., 2015. Importance of Ethiopian shade coffee farms for forest bird conservation.
6 Biol. Conserv. This SI issue.
- 7 Clark C.W., Mangel, M., 1984. Foraging and flocking strategies—information in an uncertain
8 environment. *Am. Nat.* 123, 626–641.
- 9 Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. *Aust.*
10 *J. Ecol.* 18, 117–143.
- 11 Colorado, G.J., Rodewald, A.D., 2015. Response of mixed-species flocks of specialist insectivore
12 birds to habitat alteration and deforestation in the Andes. *Biol. Conserv.* This SI issue.
- 13 Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from
14 samples. Department of Ecology and Evolutionary Biology, University of Connecticut,
15 Storrs, Connecticut, USA.
- 16 Cruz-Angón, A., Sillett, T.S., Greenberg, R., (2008). An experimental study of habitat selection by
17 birds in a coffee plantation. *Ecology* 89, 921–927.
- 18 Dinesen, L., 1995. Seasonal variation in feeding ecology of Shelley's greenbul in subtropical
19 evergreen forests. *Afr. J. Ecol.* 33, 420–425.
- 20 Dolby, A.S., Grubb Jr. T.C., 2000. Social context affects risk taking by a satellite species in a
21 mixed-species foraging group. *Behav. Ecol.* 11, 110–114.
- 22 Farine, D.R., Milburn, P.J., 2013. Social organisation of thornbill-dominated mixed-species flocks
23 using social network analysis. *Behav. Ecol. Sociobiol.* 67, 321–330.
- 24 Goodale, E., Beauchamp, G., 2010. The relationship between leadership and gregariousness in
25 mixed-species bird flocks. *J. Avian Biol.* 41, 99–103.
- 26 Goodale, E., Kotagama, S.W., 2005. Alarm calling in Sri Lankan mixed-species bird flocks.
27 *Auk* 122, 108–120.
- 28 Goodale, E., Kotagama, S.W., Shankar Raman, T.R., Sidhu, S., Goodale, U., Parker, S., Chen, J.,
29 2013. The response of birds and mixed-species bird flocks to human-modified landscapes in
30 Sri Lanka and southern India. *For. Ecol. Manag.* In Press
31 <<http://www.sciencedirect.com/science/article/pii/S0378112713005495>>.
- 32 Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the
33 measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- 34 Greenberg, R., 2000. Birds of many feathers: the formation and structure of mixed species flocks of
35 forest birds. In: Boinski, S., and Gerber, P.A. (Eds.) *On the move: How and why animals
36 travel in groups*, Chicago: University of Chicago Press, pp. 521–558.
- 37 Greig-Smith, P.W., 1978. The formation, structure and function of mixed-species insectivorous bird
38 flocks in West African savanna woodland. *Ibis* 120, 284–297.
- 39 Greig-Smith, P.W., 1981. The role of alarm responses in the formation of mixed-species flocks of
40 heathland birds. *Behav. Ecol. Sociobiol.* 8, 7–10.
- 41 Hamilton, A.C., Bensted-Smith, R., (Eds.) 1989. *Forest conservation in the East Usambara
42 Mountains, Tanzania*. IUCN: Gland.
- 43 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package
44 for Education and Data Analysis. *Palaeontol. Electron.* 4, 9.
- 45 Hino, T., 1998. Mutualistic and commensal organization of avian mixed-species foraging flocks in
46 a forest of western Madagascar. *J. Avian Biol.* 29, 17–24.
- 47 Hutto, R.L., 1994. The composition and social organization of mixed species flocks in a tropical
48 deciduous forest in Western Mexico. *Condor* 96, 105–118.
- 49 Jullien, M., Clobert, J., 2000. The survival value of flocking in Neotropical birds: reality or fiction?
50 *Ecology* 81, 3416–3430.
- 51 Jullien, M., Thiollay, J.M., 1998. Multi-species territoriality and dynamics of neotropical forest
52 understory bird flocks. *J. Anim. Ecol.* 67, 227–252.

- Kotagama, S. W., Goodale, E., 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. *Forktail* 20, 63-70.
- Legendre, P., Legendre, L., 1998. Numerical ecology, 2nd ed. Elsevier, Amsterdam, Netherlands and New York, USA.
- McClure, E., 1967. The composition of mixed species flocks in lowland and sub-montane forests of Malaya. *Wilson Bull.* 79, 130-154.
- Mkongewa, V.J., Newmark, W.D., Stanley, T.R., 2013. Breeding biology of an afro-tropical forest understory bird community in northeastern Tanzania. *Wilson J. Ornithol.* 125, 260-267.
- Moran, M.D., 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 403–405.
- Moreau, R. E., 1936. Breeding seasons of birds in East African evergreen forest. *Proc. Zool. Soc. Lond.* 1936, 631–653.
- Moynihan, M., 1962. The organization and probable evolution of some mixed-species flocks of Neotropical birds. *Smithsonian Miscellaneous Collections* 143, 1–140.
- Munn, C. A., Terborgh, J. W., 1979. Multi-species territoriality in Neotropical foraging flocks. *Condor* 81, 338–347.
- Newmark, W.D., 1991. Tropical forest fragmentation and the local extinction of understory birds in the East Usambara Mountains, Tanzania. *Conserv. Biol.* 5, 67-78.
- Newmark, W.D., 1998. Forest area, fragmentation, and loss in the Eastern Arc Mountains: implications for the conservation of biological diversity. *J. E. Afr. Nat. Hist.* 87,29-36.
- Oksanen, J., Blanchet, G., Kindt, F., Legendre, R., Minchin, P., O'Hara, P.R., Simpson, R.B., Solymos, G.L., Stevens, P., Wagner, H.H., 2013. *vegan: Community Ecology Package*. R package version 2.0.
- Perneger, T.V., 1998. What's wrong with Bonferroni adjustments. *Brit. Med. J.* 316, 1236–1238.
- Powell, G.V.N., 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Ornith. Monogr.* 36, 713–732.
- Powell, L.L., Cordeiro, N.J., Stratford, J.A., 2015. Ecology and conservation of avian insectivores of the tropical rainforest understory: an introduction to this special issue. *Special Issue. Biol. Conserv.*
- R Core Team, 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Roback, P.J., Askins, R.A., 2005. Judicious use of multiple hypothesis tests. *Conserv. Biol.* 19, 261–267.
- Rudel, T.K., 2013. The national determinants of deforestation in sub-Saharan Africa. *Phil. Trans. Royal Soc. B: Biol. Sci.* 368: doi 10.1098/rstb.2012.0405
- Satischandra, S.H.K., Kudavidanage, E.P., Kotagama, S.W., Goodale, E., 2007. The benefits of joining mixed-species flocks for a sentinel nuclear species, the Greater Racket-tailed Drongo *Dicrurus paradiseus*. *Forktail* 23, 145-148.
- Satischandra, S. H. K., Kodituwakku, P., Kotagama S. W., Goodale, E., 2010. Assessing “false” alarm calls by drongo (*Dicrurus paradiseus*) in mixed-species bird flocks. *Behav. Ecol.* 21, 396-403.
- Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* 1, 103–113.
- Şekercioğlu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandi, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proc. Nat. Acad. Sci. USA* 99, 263-267.
- Sridhar, H., Beauchamp, G., Shanker, K., 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* 78, 337-347.
- Sridhar, H., Sankar, K., 2008. Effects of habitat degradation on mixed-species bird flocks in Indian rain forests. *J. Trop. Ecol.* 24, 134-147.

- 1 Stotz, D.F., 1993. Geographic variation in species composition of mixed species flocks in lowland
2 humid forests in Brazil. *Papeis Avulsos Zoologia* 38, 61–75.
- 3 Stouffer, P. C., Bierregaard, R. O., 1995. Use of Amazonian forest fragments by understory
4 insectivorous birds. *Ecology* 76, 2429– 2445.
- 5 Stratford, J.A., Stouffer, P.C., 1999. Local extinctions of terrestrial insectivorous birds in a
6 fragmented landscape near Manaus, Brazil. *Conserv. Biol.* 13, 1316-1326.
- 7 Swynnerton, C. F. M., 1915. Mixed bird parties. *Ibis* 67, 346–354.
- 8 Terborgh, J., 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups
9 to birds and monkeys. *American. J. Primatol.* 21, 87–100.
- 10 Thiollay, J.M., 1999. Frequency of mixed-species flocking in tropical forest birds and correlates of
11 predation risk: an intertropical comparison. *J. Avian Biol.* 30, 282–294.
- 12 Thiollay, J.M., Jullien, M., 1998. Flocking behaviour of foraging birds in a neotropical rain forest
13 and the antipredator defence hypothesis. *Ibis* 140, 382–394.
- 14 van Houtan, K.S., Pimm, S.L., Bierregaard Jr, R.O., Lovejoy, T.E., Stouffer, P.C., 2006. Local
15 extinctions in flocking birds in Amazonian forest fragments. *Evol. Ecol. Res.* 8, 129-148.
- 16 Verhoeven, K.J.F., Simonsen, K.L., McIntyre, L.M., 2005. Implementing false discovery rate
17 control: increasing your power. *Oikos* 108, 643–647.
- 18 Vernon, C.J., 1980. Bird parties in central and South Africa. In: Johnson, D.N. (Ed.), *Proc. IV Pan-
19 African Ornithological Congress, Mahé, Seychelles, 6–13 November 1976. Johannesburg:
20 Southern African Ornithological Society.* pp. 313–325.
- 21 Winterbottom, J. M., 1943. On woodland bird parties in Northern Rhodesia. *Ibis* 85, 437–442.
- 22 Zou, F., Chen, G., Yang, Q., Fellows, J.R., 2011. Composition of mixed-species flocks and shifts in
23 foraging location of flocking species on Hainan Island, China. *Ibis* 153, 269-278.
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Table 1. Results of Generalized Linear Mixed Models assessing the effect of forest area on mixed-species bird foraging flocks. In all models, sites were entered as a random effect. Positive estimates indicate higher values in larger forest fragments and continuous forest. As explained in the methods section, for all species, insectivores and omnivores, the response variable in the models was the number of individuals (or species richness) in the flock, while for non-forest (includes forest generalists) and understory specialists, the response variable was the percentage of individuals (or species richness) of that group in the entire flock.

Models	Estimate±St.Err.	P
a) number of individuals		
All species	0.43±0.05	<0.001
Insectivores	0.58±0.05	<0.001
Omnivores	0.31±0.06	<0.001
Non-forest species (includes forest generalists)	-0.071±0.010	<0.001
Understorey specialists	0.040±0.013	0.006
b) species richness		
All species	0.24±0.04	<0.001
Insectivores	0.37±0.05	<0.001
Omnivores	0.11±0.04	0.001
Non-forest species (includes forest generalists)	-0.075±0.015	<0.001
Understorey specialists	0.070±0.012	<0.001

Table 2. SIMPER analysis of naturally occurring flocks. The table shows the species' diet (I = insectivore, O = omnivore), primary foraging stratum (B = broad, C = canopy, U = understorey; broad refers to foraging in understorey and canopy strata), forest dependency (F= forest-interior, specialist species; N = forest generalist and non-forest species, where strictly non-forest species are denoted with an asterisk), average multivariate dissimilarity, individual and cumulative percent contribution to total observed dissimilarity, and average abundance of each species when that species is observed in flocks in continuous forest and fragments. The last two columns show frequency of occurrence, that is, the number of flocks where that species occurred divided by the total number of flocks.

Species	Diet/Stratum/ForDej	Dissim	Contrib %	Cumul %	Abund (cont)	Abund (frag)	Freq % (cont)	Freq % (frag)
Yellow-streaked greenbul (<i>Phyllastrephus flaviostratus</i>)	I/B/F	10.7	20.1	20.1	19.6±1.2	6.6±0.6	100.0	80.0
Shelley's greenbul (<i>Andropadus masukuensis</i>)	O/B/F	4.2	7.9	28.0	9.6±0.6	5.2±0.5	100.0	90.0
Green barbet (<i>Buccanodon olivacea</i>)	O/C/F	2.5	4.6	32.6	5.7±0.3	3.7±0.4	94.4	83.3
Collared sunbird (<i>Anthreptes collaris</i>)	O/B/N	2.4	4.5	37.1	5.5±0.4	3.2±0.3	75.0	76.7
Black-headed apalis (<i>Apalis melanocephala</i>)	I/C/F	2.4	4.4	41.6	6.1±0.4	3.9±0.2	94.4	86.7
Yellow white-eye (<i>Zosterops senegalensis</i>)	O/B/N	2.4	4.4	46.0	5.3±0.5	3.7±0.5	66.7	36.7
Dark-backed weaver (<i>Ploceus bicolor</i>)	O/C/N	2.3	4.3	50.4	5.0±0.4	2.8±0.3	88.9	76.7
Olive sunbird (<i>Nectarinia olivacea</i>)	O/B/F	2.0	3.8	54.1	6.1±0.5	4.2±0.3	97.2	100.0
Stripe-cheeked greenbul (<i>Andropadus milanjensis</i>)	O/B/F	2.0	3.7	57.9	3.5±0.3	2.3±0.4	88.9	26.7
Cabanis's greenbul (<i>Phyllastrephus cabanisi</i>)	I/U/F	2.0	3.7	61.5	3.3±0.2	2.0±0.6	86.1	16.7
White-eared barbet (<i>Stactolaema leucotis</i>)	O/C/N*	1.8	3.5	65.0	5.1±0.9	4.5±0.5	27.8	43.3
Little greenbul (<i>Andropadus virens</i>)	O/U/N	1.7	3.1	68.1	4.3±0.3	2.9±0.2	88.9	90.0
Grey cuckoo-shrike (<i>Coracina caesia</i>)	I/C/F	1.4	2.6	70.7	2.6±0.2	1.5±0.2	91.7	46.7
Yellow-throated woodl. Warbler (<i>Phylloscopus ruficapillus</i>)	I/B/N	1.4	2.6	73.3	2.3±0.2	2.5±0.4	91.7	43.3
Tiny greenbul (<i>Phyllastrephus debilis</i>)	I/U/F	1.3	2.4	75.7	4.2±0.7	0.0	41.7	0.0
Forest batis (<i>Batis mixta</i>)	I/B/F	1.1	2.0	77.7	2.4±0.2	2.0±0.0	77.8	40.0
Square-tailed drongo	I/C/N	1.0	1.9	79.7	2.7±0.2	2.0±0.1	86.1	86.7

(*Dicrurus ludwigii*)

1	Uluguru violet-								
2	backed sunbird	I/C/F	1.0	1.8	81.5	2.4±0.2	1.5±0.2	58.3	20.0
3	(<i>Anthreptes</i>								
4	<i>neglectus</i>)								
5	Banded green sunbird	O/C/F	1.0	1.8	83.3	2.3±0.3	1.5±0.2	58.3	20.0
6	(<i>Anthreptes</i>								
7	<i>rubritorques</i>)								
8	Black-fronted								
9	bushshrike	I/C/F	0.9	1.7	85.0	1.8±0.2	1.2±0.2	69.4	20.0
10	(<i>Malaconatus</i>								
11	<i>multicolor</i>)								
12	Green-headed oriole	O/C/N	0.9	1.7	86.7	2.0±0.2	1.3±0.1	66.7	50.0
13	(<i>Oriolus</i>								
14	<i>chlorocephalus</i>)								
15	African paradise								
16	flycatcher	I/B/N	0.8	1.5	88.1	2.3±0.3	2.1±0.4	33.3	30.0
17	(<i>Terpsiphone</i>								
18	<i>viridis</i>)								
19	Evergreen forest								
20	warbler (<i>Bradypterus</i>	I/U/F	0.7	1.3	89.4	1.7±0.1	1.0±0.0	50.0	3.3
21	<i>mariae</i>)								
22	White-chested alethe	I/U/F	0.6	1.1	90.5	1.6±0.1	0.0	47.2	0.0
23	(<i>Alethe fuelleborni</i>)								
24	Moustached								
25	tinkerbird	O/C/F	0.6	1.1	91.6	1.3±0.1	1.1±0.1	75.0	53.3
26	(<i>Pogoniulus</i>								
27	<i>leucomystax</i>)								
28	White-tailed cr.								
29	Flycatcher (<i>Elminia</i>	I/U/F	0.6	1.1	92.7	1.6±0.2	1±0.0	47.2	3.3
30	<i>albonotata</i>)								
31	Amani sunbird								
32	(<i>Anthreptes</i>	I/C/F	0.6	1.1	93.8	1.7±0.1	1.7±0.2	38.9	23.3
33	<i>pallidigaster</i>)								
34	Black-backed								
35	puffback (<i>Dryoscopus</i>	I/B/N*	0.6	1.0	94.8	2.2±0.2	1.6±0.2	25.0	26.7
36	<i>cubla</i>)								
37	Olive woodpecker								
38	(<i>Mesopicos</i>	I/B/F	0.4	0.7	95.5	2.4±0.8	0.0	22.2	0.0
39	<i>griseocephalus</i>)								
40	Mombasa								
41	woodpecker								
42	(<i>Campethera</i>	I/C/N	0.3	0.5	96.0	1.7±0.2	1.3±0.3	16.7	10.0
43	<i>mombassica</i>)								
44	Bar-tailed trogon								
45	(<i>Apaloderma</i>	I/B/F	0.2	0.5	96.5	1.4±0.2	1±0.0	22.2	3.3
46	<i>vittatum</i>)								
47	Pale-breasted								
48	illadopsis (<i>Illadopsis</i>	I/U/F	0.2	0.4	96.9	1.5±0.2	2.0±0.0	16.7	3.3
49	<i>rufipennis</i>)								
50	Scaly-throated								
51	honeyguide (<i>Indicator</i>	I/C/N	0.2	0.4	97.3	1.0±0.0	1.0±0.0	13.9	16.7
52	<i>variegatus</i>)								
53	Fischer's turaco	O/C/N	0.2	0.3	97.6	0.0	2.3±0.3	0.0	10.0
54	(<i>Tauraco fischeri</i>)								
55	Red-tailed ant thrush								
56	(<i>Neocossyphus</i>	I/U/F	0.2	0.3	97.9	1.5±0.2	0.0	16.7	0.0
57	<i>rufus</i>)								
58	Sharpe's akalat	I/U/F	0.1	0.2	98.2	1.4±0.2	0.0	13.9	0.0
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(*Sheppardia sharpei*)

1	African dusky	I/B/N	0.1	0.2	98.4	4.0±0.0	0.0	5.6	0.0
2	flycatcher (<i>Muscicapa</i>								
3	<i>adusta</i>)								
4	Long-billed tailorbird	I/U/F	0.1	0.2	98.6	2.0±0.0	1.0±0.0	5.6	3.3
5	(<i>Artisornis moreaui</i>)								
6	Cardinal woodpecker	I/B/N*	0.1	0.2	98.8	0.0	2.0±0.0	0.0	6.7
7	(<i>Dendropicos</i>								
8	<i>fuscescens</i>)								
9	Eastern nicator	I/B/N	0.1	0.2	99.1	4.0±0.0	0.0	2.8	0.0
10	(<i>Nicator gularis</i>)								
11	Yellowbill	I/C/N*	0.1	0.2	99.2	0.0	2.0±0.0	0.0	6.7
12	(<i>Ceuthmochares</i>								
13	<i>aereus</i>)								
14	Olive thrush (<i>Turdus</i>	O/U/F	0.1	0.1	99.4	4.0±0.0	0.0	2.8	0.0
15	<i>abyssinicus</i>)								
16	White-starred robin	I/U/N	0.1	0.1	99.5	2.0±0.0	1.0±0.0	2.8	3.3
17	(<i>Pogonocichla</i>								
18	<i>stellata</i>)								
19	Brown-crowned	I/U/N*	0.1	0.1	99.6	0.0	2.0±0.0	0.0	3.3
20	tchagra (<i>Tchagra</i>								
21	<i>australis</i>)								
22	Grey-backed	I/U/N*	0.1	0.1	99.7	0.0	1.0±0.0	0.0	6.7
23	camaroptera								
24	(<i>Camaroptera</i>								
25	<i>brachyura</i>)								
26	Common bulbul	O/B/N*	0.1	0.1	99.8	0.0	1.0±0.0	0.0	6.7
27	(<i>Pycnonotus</i>								
28	<i>barbatus</i>)								
29	African broadbill	I/U/F	0.1	0.1	99.9	1.0±0.0	0.0	8.3	0.0
30	(<i>Smithornis capensis</i>)								
31	Red-faced	O/U/N	0.1	0.1	100.0	0.0	1.0±0.0	0.0	3.3
32	crimsonwing								
33	(<i>Cryptospiza</i>								
34	<i>reichenovii</i>)								
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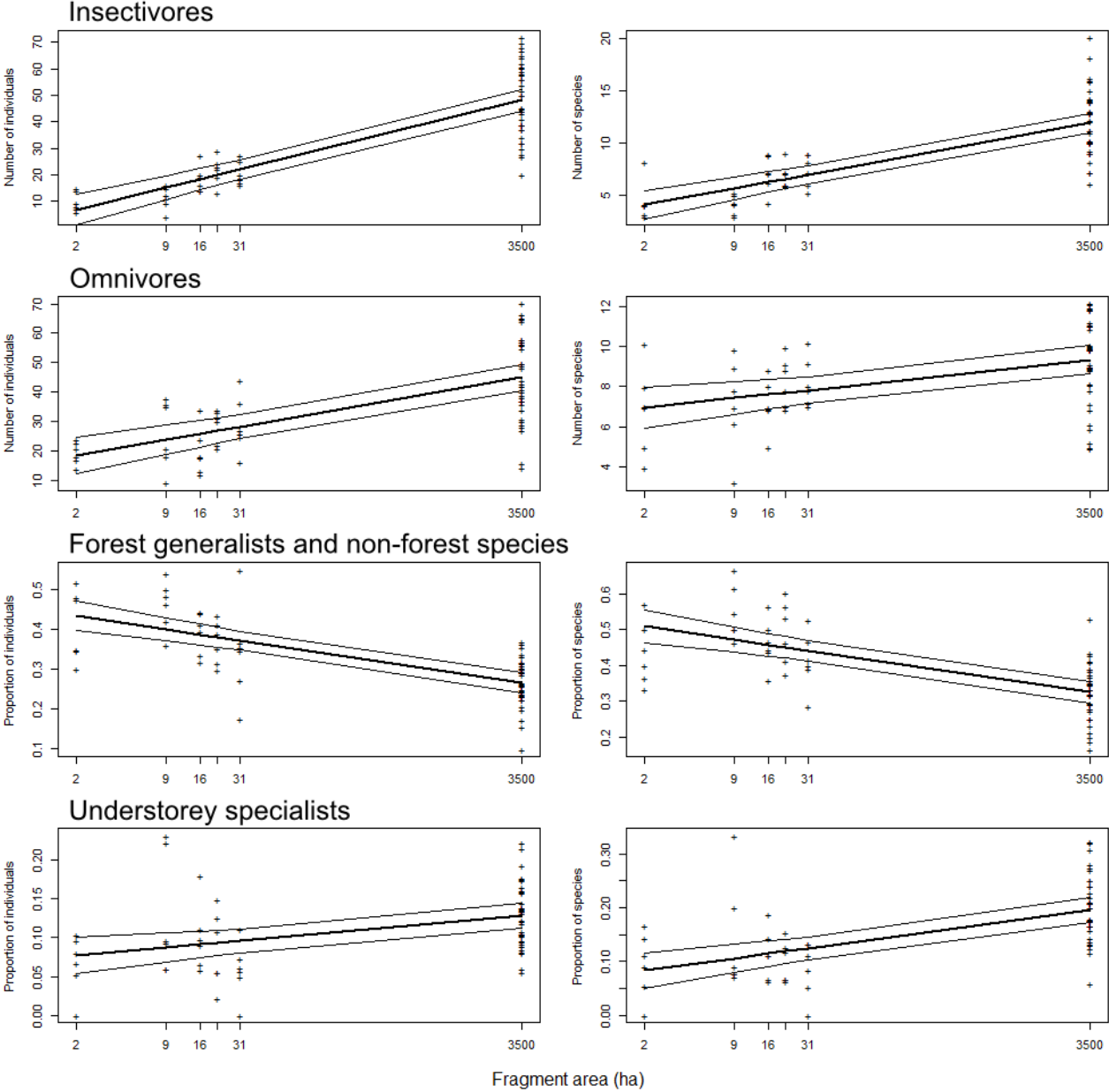
Table 3. SIMPER analysis of assemblages attracted by playback of square-tailed drongo (*Dicrurus ludwigii*) vocalisations. The table shows average multivariate dissimilarity, individual and cumulative percent contribution to total observed dissimilarity, and average abundance of each species in continuous forest and fragments. Refer to Table 2 for ecological categorisations.

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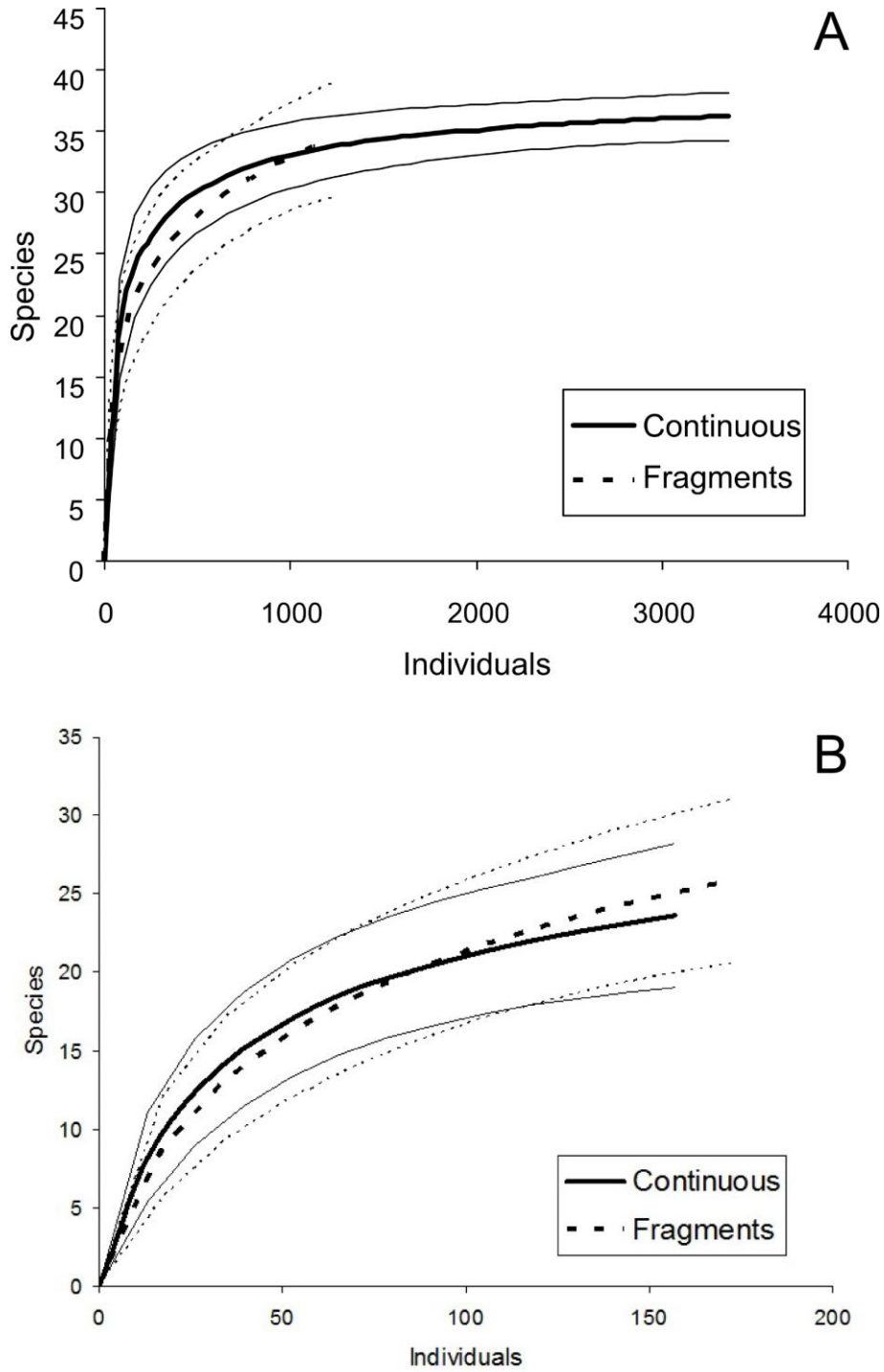
Species	Dissim.	Contrib. %	Cumul. %	Abund. (cont)	Abund. (frags)
Olive sunbird (<i>Nectarinia olivacea</i>)	7.861	11.09	11.09	1.44	3.11
Black-headed apalis (<i>Apalis melanocephala</i>)	6.262	8.833	19.92	1.11	2.56
Yellow-streaked greenbul (<i>Phyllastrephus flaviostratus</i>)	5.639	7.954	27.88	2.33	0.778
Collared sunbird (<i>Anthreptes collaris</i>)	5.477	7.725	35.6	0.333	2.22
Little greenbul (<i>Andropadus virens</i>)	5.006	7.061	42.66	1.44	1.44
Green barbet (<i>Buccanodon olivacea</i>)	4.607	6.499	49.16	1.89	1.22
Shelley's greenbul (<i>Andropadus masukuensis</i>)	3.29	4.641	53.8	1.22	0.556
Dark-backed weaver (<i>Ploceus bicolor</i>)	3.048	4.299	58.1	0.667	0.667
Grey-backed camaroptera (<i>Camaroptera brachyura</i>)	2.16	3.047	61.15	0	0.667
White-eared barbet (<i>Stactolaema leucotis</i>)	2.049	2.89	64.04	0.111	0.667
Uluguru violet-backed sunbird (<i>Anthreptes neglectus</i>)	2.02	2.849	66.89	0.556	0.222
Black-backed puffback (<i>Dryoscopus cubla</i>)	1.989	2.805	69.69	0.111	0.667
Pale batis (<i>Batis soror</i>)	1.984	2.798	72.49	0	0.778
Green-headed oriole (<i>Oriolus chlorocephalus</i>)	1.784	2.516	75	0.556	0.111
Grey cuckoo-shrike (<i>Coracina caesia</i>)	1.713	2.416	77.42	0.333	0.444
Forest batis (<i>Batis mixta</i>)	1.493	2.107	79.53	0.333	0.222
Black-throated wattle-eye (<i>Platysteira peltata</i>)	1.388	1.958	81.49	0	0.444
Moustached tinkerbird (<i>Pogoniulus leucomystax</i>)	1.307	1.844	83.33	0	0.444
Fischer's turaco (<i>Tauraco fischeri</i>)	1.168	1.647	84.98	0.222	0.222
Black-fronted bush-shrike (<i>Malaconatus multicolor</i>)	1.092	1.54	86.52	0.333	0
Pale-breasted illadopsis (<i>Illadopsis rufipennis</i>)	1.045	1.474	87.99	0.333	0
Stripe-cheeked greenbul (<i>Andropadus milanjensis</i>)	0.9687	1.366	89.36	0.222	0.222
Banded green sunbird (<i>Anthreptes rubritorques</i>)	0.821	1.158	90.51	0.111	0.222
Yellow-throated woodland warbler (<i>Phylloscopus ruficapillus</i>)	0.8048	1.135	91.65	0.222	0
Tiny greenbul (<i>Phyllastrephus debilis</i>)	0.6624	0.9343	92.58	0.222	0
Cabanis's greenbul (<i>Phyllastrephus cabanisi</i>)	0.6392	0.9016	93.49	0.111	0.111
Tropical bulbul (<i>Laniarius aethiopicus</i>)	0.6015	0.8484	94.33	0	0.222
Common bulbul (<i>Pycnonotus barbatus</i>)	0.5961	0.8408	95.17	0.111	0.111
White-crested alethe (<i>Alethe fuelleborni</i>)	0.5788	0.8164	95.99	0.222	0

	Yellow white-eye (<i>Zosterops senegalensis</i>)	0.4005	0.5649	96.56	0	0.111
1	African Dusky flycatcher (<i>Muscicapa adusta</i>)	0.4005	0.5649	97.12	0	0.111
2	Evergreen forest warbler (<i>Bradypterus mariae</i>)	0.3924	0.5535	97.67	0.111	0
3	Amani sunbird (<i>Anthreptes pallidigaster</i>)	0.3783	0.5336	98.21	0.111	0
4	Tambourine dove (<i>Turtur tympanistris</i>)	0.3376	0.4762	98.68	0	0.111
5	Red-faced crimsonwing (<i>Cryptospiza</i>	0.3376	0.4762	99.16	0	0.111
6	<i>reichenovii</i>)					
7	African broadbill (<i>Smithornis capensis</i>)	0.3312	0.4671	99.63	0.111	0
8	Long-billed tailorbird (<i>Artisornis moreau</i>)	0.2638	0.3722	100	0	0.111
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Fig. 1. Effects of forest area on the composition of 66 naturally occurring mixed-species foraging flocks. Graphs in the left column show analyses where flock size was the response variable, while in the right column the response variable was flock species richness. Lines represent GLMM model estimates and their 95% confidence intervals.



53 **Fig. 2.** Species rarefaction curves of mixed-species foraging flocks (a) observed in continuous
 54 forest and forest fragments, and (b) attracted by playback of square-tailed drongo (*Dicrurus*
 155 *ludwigii*) vocalisations in continuous forest and forest fragments. Thin lines represent unconditional
 256 95% confidence limits of the two curves.
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63 **Fig. 3.** Detrended Correspondence Analysis plots of (a) 66 naturally occurring mixed-species bird
64 flocks, and (b) 18 assemblages of birds attracted by playback of square-tailed drongo (*Dicrurus*
165 *ludwigii*) vocalisations. Filled dots = continuous forest; open dots = forest fragments. Thin lines
266 show the convex hulls enclosing all the points of the two habitat types.
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