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Forest fragmentation in an African biodiversity hotspot impacts mixed-species bird flocks

Norbert J. Cordeiro [a,b,*], Luca Borghesio [c], Martin P. Joho [d], Teodora J. Monoski [a], Victor J. Mkongewa [d], Corinna J. Dampf [a]

[a] Department of Biological, Chemical, and Physical Sciences, Roosevelt University, 430 S. Michigan Avenue, Chicago, IL 60605, USA
[b] Departments of Botany and Zoology, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA
[c] Corso Re Umberto 42, 10128 Torino, Italy
[d] BirdLife International-Tanzania Office, c/o PO Box 29, Amani, Muheza District, Tanzania

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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 behavioral 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.

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 Thiollay, 1998; Jullien and Clobert, 2000; Cruz-Angón et al., 2008),

* Corresponding author at: Department of Biological, Chemical, and Physical Sciences, Roosevelt University, 430 S. Michigan Avenue, Chicago, IL 60605, USA.
E-mail addresses: ncordeiro@fieldmuseum.org, ncordeiro@roosevelt.edu (N.J. Cordeiro), borghesio@gmail.com (L. Borghesio), martinjoho2008@yahoo.com (M.P. Joho), tjm66680@gmail.com (T.J. Monoski), victormkongewa@yahoo.com (V.J. Mkongewa), cdampf37@gmail.com (C.J. Dampf).

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and can thus be a measure of fitness, likely explaining why such flocking behavior 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; Şekercioğlu 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, understorey insectivores are among the guilds most vulnerable to fragmentation (Newmark, 1991; Stouffer and Bierregaard, 1995; Şekercioğlu 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., 2014). 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, 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 is part of one of the most globally-threatened biodiversity hotspots (Brooks et al., 2002). 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 understorey 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 understorey 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 behavior 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 affected by fragmentation than insectivores due to their broader dietary needs (Şekercioğlu et al., 2002), and that in these two guilds, understorey species with more specialized niche requirements would experience the greatest reduction through fragmentation.

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

2. Methods

2.1. Study area

The study was conducted in Amani Nature Reserve and adjacent forest fragments (Fig. S1). Amani Nature Reserve is 8380 ha in size and includes lowland and submontane forest (4°48′–5°13′S, 38°32–48′E), protecting one of the extensive wet forests of the EUM in northeastern Tanzania, which is part of the Eastern Arc Mountain range. Rising from the coast to 1506 m, the EUM are renowned for exceptionally high biodiversity, and considered a center for speciation for various taxa (Iversen, 1991; Burgess et al., 2007).