Effects of anthropogenic disturbance on bird diversity in Ethiopian montane forests

Authors: Asefa, Addisu, Davies, Andrew B., McKechnie, Andrew E., Kinahan, Anouska A., and van Rensburg, Berndt J.

Source: The Condor, 119(3) : 416-430

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-16-81.1

THE CONDOR
Ornithological Applications

AmericanOrnithology.org

Volume 119, 2017, pp. 416–430
DOI: 10.1650/CONDOR-16-81.1

RESEARCH ARTICLE

Effects of anthropogenic disturbance on bird diversity in Ethiopian montane forests

Addisu Asefa,[1a]* Andrew B. Davies,[2b] Andrew E. McKechnie,[1] Anouska A. Kinahan,[3c] and Berndt J. van Rensburg[2,4d]

[1] DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
[2] DST-NRF Centre of Excellence for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
[3] Frankfurt Zoological Society, Bale Mountains Conservation Project, Bale Mountains National Park, Ethiopia
[4] Department of Zoology, DST-NRF Centre for Invasion Biology, University of Johannesburg, Auckland Park, Johannesburg, South Africa
[a] Current address: Ethiopian Wildlife Conservation Authority, Addis Ababa, Ethiopia
[b] Current address: Department of Global Ecology, Carnegie Institution for Science, Stanford, USA
[c] Current address: Frankfurt Zoological Society, Protected Areas Commission Headquarters, National Park, Thomas Lands, Georgetown, Guyana
[d] Current address: School of Biological Sciences, The University of Queensland, Brisbane, Queensland, Australia
* Corresponding author: addisu.asefa@yahoo.com

Submitted May 9, 2016; Accepted April 7, 2017; Published June 14, 2017

ABSTRACT

The Afromontane forests of Ethiopia are global biodiversity hotspots, known for their high biological diversity and endemism. However, conservation of these areas is challenging due to increasing human threats, including encroachment of agriculture and settlements, overgrazing of livestock, and selective logging. We examined the effects of forest disturbances on birds, and highlights the potential conservation value of unprotected tropical montane forests for birds in the dry evergreen Afromontane forests of the Bale Mountains, Ethiopia. We sampled birds across 2 yr in both protected forests (characterized by low levels of cultivation, overgrazing, and logging) and unprotected forests (higher levels of disturbance). Using functional traits of birds related to habitat type, diet, and foraging stratum, we characterized the differences between protected and unprotected forests in terms of avian species richness, abundance, and assemblage composition. Overall, species richness was 27% higher and bird abundance was 19% higher in unprotected forests. In contrast, species richness and abundance of forest specialists and canopy foragers were significantly higher in protected forests. These findings suggest that unprotected, disturbed tropical montane forests in Ethiopia help to achieve conservation aims in an area recognized for its global biodiversity importance. At the same time, intact forest ecosystems need continued protection to maximize functional heterogeneity associated with specialist tropical forest taxa.

Keywords: Afromontane forest, avifaunal diversity, avian guilds, Bale Mountains, protected area, forest specialists, patch size

Effets des perturbations anthropiques sur la diversité des oiseaux dans les forêts montanes d'Éthiopie

RÉSUMÉ

Les forêts afromontanes d'Éthiopie sont des points chauds de la biodiversité mondiale, connues pour leur grande diversité biologique et leur endémisme. Cependant, la conservation de ces zones pose un défi de taille en raison des menaces humaines croissantes, dont l'empiètement de l'agriculture et des habitations, le surpâturage par le bétail et la coupe forestière sélective. Nous avons examiné l'effet des perturbations forestières et la valeur potentielle de conservation des forêts montanes tropicales non protégées pour les oiseaux dans les forêts afromontanes sèches sempervirentes du massif de Balé, en Éthiopie. Nous avons échantillonné les oiseaux pendant deux ans dans les forêts protégées (caractérisées par de faibles niveaux de culture, de surpâturage et de coupes forestières) et non protégées (niveaux de perturbation plus élevés). À l'aide des traits fonctionnels des oiseaux associés au type d'habitat, au régime alimentaire et à la strate d'alimentation, nous avons caractérisé la différence entre les forêts protégées et non protégées en termes de richesse spécifique aviaire, d'abondance et de composition de l'assemblage. Dans l'ensemble, la richesse spécifique était 27 % plus élevée et l'abondance des oiseaux était 19 % supérieure dans les forêts non protégées. En revanche, la richesse spécifique et l'abondance des spécialistes des forêts et des espèces qui s'alimentent dans la canopée étaient significativement plus élevées dans les forêts protégées. Ces résultats suggèrent que les forêts montanes non protégées et perturbées d'Éthiopie contribuent à atteindre les objectifs de conservation dans une région reconnue pour l'importance mondiale de sa biodiversité. Par ailleurs, les écosystèmes forestiers intacts nécessitent une protection continue afin de maximiser l'hétérogénéité fonctionnelle associée aux taxons des forêts tropicales spécialistes.

Mots-clés : forêt afromontane, diversité aviaire, guildes aviaires, massif de Balé, aire protégée, spécialistes des forêts, taille de la parcelle

INTRODUCTION

Degradation and destruction of habitats due to anthropogenic actions are major causes of global biodiversity declines (Brooks et al. 2006). Understanding interspecific variation in species' responses to human disturbances is important to enable effective conservation decision-making, for example, by informing habitat protection and restoration targets to maintain important ecological phenomena such as species–area thresholds (Bruner et al. 2001, Bleher et al. 2006, Maron et al. 2012, Game et al. 2013). Protected areas are frequently viewed as safeguarding ecological communities (Bruner et al. 2001); however, particularly in developing countries, where funds and national strategies for conservation and protected areas are low, protected areas frequently fail to adequately achieve this aim. Given the high rates of tropical deforestation across the globe, understanding the combined conservation role of protected and unprotected forests is critical for efficient allocation of conservation resources (Liu et al. 2001, Dirzo and Raven 2003, Buechley et al. 2015).

In forests, alteration of vegetation structure and habitat fragmentation through deforestation and forest degradation are among the main threats affecting biodiversity (Trzcinski et al. 1999, Sekercioglu 2002, Heikkinen et al. 2004, Chace and Walsh 2006). Forest birds are particularly susceptible to alterations in vegetation structure and forest extent because of their complex social structures and dependence on vertical vegetation structure (Martin and Possingham 2005, Davies and Asner 2014). However, studies of forest birds have found species' responses to disturbances to be variable and dependent on a number of factors, including species-specific ecological traits and the severity of the disturbance (Newbold et al. 2013, Mandal and Shankar Raman 2016). For example, many forest specialist species are negatively affected by forest disturbance, and insectivorous birds have disappeared from some heavily transformed forests (Canaday 1997, Şekercioğlu et al. 2002, Chace and Walsh 2006, Gove et al. 2008). In contrast, habitat generalist species that are better adapted to open and/or shrub habitats can positively exploit habitat changes induced by disturbance (Chace and Walsh 2006, Gove et al. 2008, Sekercioglu 2012). Flexibility in conservation management is therefore needed in order to differentiate between aspects of anthropogenic development and their associated impacts on biotic communities, and to manage the drivers with the greatest ecological impact (Blair 1996, Entwisle and Stern 2005). The information necessary for these important conservation actions is often lacking in biologically important areas across the globe, especially tropical forests.

The Bale Mountains massif in Ethiopia is considered a biodiversity hotspot by Conservation International (Williams et al. 2004), and Bale Mountains National Park (BMNP), the only protected area in the region, is on the tentative list for World Heritage Site listing. Almost 300 bird species are found in the region, including 6 of the 18 species endemic to Ethiopia and an additional 14 near-endemic species found only in Ethiopia and Eritrea (Asefa 2006, Shimelis et al. 2011). These mountains are designated as an Important Bird Area of Ethiopia (EWNHS 1996) and are considered to be the 4th-best birding site in Africa (African Bird Club, https://www.africanbirdclub.org/countries/Africa/hotspots). An increasing human population, and hence increased agriculture, livestock grazing, and deforestation in the region, is placing extreme pressure on the area's natural resources, resulting in large-scale alteration and degradation of habitats, even within the protected area of the park (Mitiku 2013, Asefa et al. 2015a). Such changes are likely to have profound impacts on the avifaunal assemblage of the Bale Mountains. However, the direction and severity of these impacts may vary depending on the ecological guild.

Specialist species are potentially more vulnerable than generalists to habitat degradation and fragmentation because ecological specialization in diet or habitat often leads to increased extinction risk (Sekercioglu 2011). Such selective extinction processes not only lead to shifts in species richness, assemblage composition, and relative abundance, but can also alter ecological processes and ecosystem services provided by birds (e.g., seed dispersal, pollination, and nutrient cycling; Chapin et al. 1998, Lens et al. 2002, Sekercioglu 2011, Pesendorfer et al. 2016). Therefore, understanding the ecological partitioning of avian diversity in areas with high species richness and endemism, such as the Bale Mountains, is critical for evaluating the overall ecological integrity of these ecosystems and designing appropriate conservation approaches (dos Anjos et al. 2015, Pavlacky et al. 2015, Pollock et al. 2015).

Here, we focus on bird species functionally categorized by habitat type, diet, and foraging stratum to examine the impacts of human disturbance in the Afromontane forests of the northern Bale Mountains of Ethiopia. Specifically, we examine the impacts of human disturbance on avian species richness and abundance on (1) the entire assemblage, (2) species groups that are functionally unique to a specific habitat type, and (3) forest specialist species that are functionally unique to a specific diet and a specific foraging stratum. We predicted that (1) compared with unprotected forests, protected forests (assuming lower levels of human-induced disturbance) would contain higher overall species richness and bird abundance, as well as higher richness and abundance of forest species, especially insectivores and canopy foragers; and (2) as a result of reduced forest cover and increased crop cultivation, unprotected forests would host higher richness and abundance of species associated with open land, open woodland, and shrubland habitats.

METHODS

Study Area

We conducted our study on the northern slope of the Bale Mountains in southeastern Ethiopia. Bale Mountains National Park (BMNP; 6.50°–7.17°N, 39.50°–39.92°E), at the center of these mountains, covers 2,200 km^2 and encompasses the largest expanse of Afroalpine habitat in Africa and Ethiopia's second-largest tropical montane forest (Figure 1). The area experiences 2 rainy seasons, with lighter rains from March to June and the heavy rainy season from July to October, and a dry season between November and February; mean annual rainfall is 1,219 mm (Hillman 1986). There are 5 broad vegetation types in the Bale Mountains (Hillman 1986, National Herbarium 2004): northern dry evergreen Afromontane forest (altitudinal range of 2,900–3,400 m above sea level [m asl]), northern montane grasslands (~3,000 m asl), ericaceous forest (3,400–3,800 m asl), Afroalpine moorland and grassland (3,800–4,377 m asl), and southern moist evergreen (Harenna) forest (1,500–3,200 m asl).

We undertook our study near the upper tree limit (between 2,900 and 3,400 m asl) in northern dry evergreen montane forest, referred to as juniper forest (OARDB 2007, Redman et al. 2009). This forest existed in 6 isolated patches. *Juniperus procera* was the dominant tree species in these forest patches, with *Hagenia abyssinica*, *Hypericum revolutum*, and *Rapanea melanophloeos* also present (National Herbarium 2004, OARDB 2007, Asefa et al. 2015b). Although the 6 forest patches varied in size (120–2,485 ha) and level of anthropogenic threat (Figure 1, Table 1), they occurred within a similar altitudinal range (2,900–3,400 m asl) and had comparable topography and vegetation composition (OARDB 2007, Asefa et al. 2015a, 2015b). Two of the patches (Adellay and Boditti) were fully inside BMNP, and a third (Dinsho Hill) was the park headquarters; these 3 sites were thus all in heavily managed and protected parts of the park (Figure 1) and represented protected forest (hereafter referred to as protected sites). Three other sites (Angesso, Shaya, and Darkina) were either outside BMNP or straddled the park boundary (Figure 1), and were in areas that were not as intensively protected by park management (hereafter referred to as unprotected sites). As such, these 2 sets of forest patches differed in the level of management intensity and thus the nature and degree of human disturbance. Protected sites were regularly patrolled by park rangers based at outposts near these patches (~40 person-hr day^{-1}) and were actively managed to reduce illegal land use as per the park's management plan, whereas unprotected sites were patrolled irregularly (~0.4 person-hr day^{-1}) and resource use was poorly regulated by either the national park (areas inside the park boundary) or the Bale Zone district forestry guards (areas outside the national park; Mitiku 2013, Asefa et al. 2015a). Consequently, unprotected sites had higher levels of anthropogenic disturbance

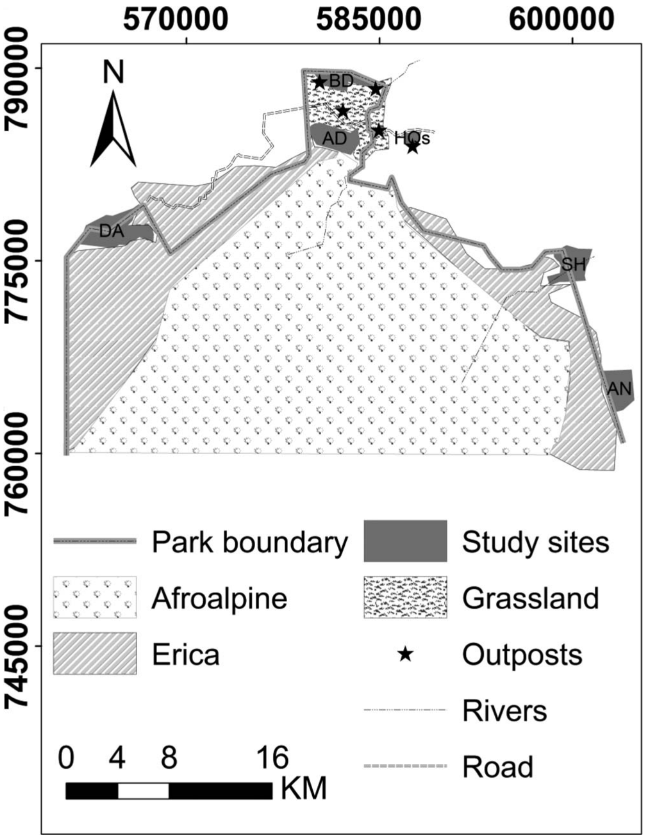

FIGURE 1. Map of the northern half of Bale Mountains National Park (BMNP), Ethiopia, showing the 6 forest patches (study sites) used to examine the effects of forest disturbance on birds and the outposts where park rangers were based. Forest patch abbreviations, protected patches: BD = Boditti, HQs = Dinsho Hill (BMNP headquarters), and AD = Adellay; unprotected patches: AN = Angesso, SH = Shaya, and DA = Darkina.

TABLE 1. Description of the forest patches (sites), including level of disturbance, in Bale Mountains National Park (BMNP), Ethiopia (Figure 1), used to examine the impacts of human disturbance on birds. Disturbance data were taken from Asefa et al. (2015a), and their values are mean ± SD number of houses ha^{-1} for settlement, number of tree stumps ha^{-1} for logging, and percentage cover ha^{-1} for agriculture. For each disturbance type in each patch, $n = 15$ transects.

	Description			Disturbance			
Site	Protection status	Area (ha)	Elevation (m)	Settlement	Logging	Grazing level	Agriculture
Adellay	Protected	784.9	2,951–3,400	0	60.0 ± 15.0	None–Low	0
Boditti	Protected	555.1	2,904–3,356	0	27.5 ± 2.5	Low–Moderate	0
Dinsho Hill	Protected	118.9	2,900–3,150	0	17.5 ± 12.5	None–Low	0
Angesso	Unprotected	2,237.9	2,915–3,270	1.2 ± 0.1	122.5 ± 12.5	Moderate–Heavy	42.1 ± 12.1
Darkina	Unprotected	1,016.6	2,922–3,348	4.5 ± 0.2	182.5 ± 32.5	Moderate–Heavy	67.1 ± 10.8
Shaya	Unprotected	2,485.1	2,967–3,391	2.4 ± 0.3	190.0 ± 32.5	Moderate–Heavy	3.4 ± 1.4

compared with protected sites (Table 1; see also Asefa et al. 2015a). Both logging (35 cut trees ha^{-1} in protected forests compared with 195 cut trees ha^{-1} in unprotected forests) and livestock grazing (none to low levels in protected forests vs. moderate to heavy levels in unprotected forests) were significantly greater in the unprotected sites. The unprotected sites were also the only patches that had human settlements (3 houses ha^{-1}) and agricultural cultivation (38% land cover ha^{-1}; Asefa et al. 2015a; Table 1).

The contrasting levels of disturbance in the unprotected and protected forest patches resulted in significant differences in the woody plant (trees, shrubs, and lianas combined) and shrub species composition. However, tree species composition was similar between the 2 forest patch types (~90% similarity; Asefa et al. 2015b). Tree abundance and canopy cover were reduced by 41% and 36%, respectively, in unprotected forests. Grazing reduced grass height by 33% and grass cover by 12% in unprotected forests. In contrast, shrub abundance was 135% higher, shrub cover was 33% higher, and proportion of bare ground was 51% higher in the unprotected sites (Asefa et al. 2015b).

Bird Surveys

In 2009 and 2012, bird surveys were carried out in the dry (November to March) and wet (July to October) seasons, thereby accounting for seasonal and temporal variation. In each of the 6 forest patches, 5 parallel line transects of 1.0 to 1.5 km were established, spanning the altitudinal range of each patch. The first transect in each forest patch was randomly located and the remaining transects were then systematically laid out to maintain a minimum distance of ~300 m between transects. Along each transect, 4 fixed bird survey points were selected systematically, again by maintaining a minimum distance of ~300 m between points to avoid double counting (Bibby et al. 1998).

Each transect was surveyed twice on 1 sampling day per season (once early in the morning, 0730–1030 hours, and again in the late afternoon, 1430–1730 hours), resulting in each transect being sampled a total of 8 times during the study. The identity and number of birds seen or heard, and their estimated sighting distances (in bands of 5 m intervals) within a radius of 50 m from the survey point were recorded for 8 min after an initial 2 min settling period (Bibby et al. 1998). Any birds that flushed away from the census point upon approach to the station or that flew away during the counting period were recorded at the point at which they were first seen (following van Rensburg et al. 2000).

Taxonomic nomenclature and order of presentation used for this study follow Clements et al. (2016). To account for species present but not detected, we used richness estimators that assumed imperfect detection (Colwell et al. 2012).

Analysis

Bird species were classified into 4 different guilds based on their broad habitat type preferences (forest, open woodland, shrubland, and open land) following Redman et al. (2009), Kissling et al. (2012), and Gove et al. (2008). Based on these broad guilds, we further classified species within the forest guild into 5 subguilds based on their diets (3 subguilds: carnivore, frugivore, and insectivore) and foraging layers (2 subguilds: ground layer and canopy layer) following Shimelis et al. (2011) and Gove et al. (2013); for species-specific guild and subguild memberships in our study, see Appendix Table 5. We identified these forest-specialist subguilds for 2 main reasons. First, the primary goal of conserving the study area's forests from an avian perspective is to maintain the diversity of bird species typically associated with forest habitats (OARDB 2007), and second, forest insectivores have repeatedly been shown to be especially sensitive to forest change (e.g., Şekercioğlu et al. 2002, Pollock et al. 2015, Powell et al. 2015).

Species richness and abundance. We used an individual-based rarefaction and extrapolation methods to calculate species richness. We chose an individual-based instead of a sample-based approach because our primary interest was to estimate (compare) species richness (the total number of species at a particular site) rather than species density (the number of species per unit area), the latter of which is computed from sample-based data (Colwell et al. 2012). We also used the Chao 1 estimator (an appropriate estimator for individual-based data; Colwell et al. 2012) to estimate asymptotic species richness (S(est), the total number of species expected in an area, including those species not observed during the survey period) for each forest type (protected vs. unprotected) to assess sampling completeness. We used the summed abundance for each forest type of the number of individuals of each species recorded along each transect as the input for the individual-based richness computation. We calculated estimated species richness (S(est)) using EstimateS 9.1.0 software (http://viceroy.eeb.uconn.edu/estimates; Colwell 2013). To compare estimated (based on extrapolation) species richness between forest types, extrapolation curves of S(est) were computed with 95% confidence intervals (CI). This approach enabled us to make statistically robust extrapolations of samples for direct comparisons among sites of different sample sizes (Colwell et al. 2012). For each comparison, if the result of doubling the smaller sample was greater than the sample size of the larger sample, both samples were extrapolated to twice the number of individuals recorded in the smaller sample in either of the 2 forest types. Otherwise, smaller samples were extrapolated to the total number of individuals recorded in the larger sample, following Colwell et al. (2012). These analyses were conducted for each forest type in each season and for all seasons combined. For each guild and subguild, however, these comparisons were made using only pooled seasonal data due to the small sample size of most guilds. Following the recommendations of Walther and Moore (2005), Colwell et al. (2012), and Colwell (2013), we used nonoverlapping 95% CIs of S(est) at the maximum extrapolated sample size for a conservative criterion of statistical difference (at $\alpha = 0.05$) in species richness between sites.

A preliminary analysis using Distance 4.2 (Thomas et al. 2010) did not show systematic differences by season or forest type in overall detection probability using the 5 m distance bands up to 50 m. Thus, given that we were not concerned with individual species, we used the raw numbers of detections within 50 m as our measures of abundance. We tested the effects of disturbance, season, and fragmentation on overall abundance (i.e. total number of individual birds recorded, regardless of species) using a generalized linear mixed model, with a Poisson probability distribution and log-link function, in SPSS 20 (IBM, Armonk, New York, USA). Bird abundance was considered the response variable, while forest type (disturbed vs. undisturbed), season, and log-transformed patch size were treated as fixed effects. Forest patch ID and transect ID were included as random effects to account for potential nonindependence of transects within a forest patch and of season along each transect. Due to the small number of forest sites in our study, we chose patch size as the main fragmentation parameter, and did not consider other potentially relevant fragmentation parameters, such as isolation, connectivity, or perimeter-to-area ratio (Gustafson and Parker 1992). As previously noted, comparisons for each guild and subguild were made using pooled seasonal data due to the small sample size of most guilds. We examined model fit for the entire assemblage and for each (sub)guild with plots of fitted data vs. standardized model residuals, which in most cases showed a satisfactory fit. Results are presented as mean ± SE, and the statistical significance of differences was tested at $\alpha = 0.05$.

Assemblage composition. We used 3 approaches to evaluate differences in assemblage composition between the 2 forest types (protected and unprotected). First, we estimated the number of shared species between the 2 forest types using the Chao 1 V(est) estimator in EstimateS 9.1.0. This estimator computes the real (actual) number of shared species, while accounting for species present but not observed (Colwell et al. 2012, Colwell 2013). Second, we used a Bray-Curtis similarity index to calculate similarities in bird species composition among assemblages using Primer v6 software (Clarke and Gorley 2006). Data were 4th-root transformed before analysis to downweight common species relative to rare ones (Clarke and Gorley 2006). We then performed an analysis of similarity (ANOSIM) to assess differences in bird species composition between forest types both within and between seasons (Clarke and Gorley 2006). Global *R* values were used to determine the degrees of similarity among treatments; the closer this value is to 1, the more dissimilar are assemblages (Clarke and Gorley 2006). Significances of differences were tested at $\alpha = 0.05$. Finally, we conducted similarity percentage analysis (SIMPER) in Primer v6 software to calculate the percentage contribution that each species made to the dissimilarity between bird assemblages of the forest types and to identify which species were contributing most to the differences (i.e. species that are characteristic of each forest type) between assemblages (Clarke and Gorley 2006). Results of this SIMPER analysis should be interpreted with caution as we undertook this analysis using raw abundance data without accounting for potential differences in intra- and inter-specific detection probability by season or forest type.

RESULTS

Species Richness

A total of 12,625 individuals comprising 66 avian species were recorded across both forest types throughout the study: 5,651 individuals from 46 species in the protected

TABLE 2. Observed (S(obs)) and estimated [(based on Chao 1 (S(est) Chao 1) and extrapolation (S(est) extrapolated))] overall avian species richness and mean abundance in protected and unprotected forest sites in Afromontane forests in the Bale Mountains, southeastern Ethiopia, during the dry season, wet season, and both seasons combined. In the case of abundance, values are mean ± SE number of individuals recorded along each transect (in each case, $n = 15$ transects); in the case of estimated richness, values are mean ± 95% CI of randomizations ($n = 100$ randomizations) in each condition. Means with no subscript letters in common denote significant differences between sites at $P < 0.05$. N is total number of individuals sighted.

Season	Status	N	S(obs)	Abundance	S(est) Chao 1	S(est) extrapolated
Dry	Protected	2,625	41	175.00 ± 7.72 ^{a}	42.0 ± 1.8 ^{a}	42.7 ± 2.2 ^{a}
	Unprotected	3,214	52	214.27 ± 3.10 ^{b}	52.0 ± 0.2 ^{b}	52.2 ± 0.7 ^{b}
Wet	Protected	3,026	39	201.73 ± 2.69 ^{a}	39.8 ± 1.4 ^{a}	40.3 ± 1.8 ^{a}
	Unprotected	3,760	53	250.67 ± 3.67 ^{c}	53.2 ± 0.5 ^{b}	53.4 ± 0.8 ^{b}
Combined	Protected	5,651	46	376.73 ± 4.00 ^{a}	47.5 ± 2.2 ^{a}	48.1 ± 2.4 ^{a}
	Unprotected	6,974	60	464.93 ± 20.44 ^{b}	60.3 ± 0.7 ^{b}	60.6 ± 1.1 ^{b}

forest sites and 6,974 individuals from 60 species in the unprotected forest patches (Table 2, Appendix Table 5). The individual-based curves almost reached an asymptote in all cases (Figure 2), and comparisons of observed and estimated (Chao 1 estimator) species richness for each dataset showed that sampling completeness among sites was >97% (Table 2).

Estimated (i.e. extrapolated) species richness of the entire bird assemblage (i.e. all species taken together) was greater in the unprotected forests than in the protected forests, both within and across seasons (Table 2, Figure 2). The estimated richness in the unprotected forests was 22% greater during the dry season, 33% greater during the wet season, and 26% greater when seasons were pooled (Table 2). Similarly, the 4 habitat guilds showed either increased or equal estimated species richness in the unprotected forests relative to the protected forests (Figure 3). Guilds with significantly higher estimated species richness in the unprotected sites were open woodland (133% higher; Figure 3B) and open land (86% higher) habitat guilds (Figure 3A). Among the 5 forest specialist subguilds considered, insectivores and canopy layer foragers were 9% and 11% lower in the unprotected forests, respectively (Figure 4). Forest specialist frugivores and ground layer foragers, however, occurred in equal numbers in both forest types, with each subguild represented by 3 species in each forest type (Appendix Table 5).

Abundance

Mean bird abundance was ~18–20% higher in unprotected forests compared with protected forests in both seasons combined, and was ~14% higher during the wet season than the dry season (Table 2). The effects of both forest type (protected vs. unprotected) and season on overall bird abundance were statistically significant (ANOVA, forest type: $F_{1,55} = 60.13$, $P < 0.05$, effect $\beta = -0.23 \pm 0.03$, $t = -6.94$, $P < 0.05$; season: mean, dry season = 194.63 ± 7.89, wet season = 226.20 ± 9.76, $F_{1,55} = 69.47$, $P < 0.05$, effect $\beta = -0.16 \pm 0.02$, $t = -6.53$, $P < 0.05$), but the effects of the interaction between these terms ($F_{1,55} = 0.17$, $P = 0.68$) and patch size ($F_{1,55} = 0.30$, $P = 0.68$) were not. However, pairwise contrasts revealed that seasonal effects were stronger in the unprotected forests, which had ~27% more individual birds during the wet season than the dry season, whereas protected forests had only 16% more birds in the wet than the dry season (unprotected: contrast estimate ± SE, wet season–dry season = 36.4 ± 13.6, $t_{56} = 2.6$, $P < 0.05$; protected: 26.7 ± 13.6, $t_{56} = 1.7$, $P = 0.05$; $n = 60$ for both forest types).

At the guild level, the forest-specialist habitat guild (ANOVA, $F_{1,27} = 12.94$, $P < 0.05$) had 36% higher abundance in the protected forests than the unprotected forests. The opposite pattern was found for the open land and shrubland habitat guilds (ANOVA, $F_{1,27} = 42.34$ and 5.19, respectively, both $P < 0.05$); these guilds were 122% and 66% higher, respectively, in the unprotected forests (Table 3A, Figure 5A). The effect of habitat patch size on guild abundance was only significant for forest habitat specialist species (ANOVA, $F_{1,27} = 5.51$, $P < 0.05$, effect $\beta = 0.34 \pm 0.15$, $t = 2.35$, $P < 0.05$).

Among the 5 forest specialist subguilds, only the abundances of insectivores (ANOVA, $F_{1,27} = 4.55$, $P < 0.05$) and canopy layer foragers ($F_{1,27} = 7.24$, $P < 0.05$) showed significant differences between protected and unprotected forests, with the abundance of forest specialist insectivores and canopy layer foragers being ~14% and ~17% higher, respectively, in the protected forests (Table 3B, Figure 5B).

Assemblage Composition

Observed (Chao 1 V(obs)) and estimated (Chao 1 V(est)) numbers of shared species between the protected and unprotected sites were 40 (61% of species) and 41 species, respectively. Despite this high degree of species overlap, the ANOSIM revealed significant differences in bird assemblage composition between the 2 forest types, both within and between seasons (dry season: Global $R = 0.7$; wet season: $R = 0.5$; across season: $R = 0.5$; in all cases, $P < 0.05$). Results of the SIMPER analysis showed that ~50% of the differences in assemblage composition between the 2

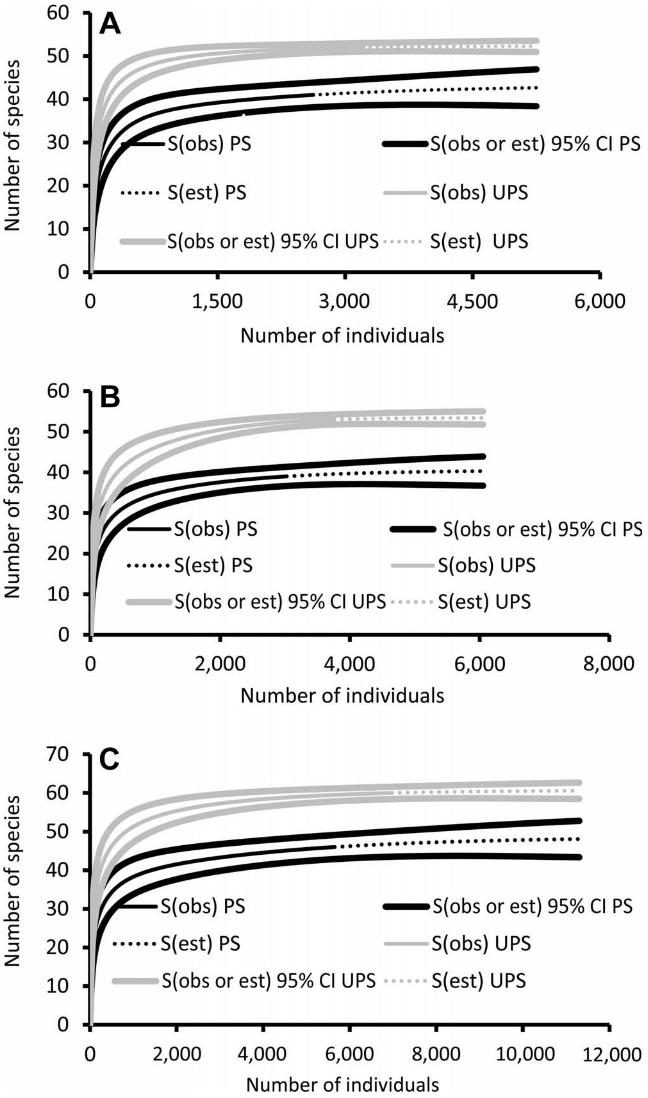

FIGURE 2. Observed (S(obs)) and estimated (S(est)) species richness values for the entire bird assemblage in protected sites (PS) and unprotected sites (UPS) of Afromontane forests in the Bale Mountains, southeastern Ethiopia, during (**A**) the dry season, (**B**) the wet season, and (**C**) both seasons combined. Values are mean ($n = 100$) species richness with 95% confidence intervals (CI); n is number of sample randomizations used.

forest patch types were driven by 11 species during the dry season (5 forest specialist and 6 nonspecialist or generalist species) and 8 species during the wet season (4 forest specialist and 4 nonspecialist species; Table 4). Forest specialists, including the White-backed Black-Tit (*Melaniparus leuconotus*), Brown Woodland-Warbler (*Phylloscopus umbrovirens*), and Broad-ringed White-eye (*Zosterops poliogastrus*), were found to be the most characteristic species of the protected sites, whereas generalist species, such as the Dusky Turtle-Dove (*Streptopelia lugens*), Abyssinian Siskin (*Serinus nigriceps*), Streaky Seedeater (*Serinus striolatus*), and Brown-rumped Seedeater (*Serinus tristriatus*), were most characteristic of the unprotected forest sites (Table 4).

TABLE 3. Results of generalized linear mixed models assessing the effects of forest type (disturbed vs. undisturbed) and forest patch size on the abundance of the different avian guilds and subguilds in Afromontane forests in the Bale Mountains, southeastern Ethiopia. Only estimates (± SE) for land use type are provided as the effect of patch size was not significant in any models, except in the case of forest habitat specialists. Positive estimates indicate higher values in the undisturbed forest sites.

Model	Estimate	t	P
(**A**) Habitat guild [a]			
Forest	0.32 ± 0.15	3.60	<0.05
Open land	−1.43 ± 0.62	−2.32	<0.05
Shrubland	−1.03 ± 0.23	−4.42	<0.05
Woodland	−0.45 ± 0.43	−1.06	0.30
(**B**) Forest specialist subguild [a]			
Carnivore	0.79 ± 0.51	1.53	0.14
Frugivore	−0.15 ± 0.53	−0.30	0.77
Insectivore	0.71 ± 0.34	2.13	<0.05
Ground layer	−0.23 ± 0.53	−0.44	0.66
Forest canopy	0.80 ± 0.30	2.69	<0.05

[a] For species-specific habitat, diet, and foraging stratum requirements, see Appendix Table 5.

DISCUSSION

Our results reveal that avian species that are functionally unique to Afromontane forests, especially forest specialist insectivores and canopy layer foragers, are dependent on intact (protected) forests with little human disturbance. These species are not only affected by disturbance-induced changes in vegetation structure and plant species composition, but also by decreased forest extent. Furthermore, the 2 forest types (protected and unprotected) that we studied differed in their bird assemblage composition, with a significant change from specialists in protected forests to generalists in unprotected forests. These results support the findings of numerous studies from around the globe that have shown specialist bird species to be among the most susceptible to forest disturbance (e.g., Stouffer and Bierregaard 1995, Sekercioglu 2012, Arcilla et al. 2015, Pavlacky et al. 2015). Thus, for the long-term conservation of forest specialists, particularly Ethiopian endemics such as the Abyssinian Woodpecker (*Dendropicos abyssinicus*), Yellow-fronted Parrot (*Poicephalus flavifrons*), White-backed Black-Tit (*Melaniparus leuconotus*), and Abyssinian Catbird (*Parophasma galinieri*), and Afrotropical species more broadly, it is important to (1) manage the drivers with the greatest ecological impact on primary forests, (2) inform, and improve on, policy responsible for habitat restoration targets, and (3) provide much-needed international support for the optimal management of

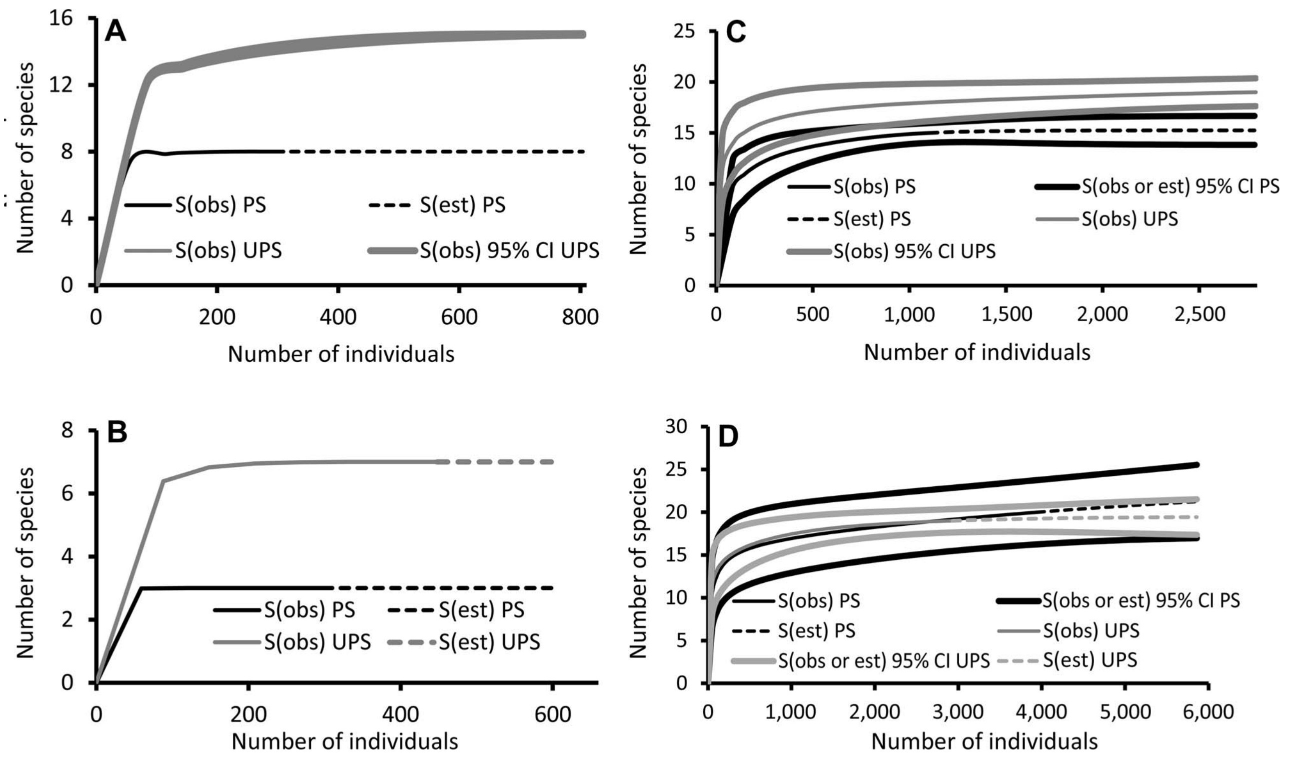

FIGURE 3. Observed (S(obs)) and estimated (S(est)) species richness values for 4 habitat guilds in protected sites (PS) and unprotected sites (UPS) of Afromontane forests in the Bale Mountains, southeastern Ethiopia: (**A**) open land, (**B**) woodland, (**C**) shrubland, and (**D**) forest. Values are mean ($n = 100$) species richness with 95% confidence intervals (CI), unless the confidence interval closes to zero (or overlaps S(obs) or S(est)); n is number of sample randomizations used.

existing protected areas in countries such as Ethiopia that still contain areas of primary forest.

In contrast to forest specialists, the species richness and abundance of birds overall (i.e. all species taken together) were higher in unprotected Afromontane forest patches compared with protected forests. This can likely be explained by the persistence of some forest species in unprotected forests, coupled with invasion by nonforest species, such as the Cape Crow (*Corvus capensis*), Pied Crow (*C. albus*), Yellow Bishop (*Euplectes capensis*), and Red-collared Widowbird (*E. ardens*), into these areas. Guilds that included species that are typically not associated with forests, such as open land, shrubland, and open woodland habitat guilds, had significantly higher species richness in the unprotected forests. These guilds are known to prefer disturbed and open habitats, so these results are not surprising (Mulwa et al. 2012, Sekercioglu 2012, Gove et al. 2013; see also Coetzee and Chown 2016 for similar findings in a savanna habitat).

However, these findings contradict the general trend of lower bird species richness in forests that have been transformed into farmland and/or undergone some other form of extensive habitat transformation (for tropical regions, see, e.g., Daily et al. 2001, Waltert et al. 2004, Seavy 2009; for temperate regions, see, e.g., Heikkinen et al. 2004, Breitbach et al. 2010). Such opposing findings could have arisen because most studies that have supported the general trend of decreased forest diversity with increased disturbance have typically investigated forests that are intensively utilized as agroecosystems or have been completely converted (e.g., Waltert et al. 2004, Seavy 2009), as opposed to forests that have been disturbed, but not heavily transformed, as with the forests in our study sites. Another potential explanation could be that, unlike in many other countries, agrofarming in rural Ethiopia consists of small-scale, traditional farming practices, where the use of insecticides and pesticides is rare and therefore unlikely to have deleterious effects on insect abundance, and therefore insectivorous birds (Gove et al. 2013).

Our findings of higher overall species richness and abundance in the more disturbed and unprotected forests do, however, support those of previous studies carried out in disturbed tropical forests in east Africa (e.g., Mulwa et al. 2012, Gove et al. 2013, Buechley et al. 2015), and there are several potential reasons why African birds might demonstrate increased resilience to human disturbance. First, the African avifauna, including functionally unique species such as understory insectivores, might be more capable of withstanding considerable habitat modification and disturbance compared with bird species found

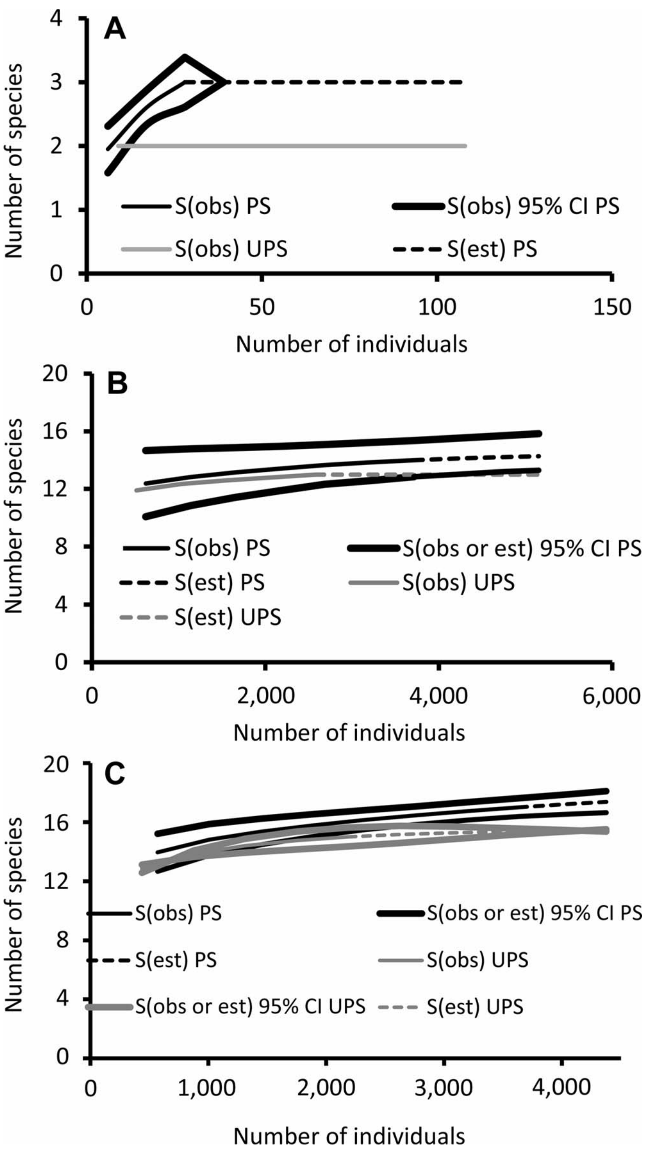

FIGURE 4. Observed (S(obs)) and estimated (S(est)) species richness values for forest specialist subguilds in protected sites (PS) and unprotected sites (UPS) of Afromontane forests in the Bale Mountains, southeastern Ethiopia: (**A**) carnivores, (**B**) insectivores, and (**C**) canopy layer foragers. Values are mean (*n* = 100) species richness with 95% confidence intervals (CI), unless the confidence interval closes to zero (or overlaps S(obs) or S(est)); *n* is number of sample randomizations used.

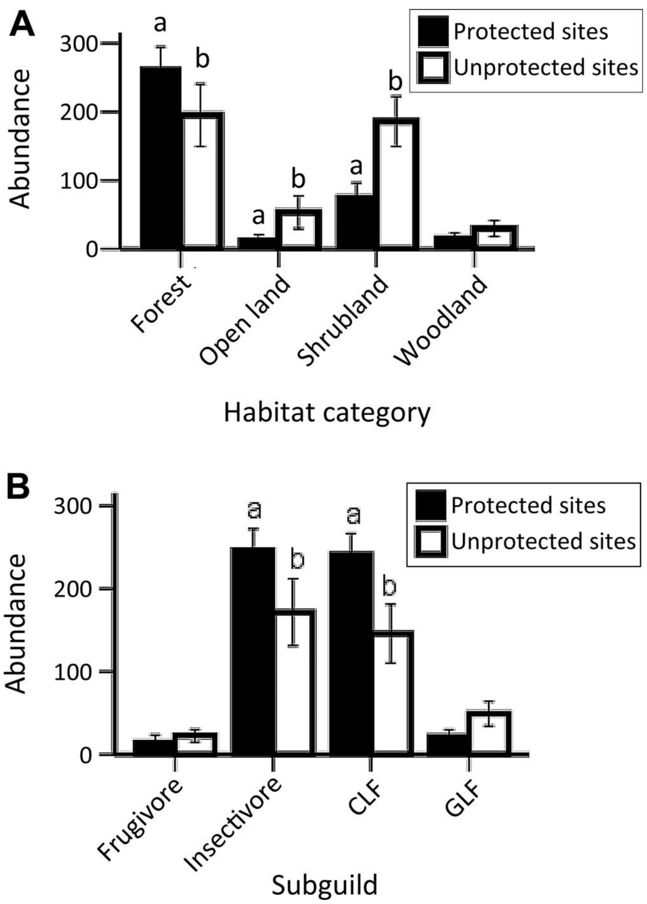

FIGURE 5. Abundances for (**A**) habitat guild and (**B**) forest specialist subguild categories in protected sites and unprotected sites of Afromontane forests in the Bale Mountains, southeastern Ethiopia. Values are mean ± SE. In all cases, $n = 15$. Letters indicate a significant difference between sites at $\alpha = 0.05$. Abbreviations for the forest specialist subguilds in panel B: CLF = canopy layer forager (i.e. forest specialist species that forages in the tree canopy); GLF = ground layer forager (i.e. forest specialist that forages on the ground).

elsewhere due to the longer history of anthropogenic forest clearance and agrarian activity in Africa (Chapman and Chapman 1996, Darbyshire et al. 2003). Such resilience of the African fauna to disturbance has been suggested by several previous studies that focused on birds and spanned a wide range of ecosystems and biogeographical regions (Karr 1976, van Rensburg et al. 2004, Gove et al. 2008, 2013, Mulwa et al. 2012). Second, previous studies have found intact forest habitats, particularly in Ethiopia, to have fewer bird species than the surrounding or nearby open (disturbed) forests, attributing such findings to the relatively young age of Ethiopian forests and the possibility that they have been regularly affected by climatic changes due to their topography (Gove et al. 2008, 2013, Buechley et al. 2015). Ethiopian forest habitats not only have fewer bird species than nearby open habitats, but also have relatively fewer specialist species compared with other tropical forests (Buechley et al. 2015). Third, it is well understood that spatial heterogeneity is an important driver of species richness across taxa (van Rensburg et al. 2002, Sekercioglu et al. 2007, Gove et al. 2008, Stein et al. 2014). In our study sites, the disturbed forests comprised both primary and secondary forest patches, in addition to galleries and open areas (cultivated lands) with retained canopy trees, whereas the protected forest patches were

TABLE 4. Similarity percentage analysis (SIMPER) of bird abundance between protected (PS) and unprotected (UPS) forest sites in Afromontane forests in the Bale Mountains, southeastern Ethiopia, in each season, to determine the percentage contribution that each species made to the dissimilarity between bird assemblages of the forest sites and to identify which species were contributing most to the differences between assemblages.

Species [a]	Average abundance (PS)	Average abundance (UPS)	Average dissimilarity	Percentage of contribution to overall dissimilarity	Cumulative percentage of dissimilarity
Dry season					
White-backed Black-Tit (*Melaniparus leuconotus*)	31.67	9.47	5.97	9.48	9.48
Broad-ringed White-eye (*Zosterops poliogastrus*)	27.27	9.60	4.89	7.77	17.25
Common Chiffchaff (*Phylloscopus collybita*)	16.73	1.47	4.04	6.42	23.67
Brown Woodland-Warbler (*Phylloscopus umbrovirens*)	22.67	14.47	2.87	4.55	28.22
Brown-rumped Seedeater (*Serinus tristriatus*)	1.73	10.40	2.50	3.98	32.20
Dusky Turtle-Dove (*Streptopelia lugens*)	7.60	13.93	2.41	3.82	36.02
Abyssinian Thrush (*Turdus abyssinicus*)	6.87	13.13	2.26	3.58	39.60
Streaky Seedeater (*Serinus striolatus*)	2.53	9.27	2.09	3.31	42.91
Common Bulbul (*Pycnonotus barbatus*)	0.47	7.20	1.82	2.88	45.79
Wattled Ibis (*Bostrychia carunculata*)	5.07	5.20	1.81	2.87	48.66
Abyssinian Siskin (*Serinus nigriceps*)	0.47	6.93	1.77	2.80	51.46
Wet season					
White-backed Black-Tit	32.87	8.87	5.69	9.95	9.95
Yellow-crowned Canary (*Serinus flavivertex*)	17.27	25.80	4.74	8.30	18.25
Broad-ringed White-eye	27.67	17.47	4.08	7.13	25.38
Abyssinian Catbird (*Parophasma galinieri*)	15.87	22.87	3.54	6.20	31.58
Brown Woodland-Warbler	22.93	11.53	3.09	5.41	36.99
Tacazze Sunbird (*Nectarinia tacazze*)	18.27	12.87	2.84	4.97	41.96
Slender-billed Starling (*Onychognathus tenuirostris*)	0.40	13.60	2.83	4.96	46.92
Streaky Seedeater	6.47	17.93	1.64	4.86	51.78

[a] For species-specific habitat requirements, see Appendix Table 5.

typically dominated by primary growth with less shrubby understory and open habitat (Mitiku 2013, Asefa et al. 2015b). Therefore, it is possible that the higher bird species richness and abundance in the unprotected forests resulted from the high diversity of structural habitat elements in these forests compared with the less disturbed forest patches. Indeed, structural heterogeneity of vegetation is known to exert a stronger influence on bird diversity than canopy cover (Davies and Asner 2014). As such, some forest specialist species are able to persist in unprotected forests, as well as several nonforest species, thereby leading to higher species richness in disturbed environments (see also Gascon et al. 1999, Sekercioglu et al. 2007, Gove et al. 2008).

Similarly to urban environments, where the best opportunities to conserve species may exist in degraded or even artificial environments (Sushinsky et al. 2013, Thomas 2013; but see also Coetzee and Chown 2016), the higher overall avian diversity in the unprotected forests might indicate the potential importance of disturbed habitats for bird conservation. These findings are particularly pertinent given the current unprecedented rate of forest degradation that is occurring globally, with the greatest proportion of loss occurring in developing Afrotropical countries such as Ethiopia (FAO 2010). It is therefore likely that the remaining primary forests in such countries will not survive or be available for the adequate, long-term conservation of forest birds, and the long-term perpetuity of several forest species may instead depend on well-managed, disturbed forestscapes. Other similar suggestions have been made for the region, for example "bird friendly" shade coffee farms, that, although they result in the loss of primary forests, maintain high overall avian species richness (Buechley et al. 2015). However, the viability of such disturbed forests as breeding habitats for forest birds requires further study, including species-specific population dynamics and ranging patterns. It is possible that disturbed forest patches could act as stepping stones for forest birds searching for more suitable habitat (Buechley et al. 2015), but they could also function as ecological traps and local population sinks for many functionally unique species, which could lead to functional homogenization and further conservation concern (Aerts et al. 2008, Coetzee and Chown 2016).

In conclusion, changes in vegetation composition and structure caused by human disturbance in our study region (Asefa et al. 2015a, 2015b) have led to considerable changes in bird richness, abundance, and assemblage composition. While habitat disturbance has led to an overall increase in avian diversity, and in the abundance of most avian functional guilds, it has negatively affected forest specialist species, which could lead to functional homogenization, although the ubiquity of this pattern remains to be examined. Therefore, it is critically important that we obtain a better understanding of the value and adequate management of unprotected habitats to maximize conservation targets. Corroborating the findings of Buechley et al. (2015), who compared avian diversity between primary forests and shade coffee farms in Ethiopia, our study supports the value of unprotected habitats for bird conservation, even if they are somewhat disturbed. It is, however, important to note that our study also highlights the need for proper protection of intact forest ecosystems if our aim is to maximize functional heterogeneity associated with tropical forest taxa. This is particularly true for global biodiversity hotspots, such as the Ethiopian Afromontane forests, where species endemism is typically high.

ACKNOWLEDGMENTS

We are grateful to Jemal Kassim and Usman Abdella for their assistance during data collection. We thank the Ethiopian Wildlife Conservation Authority and Bale Mountains National Park for permission to conduct the study. Several anonymous referees provided constructive reviews that greatly improved the final version of the manuscript.

Funding statement: This study was undertaken with financial support from DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Pretoria, and Frankfurt Zoological Society, Bale Mountains Conservation Project. None of our funders had any influence on the content of the submitted or published manuscript, and none of them required approval of the final manuscript to be published.

Ethics statement: Research permission was obtained from the Ethiopian Wildlife Conservation Authority.

Author contributions: A.A., A.A.K., and B.J.v.R. conceived the idea, design, experiment (supervised research, formulated question or hypothesis); A.A. and B.J.v.R. developed or designed methods; A.A. performed the experiments (collected data, conducted the research) and analyzed the data; and all authors wrote the paper (or substantially edited the paper).

LITERATURE CITED

Aerts, R., F. Lerouge, E. November, L. Lens, M. Hermy, and B. Muys (2008). Land rehabilitation and the conservation of birds in a degraded Afromontane landscape in northern Ethiopia. Biodiversity and Conservation 17:53–69.

Arcilla, N., L. H. Holbech, and S. O'Donnell (2015). Severe declines of understory birds follow illegal logging in Upper Guinea forests of Ghana, West Africa. Biological Conservation 188: 41–49.

Asefa, A. (2006). Birds of Bale Mountains National Park (BMNP), southeast Ethiopia. Walia 25:22–33.

Asefa, A., Y. Mamo, G. Mengesha, and A. Shimelis (2015b). Woody plant diversity along disturbance gradients in the northern Afro-montane forests of the Bale Mountains, Ethiopia. International Journal of Development Research 5: 3745–3754.

Asefa, A., A. Shimelis, and A. A. Kinahan (2015a). Assessment of threat status in the northern woodlands of the Bale Mountains, Ethiopia: Indicator for management effectiveness. Ethiopian Journal of Environmental Studies and Management 8:318–329.

Bibby, C., M. Jones, and S. Marsden (1998). Expedition Field Techniques: Bird Surveys. Expedition Advisory Centre, Royal Geographical Society, London, UK.

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Bleher, B., D. Uster, and T. Bergsdorf (2006). Assessment of threat status and management effectiveness in Kakamega Forest, Kenya. Biodiversity and Conservation 15:1159–1177.

Breitbach, N., I. Laube, I. Steffan-Dewenter, and K. Böhning-Gaese (2010). Bird diversity and seed dispersal along a human land-use gradient: High seed removal in structurally simple farmland. Oecologia 162:965–976.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues (2006). Global biodiversity conservation priorities. Science 313:58–61.

Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. da Fonseca (2001). Effectiveness of parks in protecting tropical biodiversity. Science 291:125–128.

Buechley, E. R., Ç. H. Şekercioğlu, A. Atickem, G. Gebremichael, J. K. Ndungu, B. A. Mahamued, T. Beyene, T. Mekonnen, and L. Lens (2015). Importance of Ethiopian shade coffee farms for forest bird conservation. Biological Conservation 188:50–60.

Canaday, C. (1997). Loss of insectivorous birds along a gradient of human impact in Amazonia. Biological Conservation 77: 63–77.

Chace, J. F., and J. J. Walsh (2006). Urban effects on native avifauna: A review. Landscape and Urban Planning 74:46–69.

Chapin, F. S., III, O. E. Sala, I. C. Burke, J. P. Grime, D. U. Hooper, W. K. Lauenroth, A. Lombard, H. A. Mooney, A. R. Mosier, S. Naeem, S. W. Pacala, et al. (1998). Ecosystem consequences of changing biodiversity: Experimental evidence and a research agenda for the future. Bioscience 48:45–52.

Chapman, C. A., and L. J. Chapman (1996). Mid-elevation forests: A history of disturbance and regeneration. In East African Ecosystems and Their Conservation (T. R. McClanahan and T. P. Young, Editors). Oxford University Press, Oxford, UK. pp. 385–400.

Clarke, K. R., and R. N. Gorley (2006). PRIMER v6: User Manual/ Tutorial. PRIMER-E, Plymouth, Devon, UK.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, D. Roberson, T. A. Fredericks, B. L. Sullivan, and C. L. Wood (2016). The eBird/ Clements Checklist of Birds of the World: v2016. http://www.birds.cornell.edu/clementschecklist/download/

Coetzee, B. W. T., and S. L. Chown (2016). Land-use change promotes avian diversity at the expense of species with unique traits. Ecology and Evolution 6: 7610–7622.

Colwell, R. K. (2013). EstimateS 9.1: Statistical estimation of species richness and shared species from samples. http://viceroy.colorado.edu/estimates/index.html

Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3–21.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa (2001). Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications 11:1–13.

Darbyshire, I., H. Lamb, and M. Umer (2003). Forest clearance and regrowth in northern Ethiopia during the last 3000 years. The Holocene 13:537–546.

Davies, A. B., and G. P. Asner (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends in Ecology & Evolution 29:681–691.

Dirzo, R., and P. H. Raven (2003). Global state of biodiversity and loss. Annual Review of Environment and Resources 28:137–167.

dos Anjos, L., C. D. Collins, R. D. Holt, G. H. Volpato, E. V. Lopes, and G. M. Bochio (2015). Can habitat specialization patterns of Neotropical birds highlight vulnerable areas for conservation in the Atlantic rainforest, southern Brazil? Biological Conservation 188:32–40.

Entwisle, B., and P. C. Stern (Editors) (2005). Population, Land Use, and Environment: Research Directions. National Academies Press, Washington, DC, USA.

EWNHS (Ethiopian Wildlife and Natural History Society) (1996). Important Bird Areas of Ethiopia: A First Inventory. Ethiopian Wildlife and Natural History Society, Addis Ababa, Ethiopia.

FAO (2010). Global Forest Resources Assessment 2010: Country Report: Ethiopia. Report FRA2010/065, Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy. http://www.fao.org/docrep/013/al501E/al501e.pdf

Game, E. T., P. Kareiva, and H. P. Possingham (2013). Six common mistakes in conservation priority setting. Conservation Biology 27:480–485.

Gascon, C., T. E. Lovejoy, R. O. Bierregaard, Jr., J. R. Malcolm, P. C. Stouffer, H. L. Vasconcelos, W. F. Laurance, B. Zimmerman, M. Tocher, and S. Borges (1999). Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91:223–229.

Gove, A. D., K. Hylander, S. Nemomisa, and A. Shimelis (2008). Ethiopian coffee cultivation—Implications for bird conservation and environmental certification. Conservation Letters 1: 208–216.

Gove, A. D., K. Hylander, S. Nemomissa, A. Shimelis, and W. Enkossa (2013). Structurally complex farms support high avian functional diversity in tropical montane Ethiopia. Journal of Tropical Ecology 29:87–97.

Gustafson, E. J., and G. R. Parker (1992). Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecology 7:101–110.

Heikkinen, R. K., M. Luoto, R. Virkkala, and K. Rainio (2004). Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in agricultural–forest mosaic. Journal of Applied Ecology 41:824–835.

Hillman, J. C. (1986). Bale Mountains National Park Management Plan. Ethiopian Wildlife Conservation Organization, Addis Ababa, Ethiopia.

Karr, J. R. (1976). Within- and between-habitat avian diversity in African and Neotropical lowland habitats. Ecological Monographs 46:457–481.

Kissling, W. D., C. H. Sekercioglu, and W. Jetz (2012). Bird dietary guild richness across latitudes, environments and biogeographic regions. Global Ecology and Biogeography 21:328–340.

Lens, L., S. Van Dongen, K. Norris, M. Githiru, and E. Matthysen (2002). Avian persistence in fragmented rainforest. Science 298:1236–1238.

Liu, J., M. Linderman, Z. Ouyang, L. An, J. Yang, and H. Zhang (2001). Ecological degradation in protected areas: The case of Wolong Nature Reserve for giant pandas. Science 292:98–101.

Mandal, J., and T. R. Shankar Raman (2016). Shifting agriculture supports more tropical forest birds than oil palm or teak plantations in Mizoram, northeast India. The Condor: Ornithological Applications 118:345–359.

Maron, M., M. Bowen, R. A. Fuller, G. C. Smith, T. J. Eyre, M. Mathieson, J. E. M. Watson, and C. A. McAlpine (2012). Spurious thresholds in the relationship between species richness and vegetation cover. Global Ecology and Biogeography 21:682–692.

Martin, T. G., and H. P. Possingham (2005). Predicting the impact of livestock grazing on birds using foraging height data. Journal of Applied Ecology 42:400–408.

Mitiku, A. A. (2013). Afromontane avian assemblages and land use in the Bale Mountains of Ethiopia: Patterns, processes and conservation implications. M.S. thesis, University of Pretoria, Pretoria, South Africa.

Mulwa, R. K., K. Böhning-Gaese, and M. Schleuning (2012). High bird species diversity in structurally heterogeneous farmland in western Kenya. Biotropica 44:801–809.

National Herbarium (2004). Biodiversity Assessment of the Bale Mountains National Park and Surrounding Areas. National Herbarium of Addis Ababa University, Addis Ababa, Ethiopia.

Newbold, T., J. P. W. Scharlemann, S. H. M. Butchart, Ç. H. Şekercioğlu, R. Alkemade, H. Booth, and D. W. Purves (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B 280: 20122131. http://dx.doi.org/10.1098/rspb.2012.2131

OARDB (Oromia Agriculture and Rural Development Bureau) (2007). Bale Mountains National Park General Management Plan. Oromia Agriculture and Rural Development Bureau, Addis Ababa, Ethiopia.

Pavlacky, D. C., Jr., H. P. Possingham, and A. W. Goldizen (2015). Integrating life history traits and forest structure to evaluate the vulnerability of rainforest birds along gradients of deforestation and fragmentation in eastern Australia. Biological Conservation 188:89–99.

Pesendorfer, M. B., T. S. Sillett, W. D. Koenig, and S. A. Morrison (2016). Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. The Condor: Ornithological Applications 118:215–237.

Pollock, H. S., Z. A. Cheviron, T. J. Agin, and J. D. Brawn (2015). Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. Biological Conservation 188:116–125.

Powell, L. L., N. J. Cordeiro, and J. A. Stratford (2015). Ecology and conservation of avian insectivores of the rainforest understory: A pantropical perspective. Biological Conservation 188:1–10.

Redman, N., T. Stevenson, and J. Fanshawe (2009). Birds of the Horn of Africa: Ethiopia, Eritrea, Djibouti, Somalia and Socotra. Princeton University Press, Princeton, NJ, USA.

Seavy, N. E. (2009). Bird use of banana plantations adjacent to Kibale National Park, Uganda: Evaluating the conservation value of a matrix habitat. Journal of East African Natural History 98:211–222.

Sekercioglu, C. H. (2002). Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. Biological Conservation 107:229–240.

Sekercioglu, C. H. (2011). Functional extinctions of bird pollinators cause plant declines. Science 331:1019–1020.

Sekercioglu, C. H. (2012). Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. Journal of Ornithology 153 (Suppl. 1):153–161.

Şekercioğlu, Ç. H., P. R. Ehrlich, G. C. Daily, D. Aygen, D. Goehring, and R. F. Sandí (2002). Disappearance of insectivorous birds from tropical forest fragments. Proceedings of the National Academy of Sciences USA 99:263–267.

Sekercioglu, C. H., S. R. Loarie, F. Oviedo Brenes, P. R. Ehrlich, and G. C. Daily (2007). Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology 21:482–494.

Shimelis, A., A. Bekele, A. Asefa, S. Williams, A. Gove, and S. Thirgood (2011). Structuring of the birds of the Bale Mountains National Park. Walia Special Edition on the Bale Mountains:15–27.

Stein, A., K. Gerstner, and H. Kreft (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.

Stouffer, P. C., and R. O. Bierregaard, Jr. (1995). Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76:2429–2445.

Sushinsky, J. R., J. R. Rhodes, H. P. Possingham, T. K. Gill, and R. A. Fuller (2013). How should we grow cities to minimize their biodiversity impacts? Global Change Biology 19:401–410.

Thomas, C. D. (2013). The Anthropocene could raise biological diversity. Nature 502:7.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Trzcinski, M. K., L. Fahrig, and G. Merriam (1999). Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9:586–593.

van Rensburg, B. J., S. L. Chown, and K. J. Gaston (2002). Species richness, environmental correlates, and spatial scale: A test using South African birds. The American Naturalist 159:566–577.

van Rensburg, B. J., S. L. Chown, A. S. van Jaarsveld, and M. A. McGeoch (2000). Spatial variation and biogeography of sand forest avian assemblages in South Africa. Journal of Biogeography 27:1385–1401.

van Rensburg, B. J., P. Koleff, K. J. Gaston, and S. L. Chown (2004). Spatial congruence of ecological transition at the regional scale in South Africa. Journal of Biogeography 31:843–854.

Waltert, M., A. Mardiastuti, and M. Mühlenberg (2004). Effects of land use on bird species richness in Sulawesi, Indonesia. Conservation Biology 18:1339–1346.

Walther, B. A., and J. L. Moore (2005). The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography 28:815–829.

Williams, S., J. L. Vivero Pol, S. Spawls, A. Shimelis, and K. Kelbessa (2004). Ethiopian highlands. In Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions (R. A. Mittermeier, P. Robles Gill, M. Hoffmann, J. Pilgrim, T. Brooks, C. Goettsch Mittermeier, J. Lamoreux, and G. A. B. da Fonseca, Editors). Conservation International and CEMEX, Mexico City, Mexico. pp. 262–273.

APPENDIX TABLE 5. List of species and their overall abundances recorded in unprotected and protected sites of Afromontane forests in the northern Bale Mountains, Ethiopia. Taxonomic order and nomenclature follow Clements et al. (2016). Species indicated by the superscript letter "a" are migrants.

Common name	Scientific name	Habitat	Food type	Substrate	Unprotected	Protected
Chestnut-naped Francolin	*Pternistis castaneicollis*	Shrubland	Omnivore	Ground layer	106	141
Wattled Ibis	*Bostrychia carunculata*	Open land	Insectivore	Ground layer	102	134
African Goshawk	*Accipiter tachiro*	Forest	Carnivore	Tree canopy	2	5
Little Sparrowhawk	*Accipiter minullus*	Forest	Carnivore	Tree canopy	0	1
Rufous-chested Sparrowhawk	*Accipiter rufiventris*	Forest	Carnivore	Tree canopy	4	22
Rouget's Rail	*Rougetius rougetii*	Shrubland	Omnivore	Ground layer	0	2
Speckled Pigeon	*Columba guinea*	Open land	Granivore	Ground layer	12	0
Rameron Pigeon	*Columba arquatrix*	Forest	Frugivore	Tree canopy	47	0
Dusky Turtle-Dove	*Streptopelia lugens*	Woodland	Granivore	Ground layer	336	184
Red-eyed Dove	*Streptopelia semitorquata*	Woodland	Granivore	Ground layer	10	0
White-Cheeked Turaco	*Tauraco leucotis*	Forest	Frugivore	Tree canopy	125	14
African Emerald Cuckoo [a]	*Chrysococcyx cupreus*	Shrubland	Insectivore	Shrub layer	1	0
Speckled Mousebird	*Colius striatus*	Woodland	Frugivore	Tree canopy	10	0
Narina Trogon	*Apaloderma narina*	Forest	Insectivore	Tree canopy	0	1
Eurasian Hoopoe [a]	*Upupa epops*	Woodland	Insectivore	Ground layer	17	0
Abyssinian Ground-Hornbill	*Bucorvus abyssinicus*	Open land	Insectivore	Ground layer	2	0
Rufous-necked Wryneck	*Jynx ruficollis*	Woodland	Insectivore	Tree canopy	5	1
Nubian Woodpecker	*Campethera nubica*	Forest	Insectivore	Tree canopy	0	2
Abyssinian Woodpecker	*Dendropicos abyssinicus*	Forest	Insectivore	Tree canopy	16	39
Mountain Gray Woodpecker	*Dendropicos spodocephalus*	Forest	Insectivore	Tree canopy	1	13
Black-winged Lovebird	*Agapornis taranta*	Forest	Frugivore	Tree canopy	171	157
Yellow-fronted Parrot	*Poicephalus flavifrons*	Forest	Frugivore	Tree canopy	0	59
Northern Puffback	*Dryoscopus gambensis*	Forest	Insectivore	Tree canopy	6	0
Ethiopian Boubou	*Laniarius aethiopicus*	Forest	Insectivore	Tree canopy	104	33
Northern Fiscal	*Lanius humeralis*	Woodland	Carnivore	Shrub layer	15	0
Cape Crow	*Corvus capensis*	Open land	Omnivore	Ground layer	50	0
Pied Crow	*Corvus albus*	Open land	Omnivore	Ground layer	4	0
Fan-tailed Raven	*Corvus rhipidurus*	Open land	Omnivore	Ground layer	42	24
Thick-billed Raven	*Corvus crassirostris*	Open land	Omnivore	Ground layer	11	22
Thekla Lark	*Galerida theklae*	Open land	Insectivore	Ground layer	24	4
White-backed Black-Tit	*Melaniparus leuconotus*	Forest	Insectivore	Tree canopy	275	968
Common Bulbul	*Pycnonotus barbatus*	Shrubland	Omnivore	Shrub layer	228	9
Brown Woodland-Warbler	*Phylloscopus umbrovirens*	Forest	Insectivore	Tree canopy	390	684
Common Chiffchaff [a]	*Phylloscopus collybita*	Forest	Insectivore	Tree canopy	22	251
Cinnamon Bracken-Warbler	*Bradypterus cinnamomeus*	Shrubland	Insectivore	Shrub layer	234	98
Winding Cisticola	*Cisticola galactotes*	Shrubland	Insectivore	Shrub layer	30	3
Tawny-flanked Prinia	*Prinia subflava*	Shrubland	Insectivore	Shrub layer	120	30
Abyssinian Catbird	*Parophasma galinieri*	Forest	Insectivore	Tree canopy	558	420
Broad-ringed White-eye	*Zosterops poliogastrus*	Forest	Omnivore	Tree canopy	406	824
Dusky-brown Flycatcher	*Muscicapa adusta*	Forest	Insectivore	Tree canopy	61	142
Abyssinian Slaty-Flycatcher	*Melaenornis chocolatinus*	Woodland	Insectivore	Tree canopy	55	93
Rüppell's Robin-Chat	*Cossypha semirufa*	Forest	Insectivore	Ground layer	195	84
Moorland Chat	*Cercomela sordida*	Open land	Insectivore	Ground layer	178	12
Abyssinian Ground-Thrush	*Geokichla piaggiae*	Forest	Insectivore	Ground layer	80	48
Groundscraper Thrush	*Psophocichla litsitsirupa*	Open land	Insectivore	Ground layer	95	18
Abyssinian Thrush	*Turdus abyssinicus*	Forest	Insectivore	Ground layer	462	203
Slender-billed Starling	*Onychognathus tenuirostris*	Shrubland	Omnivore	Shrub layer	235	10
Collared Sunbird	*Hedydipna collaris*	Shrubland	Nectarivore	Tree canopy	18	0
Tacazze Sunbird	*Nectarinia tacazze*	Shrubland	Nectarivore	Shrub layer	274	299
Malachite Sunbird	*Nectarinia famosa*	Shrubland	Nectarivore	Shrub layer	0	1
Western Yellow Wagtail	*Motacilla flava*	Open land	Insectivore	Ground layer	26	0
Gray Wagtail [a]	*Motacilla cinerea*	Open land	Insectivore	Ground layer	3	0
Red-Throated Pipit [a]	*Anthus cervinus*	Open land	Insectivore	Ground layer	50	0
Yellow-crowned Canary	*Serinus flavivertex*	Shrubland	Granivore	Shrub layer	440	291
Abyssinian Siskin	*Serinus nigriceps*	Open land	Granivore	Ground layer	155	16
African Citril	*Serinus citrinelloides*	Shrubland	Granivore	Shrub layer	8	2
Streaky Seedeater	*Serinus striolatus*	Shrubland	Granivore	Shrub layer	408	135
Brown-rumped Seedeater	*Serinus tristriatus*	Shrubland	Granivore	Ground layer	277	66
Swainson's Sparrow	*Passer swainsonii*	Open land	Granivore	Ground layer	50	0

APPENDIX TABLE 5. Continued.

Common name	Scientific name	Habitat	Food type	Substrate	Unprotected	Protected
Baglafecht Weaver	*Ploceus baglafecht*	Shrubland	Insectivore	Shrub layer	78	9
Yellow Bishop	*Euplectes capensis*	Shrubland	Granivore	Shrub layer	9	0
Red-collared Widowbird	*Euplectes ardens*	Shrubland	Granivore	Shrub layer	26	0
Yellow-bellied Waxbill	*Coccopygia quartinia*	Shrubland	Granivore	Shrub layer	174	67
Abyssinian Crimson-wing	*Cryptospiza salvadorii*	Forest	Granivore	Shrub layer	4	0
Common Waxbill	*Estrilda astrild*	Shrubland	Granivore	Shrub layer	125	10
Pin-tailed Whydah	*Vidua macroura*	Shrubland	Granivore	Shrub layer	2	0