

## RESEARCH ARTICLE

# Community characteristics of forest understory birds along an elevational gradient in the Horn of Africa: A multi-year baseline

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Submission Date: June 30, 2020; Editorial Acceptance Date: February 7, 2021; Published April 27, 2021

## ABSTRACT

Tropical mountains are global hotspots for birdlife. However, there is a dearth of baseline avifaunal data along elevational gradients, particularly in Africa, limiting our ability to observe and assess changes over time in tropical montane avian communities. In this study, we undertook a multi-year assessment of understory birds along a 1,750 m elevational gradient (1,430–3,186 m) in an Afrotropical moist evergreen montane forest within Ethiopia's Bale Mountains. Analyzing 6 years of systematic bird-banding data from 5 sites, we describe the patterns of species richness, abundance, community composition, and demographic rates over space and time. We found bimodal patterns in observed and estimated species richness across the elevational gradient (peaking at 1,430 and 2,388 m), although no sites reached asymptotic species richness throughout the study. Species turnover was high across the gradient, though forested sites at mid-elevations resembled each other in species composition. We found significant variation across sites in bird abundance in some of the dietary and habitat guilds. However, we did not find any significant trends in species richness or guild abundances over time. For the majority of analyzed species, capture rates did not change over time and there were no changes in species' mean elevations. Population growth rates, recruitment rates, and apparent survival rates averaged 1.02, 0.52, and 0.51 respectively, and there were no elevational patterns in demographic rates. This study establishes a multi-year baseline for Afrotropical birds along an elevational gradient in an under-studied international biodiversity hotspot. These data will be critical in assessing the long-term responses of tropical montane birdlife to climate change and habitat degradation.

## LAY SUMMARY

- There is a dearth of baseline avifaunal data along elevational gradients, especially in Africa, impeding efforts to evaluate temporal changes in tropical montane bird communities.
- We assessed species richness, community composition, abundance, elevational occurrence, and demographic rates of montane understory avifauna along an elevational gradient in Ethiopia's Bale Mountains.
- We found a bimodal pattern is observed and estimated species richness, with high species turnover across the gradient.
- There were few significant changes in guild or species capture rates over time, yet we documented eight species at elevations higher than documented in the established literature.
- This six-year study establishes an important baseline for East African understory montane birds along an elevational gradient in an under-studied international biodiversity hotspot.

*Keywords:* abundance, avian ecology, community composition, demographic rates, Ethiopia, species richness, tropical mountains

## Caractéristiques des communautés d'oiseaux de sous-bois le long d'un gradient d'altitude dans la Corne de l'Afrique: un état de référence pluriannuel

### RÉSUMÉ

Les montagnes tropicales sont des points chauds de diversité aviaire dans le monde. Cependant, il manque des données de base sur l'avifaune le long de gradients altitudinaux, particulièrement en Afrique, ce qui limite notre capacité à observer et à évaluer les changements temporels dans les communautés aviaires des montagnes tropicales. Dans cette étude, nous avons entrepris une évaluation sur plusieurs années des populations d'oiseaux de sous-bois le long d'un gradient altitudinal de 1750 m (1 430 – 3 186 m) de la forêt montagnarde sempervirente humide afrotropicale du massif du Balé, en Éthiopie. En analysant 6 années de données systématiques de baguage provenant de cinq sites, nous décrivons les patrons de richesse spécifique, d'abondance, de composition des communautés aviaires et de taux démographiques dans l'espace et le temps. Nous avons trouvé des patrons bimodaux dans la richesse spécifique observée et estimée le long du gradient altitudinal (culminant à 1 430 et 2 388 m), bien que la richesse spécifique n'ait atteint d'asymptote pour aucun des sites au cours de l'étude. Le renouvellement en espèces était élevé sur l'ensemble du gradient, mais les sites forestiers à mi-altitude se ressemblaient en termes de composition spécifique. Nous avons trouvé une variation significative entre les sites pour ce qui est de l'abondance aviaire dans certaines guildes alimentaires et guildes d'habitats. Toutefois, nous n'avons pas trouvé de tendance significative pour la richesse spécifique ou les abondances des guildes dans le temps. Pour la majorité des espèces analysées, les taux de capture n'ont pas changé au fil du temps et il n'y avait aucun changement dans les altitudes moyennes des espèces. Les taux de croissance des populations, les taux de recrutement et les taux de survie apparente étaient en moyenne de 1,02, 0,52 et 0,51 respectivement, et il n'y avait aucun patron altitudinal dans les taux démographiques. Cette étude établit un état de référence pluriannuel pour les oiseaux afrotropicaux le long d'un gradient altitudinal dans un point chaud de biodiversité international sous-étudié. Ces données seront essentielles pour évaluer les réponses à long terme de l'avifaune des montagnes tropicales aux changements climatiques et à la dégradation des habitats.

*Mots-clés:* abondance, écologie aviaire, composition des communautés, taux démographiques, Éthiopie, richesse spécifique, montagnes tropicales

### INTRODUCTION

Mountain ranges are diverse hotspots of endemism, ecological specialization, and evolution in birds (Harris et al. 2014, White and Bennett 2015, Abebe et al. 2019), resulting in high global conservation value, especially in the tropics (Wormworth and Şekercioglu 2011). Within the tropics, birds occur over much narrower temperature ranges than do their temperate counterparts (Dulle et al. 2016), likely due to the lower variation in tropical environmental conditions (Janzen 1967, Polato et al. 2018). Beyond temperature, a multitude of other factors including precipitation (Lenoir et al. 2010, Larsen et al. 2011, Tingley et al. 2012, Abebe et al. 2019, Santillán et al. 2020), habitat (Freeman et al. 2018a, Forero-Medina et al. 2011), vegetation (Forero-Medina et al. 2011, Jankowski et al. 2013, Santillán et al. 2020), interspecific competition (Jankowski et al. 2010, Lenoir et al. 2010), resource availability (Forero-Medina et al. 2011, Santillán et al. 2020), and evolutionary history (Santillán et al. 2020) may also exert strong control on the distributional limits and diversity of birds along elevational gradients.

Within the next century, warming temperatures are forecast to cause range shifts in temperate and tropical species that may lead to widespread range shifts (Abolafya et al. 2013) and extinctions (Şekercioglu et al. 2008). While the magnitude of climate change may be higher in temperate areas (Zuckerberg et al. 2009, Brommer et al. 2012, Virkkala and Lehikoinen

2014, Massimino et al. 2015), the effects on biodiversity may be greater in the tropics due to the heightened sensitivity of tropical species to rising temperatures (Şekercioglu et al. 2012, Freeman and Class Freeman 2014, Bender et al. 2019), which results from many factors such as low variability in climate, decreased dispersal ability, and complex biotic interactions (Janzen 1967, Jankowski et al. 2012, Polato et al. 2018, Sheard et al. 2020). Already, upslope shifts have been observed in tropical montane species, particularly in the Neotropics and Southeast Asia (e.g., Peh 2007, Forero-Medina et al. 2011, Freeman et al. 2018a, Neate-Clegg et al. 2018). Warming can cause montane endemics and specialist species to undergo substantial range contractions and may eventually lead to mountain-top extinctions (Şekercioglu et al. 2008, 2012, Cronin et al. 2014, Avalos and Hernández 2015, Freeman et al. 2018a) in a process termed the “escalator to extinction” (Şekercioglu 2007, Tobias et al. 2013, Freeman et al. 2018b).

Deforestation and habitat fragmentation are also significant impacts threatening montane ecosystems. Habitat or diet specialists that are functionally unique and restricted to high elevational forests (Buechley et al. 2015, Asefa et al. 2017) or are denizens of forest interior habitat (Turner 1996, O'Dea and Whittaker 2007) are especially sensitive and vulnerable to forest degradation, with specialized bird species more likely to be threatened with extinction (Şekercioglu 2011). Deforestation can cause interior forest

birds to shift upslope in search of suitable habitat (Ocampo-Peñuela and Pimm 2015). Loss of forested habitat can likewise lead to a decrease in the extent of montane bird ranges (Ocampo-Peñuela and Pimm 2015) and population sizes (Husemann et al. 2015), pushing to extinction small and isolated populations that are already elevationally constrained (Kattan et al. 1994). Furthermore, habitat loss at low-to-mid elevations can interact synergistically with climate change (Buechley et al. 2015, Fergler et al. 2017, Neate-Clegg et al. 2018) to drive bird extinctions. Finally, forest fragmentation can impede elevational movements, altitudinal migration, and recolonization efforts (Kattan et al. 1994), amplifying the impacts of rising temperatures on birds.

Baseline data are urgently needed to document how tropical species along elevational gradients have responded and will respond to rising temperatures, deforestation, and other anthropogenic threats (Freeman and Beehler 2018). However, there is a scarcity of baseline data in the tropics on species' distributions (Collen et al. 2008, van der Hoek et al. 2020). There are few published elevational baselines of raw data that include the number of individuals of each species detected (e.g., Pagaduan and Afuang 2012, Freeman and Beehler 2018, Freeman et al. 2018a). Additionally, published elevational baselines often comprise a single year or season of historical data, which is compared to a modern dataset of similar duration (Freeman and Class Freeman 2014, Dulle et al. 2016, Campos-Cerqueira et al. 2017). While decades may have elapsed between surveys, each survey represents a snapshot in time that does not capture the interannual variation in distributions, population size, and demographic rates (Forero-Medina et al. 2011, Dulle et al. 2016), even though this variation can shed light on fine-scale patterns or generational changes in birdlife. Finally, few elevational studies have focused on the abundances of individual species (Stiles et al. 2017, Freeman and Beehler 2018), even though abundance can be an earlier and perhaps better indicator of population change than range size or species richness (Dulle et al. 2016).

Within the tropics, baseline data on species' elevational distributions and dynamics are particularly lacking in Africa (Harris et al. 2011, Sintayehu 2018, Sheldon 2019), a continent that tends to have steep montane elevational gradients (La Sorte et al. 2014) which receive little protection (Elsen et al. 2018). Recent studies in the Albertine Rift of Rwanda have found upslope shifts in rainforest bird communities (Neate-Clegg et al. 2020), with close to a hundred bird species at elevations higher than recorded in published literature (van der Hoek et al. 2020). Recent surveys in Ethiopia have likewise documented new avian elevational records (Dowsett and Dowsett-Lemaire 2015, Rannestad 2016). However, without well-established empirical data in these regions, it is unclear whether new avian elevational

records represent true changes in species' distributions in response to anthropogenic factors or whether they result from the lack of standardized surveys in the Afrotropics (Sam and Koane 2014, Marki et al. 2016).

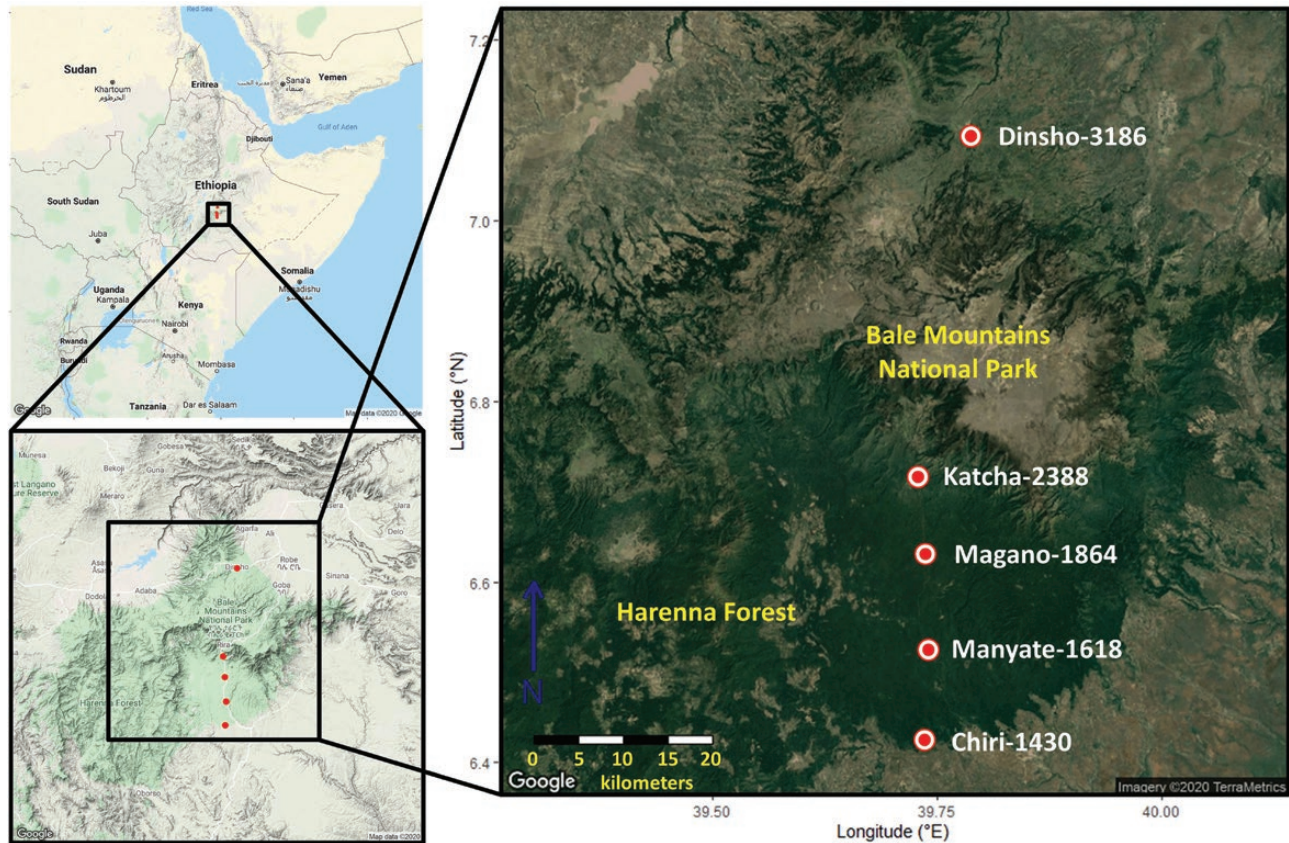
In the Horn of Africa, Ethiopia receives relatively little research despite the country's high avian biodiversity and endemism. Ethiopia's highland forests support a large number of endemic and range-restricted bird species (Ash and Atkins 2009, Buechley et al. 2015, Redman et al. 2016), which are forecast to undergo range contractions as arid areas expand under climate change (Huntley et al. 2006). Temperatures in Ethiopia have risen by an average of 0.28°C per decade over the last 60 years (Simane et al. 2016), and are predicted to increase further (Teshome and Zhang 2019). In addition, habitat degradation is a persistent issue, especially at higher elevations (Shiferaw and Suryabhagavan 2019). It is therefore critical to establish baseline data on bird community composition and distributions before the unique ecosystems of Ethiopia change further.

In this study, we undertook a multi-year assessment of the tropical understory avifauna along an elevational gradient in Ethiopia. We used mist-nets to survey the understory bird community at 5 sites spanning a 1,750 m gradient in and around the Haremma Forest and Bale Mountains National Park, which comprise a critical part of the Eastern Afrotropical and Horn of Africa global biodiversity hotspots (Asefa et al. 2017, Kidane et al. 2019). We used 6 years of systematic bird banding data to assess community-level and population-level parameters in relation to elevation and year. First, we calculated and described patterns in species richness and guild-specific captures across the elevational gradient, and assessed how those parameters changed over time. Next, we conducted a community composition analysis of the bird community at each elevation and quantified species turnover along the elevational gradient. We then quantified species-specific abundances and mean elevational distributions for a subset of species along the elevational gradient over time to determine if there was any preliminary evidence of range shifts. Finally, we used mark-recapture analyses to estimate the demographic rates of focal species in relation to elevation. Our data provide a critical multi-year baseline of Afrotropical montane forest understory avifauna against which future surveys can be compared.

## METHODS

### Study Site

Fieldwork was conducted in and around the Haremma Forest and Bale Mountains National Park (Figure 1), in coordination with the Oromia Forest and Wildlife Enterprise



**FIGURE 1.** Location of the 5 study sites in and around the Bale Mountains National Park, Ethiopia. The panel on the right depicts the study sites overlaid on satellite imagery. The 4 lower sites are also located within the Harena Forest. Elevation (m) for each site is included next to its name.

and permitted by the Ethiopia Wildlife Conservation Authority. Bale Mountains National Park (6.483–7.167°N, 39.467–39.950°E) is located in the southeastern highlands of Ethiopia and encompasses an area of 2,200 km<sup>2</sup>, ranging in elevation from ~1,500 to 4377 m.a.s.l. (meters above sea level) (Asefa 2006, Shimelis et al. 2013). It was established in 1970 with the primary objective of conserving wildlife and other valuable natural resources, particularly the rare, endemic, and endangered Mountain Nyala (*Tragelaphus buxtoni*) and Ethiopian wolf (*Canis simensis*) (Gashaw 2015). Bale Mountains National Park contains some of the largest contiguous Afromontane forest habitats on the continent, supporting high levels of species richness, endemism, and evolutionary processes (Asefa 2006, Gashaw 2015, Asefa et al. 2017). The park features 5 main vegetation zones, including the northern dry evergreen Afromontane forest (dominated by *Juniperus procera*) and the Southern Harena moist tropical forest (Asefa et al. 2017). The latter covers ~7,000 km<sup>2</sup> of the southern slope of the Bale Mountains, of which only 14% is located within the park boundaries (Tesfaye et al. 2002).

Bale Mountains National Park is designated as an Important Bird Area and Key Biodiversity Area (BirdLife International 2020) and is part of the Eastern Afromontane Biodiversity Hotspot, one of 36 international biodiversity hotspots of global conservation significance (CEPF 2020). Almost 300 bird species have been recorded in the Bale region, including 6 of Ethiopia's 17 endemic bird species (BirdLife International 2020) and 14 near-endemic species found only in Ethiopia and Eritrea (Asefa et al. 2017). Despite its high conservation value, Bale Mountains National Park is under increasing threat from habitat degradation due to human population growth, agriculture, livestock, and deforestation throughout the park (Shimelis et al. 2013, Asefa et al. 2017).

For our study, we chose 4 research sites within the Harena Forest along a 538 m elevational gradient: Chiri (elevation: 1,430 m.a.s.l.), Manyate (1,618 m), Magano (1,864 m) and Katcha (2,388 m) (Supplemental Material Table S1). Chiri was positioned in the southern extent of the Harena Forest and bordered agricultural land (Figure 1), whereas the other 3 sites were located within the moist tropical forest inside the park, distributed ~11 km from

one another along a single north–south elevational gradient on the south side of the Bale Mountains (Figure 1). Katcha was located in close proximity to a meadow. To sample a higher elevation site along this gradient that was also forested, we located a fifth site, Dinsho (3,186 m), ~40 km north of the other sites near the park headquarters (Figure 1). This site was just outside the national park boundary in heavily managed juniper forest (Asefa et al. 2017) but was protected from livestock grazing, unlike the high-elevation (>2,500 m) sites in the Harena Forest where the understory was extensively overgrazed and open. Hereafter, we refer to the sites with their associated elevations. The map of our study sites (Figure 1) was created using the R packages *ggmap* (Kahle and Wickham 2013) and *ggplot2* (Wickham 2016).

### Bird Surveys

Bird banding occurred annually from 2011 to 2016. While the initial intent of this study was to monitor bird populations yearly for decades, due to the political and bureaucratic challenges in the country, fieldwork could not be continued after 2016. Each banding season lasted from early October to early December, mostly during the region's dry season (Asefa et al. 2017). Sampling during a single season allowed us to control for potential inter-seasonal elevational movement of birds, as some montane species in East Africa can seasonally move to lowland forest sites (Burgess and Mlingwa 2000). We used twenty 38-mm mesh mist-nets, measuring 12 × 3 m. Nets were erected at consistent locations across years through the use of GPS locations and flagging marking net sites between field seasons. At each site, nets were spaced along a roughly circular pattern ~300 m in circumference, with some nets connected to create a long net wall. We opened the nets 30 min before sunrise (~05:30) and checked every half-hour for the next 6 hr, 1–2 days a week at each study site in each of the 6–8 rotations. We extracted all birds from the nets, identified the species, and, if possible, determined their age and sex. Numbered aluminum leg bands (East African Ringing Scheme, National Museum of Nairobi) were fitted on the legs of the newly-captured birds, and the band numbers of recaptured birds were recorded.

Mist-netting enables the detection of cryptic understory bird species, reliable identification, and repeatability of survey effort with minimal observer bias (Blake and Loiselle 2000, Buechley et al. 2015). Other recent studies of tropical montane birds along elevational gradients have used mist nets as the preferred method for gathering data on birds (Forero-Medina et al. 2011, Dulle et al. 2016, Freeman and Beehler 2018, Freeman et al. 2018b, Boyce et al. 2019), including for specifically surveying the understory bird community (Werema and Howell 2016).

### Statistical Analyses

**Community-level analyses.** To test whether our survey effort had adequately surveyed the local bird community, we calculated rarified species accumulation curves across sampling days for each site, based on observed and expected (sample-based rarefaction) species richness (Colwell et al. 2012) using the “exact” method of the *specaccum* function from the R package *VEGAN* (Oksanen et al. 2019). Since our species accumulation curves did not reach asymptotes for species richness, observed species richness likely does not capture true species richness. We, therefore, used sample-size-based rarefaction and extrapolation (R/E) of Hill numbers (the effective number of species, which integrates species richness and relative abundances; Chao et al. 2014). Sample-size-based rarefaction and extrapolation of Hill numbers is an emerging approach used to standardize and compare estimates of diversity between samples (see Cox et al. 2017, Fair et al. 2018, Baumel et al. 2018, Chao et al. 2019, Debela et al. 2020). Specifically, we used this framework to estimate two values of Hill number 0 (i.e. estimated species richness). First, we calculated standardized species richness. We used the function *iNEXT* from the R package *iNEXT* (Hsieh et al. 2016) to calculate R/E curves, standardizing our curve parameters to a maximum of 1,000 individual bird captures (endpoint = 1,000), knots = 500, and a bootstrap replication of 1,000 (nboot = 1,000). From these curves, we provide standardized estimates of species richness based on the sampling of 1,000 individuals at each site. We also estimated asymptotic species richness using the function *ChaoRichness* from the package *iNEXT* (Hsieh et al. 2016). Although the asymptotic species richness is an estimate of true species richness, in practice, reaching an asymptote can take a long time and a lot of sampling. We then plotted the R/E curves of standardized species richness (i.e. over 1,000 individuals) for each site as a function of sample size using the function *ggiNEXT* (Hsieh et al. 2016). We also visualized asymptotic species richness by setting the endpoint of the *iNEXT* function to 10,000 individuals.

Next, we assessed the spatial and temporal patterns in observed species richness and guild-specific captures. For guild-specific captures, we identified the primary diet and habitat association of each species using a global dataset of avian ecological traits (Table 1; see Şekercioğlu et al. 2004, 2019 for a description of the dataset) and summed captures for each separate guild based on either primary diet or habitat. We restricted our analyses to guilds that had ≥40 captures and ≥5 species over the study period and modeled each guild independently. We chose a ≥40 capture threshold as our cutoff between infrequently and frequently encountered species. Most species above this threshold were recorded each year and more than once or twice in each year (the few species that were not recorded each year were recorded multiple times in the other years),

**TABLE 1.** The total number of captures per species at each site over 6 years in and around the Hareenna Forest and Bale Mountains National Park, Ethiopia. The primary dietary and habitat association guilds for each species originate from a global dataset of avian ecological traits.

Scientific Name	English Name	Diet Guild	Habitat Guild	Chiri-1430	Manyate-1618	Magano-1864	Katcha-2388	Dinsho-3186
<i>Pternistis castaneicollis</i>	Chestnut-naped Francolin	Seed	Forest	0	0	0	0	2
<i>Aplopelia larvata</i>	Lemon Dove	Herbivore	Forest	4	25	25	12	0
<i>Streptopelia lugens</i>	Dusky Turtle-dove	Seed	Forest	0	0	0	0	1
<i>Turtur afer</i>	Blue-spotted Wood-dove	Invertebrate	Forest	2	0	0	0	0
<i>Turtur tympanistria</i>	Tambourine Dove	Omnivore	Forest	129	40	51	0	0
<i>Clamator levaillantii</i>	Levaillant's Cuckoo	Invertebrate	Woodland	1	0	0	0	0
<i>Bostrychia carunculata</i>	Wattled Ibis	Invertebrate	Riparian	0	0	0	1	0
<i>Rhinoptilus cinctus</i>	Three-banded Courser	Invertebrate	Shrub	1	0	0	0	0
<i>Accipiter tachiro</i>	African Goshawk	Vertebrate	Forest	0	1	0	1	1
<i>Accipiter badius</i>	Shikra	Vertebrate	Woodland	0	0	0	0	1
<i>Accipiter rufiventris</i>	Rufous-breasted Sparrowhawk	Vertebrate	Forest	0	1	0	1	0
<i>Apaloderma narina</i>	Narina Trogon	Invertebrate	Forest	4	6	8	0	0
<i>Rhinopomastus aterrimus</i>	Black Scimitarbill	Invertebrate	Savanna	1	0	0	0	0
<i>Ispidina picta</i>	African Pygmy-kingfisher	Invertebrate	Forest	60	3	1	0	0
<i>Pogoniulus chrysoconus</i>	Yellow-fronted Tinkerbird	Fruit	Shrub	0	0	0	2	0
<i>Indicator minor</i>	Lesser Honeyguide	Omnivore	Woodland	0	0	2	2	0
<i>Indicator variegatus</i>	Scaly-throated Honeyguide	Omnivore	Woodland	0	1	8	0	0
<i>Campethera nubica</i>	Nubian Woodpecker	Invertebrate	Shrub	1	0	0	0	0
<i>Oriolus monacha</i>	Ethiopian Black-headed Oriole	Fruit	Woodland	1	0	1	5	0
<i>Prionops plumatus</i>	White-crested Helmetshrike	Invertebrate	Savanna	6	0	0	0	0
<i>Platysteira cyanea</i>	Brown-throated Wattle-eye	Invertebrate	Forest	2	2	3	4	0
<i>Malacoonotus blanchoti</i>	Grey-headed Bush-shrike	Carnivore	Savanna	6	0	0	0	0
<i>Dryocopus gambensis</i>	Northern Puffback	Invertebrate	Savanna	6	0	0	0	0
<i>Laniarius aethiopicus</i>	Tropical Boubou	Invertebrate	Forest	2	0	1	1	0
<i>Terpsiphone viridis</i>	African Paradise-flycatcher	Invertebrate	Woodland	26	4	1	3	0
<i>Lanius collurio</i>	Red-backed Shrike	Invertebrate	Woodland	1	0	0	0	0
<i>Lanius collaris</i>	Common Fiscal	Invertebrate	Grassland	4	0	0	0	0
<i>Corvus crassirostris</i>	Thick-billed Raven	Omnivore	Rocky	0	0	0	0	1
<i>Melaniparus leuconotus</i>	White-backed Black Tit	Invertebrate	Forest	0	0	0	0	10
<i>Galerida theklae</i>	Thekla Lark	Invertebrate	Shrub	0	0	0	0	1
<i>Camaptera brachyura</i>	Bleating Camaroptera	Invertebrate	Forest	9	7	16	0	0
<i>Prinia subflava</i>	Tawny-flanked Prinia	Invertebrate	Savanna	0	0	0	9	3
<i>Bradypterus</i>	Cinnamon Bracken-warbler	Invertebrate	Forest	0	0	4	28	2
<i>Cinnamomeus</i>								
<i>Phyllastrephus strepitans</i>	Northern Brownbul	Fruit	Woodland	1	0	0	0	0
<i>Pycnonotus barbatus</i>	Common Bulbul	Fruit	Woodland	18	4	3	9	0
<i>Phylloscopus trochilus</i>	Willow Warbler	Invertebrate	Forest	0	0	0	1	2
<i>Phylloscopus collybita</i>	Common Chiffchaff	Invertebrate	Forest	0	0	0	42	5
<i>Phylloscopus umbrovirens</i>	Brown Woodland-warbler	Invertebrate	Forest	0	0	1	12	43
<i>Sylvia atricapilla</i>	Eurasian Blackcap	Invertebrate	Woodland	8	0	0	1	0
<i>Sylvia abyssinica</i>	African Hill-babbler	Invertebrate	Forest	0	11	25	28	0
<i>Sylvia curruca</i>	Lesser Whitethroat	Invertebrate	Shrub	1	0	0	0	0
<i>Sylvia communis</i>	Common Whitethroat	Invertebrate	Shrub	0	0	0	1	0
<i>Parophasma galinieri</i>	Abyssinian Catbird	Fruit	Shrub	0	0	0	6	14

TABLE 1. Continued

Scientific Name	English Name	Diet	Habitat	Chiri-1430	Manyate-1618	Magano-1864	Katcha-2388	Dinsho-3186
<i>Zosterops polioastrus</i>	Ethiopian White-eye	Omnivore	Forest	117	7	25	35	37
<i>Turdoides leucopygia</i>	White-rumped Babbler	Fruit	Woodland	1	0	0	0	0
<i>Geokichla piaggiae</i>	Abyssinian Ground-thrush	Invertebrate	Forest	17	100	65	111	6
<i>Turdus abyssinicus</i>	Abyssinian Thrush	Invertebrate	Forest	77	27	26	32	39
<i>Turdus pelios</i>	African Thrush	Invertebrate	Woodland	8	0	0	0	0
<i>Muscicapa adusta</i>	African Dusky Flycatcher	Invertebrate	Forest	62	7	14	15	9
<i>Melaenorhis chocolatinus</i>	Abyssinian Slaty-flycatcher	Invertebrate	Woodland	2	4	13	13	48
<i>Melaenorhis edoloides</i>	Northern Black-flycatcher	Invertebrate	Woodland	2	0	0	0	0
<i>Cossypha semirufa</i>	Rüppell's Robin-chat	Invertebrate	Forest	2	49	44	56	18
<i>Cossypha natalensis</i>	Red-capped Robin-chat	Invertebrate	Forest	29	0	0	0	0
<i>Hedydipna collaris</i>	Collared Sunbird	Invertebrate	Forest	0	1	0	0	0
<i>Cyanomitra olivacea</i>	Olive Sunbird	Invertebrate	Forest	42	69	117	34	0
<i>Nectarinia tacaze</i>	Tacaze Sunbird	Nectar	Forest	0	0	0	39	8
<i>Cinnyris venustus</i>	Variable Sunbird	Nectar	Woodland	0	0	1	6	0
<i>Ploceus baglafaecht</i>	Baglafaecht Weaver	Invertebrate	Shrub	0	0	1	2	0
<i>Anaplectes leuconotus</i>	Northern Red-headed Weaver	Invertebrate	Woodland	10	0	0	0	0
<i>Lagonosticta senegala</i>	Red-billed Firefinch	Seed	Grassland	1	0	0	0	0
<i>Mandingoa nitidula</i>	Green Twinspot	Seed	Shrub	17	30	5	0	0
<i>Cryptospiza salvadorii</i>	Abyssinian Crimsonwing	Seed	Forest	0	1	78	111	0
<i>Coccyppiza quartina</i>	Yellow-bellied Waxbill	Seed	Grassland	0	0	1	3	2
<i>Spermestes bicolor</i>	Black-and-white Mannikin	Seed	Grassland	1	0	0	0	0
<i>Vidua macroura</i>	Pin-tailed Whydah	Seed	Savanna	0	0	0	3	0
<i>Passer swainsonii</i>	Swainson's Sparrow	Seed	Shrub	0	0	0	1	0
<i>Anthus trivialis</i>	Tree Pipit	Invertebrate	Woodland	0	0	0	1	0
<i>Motacilla clara</i>	Mountain Wagtail	Invertebrate	Forest	1	0	0	0	0
<i>Crithagra citrinelloides</i>	Abyssinian Citril	Seed	Shrub	0	0	0	1	0
<i>Crithagra tristriata</i>	Brown-rumped Seedeater	Seed	Woodland	0	0	0	0	47
<i>Crithagra striolata</i>	Streaky Seedeater	Seed	Grassland	0	0	0	29	11
<i>Serinus flavivertex</i>	Yellow-crowned Canary	Seed	Forest	0	0	0	0	5
Total number				683	410	539	657	316

whereas individuals under this threshold tended to have few captures across more than one year. We chose a  $\geq 5$  species threshold for the guild models to ensure that results for these metrics represented more than a few species.

We constructed models comparing each response variable (observed species richness, dietary, and habitat guild-specific captures) as a function of the site, and included the number of survey days per site and year (Table 2) as a covariate to control for the variation in the sampling effort. We used generalized linear models (GLMs) for species richness and guild-specific captures, as these represent count data. Within the GLMs, we used a Poisson error structure for species richness, and for guild-specific captures, we used a quasi-Poisson error structure to account for over-dispersion in the count data. To assess changes in the bird community over time, we ran an additional model for each response variable that contained year and site, with a year \* site interaction (error structures were applied as above). We tested the significance of the explanatory variables in the GLMs with an analysis of deviance.

We assessed species dissimilarity between sites along the elevational gradient by calculating the Sørensen dissimilarity index ( $S_g$ ) for pairs of sites adjacent to each other along the elevational gradient, as well as for Chiri-1430 and Dinsho-3186 at either end of the gradient.  $S_g$  can range from complete dissimilarity ( $S_g = 1$ ) to complete similarity ( $S_g = 0$ ). This dissimilarity can be further decomposed into turnover and nestedness, which we calculated using the function *beta.pair* in the package *betapart* (Baselga et al. 2020). Finally, to compare community composition (captures of different species, weighted by abundance), we ran a principal coordinate analysis (PCoA) based on a Bray-Curtis dissimilarity matrix (Legendre and Legendre 2012). A PCoA extracts the greatest orthogonal axes of variation in community composition, plotting them in multidimensional space such that more similar communities are closer to each other in Euclidean space. We extracted the first two axes from the PCoA that represent the greatest variation in community composition.

**Species-level analyses.** As a proxy for species abundance (Dulle et al. 2016), we calculated species-specific captures (the number of captured and recaptured individuals of a particular species) per site and year for the most frequently-captured species ( $\geq 40$  captures over the study period). To assess the variation in species' elevational distributions, we calculated the mean elevation at which each species was detected each year (hereafter “mean elevation”) for frequently-captured species that were detected at least once in every year of the study. Smaller range shifts in tropical birds are more detectable when analyzing mean elevational occurrence rather than the changes in upper or lower range boundaries, as

**TABLE 2.** Total captures, observed species richness, and sampling effort of mist-netted birds at 5 study sites for each research season in the Bale Mountains, Ethiopia. TC = total captures (number of newly banded and recaptured birds), SR = species richness, and FD = field days. Total TC, SR, and FD for each site encompass the entire 6 years.

Year	Chiri-1430			Manyate-1618			Magano-1864			Katcha-2388			Dinsho-3186		
	TC	SR	FD	TC	SR	FD	TC	SR	FD	TC	SR	FD	TC	SR	FD
2011	123	20	6	62	12	6	125	19	7	166	23	6	63	14	6
2012	86	16	9	61	12	7	92	12	8	84	21	8	37	12	8
2013	77	15	8	76	15	8	71	14	8	106	19	9	99	18	8
2014	87	20	7	63	13	4	59	12	4	71	17	4	37	10	4
2015	112	13	7	48	9	7	88	16	6	101	21	7	30	13	6
2016	198	23	9	100	13	10	104	21	11	129	25	10	50	9	9
Total	683	39	46	410	22	42	539	27	44	657	37	44	316	24	41



the position of range boundaries is strongly dependent on the sampling effort (Shoo et al. 2006).

We regressed both species-specific captures (in a GLM with a quasi-Poisson error structure) and mean elevation (in a simple linear model) against year. Since the Dinsho-3186 site was located far from the other sites, we decided to re-run the species-level analyses with Dinsho-3186 data removed. The results remained similar with Dinsho-3186 excluded (Supplemental Material Tables S2 and S3) and, therefore, we retained Dinsho-3186 data in the analyses to increase our statistical power. Additionally, we compared our elevational records for banded birds with those reported in the literature for Ethiopia and the Horn of Africa (Ash and Atkins 2009, Dowsett and Dowsett-Lemaire 2015, Rannestad 2016) in order to assess whether any species were detected outside of their recorded elevational distributions. We used an elevational difference of at least 150 m to indicate whether a species had clearly been recorded in our study higher or lower than previously reported in Ethiopia, a distance previously used to signify extralimital records of birds in Ethiopia (Dowsett and Dowsett-Lemaire 2015). A difference of <150 m could result from chance, whereas a difference >150 m is more likely to result from a systematic change in the elevational range.

At the population level, we used Pradel models (Pradel 1996) implemented with the package *RMark* (Laake and Rexstad 2012) to estimate the rates of apparent survival ( $\phi$ ), recruitment ( $F$ ), and realized population growth ( $\lambda$ ) while controlling for encounter probabilities ( $p$ ).  $\phi$  is the rate at which individuals remain in the population;  $F$  is the rate at which new individuals join the population via birth or immigration, and  $\lambda$  is the combined effect of survival and recruitment. A population does not change in size when  $\lambda = 1$ , declines when  $\lambda < 1$ , and grows when  $\lambda > 1$ . These mark-recapture models cannot distinguish movement in and out of a study area (immigration/emigration) from true birth and survival. However, birds living in tropical mountains are known to have small range sizes (Orme et al. 2006), and tropical understory birds of interior forests have limited dispersal ability (Janzen 1967, Moore et al. 2008, Lees and Peres 2009, Visco et al. 2015, Polato et al. 2018, Sheard et al. 2020), suggesting that the differences in recruitment or apparent survival rates of understory birds at our study sites are unlikely to be highly affected by immigration and emigration.

We initially considered all species with >50 captures. For every species we estimated all 4 demographic parameters in constant (time-invariant) Pradel models, extracting the parameter estimates and their 95% confidence intervals (CI). We then censored any species where the models failed to estimate parameters, or where the 95% CI on the parameter estimates were exceedingly large. Then, to

assess whether the population growth rates depended on elevation, we modeled  $\lambda$  as a function of the site for each species. Additionally, we ran models where both  $\lambda$  and  $p$  were constrained by site, but these models involved many parameters and they were, therefore, suitable only for those species with the largest sample size.

All statistical analyses and graphing were conducted in R (R Core Team 2020; version 4.0.2, 2020-06-22).

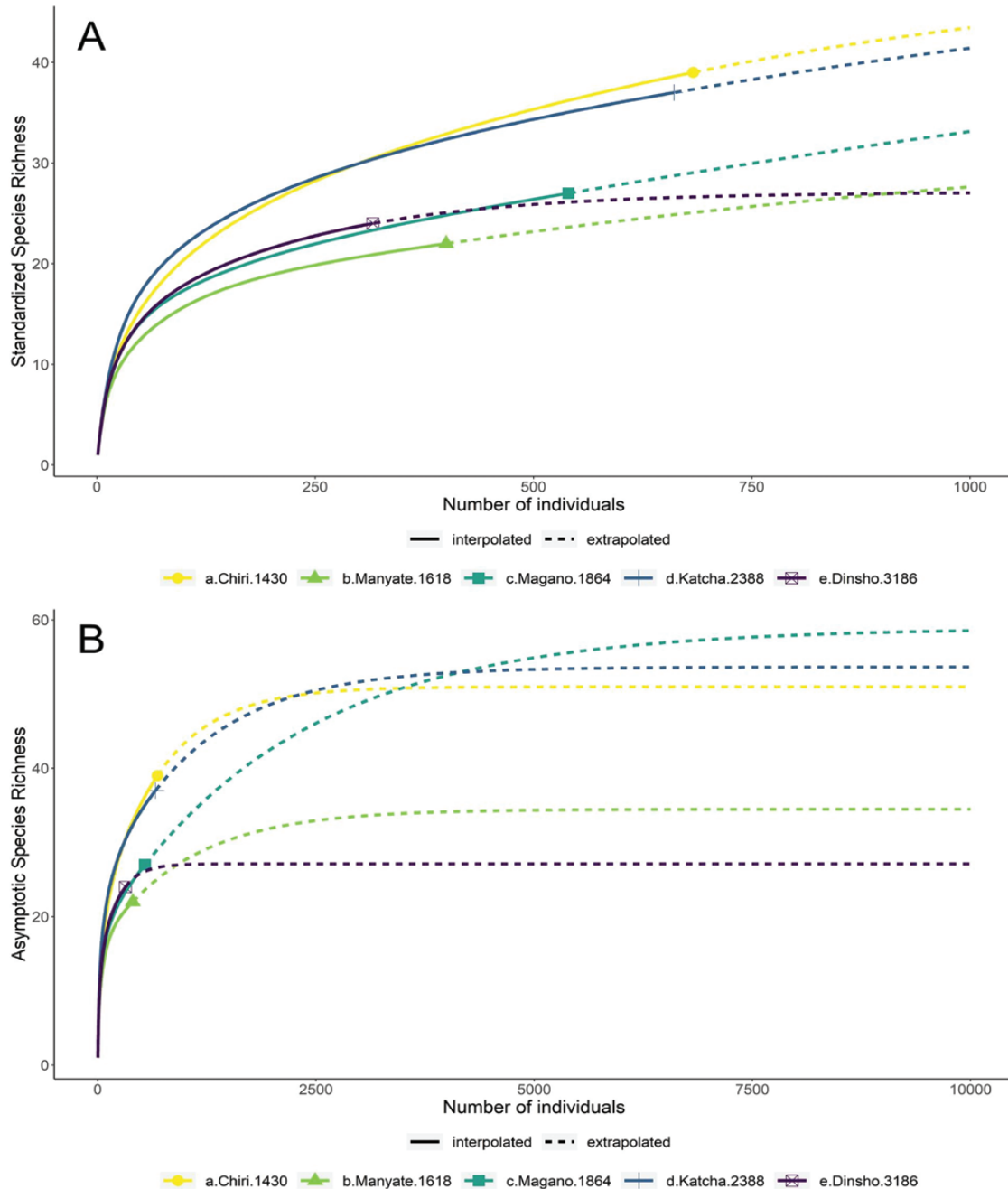
## RESULTS

### Community-Level

During 6 years of banding in the Bale Mountains, we caught 2,605 birds of 72 species (Tables 1 and 2), including 6 species endemic to the Abyssinian highlands (Supplemental Material Table S4). After 6 seasons of sampling, none of the sites reached an asymptote in species richness (Figure 2A). Observed species richness varied significantly across sites (GLM,  $\chi^2 = 19.512$ ,  $df = 4$ ,  $p < 0.001$ ). Observed species richness showed a bimodal pattern that peaked at both the lowest elevation site, Chiri-1430 (39 species), and at Katcha-2388, the second-highest site, (37 species; Table 3 and Figure 3A), whereas Manyate-1618 had the lowest observed species richness (22 species). Standardized species richness (richness estimated over 1,000 individuals) matched this bimodal pattern (Table 3 and Figure 2A), peaking with Chiri-1430 ( $43.45 \pm 3.27$ ) and Katcha-2388 ( $41.48 \pm 3.77$ ). However, Dinsho-3186, the highest-elevation site, had the lowest standardized species richness ( $27.02 \pm 3.97$ ). Asymptotic species richness was high at 3 sites (Table 3 and Figure 2B): Magano-1864 ( $58.94 \pm 39.52$ ), Katcha-2388 ( $53.64 \pm 14.82$ ), and Chiri-1430 ( $50.98 \pm 9.15$ ).

For guild-specific captures by site, there were 4 diet and habitat guilds with  $\geq 40$  captures and  $\geq 5$  species. Insectivores were far more numerous than the other dietary guilds, with omnivores and granivores the next most abundant understory birds, followed by frugivores (Figure 3B). All 4 of these dietary guilds varied significantly across the 5 sites in the number of captures (insectivores: GLM,  $\chi^2 = 97.134$ ,  $df = 4$ ,  $p = 0.013$ ; omnivores: GLM,  $\chi^2 = 285.188$ ,  $df = 4$ ,  $p < 0.001$ ; granivores: GLM,  $\chi^2 = 129.183$ ,  $df = 4$ ,  $p < 0.001$ ; frugivores: GLM,  $\chi^2 = 25.581$ ,  $df = 4$ ,  $p = 0.019$ ). Forest birds were far more abundant than species belonging to other habitat guilds, with woodland, shrub, and grassland guilds clustered closely together in the number of captures (Figure 3C). All of these habitat guilds varied significantly in guild captures across the elevational gradient (forest: GLM,  $\chi^2 = 269.020$ ,  $df = 4$ ,  $p < 0.001$ ; grassland: GLM,  $\chi^2 = 66.449$ ,  $df = 4$ ,  $p < 0.001$ ; shrub: GLM,  $\chi^2 = 34.330$ ,  $df = 4$ ,  $p = 0.001$ ; woodland: GLM,  $\chi^2 = 108.806$ ,  $df = 4$ ,  $p < 0.001$ ).

Temporally, observed species richness did not significantly vary at any of the sites over the study period (GLM,



**FIGURE 2.** Sample-size-based rarefaction and extrapolation (R/E) curves of species richness at the 5 study sites over 6 years along an elevational gradient in the Bale Mountains, Ethiopia. These R/E curves plot the interpolated (rarefaction) and extrapolated species richness estimates as a function of the number of individual birds. An endpoint of 1,000 individual bird captures is utilized to display (A) standardized species richness, whereas an endpoint of 10,000 captures is utilized to display (B) asymptotic species richness. In both plots, R/E curves were estimated with 500 knots and 1,000 bootstraps.

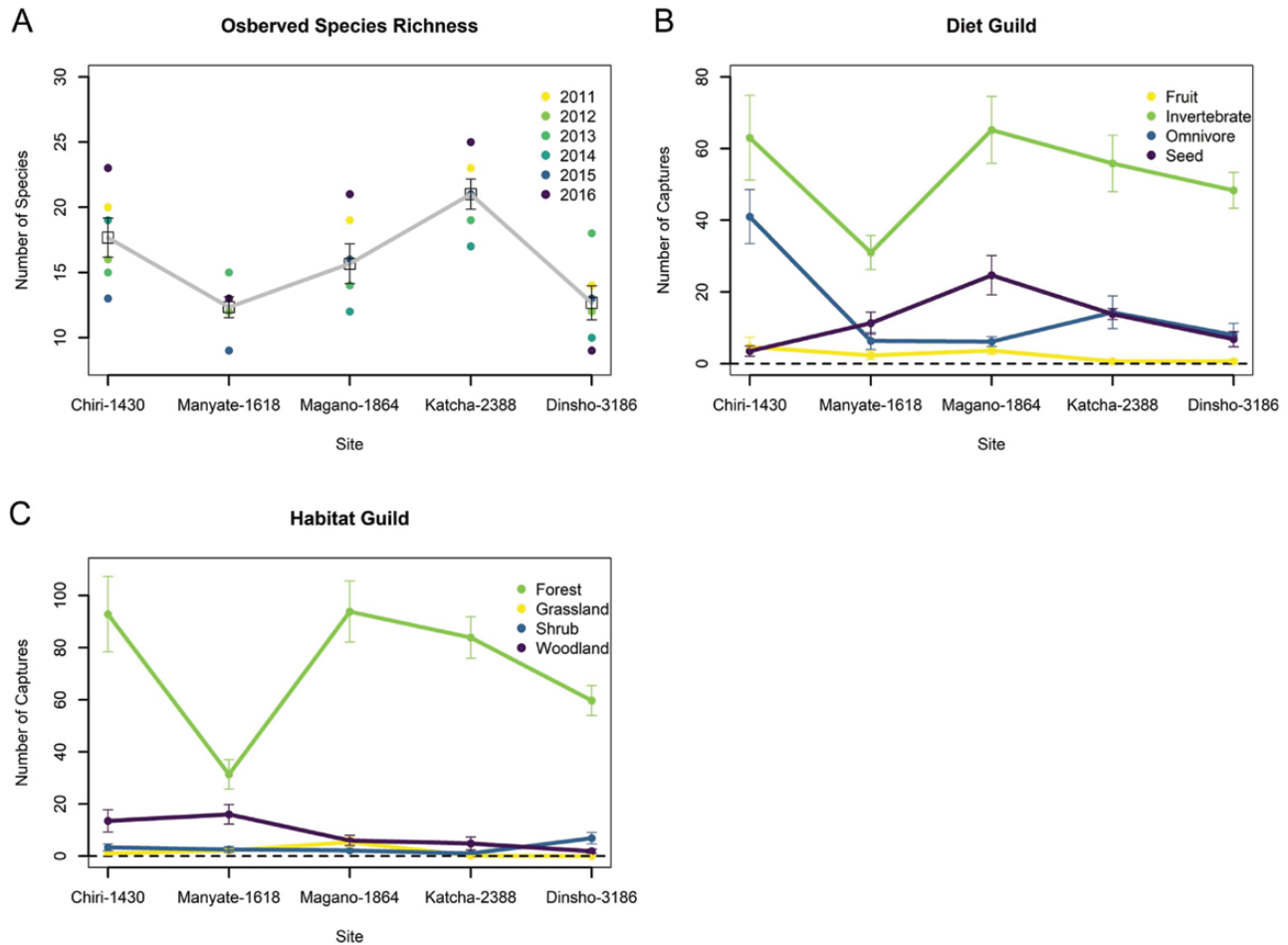
$\chi^2 = 0.002$ ,  $p = 0.96$ ) and the year\*site interaction term was also not significant ( $\chi^2 = 1.42$ ,  $df = 4$ ,  $p = 0.70$ ). For guild captures, the year\*site interaction term was significant for frugivores (GLM,  $\chi^2 = 23.425$ ,  $df = 4$ ,  $p = 0.029$ ) and shrubland species (GLM,  $\chi^2 = 20.498$ ,  $df = 4$ ,  $p = 0.014$ ) such that the number of captures increased over time at

low-elevation sites, but decreased at high-elevation sites (Table 4 and Figure 4A and B). In addition, grassland species increased significantly over time (GLM,  $\chi^2 = 9.713$ ,  $p = 0.006$ ; Table 4 and Figure 4C).

When comparing community composition, Manyate-1618 and Magano-1864, two intermediate-elevation sites which

**TABLE 3.** Observed, standardized, and asymptotic species richness for the 5 bird banding sites in the Bale Mountains, Ethiopia. Standardized and asymptotic species richness were both estimated from rarefaction/extrapolation curves. Standardized species richness was based on a standardized sample of 1000 individuals. Standard errors are provided for both estimates.

Site	Observed	Standardized		Asymptotic	
		Estimate	SE	Estimate	SE
Chiri-1430	39	43.45	3.27	50.98	9.15
Manyate-1618	22	27.63	4.23	34.47	17.10
Magano-1864	27	33.14	4.63	58.94	39.53
Katcha-2388	37	41.41	3.77	53.64	14.82
Dinsho-3186	24	27.02	3.87	27.12	3.65



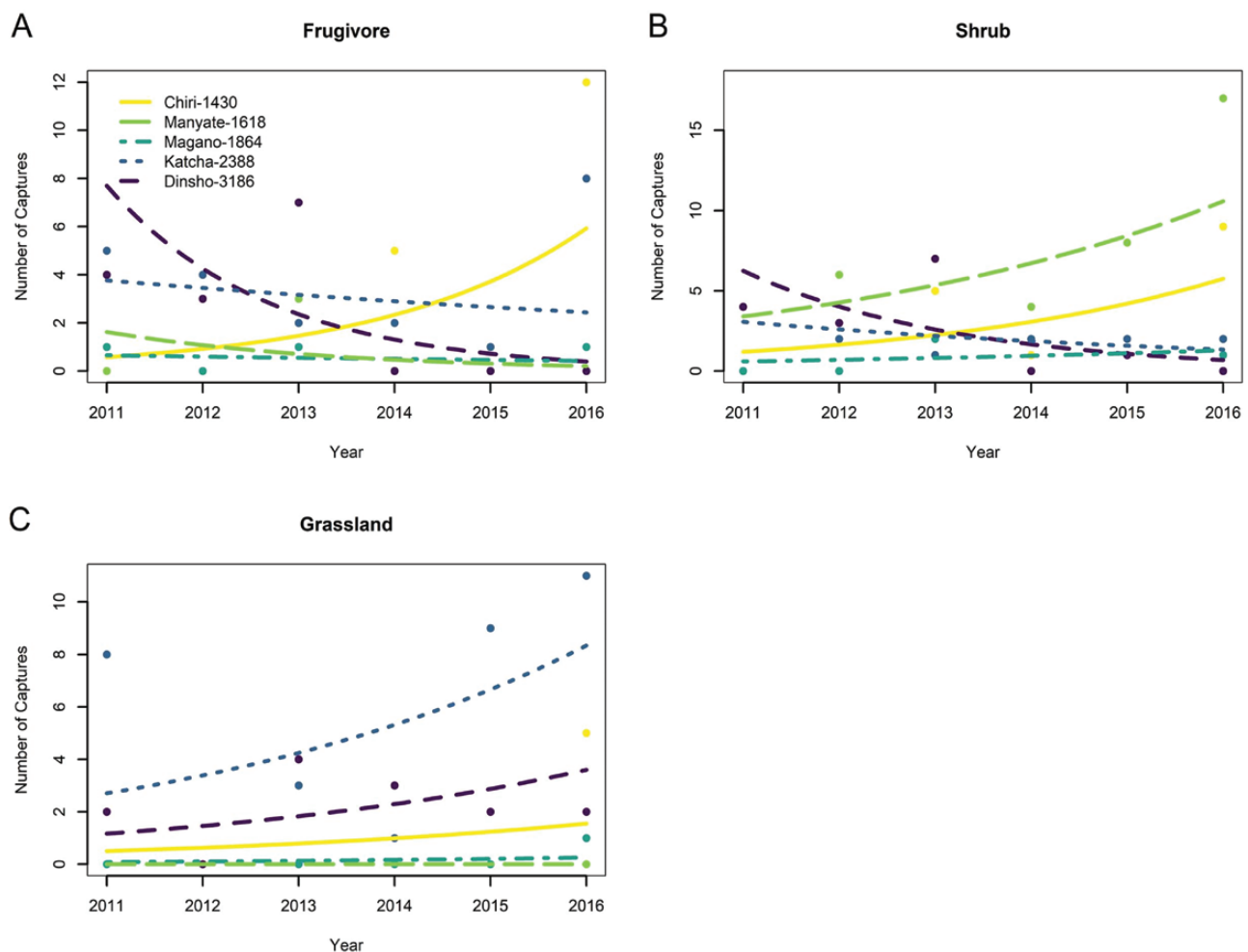
**FIGURE 3.** Variation in the bird community along an elevational gradient of 5 sites in the Bale Mountains, Ethiopia. Trends are shown for (A) observed species richness, (B) dietary, and (C) habitat guilds calculated for each site and year. Means and standard errors are given for each site. Guilds were only included if they had  $\geq 40$  captures and  $\geq 5$  species.

were composed of the most pristine old-growth forest, clustered most closely together and overlapped greatly in species composition (Figure 5). Katcha-2388, which was located on the edge of a meadow, was most similar to these two sites. Both Chiri-1430 and Dinsho-3186 clustered away from these 3 sites on different sides of the PCoA, meaning these two sites had the most different community compositions. This was expected as they represent the lowest

and highest elevation sites, respectively, and were also both located along margins of the forest. Species dissimilarity ( $S_g$ ) between adjacent sites (Figure 5) averaged 0.38. Dissimilarity can be parsed out into species turnover and species nestedness, and the proportion of dissimilarity due to species turnover averaged 66.7%. Dissimilarity was lowest between Manyate-1618 and Magano-1864 ( $S_g = 0.24$ ), of which 70.8% was due to turnover, and was highest between

**TABLE 4.** Chi-squared ( $\chi^2$ ) values, degrees of freedom (df), and  $p$ -values from GLMs of bird captures for specific dietary and habitat guilds ( $\geq 40$  captures,  $\geq 5$  species) at 5 sites over 6 years in the Bale Mountains, Ethiopia. Values are shown for guilds across year, site, and a year\*site interaction term. Statistically significant results ( $p \leq 0.05$ ) are in bold.

Site	Year			Site			Year*Site		
	$\chi^2$	df	$p$	$\chi^2$	df	$p$	$\chi^2$	df	$p$
Frugivore	0.649	1	0.584	25.581	4	<b>0.019</b>	23.425	4	<b>0.029</b>
Insectivore	0.235	1	0.861	97.134	4	<b>0.013</b>	24.060	4	0.535
Omnivore	1.630	1	0.607	285.188	4	<b>&lt;0.001</b>	20.273	4	0.511
Granivore	3.366	1	0.347	129.183	4	<b>&lt;0.001</b>	18.345	4	0.306
Forest	0.007	1	0.976	269.020	4	<b>&lt;0.001</b>	27.643	4	0.437
Woodland	0.008	1	0.967	108.806	4	<b>&lt;0.001</b>	22.760	4	0.333
Shrub	5.382	1	0.070	34.330	4	<b>&lt;0.001</b>	20.498	4	<b>0.014</b>
Grassland	9.713	1	<b>0.006</b>	66.449	4	<b>&lt;0.001</b>	10.890	4	0.074

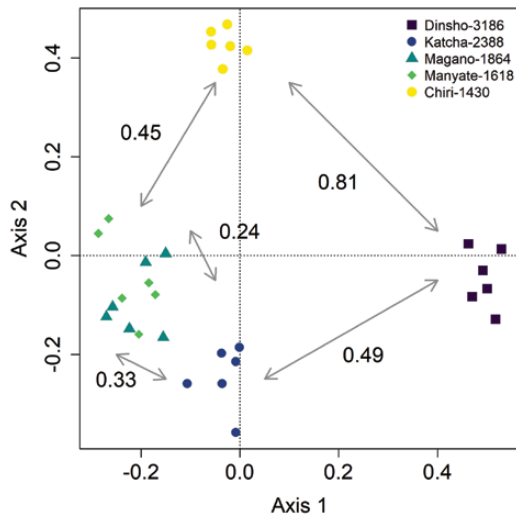


**FIGURE 4.** Bird captures for specific dietary and habitat guilds ( $\geq 40$  captures,  $\geq 5$  species) at 5 sites over 6 years in the Bale Mountains, Ethiopia. Lines represent quasipoisson GLM trendlines indicating change over time in captures for these sites. Effect of year\*site was significant for the (A) frugivore (GLM,  $\chi^2 = 23.425$ ,  $df = 4$ ,  $p = 0.029$ ) and (B) shrub (GLM,  $\chi^2 = 20.498$ ,  $df = 4$ ,  $p = 0.014$ ) guilds. Effect of year was significant for the (C) grassland guild (GLM,  $\chi^2 = 9.713$ ,  $df = 1$ ,  $p = 0.006$ ).

Katcha-2388 and Dinsho-3186 ( $S_g = 0.49$ ), of which 71.4% was due to turnover. Dissimilarity was very high between Chiri-1430 and Dinsho-3186 ( $S_g = 0.81$ ), with 91.4% of this dissimilarity due to turnover.

#### Species-Level

Eighteen species (25% of all species captured) had  $\geq 40$  captures, representing 92% of total bird captures. Green Twinspot (*Mandingoa nitidula*) experienced a significant



**FIGURE 5.** Community composition of the 5 sites along an elevational gradient in the Bale Mountains, Ethiopia. Each site consists of 6 points, representing the 6 years of the study. Community composition was extracted from the first two axes of a principal coordinate analysis based on a Bray-Curtis dissimilarity matrix. The closer the points are to one another, the more similar the community composition. Sørensen dissimilarity index was used to estimate species dissimilarity between sites (arrows and numbers), where 1 = complete turnover and 0 = no turnover.

increase in captures over the 6 years (GLM,  $t_5 = 7.818$ ,  $p = 0.004$ ; Supplemental Material Figure S1A). For the remaining seventeen species, capture rates did not significantly change over time (Supplemental Material Table S2). Of the most frequently captured birds, 15 species were caught at least once each year. One species, Brown Woodland-warbler (*Phylloscopus umbrovirens*), underwent a significant decrease in mean elevation from an average of 3,186 to 2,735 m.a.s.l. (LM,  $t_3 = -3.257$ ,  $p = 0.047$ ; Supplemental Material Figure S1B). The remaining 14 species did not significantly shift in mean elevation of detection during the study period ( $p \geq 0.05$ ) (Supplemental Material Table S3). However, we captured 6 species at elevations higher than previously reported in the literature for Ethiopia (Supplemental Material Table S5).

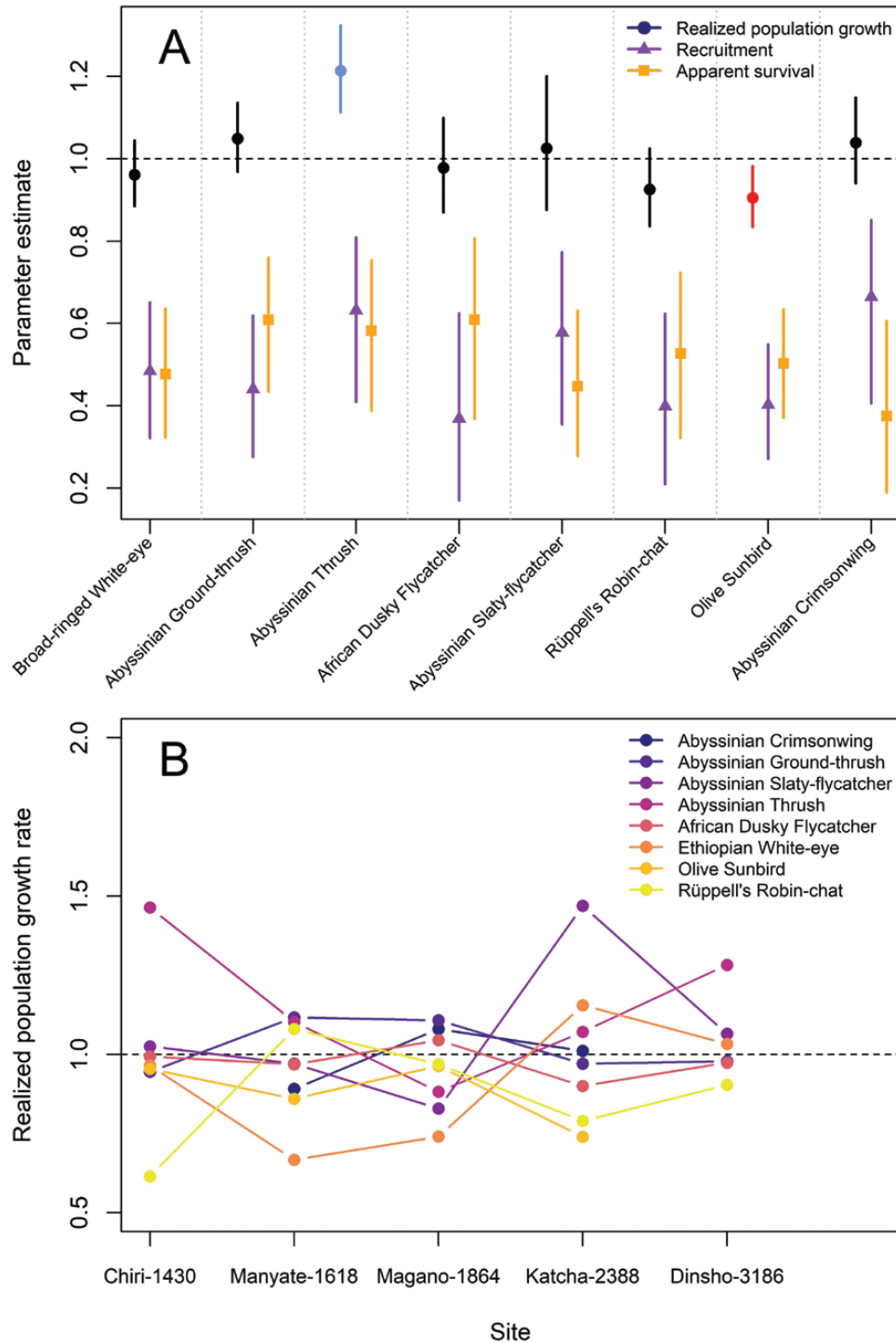
We had sufficient data to conduct mark–recapture models on 8 species (Figure 6A and Supplemental Material Table S6). Encounter probabilities,  $p$ , ranged from 0.21 for African Dusky Flycatcher (*Muscicapa adusta*) to 0.63 for Abyssinian Slaty-flycatcher (*Melaenornis chocolatinus*), with a mean of 0.30 (Supplemental Material Table S6). Apparent survival rates ranged from 0.38 for Abyssinian Crimsonwing (*Cryptospiza salvadorii*) to 0.61 for African Dusky Flycatcher with a mean of 0.52 (Supplemental Material Table S6). Recruitment rates ranged from 0.37 for African Dusky Flycatcher to 0.66 for Abyssinian Crimsonwing with a mean of 0.52 (Supplemental Material Table S6). Realized population growth rates ranged from

0.91 for Olive Sunbird (*Cyanomitra olivacea*) to 1.21 for Abyssinian Thrush (*Turdus abyssinicus*) with a mean of 1.02 (Supplemental Material Table S6). For Abyssinian Thrush,  $\lambda > 1$  meaning that on average the population grew from year to year, while for Olive Sunbird  $\lambda < 1$  meaning that on average the population declined from year to year (Figure 6A). We estimated  $\lambda$  as a function of site for the same 8 species (Supplemental Material Table S7). There was, however, no consistent effect of elevation on  $\lambda$  (Figure 6B). When, in addition to  $\lambda$ , we constrained  $p$  by site, we could only conduct the model on 2 species (Supplemental Material Table S7), Abyssinian Thrush and Olive Sunbird, and the estimates of  $\lambda$  were very similar to the unconstrained- $p$  model.

## DISCUSSION

Our 6-year study represents the first comprehensive multi-year assessment of understory birds along an elevational gradient in the Bale Mountains and the Horn of Africa in general. Prior studies on the relationship between species richness and elevation in tropical birds have reported either a unimodal, hump-shaped pattern in historically fragmented areas with a mixture of natural forest (Kattan and Franco 2004, Herzog et al. 2005) or in primary forest (Burner et al. 2018), or a general decline with elevation in pristine, old-growth, forest (Blake and Loiselle 2000) or within protected areas facing increasing human pressure (Basnet and Badola 2012, Mallet-Rodrigues et al. 2015, Neate-Clegg et al. 2018). In contrast, we found a bimodal pattern in both observed and standardized species richness (Figures 2A and 3A), with peaks at low (Chiri-1430) and mid-high (Katcha-2388) elevations (Table 3). This bimodal pattern is similar to the pattern found along an elevational gradient of primary forest in Papua New Guinea (Freeman and Beehler 2018), though the lower elevation peak was higher in that study. Interestingly, our bimodal species richness pattern differed from the hump-shaped pattern of a prior bird community study in the Horn of Africa (Abebe et al. 2019), though those authors were looking at birds in general across the entire region rather than the understory community on a single elevational gradient. Across the elevational gradient, we also found high species turnover between sites, ranging from 70.8% of the dissimilarity between Manyate-1618 and Magano-1864, to 91.4% of the dissimilarity between Chiri-1430 and Dinsho-3186. These turnover rates are similar to those from other studies that have found high species turnover of birds along elevational gradients (Young et al. 1998, Blake and Loiselle 2000, Jankowski et al. 2013).

The bimodal distribution of species richness is more likely linked to habitat than elevation per se, as Chiri-1430 and Katcha-2388, the sites with the highest standardized species richness, were more disturbed, in closer proximity



**FIGURE 6.** Demographic rates of 8 frequently-caught Afrotropical bird species in the Bale Mountains, Ethiopia. **(A)** We used constant mark–recapture models to estimate the rates of apparent survival ( $\phi$ ), recruitment ( $F$ ), and realized population growth ( $\lambda$ ) while controlling for encounter probabilities ( $p$ ). For  $\lambda$ , points and 95% confidence intervals are blue when the confidence intervals on the estimate are greater than 0, red when less than 0 and black otherwise. **(B)** Site-specific estimates of  $\lambda$  are given from low elevation (Chiri-1430 m) to high elevation (Dinsho-3186 m).

to habitat degradation, and adjacent to more open habitats (bordering agriculture and meadows respectively) than were Manyate-1618 and Magano-1864 in the Hareenna

Forest. Nearby anthropogenic land use (Connell 1978) and forest edge habitat (Ries and Sisk 2004) could result in intermediate levels of disturbance that has been shown

to bolster diversity (Connell 1978). Previous research in the Dinsho area has shown that habitat disturbance and human-induced changes to vegetation structure can alter the bird community, leading to an overall increase in diversity (Asefa et al. 2017). Similarly, a study of Ethiopian shade coffee farms also found that avian diversity was higher in disturbed agroforest compared to nearby pristine forest understory (Buechley et al. 2015). In the Harenna Forest, habitat loss is common across elevations (Shiferaw and Suryabagavan 2019). For example, over a 21-year period, forest cover in an adjacent section of Harenna Forest (Harenna Buluk district) decreased by 119.2 km<sup>2</sup> (6.19%), largely due to selective logging, forest conversion to farmland, and livestock presence (Asefa et al. 2017, Shiferaw and Suryabagavan 2019). The potential effects of disturbance are further seen in our community composition analysis, as Magano-1864 and Katcha-2388, which are only a few kilometers apart, are more different in community composition than the similarly-distanced Magano-1864 and Manyate-1618 (Figure 5), which are both similarly undisturbed sites in pristine old-growth forest. Similarly, omnivores peaked at both Chiri-1430 and Katcha-2388 (Figure 3B), with the number of captures at Katcha-2388 significantly higher than Magano-1864. Thus, habitat disturbance is likely an important driver of the bimodal species richness pattern.

None of our sites reached an asymptote in species richness over the study period (Figure 2A), indicating that we did not sample the full community at any of these locations during our 6 seasons of sampling. While asymptotic species richness was also bimodally peaked across the elevational gradient, the highest peak for asymptotic richness was at Magano-1864 (Table 3), the intermediate elevation site mostly composed of pristine old-growth forest, a result of a R/E curve that was slower to reach saturation (Figure 2B). By not taking into account the number of individual birds, observed species richness was therefore limited by sample size, thereby underestimating true species richness along the elevational gradient. We also found that, while Manyate-1618 had the lowest observed species richness, Dinsho-3186 had the lowest standardized and asymptotic species richness (Table 3 and Figure 2). Dinsho-3186 thus accumulated species faster than Manyate-1618 but resulted in lower overall species richness. As the highest elevation site, it is not surprising that Dinsho-3186 also had the lowest estimated species richness (Mallet-Rodrigues et al. 2015, Quintero and Jetz 2018, Abebe et al. 2019).

We found few significant changes in species-specific capture rates over time, and the population growth rates of a subset of these species were also relatively stable ( $\lambda \approx 1$ , Figure 5B). While the captures of grassland species increased significantly over time across all elevations (Figure 4C), we found that frugivores and shrubland species increased over time at lower-elevation sites, specifically

Chiri-1430, but decreased at higher-elevation sites (Figure 4A and B). This result for frugivores compares to a recent study showing that large frugivores are more likely to move downslope in Rwanda (Neate-Clegg et al. 2020). Further studies are needed to determine whether observed population trends represent longer-term changes in the understory community due to anthropogenic factors, or are shorter-term fluctuations in populations driven by ecosystem-level factors such as resource availability. While our study was a multi-year continuous effort, it occurred over a relatively short time span relative to the long life-spans of tropical birds (Korfanta et al. 2012). If there have been systematic changes in the bird community, we likely lack the power to detect significant changes over time in some of our parameters. Since forest bird species in East Africa may live for more than ten years (Korfanta et al. 2012), they may be slow to respond to anthropogenic change. Therefore, a resampling study in the Bale Mountains should preferentially run for more than a ten-year period to assess potential inter-generational changes against our baseline.

Similar to several recent studies in East Africa (van der Hoek et al. 2020), Southeast Asia (Peh 2007), and Papua New Guinea (Sam and Koane 2014), our study provides documentation of some species at previously unrecorded elevations (Supplemental Material Table S5). We detected 6 species at elevations higher than reported in the literature for Ethiopia (Ash and Atkins 2009, Dowsett and Dowsett-Lemaire 2015, Rannestad 2016; Supplemental Material Table S5). These new elevational records could be an indication of birds expanding their ranges upslope in response to climate change (Neate-Clegg et al. 2020). However, like Peh (2007), Sam and Koane (2014), and van der Hoek et al. (2020), our study took place in an understudied region with a general paucity of historical records. In the absence of prior well-established baselines of species' montane distributions, it is best to treat the importance of these elevational records cautiously (Sam and Koane 2014, Marki et al. 2016).

Although most species showed no change in mean elevation, one species showed a significant decrease in mean elevation (Supplemental Material Figure S1B). We also detected one species at elevations lower than previously reported in the literature (Ash and Atkins 2009; Supplemental Material Table S5). While an upslope range shift is the most expected response of montane avifauna to climate warming (Peh 2007, Larsen et al. 2011, Avalos and Hernández 2015, Freeman et al. 2018b, van der Hoek et al. 2020), some studies have reported that many species appear to shift downslope or exhibit no movement at all over time (Lenoir et al. 2010, Harris et al. 2012, Tingley et al. 2012, Freeman et al. 2018b). Downslope movements could be due to changes in abiotic variables other than temperature, such as precipitation, humidity, or seasonality parameters that occur in directions other than upslope (Larsen

et al. 2011, Tingley et al. 2012). Alternatively, downslope shifts could result from biotic changes such as competitor release whereby superior competitors at lower elevations disappear, allowing inferior competitors to move downslope (Lenoir et al. 2010).

Our research provides the first comprehensive assessments of various species richness, population, and demographic parameters for the bird community in the Bale region. Anthropogenic stressors that affect montane birdlife in Ethiopia are forecasted to become more severe, and average temperature minima in Ethiopia are projected to increase by approximately 0.72°C to 2.8°C by 2100 (Teshome and Zhang 2019). Furthermore, habitat degradation from deforestation and livestock continues to be pressing issues in the Harena Forest (Asefa et al. 2017, Shiferaw and Suryabhagavan 2019). If researchers are to assess how birds in tropical montane regions are responding to anthropogenic change, it is imperative that ecological baselines be established now. Our study provides an important ecological baseline of the understory bird community for the Bale Mountains in an understudied biodiversity hotspot and a blueprint for future studies. We believe that our mist-netting data is now one of the most comprehensive publicly-available datasets of its kind for elevational studies of tropical montane avifauna (Table 1) and, to our knowledge, the only one consisting of multiple continuous years of sampling. We hope that future studies monitoring understory avifauna in the Bale Mountains will utilize these data to monitor and evaluate anthropogenic impacts such as climate change and habitat degradation on this unique montane avifaunal community.

## SUPPLEMENTAL MATERIAL

Supplemental Material is available at *Ornithological Applications* online.

## ACKNOWLEDGEMENTS

We are grateful to Khalifa Ali, Mike Ford, Daniel Froehlich, Brett Hellstrom, Jordan Herman, Abdu Ibrahim, Sedat İnak, James Kuria Ndungu and Sisay Sayfu for their dedicated field assistance and to the people of Ethiopia for their kindness, friendship and hospitality. We thank the Ethiopia Wildlife Conservation Authority for providing us with the research permits for this study. We greatly appreciated the generous support of Barbara Watkins and the Bale Mountain Lodge, the kind hospitality of Guy and Yvonne Levene, and the friendship of the lodge staff. We also thank our colleagues and friends at the Ethiopian Wildlife and Natural History Society, especially Yilma Dellelegn Abebe, Bruktawit Abdu Mahamued and Mengistu Wondfarash, for their support, advice, and friendship through the years.

**Funding statement:** This research was supported by the USA National Science Foundation, University of Utah School of Biological Sciences, Environmental Studies Graduate Fellowship Fund, University of Utah Global Change and Sustainability Center and the National Geographic Society.

**Ethics statement:** Research permits for banding birds were provided by the Ethiopia Wildlife Conservation Authority.

**Author contributions:** K.D.K. wrote the manuscript with assistance from M.H.C.N.C.; Ç.H.Ş. conceived and administered the project, with support from E.R.B. and M.H.C.N.C.; Ç.H.Ş. acquired funding and resources, with support from ERB; Ç.H.Ş. supervised field research, which was led by E.R.B.; K.D.K. and M.H.C.N.C. analyzed the data; K.D.K. created the figures, with M.H.C.N.C. analyzing community composition; all co-authors contributed to and gave final approval of the manuscript.

**Data availability:** Analyses reported in this article can be reproduced using the data provided by Kittelberger et al. (2021).

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