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Comparison of acoustic and traditional point count methods to assess bird diversity and composition in the Aberdare National Park, Kenya

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Abstract

Afromontane forests, like those in the Aberdare National Park (ANP) in Kenya, sustain unique avifaunal assemblages. There is a growing need for biodiversity inventories for Afromontane forests, especially through the utilisation of unskilled observers. Acoustic surveys are a potential aid to this, but more comparisons of this technique with that of traditional point counts are needed. We conducted a systematic survey of the ANP avifauna, assessing whether acoustic and traditional surveys resulted in different species richness scores, and whether this varied with habitat and species characteristics. We also investigated the role of habitat and elevation in driving variation in species richness. The ANP provides habitat types including scrub, moorland, montane, hagenia and bamboo forests. Overall, the surveys yielded 101 identified species. The acoustic method resulted in higher species richness scores compared to the traditional method across all habitats, and the relative performance of the two methods did not vary with habitat type or visibility. The methods detected different species, suggesting that they should be used together to maximise the range of species recorded. We found that habitat type was the primary driver of variation in species richness, with scrub and montane forest having higher species richness scores than other habitats.

Résumé

Les forêts afromontane, comme celles du parc national d'Aberdare (ANP) au Kenya, présentent des assemblages d'avifaune uniques. D'où, le besoin croissant d'inventaires de la biodiversité de ces forêts afromontanes, notamment réalisés par des observateurs non qualifiés. Les relevés acoustiques en sont une aide potentielle, mais il est nécessaire d'avoir un plus grand nombre de comparaison entre les relevés acoustiques et le dénombrement par point traditionnel afin d'évaluer la meilleure méthode à utiliser. Ainsi, nous avons effectué une étude systématiques de l'avifaune de l'ANP, en évaluant si les relevés acoustiques et traditionnels entraînaient des résultats de richesse d'espèces différents et s'ils variaient en fonction des caractéristiques d'habitat et d'espèce. Nous avons également étudié le rôle de l'habitat et de l'élévation

dans la variation de la diversité des espèces comme l'ANP contient différent types d'habitats, tells que de la brousse, la lande et des forêts subalpines, d'Hagenia et de bambou. Pour tous les habitats, la méthode acoustique a donné des résultats plus élevés de richesse d'espèces que la méthode de dénombrement par point traditionnelle, qui a dans l'ensemble, a permis d'identifier 101 espèces d'oiseaux. La performance relative des deux méthodes n'a pas variée en fonction du type d'habitat ou de la visibilité. Les deux des méthodes ont détecté différentes espèces d'oiseaux, ce qui suggère qu'elles devraient être utilisées ensemble afin de maximiser la gamme d'espèces enregistrées. Nous avons constaté que le type d'habitat était le principal moteur de variation de la richesse des espèces et que la brousse et la forêt subalpine en particulier, donnent des résultats de richesse en espèces plus élevés que les autres habitats.

KEYWORDS
bioacoustics, bird survey, habitat heterogeneity, Kenya, species richness, survey techniques

1 | INTRODUCTION

Afromontane forests are biodiversity hotspots (Mittermeier et al., 2004) and host many species threatened on global and national scales. However, these habitats are threatened by a range of anthropogenic pressures, including logging and expansion of agriculture (Hitimana, Kiyiapi, Njunge, & Bargerei, 2010; Willcock et al., 2016). Conservation of these forests is vital to preserve forest specialist fauna (Fanshawe & Bennun, 1991), but better knowledge of their biodiversity value is needed in order to identify priority areas for protection (Brooks & Thompson, 2001).

Various techniques can be employed to survey bird communities. The traditional point count method requires experienced observers who can reliably identify, both by sight and sound, the bird species within the survey area (Bibby, Burgess, & Hill, 1993; Sedlacek et al., 2015). However, the availability of skilled observers can be a limitation of this survey method, particularly in the tropics, where the large diversity of species means that intense training is required to ensure all species can be reliably detected and identified (Ralph, Sauer, & Droege, 1995). More recently, there has been a growing interest in acoustic point count methods (e.g. Haselmayer & Quinn, 2000; Sedlacek et al., 2015). In acoustic point counts, recordings are made of the birds within the vicinity of the transect point and the recorded songs and calls are identified at a later date (Haselmayer & Quinn, 2000). A major advantage of the acoustic method is the ability for less skilled observers to conduct field recordings. Later, reference recordings can be used to assist identification, reducing the need for skilled observers in the field. This can increase the pool of available observers and therefore increase survey effort. In addition, recordings can be archived as a permanent record for a certain area and time, and used as documentary evidence for species identification, distribution and population trends (Lees et al., 2014). Such collections are especially important in tropical systems where criteria for identification and taxonomy are regularly updated (Baker et al., 2017). Despite the potential value of acoustic point counts, it is important to understand whether they give similar inferences in terms of species richness and composition to traditional point counts within different habitat types. Although there is growing understanding that acoustic methods can provide similar species richness estimates to traditional methods (see Shonfield and Bayne (2017) for a review), data are limited from tropical regions and associated habitats. In some tropical studies, acoustic methods have been shown to yield higher species detection, irrespective of habitat structure, (Celis-Murillo, Deppe, & Allen, 2009; Celis-Murillo, Deppe, & Ward, 2012). However, other studies have found that both methods yield similar results (e.g. Sedlacek et al. (2015) in Cameroonian Afromontane forests), or that traditional point counts outperform acoustic methods (Leach, Burwell, Ashton, Jones, & Kitching, 2016). The variation inferences from tropical studies suggest that further work is needed to better understand how the performance of the two methods vary (Shonfield & Bayne, 2017).

We apply both traditional and acoustic point counts to survey bird communities in a range of habitats in the Aberdare National Park (ANP), Kenya. Previous surveys have recorded over 270 bird species there, some of which are specialised montane species (Fishpool & Evans, 2001; Lambrechts, Woodley, Church, & Gachanja, 2003), such as the endangered Aberdare cisticola (*Cisticola aberdare*) (BirdLife International, 2018). Although the ANP is protected, birds within the national park may be affected by changes in fire frequency and browsing pressure (Reside, Wal, Kutt, Watson, & Williams, 2012), which could alter the extent of different habitats, while climate change may force species to move to higher elevations (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011). It is necessary to understand how elevation

and habitat control bird species richness and community composition in order to evaluate the consequences of these changes. We assess whether traditional and acoustic point counts provide different estimates of the avifauna community in the ANP, and whether these estimates are influenced by habitat or species characteristics. We also examine the role of habitat type and elevation in influencing species richness and community composition across the ANP.

2 | MATERIALS AND METHODS

2.1 | Study site

The Aberdare National Park (ANP) is a mountainous, volcanic region located in the central province of Kenya (0°25'0.85"S, 36°40'0.116"E). ANP protects a forested area of 774 km^2 and is part of the Great Rift Valley. The ANP is an important water source for much of Kenya with four of the country's seven largest rivers originating there. The large elevational range of the park (from 1,800 to 4,001 m above sea level) results in a diverse range of habitats. Woody forest and scrubland is below 2,500 m with dense bamboo forest (*Yushania alpina*) found from 2,500 to 3,000 m. Hagenia forest (*Hagenia abyssinica-Hypericum revolutum*) is found at elevations between 3,000 and 3,300 m, with moorland habitat made up of alpine grassland and heathland lying above 3,300 m (Lambrechts et al., 2003). Climate in the Aberdare NP follows a pattern of wet and dry seasons, with two rainy seasons occurring from April to May and from October to November. Temperatures stay relatively constant throughout the year but do vary with altitude (Estes, Reillo, Mwangi, Okin, & Shuagrt, 2010; Lambrechts et al., 2003). The ANP is surrounded by areas of high population density and intense agricultural practice. Human activities encroaching on the National Park have led to high levels of habitat degradation through unmanaged logging and livestock grazing. A 400 km long perimeter fence was erected, between 1989 and 2009, surrounding the park to help preserve the ecosystem, while protecting neighbouring communities from damage caused by wildlife (Morrison et al., 2018; Mworia et al., 2011).

2.2 | Point counts

We surveyed the five most extensive habitats in ANP. Three separate transects of 2 km each were conducted across four different habitat types (scrub, moorland, montane forest and bamboo), while there was one 2 km transect in hagenia forest. The transects occurred between 2,000 and 3,282 m, with a mean elevation range within transects of 89.5 m. Each transect contained five point count locations, distributed evenly along the transect with a separation of 500 m to reduce the chance of repeat counts of individual birds. Surveys took place between June and August 2015 and were conducted between 06:00 (i.e. at or around dawn) and 12:00. Repeat surveys of transects in the scrub, moorland and montane forest were conducted. Time constraints prevented repeat sampling in the hagenia and bamboo habitats.

Each point count survey lasted a total of 10 min with an initial 2-min habituation period, followed by 8 min of observation, as this is proposed as the optimal duration to obtain reliable species richness estimates for one point (Mattos & Peris, 2008). At each point, all individual birds observed by sight or sound were included in the traditional point count. During the 8-min observation period, the direction of observation, initially chosen randomly, was rotated clockwise at 90 degrees every 2 min. Bird taxonomy follows Clements et al. (2018). One bird observer (AW) with experience in Europe, but with no prior experience of Kenyan avifauna, conducted all surveys. A 2-week training period preceded the surveys to improve identification skills of local bird species, as well as intense study in the UK before arrival in Kenya.

2.3 | Acoustic recordings

Acoustic point counts were conducted simultaneously to the traditional point counts. A Sennheiser ME66 directional microphone with a foam wind guard and Marantz PMD661 recorder were set up on a tripod and turned every 2 min to face the same direction as the point count. The microphone was placed at an upward angle of approximately 45 degrees at 1 m above ground. Recordings were made at a sampling frequency of 44.1 kHz, 16 bits in WAV format. Spectrograms and recordings were compared to reference recordings in databases (eGuide to Birds of East Africa, 2014; xeno-canto, 2014) if species were not identified when in the field. HM, MS and SdK verified the species identification based on recordings, and they have between them two decades of experience of ornithology in the region and in other parts of Africa.

2.4 | Habitat measurements

For each point count location, the habitat type as well as the maximum distance at which birds could be identified was assessed. As a proxy for the latter, a range finder (Bushnell Yardage Pro Sport 450) was used to measure the distance to the nearest dense foliage in each direction of the point counts. The elevation of each point count location was measured using a Garmin GPS, marking each individual point along a transect. Waypoints marked by the GPS were later used to return to the points when conducting repeat transects.

2.5 | Statistical analysis

All analyses were conducted using R (R Core Team, 2018, version 3.5.0). We observed 101 species in the surveys (Supporting Information Table S1). We had 16 sound recordings that we could not attribute to a species. These recordings were either very short or of low quality. We therefore excluded these recordings from all statistical analyses, and the results are a conservative estimate of the species recorded.

For analyses with species richness as a response variable, we used generalised linear models with Poisson errors and a log link function. We first tested whether survey method affected the number

of species recorded using a Poisson GLM with species richness as a response variable and survey method (acoustic or traditional) as an explanatory variable. Each combination of point count and survey method was treated as an independent observation (n = 220, i.e. 110 point counts by two methods). To test whether the effect of survey method varied among habitats or with habitat structure, we added interaction terms with habitat and visible range, respectively. Finally, we added an interaction term with survey date to test whether the effect of survey method changed over the study period. If there were a change then this could be attributed to increasing observer experience over the study period, or to changes in detectability as a result of changes in the breeding cycle.

We then investigated the factors that influence species distribution. For this, we combined birds recorded by traditional and acoustic methods to give a dataset of 110 point count locations. Our aim was to model species richness as a function of habitat, elevation, visible range and their interactions, but strong collinearity between habitat and elevation (variance inflation factors > 4) meant that the effects of habitat and elevation could not be statistically disentangled. We therefore first conducted analyses with habitat and visible range as explanatory variables, before repeating them with elevation as an explanatory variable. Differences in community composition among habitats were visualised using non-metric multidimensional scaling ordination (implemented using the vegan R package (Oksanen et al., 2017)), with habitats highlighted by drawing ellipses to show the standard deviation of points (ordiellipse function). The relationship of points with elevation was shown using the ordisurf function, which fits a smooth surface of how elevation varies in ordination space. Formal statistical inference of how elevation and habitat affected community composition was made using multivariate binomial GLMs implemented using the mvabund R package (Wang, Naumann, Wright, & Warton, 2012).

The analyses described above use point counts as their unit of replication so are robust to the differing sampling intensity in terms of number of point counts in different habitats. However, assessments of total species richness in each habitat would be affected by this unbalanced sampling. To account for this, we used rarefaction and extrapolation implemented in the iNEXT R package (Chao et al., 2014; Hsieh, Ma, & Chao, 2016), and estimated the species richness in each habitat with sampling efforts of five point counts (the minimum sampling effort in a habitat) and 30 point counts (the maximum sampling effort in a habitat). We also use the iNEXT package to estimate sample coverage, defined as the proportion of individuals in a community that belong to the species present in our sample (Chao & Jost, 2012), and thus provides a measure of the degree to which our dataset represents a complete sample of the species present. We use extrapolation to estimate the species richness in each habitat if sampling was complete (Hsieh et al., 2016).

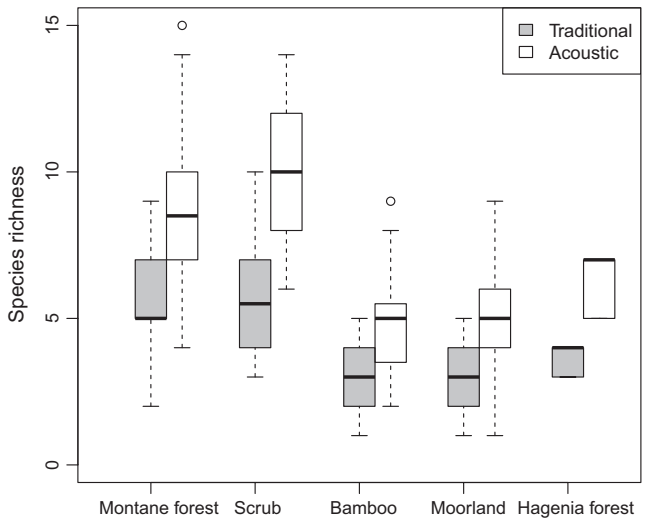

FIGURE 1 Variation in the number of species recorded in point counts between traditional and acoustic methods and among habitats. N = 220 point count/method combinations

3 | RESULTS

3.1 | Avifauna of the Aberdare NP

We observed and identified 101 species in the surveys (Supporting Information Table S1). Hunter's cisticola (*Cisticola hunteri*) and tropical boubou (*Laniarius major*) were detected using the traditional method across all five habitat types. Nine acoustically detected species were common in all habitat types, including Abyssinian crimson-wing (*Cryptospiza salvadorii*) and brown woodland-warbler (*Phylloscopus umbrovirens*). Most species detected were rare with 78 species detected in ten or fewer of the 101 point counts.

3.2 | Comparison of survey methods

In total, 82 species were observed using acoustic point counts and 63 species were observed using traditional point counts (n = 110 for each). Thirty-eight species were only recorded by acoustic point count, 19 only by traditional point count and 44 with both survey methods. The acoustic point count method resulted in a significantly higher species richness score than the traditional point count method (Poisson GLM: $\beta = 0.50 \pm 0.06$ *SE*, $z = 8.7$, $df = 214$, $p < 0.001$, Figure 1), with a mean of 7.3 ± 3.1 *SD* species recorded in each acoustic point count compared to 4.4 ± 1.9 *SD* species recorded in each traditional point count. The interaction between point count method and habitat was non-significant (Poisson GLM, $\chi^2_{4,210} = 1.20$, $p = 0.878$, Figure 1), as was the interaction between method and average visibility (Poisson GLM, $\chi^2_{1,216} = 1.54$, $p = 0.215$), indicating that the differences in the number of species detected by each method did not differ between habitats or with the density of a habitat. The interaction between method and survey date was also non-significant (Poisson GLM, $\chi^2_{1,212} = 1.78$, $p = 0.182$), indicating that the observed differences between methods were not affected by increasing observer experience during the study period.

3.3 | Factors affecting bird distribution and richness

Species richness decreased with visibility range (Poisson GLM, $\beta = -0.008 \pm 0.002$ *SE*, $z = 4.1$, $df = 108$, $p < 0.001$) and varied with habitat type (Poisson GLM, $\chi^2_{4,105} = 104.3$, $p < 0.001$,

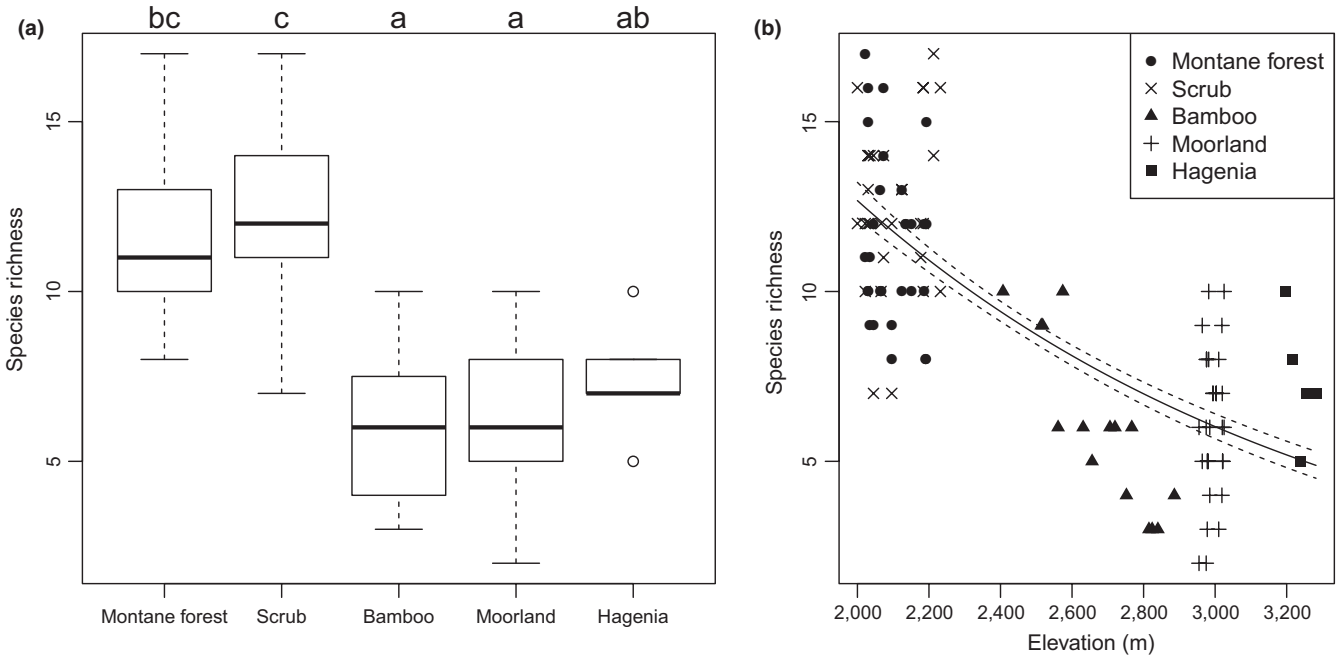

FIGURE 2 (a) Variation in species richness among habitats. Different letters above the boxplots indicate significant differences between habitats following pairwise post hoc tests. (b) Relationship between species richness and elevation. Note that elevation and habitat type also show strong collinearity and so their effects cannot be disentangled confidently. N = 110 point counts

TABLE 1 Variation in bird species richness among habitats in the Aberdare National Park. For estimated values, 95% confidence intervals are shown in parentheses

	Montane forest	Scrub	Bamboo	Moorland	Hagenia forest
Species richness	64	77	24	32	15
Number of point counts	30	30	15	30	5
Number of species unique to habitat	13 (20.3%)	23 (29.9%)	0 (0%)	12 (37.5%)	1 (6.7%)
Sample completeness	0.942 (0.921–0.963)	0.932 (0.911–0.954)	0.892 (0.812–0.972)	0.941 (0.911–0.972)	0.834 (0.730–0.939)
Estimated species richness: five point counts	30.5 (28.3–32.8)	35.4 (32.9–38.0)	15.5 (13.2–17.9)	15.5 (13.8–17.1)	15 (11.4–18.5)
30 point counts	64 (57.8–70.2)	77 (68.9–85.1)	32.9 (19.7–46.2)	32 (27.3–36.7)	24.5 (11.7–37.2)
100% sample coverage	81.8 (70.2–114.6)	104.1 (87.5–146.8)	70.7 (31.4–318.8)	46.6 (35.6–92.1)	24.8 (16.7–70.1)

Figure 2). However, backwards simplification of a model with visibility range, habitat type and their interaction resulted in a model with only habitat type (Poisson GLM, non-significant interaction, $\chi^2_4 = 5.1$, $p = 0.275$, non-significant additive effect of visibility range, $\chi^2_1 = 0.76$, $p = 0.383$). Species richness was highest in scrub and montane forest, and lowest in bamboo and moorland (Tukey post hoc tests $p < 0.05$, Figure 2). Species richness in hagenia forest was lower than in scrub, but not significantly different to other habitats (Tukey post hoc tests $p \geq 0.05$, Figure 2).

Overall, scrub was the most speciose habitat (72 species recorded), followed by montane forest (64 species), moorland (32 species), bamboo (23 species) and hagenia forest (15 species). The higher species richness in scrub and montane forest compared to other habitats remained when using rarefaction and extrapolation to account for variation in sampling effort (Table 1), with scrub still estimated to be the most speciose habitat at 100% sample completeness (92 species, Table 1). Although sample completeness was estimated to be high in all habitats (0.834–0.941, Table 1), substantial additional sampling would be needed to attain complete coverage, with>150 point counts needed in all habitats except hagenia forest.

Compositional differences were also evident among habitats (multivariate binomial GLM, Deviance = 1,092, $p = 0.002$). Ordination (stress = 0.23) revealed greatest separation in bird community composition between moorland and both montane forest and scrub, and some separation in community composition between scrub and montane forest (Figure 3). Bamboo and hagenia forest had

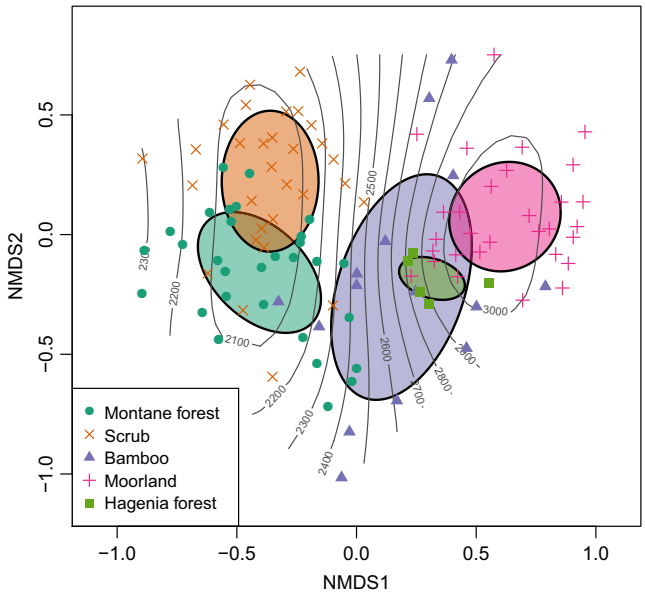

FIGURE 3 Ordination plot of the community compositions for the different habitat types. Note that stress is relatively high (stress = 0.226). Ellipses show the standard deviation of points in each habitat type. Contour lines show point count elevation (m) modelled as a function of the ordination axes. N = 110 point counts [Colour figure can be viewed at wileyonlinelibrary.com]

intermediate community composition between moorland and montane forest (Figure 3). All habitats except bamboo contained at least one species not recorded in any other habitat, with the highest proportion of unique species (38%) in moorland (Table 1).

Elevation could also exert a control on species richness and community composition. Species richness decreased with elevation (Poisson GLM, $\beta = -0.0007 \pm <0.0001$ SE, $z = 9.3$, $df = 108$, $p < 0.001$, Figure 2), while community composition varied with elevation (multivariate binomial GLM, Deviance = 763.3, $p = 0.002$). Elevation was less supported as a predictor of species richness than habitat (AIC of model with elevation = 523.0, AIC of model with habitat = 519.6), although high collinearity means that habitat type and elevation are too strongly correlated to robustly separate their effects on species richness. The elevation range species occurred across was positively correlated with the mean elevation species occur at (Kendall's tau correlation, $\tau = 0.36$, $df = 72$, $p < 0.001$, note species that only occurred in one point count were removed from this analysis).

4 | DISCUSSION

A total of 101 species were recorded during 2 months surveying birds in the Aberdare National Park. When comparing survey methods, the acoustic recording method showed higher species richness scores across all habitat types compared to the traditional survey method. A total of 82 species were detected with the acoustic recording method, while the traditional method resulted in 63 species. Scrub and montane forest habitat types harboured higher species richness scores than other habitat types. This may be due to greater habitat heterogeneity in these habitats or the low elevations these habitats are found at (Ferger, Schleuning, Hemp, Howell, & Bohning-Gaese, 2014; Martin & Proulx, 2016; McCain, 2009).

4.1 | Comparison of survey methods

We hypothesised that acoustic point counts would detect more species relative to traditional point counts in enclosed habitats with poor visibility, but instead found that neither habitat type nor visibility influenced the difference in species richness between point count methods. This could be because the observer could detect and identify more species in acoustic point counts in all habitats because there was a permanent record. These recordings could be cross referenced to acoustic data bases and verified by more experienced ornithologists (Haselmayer & Quinn, 2000). Notably, only 44% of species were recorded using both methods. Certain species may be visually cryptic but acoustically loud, such as the yellow-rumped tinkerbird (*Pogoniulus bilineatus*), whereas, others such as the augur buzzard (*Buteo augur*) may be visibly obvious but rarely use vocalisations. In this study, 19 species were not detected by acoustic census techniques alone, while 38 species were not detected by traditional census techniques alone. As observer experience increases it is likely that the proportion of species missed by traditional census techniques will be reduced. In contrast, the 19 species missed by acoustic census techniques would remain the same, irrespective of experience, as the species did not vocalise during the census. In this study, the observer was trained for two weeks on the local avifauna prior to fieldwork, so perhaps had a representative skill level for a newly trained observer. There was no change in the relative performance of the methods during the study, indicating that substantially more training or experience would be needed to identify all species by sound in real-time. For this reason, it appears prudent to use both methods combined to get a better representation of birds in a certain area (Celis-Murillo et al., 2012; Sedlacek et al., 2015), especially when observers have limited experience.

4.2 | Effect of sampling effort

Previous surveys combined have observed 270 bird species in the Aberdare (Lambrechts et al., 2003; Mworia et al., 2011), while this study recorded 101 identified species. The rarefaction and extrapolation analysis revealed that while this survey recorded on average 63% of the species predicted to be present in each habitat (Table 1), it would require an increase in survey effort of over fourfold to perform a complete species inventory. This result is likely to be generalizable to many tropical regions, where highly skewed species abundance distributions mean that the majority of species are rare (ter Steege et al., 2013). Our results indicate that repeat sampling in the same location can substantially increase species richness estimates. One explanation for this is that tropical species often form wide ranging interspecific feeding flocks (Jullien & Thiollay, 1998), so the species recorded in a particular location are likely to be highly temporally variable. In addition, elevational migration or seasonal migration of certain species may also affect the temporal variation

(Loiselle & Blake, 1992). The huge survey effort needed to capture rare species reinforces the need to develop survey methods that can be used by fieldworkers with limited training such as the placement of passive acoustic recorders (Celis-Murillo et al., 2012).

The timing of our study will mean that Palearctic migrants that winter in Kenya will not have been present, as these arrive between August and October (Jones, 1995). The detectability of resident species will also vary with their breeding cycle. The breeding season for Kenyan bird species is somewhat varied; however, most seem to follow the trend of breeding within the two rainy seasons (Moreau, 1950). The rainy season for the Aberdare National Park is from April to May and October to November (Lambrechts et al., 2003). Therefore, it is likely that many species were not breeding during the survey period. This means that certain species may have been less vocal and less likely to be detected acoustically. Additionally, some species exhibit elevational migration, which may influence how species richness varies with elevation; additional surveys at other times of the year would allow these elevational movements to be quantified.

4.3 | Drivers of bird species richness in the Aberdare National Park

Avian species richness declined monotonically with elevation, although as our gradient begins at mid-elevations (lowest elevation in our survey area is 1,111 m), our results cannot distinguish between monotonic declines in diversity across all elevations and mid-elevation peaks (McCain, 2009). Changes in diversity and composition with altitude could be driven by climatic factors influencing bird species richness (Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2007), by declines in habitat heterogeneity and quality with altitude (LaSorte & Jetz, 2010; Terborgh, 1977), or by altitudinal zonation in vegetation types (Hamilton & Perrott, 1981). Identifying whether elevational changes in bird diversity and composition is a function of altitude or results from habitat zonation is difficult, as habitat is correlated with elevation (McCain, 2009). However, these processes do generate subtly differing predictions for how richness and composition vary; if elevation drives richness and composition we would predict continuous changes across the gradient, but if habitat drives richness and composition then we would expect no change within habitat, but sharp changes at habitat boundaries. Our results can be tentatively interpreted as providing greater support for the role of habitat over direct effects of elevation, as habitat had greater explanatory power in models of species richness and community composition. Additionally, hagenia forest had higher species richness than expected for their elevation (Figure 2). However, the lower species richness of hagenia forest compared to montane forest, and the decline in species richness with elevation within the bamboo zone (Figure 2), suggest that elevation does exert some direct control on bird distributions.

Scrub and montane forest habitats both have higher species richness than moorland and bamboo forest, with hagenia forest having intermediate diversity (Figure 2). One potential reason for differences in species richness between these habitats is differences in spatial heterogeneity in habitat structure, where higher spatial heterogeneity results in a higher species richness through greater niche diversity (Ferger et al., 2014; Martin & Proulx, 2016). Spatial heterogeneity within this study is represented through visible range measurements, where habitats with low visible ranges had higher vegetation density, and hence likely higher spatial heterogeneity. We found that dense habitats had higher bird species richness, but visible range had no effect in models also containing habitat. This could point to a limitation in the use of visible range to quantify habitat heterogeneity, as illustrated by comparing bamboo to montane forest. Bamboo forests were denser than montane forests but have a simpler structure (Hamilton & Perrott, 1981), and hold fewer bird species. Moreau (1966) suggested that bamboo habitat is of little ornithological importance, and we found no unique species in this habitat; this may be due to the dominance of a single *Yushania* species (Estes et al., 2010). Hagenia forest had a similar range of visibility to montane forest but had a lower bird species richness, which, in additional to elevational effects, could be due to reduced structural complexity and fewer lianas than lower elevation forests (Hamilton & Perrott, 1981; Lange, Bussmann, & Beck, 1997).

4.4 | Consequences of changes in habitat within the Aberdare National Park

Several drivers of change are currently operating within the Aberdare National Park which could lead to changes in the extent of different habitats. The completion of fencing around the park boundary means that elephants are forced to stay in the park year-round. A consequence of this could be increasing conversion of montane forest to scrub (Laws, 1970), although there is no evidence for this at present (Morrison et al., 2018). We found scrub to be the habitat with the highest bird richness and it contained the most species only found in one habitat (23 species). However, these species are not habitat specialists, so it is unlikely that the scrub habitat in the Aberdare NP is of any conservation importance to them. In contrast, many of the species only found in the montane forest were more strongly associated with this habitat, such as lemon dove (*Aplopelia larvata*). A higher degree of habitat specialism occurred in species unique to the moorland. While none of these species are of IUCN conservation concern (BirdLife International, 2018), the Aberdare NP may support an important part of their population. For example, the Jackson's francolin (*Pternistis jacksoni*) and red-tufted sunbird (*Nectarinia johnstoni*) are restricted to a few mountain systems in East Africa; other species (not recorded in this survey) for which the Aberdare moorland may be critical include Aberdare cisticola (*Cisticola aberdare*) and Sharpe's longclaw (*Macronyx sharpie*), although the status of the latter is currently uncertain (Muchai, Bennun, Lens, Rayment, & Pisano, 2002). Therefore, changes that degrade the moorland or montane forest habitats are likely to have greater conservation consequences to birds than changes to the scrub. An additional driver of change in the park is increased fire frequency. This could lead to conversion of montane forest to scrub, and at higher elevations could reduce the extent of mature hagenia forest (Lange et al., 1997). Only one bird species was only recorded in hagenia forest, but this was also the habitat with the lowest estimated

sampling coverage. Bamboo forest had low species richness and contained no unique bird species. While this might indicate relatively low conservation value of bamboo forest for birds, the habitat is important for water conservation, the prevention of soil erosion and the storage of carbon dioxide (Zhao et al., 2005).

5 | CONCLUSION AND FUTURE RESEARCH DIRECTIONS

In terms of survey methodology, acoustic point counts yield higher species richness scores than traditional point counts due to the ability to listen to sound recordings more than once. However, it is suggested that the both traditional and point count methods be used to gain a full representation of bird species within an area. Our results demonstrate the role of habitat in shaping bird community composition and species richness, with some support for higher species richness in habitats with greater spatial heterogeneity. There was also some evidence for an effect of elevation on bird communities. Climate change is leading to elevational shifts in species distributions (Chen et al., 2011), but our current understanding of the effects of this is limited by the availability of data, especially in species-rich tropics where many species have narrow elevation ranges (Anderson, Storlie, Shoo, Pearson, & Williams, 2013; Laurance et al., 2011). It would therefore be valuable to monitor year to year variation in species richness, and analyse whether climate change is affecting the montane bird species within the ANP. The acoustic point count method is advantageous for this as it does not require experienced observers and makes assessments quicker and easier to obtain, so is potentially more amenable to long-term monitoring schemes. Knowing which habitat types hold rare species and which have the highest richness allows for the better protection of habitats from human habitat exploitation and protects species from further decline (Fleishman, Noss, & Noon, 2006; Owens & Bennett, 2000), and these assessments will also be helped by using acoustic point counts alongside traditional ones.

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